行政院國家科學委員會專題研究計畫　期中精簡報告

南灣海域上層水體生物源有機碳循環及物理流場之研究

-II(1/2)

計畫類別： 整合型計畫
計畫編號： NSC91-2621-B-002-012-
執行期間： 91 年 08 月 01 日至 92 年 07 月 31 日
執行單位： 國立臺灣大學海洋研究所

計畫主持人： 夏復國

報告類型： 精簡報告

處理方式： 本計畫可公開查詢

中　華　民　國 92 年 5 月 12 日

本計劃為『墾丁國家公園海域長期生態研究 - 整合與模式建構』整合型計劃中子計劃一。主要係研究南灣海域上層水體 1.物理流場（船載 ADCP 測量, 船載 CTD 測量,錨定潮位計及錨定流速儀測量），2.細菌生產力(bacterial production; BP; ^{3}H-thymidine 培養法），3.水體群聚呼吸率（community respiration rates; CR; 暗瓶培養法），4.浮游植物初級生產力（phytoplankton primary production; PP; in situ ^{14}C 培養法）, 5.顆粒態有機碳（particulate organic carbon; POC; 元素分析燃燒法）及 6.溶解態有機碳（dissolved organic carbon; DOC;高溫氧化燃燒法）之時空分布。生物源有機碳在上層水體之來源(source)以 PP 測量，消耗(sink)以 BP 及 CR 的測量而加以評估，POC 及 DOC 則可顯示有機碳庫存量（stock)之變化。

本團隊於計劃年度內於南灣設立的 15 個測站，每 2 個月進行一次為期 2-3 天的 8 個航次調查。包括 OR1-634, OR1-663, OR2-735, OR2-743, OR2-759, OR2-765, OR2-795 及 OR2-840 航次。此 8 航次所得之結果，已分別由主持人的二位碩士班 2 年級學生做為畢業論文，目前仍在撰寫之中。學生姓名及論文題目分別為：曾于芳：南灣珊瑚礁海域初級生產力季節變異及光模式的應用性分析。

林慧雯：南灣珊瑚礁海域細菌生產力季節變異及生長控制因子分析。

此外本團隊亦利用 2001 年 2 月航次所得之結果，完成論文之撰寫，預定於近期內投稿至 Aquatic Microbial Ecology。檢附論文全稿於下。圖，表及引用文獻尚在整理之中。

Short-termed differential responses of biomass, production and turnover rate of phytoplankton as well as bacterioplankton in a coral reef system with spring tide induced upwelling

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Keywords: Dissolved inorganic nutrients, chlorophyll, POC, C-limitation, conveyor-belt hypothesis, tidal cycle.

ABSTRACT

To exam hourly responses of phytoplankton and heterotrophic bacteria to an upwelling caused by spring tide, a 2-days cruise with 11 stations was conducted in the Nan-Wan Bay coral reef ecosystem in Feb. 2001. Nitrate concentrations (NO_3, <0.15 ~ 10.2 μM) correlated negatively with temperature (16 ~ 26 ^oC). Estimated NO_3 flux was ~60 mmolN m^{-2} h^{-1} with <1% of it utilized by phytoplankton. Chlorophyll (Chl-a) concentrations doubled in 9 hrs after the upwelling but with maximal concentrations <0.30 μg l^{-1}. Daily euphotic zone integrated primary production (IPP_{Ze}, 118 ~ 389 mgC m^{-2} d^{-1}) and algal turnover rate (Pμ, 0.27 ~ 0.76 d^{-1}) responded to the upwelling ~5 hrs earlier than that of Chl-a. Such differential changes in growth rates and biomass accumulation could be explained by the “conveyor-belt” theory. The observed HNLC (High Nutrient Low Chlorophyll) phenomenon might due to shorter residence time of water mass (<1 d) within the Bay in comparison with those of algal turnover time (1.3 ~ 3.7 d). Euphotic zone integrated bacterial production (IBP_{Ze}; (7.2 ~3 9.7 mgC m^{-2} d^{-1}) and bacterial turnover rate (0.56 ~ 0.82 d^{-1}) were positively correlated with IPP_{Ze}, Pμ and depth integrated POC (540 ~ 6575 mgC m^{-2}, suggesting

a high possibility of “bottom-up” (organic substrate supply) control. This was confirmed by the results of 3 enrichment experiments showing that bacterial growth was C-limited. Our study provide mechanistic information regarding the magnitude of coupling among physical, chemical and biological process since the time scale adopted by this study was similar to the turnover time of auto- and heterotrophic planktoners.

Introduction

Upwelling is an important marine phenomenon providing opportunity for the understanding of the magnitude of coupling among physical, chemical and biological processes. In 2003, there are still >100 researches concentrating on this issue (source, http://wos.stic.gov.tw/). Upwelling system is also one of the ecosystems having the highest “new or export production” that might have profound effects in regulating global carbon cycle (Murray et al., 1995). As one may note that most of these upwelling studies were performed to address biological responses at longer time scales (days to inter-annual). We now know that at larger scales, physical, chemical and biological processes tend to be coupled, but it has not been clear at what smaller scales their relationships also hold particularly in the field (cf. Wilkerson and Dugdale 1987). Determining the temporal and spatial variability of biological phenomenon has become an important issue during the last decade (Steel 1991). Dickie et al. (1987) suggested that the prime requisite for understanding controlling mechanisms is determination of the spatial and temporal scales on which interactions take place, and it is at the smaller scales that mechanistic relationships are expressed.

Coral reef ecosystem is well known for its high productivity and biodiversity in the benthic system (Odum, 1955, Connell 1978), the pelagic system in reef region is however much less productive (e.g. Lewis 1977). The ecological roles planktonic-trophodynamics play in the reef pelagic system have therefore received less attention until recently (Wolanski 1983, Leichter, 1996, Torreton et al., 2002 and citations therein). Tidal induced upwelling in the reef system was initially observed by Maxwell (1968) and documented by Rory et al. (1981), Leichter (1996) and Hatcher (1997). One of the interesting phenomena is that chlorophyll concentrations in the reef pelagic systems are generally very low as if it were an oligotrophic system. In a reef system with frequent or periodic upwelling, does algal bloom occur in the upper column? If not, what causes it? How fast do auto- (phytoplankton primary production) and heterotrophic (bacterial production) processes couple in this system? We believe that these questions are basic but very important since phytoplankton biomass constitutes the base of organic supply that regulates the magnitude of the

pelagic-benthic coupling in the reef system, and that heterotrophic bacteria have been recognized as one of the most important agents of C and N cycling in coral reefs (Ferrier-Pages et al. 2000 and citations therein).

The Nan-Wan Bay, part of the Kenting National Park, locates at the tropical southern Taiwan (Fig. 1). It is semi-enclosed embayment with coral reef distributed along the coastal line within depths <30 – 50 m. Previous study showed that there was monthly periodical upwelling during spring tide (Lee, 1997). Upwelling formation might be associated with cyclonic eddy pumping induced by the combined effects of tidal flow and topography (Lee 1997, 1999 1999a). Circulation dominated by strong tidal current, and the prevailing tidal currents were essentially zonal and contained sizable diurnal and semidiurnal components in the study area (Liang 1987). Tidal current flows west- and eastward during flood and ebb tide outside the Bay, respectively. The duration from its initiation to disappearance of this eddy pumping upwelling was <1 day (Lee 1997).

Based on the above reasoning, we designed a cruise survey to explore how planktonic communities respond to upwelling in the reef systems at time scales of hrs-days, which are approximately at the same scale of planktoners' turnover time.

Materials and methods

Study area and sampling.

Cruise survey was conducted with R/V *Ocean Researcher I* in late Feb., 2001 with 11 sampling stations deployed in the Nan-Wan Bay (Fig. 1). For tidal variation study, a total of 25 continuous hydrocasts with an interval of 1~2 hrs was performed at the predicted upwelling center (i.e. St. 5). Water samples were collected using 10-L Teflon coated Go-Flo bottles mounted on a General Oceanic rosette assembly. Sampling depths ranged 4~9, depending on bottom depths. Temperature and salinity profiles were recorded with a SeaBird CTD (SBE 9/11 puls, SBE Inc. USA). For each station, there were at least 2 CTD cast with at least 1 cast for chemical and biological measurements (Table 1). For the daytime casts, surface and subsurface photosynthetic available radiance (PAR) were recorded to calculate the euphotic zone depths (depth with 1% surface PAR) and light extinction coefficients.

Inorganic nutrients, chlorophyll *a* and Primary production

Water subsamples for nutrients (i.e., nitrate, phosphate, and silicate) analyses were collected with 100 ml polypropylene bottles and frozen immediately with liquid-N_2. A custom-made flow injection analyzer was used for nutrients (i.e., PO_4^{-3}, SiO_2, and NO_3^-) analysis (Gong et al., 1992). Nutrients data for stations 6, 8 and 10 were not measured (Table 1). Chlorophyll *a* (Chl-a) fluorescence profile was measured with a Sea Tech fluorometer attached to CTD. The readings of *in vivo*

fluorescence then were calibrated (Chl-a = -0.0080 + 1.47 x Fluo, n = 124, R^2 = 0.60, p<0.001) by *in vitro* fluorometery (Turner Design 10-AU-005) following acetone extraction (Parson et al., 1984).

Primary production was measured by the ^{14}C assimilation method (Parsons et al. 1984). In brief, two light and one dark 250-ml clean PC bottles were filled with water samples taken from the euphotic zone. After inoculation with $H^{14}CO_3^-$ (final conc., 10 μCi ml^{-1}), samples were wrapped with 9 neutral density filters (LEE filters) and incubated for 2-4 h in a self-designed tank with an artificial light source (2000 μE m^{-2} s^{-1}). Water temperature was maintained with running seawater. Following retrieval, samples were immediately filtered through Whatman 25 mm GF/F filters. The filters were then placed in scintillation vials, and 0.5 ml of 0.5 N HCl was added to remove residual $H^{14}CO_3^-$. Radioactivity was counted in a liquid scintillation counter (Packard 1600) after the addition of 10 ml scintillation cocktail (Ultima Gold, Packard) into the vials. The Webb et al (1974) model was applied to estimate the maximal Chl-a normalized photosynthetic rate (i.e. P^B_{max}) and the initial slope (i.e. α). Daily primary production (i.e. PP) then estimated with the values of the euphotic zone depth, P^B_{max}, α, Chl-a profile, subsurface PAR profile and daytime surface PAR (2 days' average, 19.1 mEins/m^2/d). Phytoplankton turnover rate was calculated as depth integrated PP divided by depth integrated Chl-a with a conversion factor of 58 gC gChl-a^{-1} (Eppley et al. 1992). PP measurements were conducted only during daytime at sts. 2, 4, 5, 7 and 9 (Table 1). Since P^B_{max} and α derived from these stations were similar to each other (Table 1), PP for the other 6 stations were calculated using the averaged P^B_{max} (7.27 ± 1.09 gC gChl-a^{-1} h^{-1}) and α (0.0182 ± 0.019 gC gChl-a^{-1} h^{-1} $\mu E^{-1}m^{-2}$ s^{-1}) of these 5 stations.

Particulate organic carbon, bacterial abundance and bacterial production

Samples for particulate organic carbon (POC) were filtered through a Whatman 25 mm GF/F filter, wrapped in aluminum foil and then stored at 4 ℃. Both filters and aluminum foils were pre-combusted at 550°C for 1 hour. After drying and acid-fuming, Samples were measured by combustion method (HORIBA EMIA-510). POC were not measured at sts. 6, 8 and 10 (Table1). Bacterial abundance was measured by the acridine orange epifluorescence microscopy (Hobbie et al. 1977). Biomass was calculated with a carbon conversion factor of 20 fgC $cell^{-1}$ (Lancelot & Billen 1984). Bacterial production (i.e. BP) was measured with triplicates by ^3H-thymidine incorporation with thymidine and carbon conversion factors of 0.7 x 10^{18} cell $mole^{-1}$, Torreton 1999) and 20 fgC $cell^{-1}$, respectively. BB and BP data were only available for sts. 2, 4, 5, 7 and 9 (Table 1).

Bacterial enrichment experiments and data analysis

Experiments were conducted at stations 2, 5 and 7. Water samples collected at

the surface (ca. 5 m) were filtered through a pre-acid (0.5 N HCl) washed then MilliQ H_2O rinsed 0.8 μ polycarbonate (Nucleopore) filter. The filtrates then were assigned to four treatments that were incubated in duplicate 2-L polycarbonate (Nalgene) bottles at *in situ* temperature for 12 hrs. Treatments included (1) unamended control, (2) glucose addition, (3) NH_4^+ plus PO_4^{-3} addition (N+P treatment) and (4) glucose plus NH_4^+ plus PO_4^{-3} addition (C+N+P treatment). The final concentrations of glucose, NH_4^+ and PO_4^{-3} were 100 μM, 1.0 μM and 1.0 μM, respectively.

Depth integrated data if used, were integrated (trapezoidal method) down to the euphotic zone depth or bottom depth depending on which one is deeper. The StatView II^{TM} in Macintosh was used for statistical analysis.

Results

The Nan-Wan Bay locates at southern Taiwan. Geographically, water properties within the Bay are primarily affected by the water masses from the Western Philippine Sea (i.e. the WPS) and the South China Sea (The SCS, Lee 1997). The temperature-salinity (i.e. T-S) diagram showed that the temperatures and salinities taken from all sampling casts lied between those of the WPS and SCS (Fig. 2), and also indicated that there was no trace for coastal and/or freshwater effects. The bottom depths and euphotic zone depths of the study area ranged 47~131 and 36~91 m, respectively (Table 1). Light extinction coefficients were lower (-0.04 m^{-1}) for the outer Bay stations and then increased toward the inner Bay stations reaching a value of -0.07 m^{-1} (Table 1). For the following sections, we used temperature as criteria to describe the changes of mater mass within the Bay.

To identify that station 5 was the upwelling center, the temperature profile along transect across sts. 10, 11, 2, 5 and 7 were examined during the predicted upwelling and non-upwelling periods. During upwelling period, the temperature profile formed a dome-shape with the lowest T (<16 ^oC) centering at st. 5. During the non-upwelling period, this temperature dome-shape became much less significant (Figs. 3A-B). Spatial distribution of temperature at 30 m depth showed that during upwelling, st. 5 located at center of cold water mass with a temperature variation >3 ^oC (Fig. 4A). During the non-upwelling period, this temperature contour almost disappeared with a temperature variation <1 ^oC (Fig. 4B).

Temperature (Fig. 5A, 15.9~25.1 ^oC) and salinity (Fig. 5B, 34.32~43.65 psu) varied periodically at st. 5 within 42 hrs. The 23 ^oC isotherm elevated form 70 m depth to ca. 20 m depth within 8 hrs and then descended down to >100 m depth in 12 hrs. The 2nd cycle was more dramatic than the 1st one with the 23 ^oC isotherm intruded upward to 10 m depth. Nitrate (NO_3) concentrations at st. 5 ranged from <detection limit (0.15 μM) to 10.2 μM (Fig. 5C) and showed a negative correlation with

temperature (Fig. 6A, NO_3 = 26.9 - 1.06 x T, n = 82, R^2 = 0.92, p< 0.01). This suggested that NO_3 behaved quite conservatively (i.e. no or low biological uptake or release) during the upwelling. For the 14 casts where NO_3 concentrations were not measured, their NO_3 profiles could be estimated quite conceivably with the linear relation presented above. Phosphate (PO_4) concentrations (<detection limit ~ 0.82 μM) were positively correlated with NO_3 with an N:P ratio of 12.7 (Fig. 6B), which was significantly lower than the Redfield ratio (N:P=16; n = 82, p< 0.01).

Profile of Chl-a concentrations ranged <0.1~0.29 μgChl l^{-1} (Fig. 5C). The euphotic zone integrated Chl-a concentrations (Fig. 7A, $IChl_{Ze}$; 5.2~11.7 mgChl-a m^{-2}) seemed to be out of phase with those of 70 m integrated NO_3 concentrations (INO_{70}; 50~258 mmol m^{-2}, r = -0.92, n = 25, p< 0.01). When INO_{70} reached the highest value at sampling time of 9 hr, $IChl_{Ze}$ was the lowest. INO_{70} started decreasing with increasing $IChl_{Ze}$ that reached maximum at sampling time of 18 hr. After that, $IChl_{Ze}$ dropped but still remained values >9.4 mgChl-a m^{-2}. The same phenomenon repeated again after sampling time of 28 hr. From the temporal change of INO_{70}, we estimated the highest NO_3 flux at st. 5 to be ~60 mmolN m^{-2} h^{-1}. In the 1st tidal cycle, $IChl_{Ze}$ increased from 6.7 to 11.7 mgChl m^{-2} in 9 hrs, assuming phytoplankton C:N ratio follows that of Redfield (C:N = 106:16) and a Chl-a to carbon ratio of 58 gC gChl-a^{-1} (Epply et al. (1992), this gave a nitrate uptake rate of 0.35 mmolN m^{-2} h^{-1}. This accounted for 0.6% of the NO_3 flux from the upwelling.

Daily euphotic zone integrated phytoplankton production (IPP_{Ze}; 118~389 mgC m^{-2} d^{-1}) and its turnover rates (P_μ = $IPP_{Ze}/IChl_{Ze}$; 0.27~0.76 d^{-1}) varied ~3-folds and seemed to respond to the upwelling ~5 hrs earlier than that of $IChl_{Ze}$ (Fig. 7B). IPPZe was positively correlated with P_μ (r = +0.85, n = 12, p< 0.01). The 1st maximal IPP_{Ze} (and P_μ) appeared at sampling time of 14 hr when INO_{70} dropped to an intermediate value of 139 mmol/m^2. Both IPP_{Ze} and P_μ seemed to have a trend with increasing values during the mid upwelling relaxation period. After that, both parameters kept decreasing during the late upwelling relaxation period when surface waters were depleted of nutrients (Fig. 5C). Noted that in calculating IPP_{Ze} of different daytime samples, we used the same parameters derived from the P^B-E curve of st. 5 and the same daytime surface PAR (19.1 mEins m^{-2} d^{-1}). Assuming phytoplankton C:N uptake ratio follows that of Redfield (C:N = 106:16) and that a daylight hour of 12, the maximal IPPze was ~0.35 mmolN m^{-2} h^{-1}. Noted that this value was exactly the same as the one calculated from the $IChl_{Ze}$ data. The negative relationship between INO_{70} vs. $IChl_{Ze}$ also observed at st. 7 (r = -0.94, n = 5, p< 0.01) which located at the left of st. 5. In fact, the 5 data points of INO_{70} and $IChl_{Ze}$ calculated from st. 7 fitted very

well with the INO_{70} and $IChl_{Ze}$ curves of st. 5 (Fig. 7C).

Bacterial biomass (BB) ranged 0.30~0.63 mgC $m^{-3}$with an average of 0.46± 0.09 mgC m^{-3} (Figs. 8A-B). For most sampling stations, BB decreased with depths. The highest and lowest BB values were observed at sts. 4 and 9, which located at the inner and outer bay respectively. Bacterial production varied 2-fold (BP, 0.20~0.44 mgC m^{-3} d^{-1}, 0.31 ±0.05 mgC m^{-3} d^{-1}) with higher values in the surface then decreased with depths (Figs. 8C-D). Particulate organic carbon (i.e. POC) concentrations varied 3-fold among stations ranging 41~145 mgC m^{-3} (Table 1). No regular pattern for POC profiles (data not shown). The values of euphotic zone integrated BB (IBB_{Ze}, 27.7~36.7 mgC m^{-2}) showed no correlations with any physical and measured variables. On the other hand, the euphotic zone integrated BP (IBP_{Ze}, 16.5~27.6 mgC m^{-2} d^{-1}) and bacterial turnover rates ($B\mu = IBP_{Ze}/IBB_{Ze}$, 0.56~0.82 d^{-1}) were positively correlated with euphotic zone integrated POC ($IPOC_{Ze}$, 3,125~9,163 mgC m^{-2}), IPPze and P_{μ}. (Table 3). Noted that these analysis were using data taken from different stations and sampling times.

Field data for the 3 enrichment experiments performed at sts. 2, 5 and 7 were listed in Table 2. Water samples were warmed (>23.0 ^{o}C), saline (>34.47 psu) with detectable NO_3 (0.83~1.24 μM) and PO_4 (0.10~0.14 μM). Results for the 3 enrichment experiments were identical (Figs. 10A-C). Taking st. 2 as an example, BP of the N+P treatment showed no difference with those of control (<0.01 ~ 0.018 mgC m^{-3} h^{-1}) over 12 hrs incubation. BP in the glucose treatment at sampling hour 6 (0.052 mgC m^{-3} h^{-1}) was 4-fold of the control (0.012 mgC m^{-3} h^{-1}). After that, the difference between control and the glucose treatment became more and more significant. The C+N+P treatment behaved almost exactly as the glucose treatment. All these suggested that bacterial growth at these 3 stations were limited by the supply of dissolved organic carbon only.

Discussions and conclusions

The enhancement of biological activities due to upwelling has been well demonstrated in several ecosystems in the past decade (Spitz et al., 2003; Wieters et al., 2003 and citations therein). Our results, via a field study performed at shorter time scales, demonstrate much more clearly the sequential responses of auto- and hetero-trophic processes to the increase of inorganic nutrients induced by eddy pumping in a coral reef system. The formation of cyclonic eddy depends upon the tidal amplitude that is the largest in spring tide. The disappearance of the cold and nutrient-riched waters right after the upwelling (Fig. 5, after sampling hr. 9) was primarily due to the quick mixing with adjacent warm (and oligotrophic) waters instead of the withdraw of the spring tide or biological uptake (see below). A

"conveyor-belt" hypothesis has been proposed (Jones et al., 1983) and testified (Wilkerson & Dugdale, 1987) to explain upwelling effect on the growth of phytoplankton. This hypothesis stated that newly upwelled phytoplankton near the upwelling center are "shift-down", growing and taking up nutrients slowly. To have a positive influence (shift-up) on phytoplankton physiology (i.e. growth), the upwelled water has to be "conditioned" in some way. As the algae adapt to the high light (or warm temperature) downstream, algal rate processes start to "shift-up". Macromolecules are synthesized, leading to increased growth rate and biomass. Nutrient concentrations are rapidly decreased, and the cells respond by undergoing rate decreases or shift-down. Our results basically repeated exactly processes proposed by this hypothesis. But further indicates that such hypothesis can be applied to shorter time scales. We found that there were time lag for the occurrence of maximal nutrient concentrations, phytoplankton growth and biomass accumulation. In the 1st tidal cycle, maximal phytoplankton C-fixation and turnover rates appeared during the mid relaxation of upwelling (shift-up) where concentrations of INO_{70} were in the medium range (~150 mmolN m^{-2}). Phytoplankton turnover rates (Pμ) decreased (shift-down) dramatically during the late relaxation period when NO_3 in the surface waters were depleted (or very low), indicating a possibility of nutrient limitation on algal turnover (growth) rate. The same phenomenon repeated in the 2nd tidal cycle. Maximal algal biomass ($IChl_{Ze}$) always occurred after maximal Pμ (and IPP_{Ze}), which is reasonable if (zooplankton) grazing does not catch up immediately (see below). The results from st. 7, although only with 5 data points, also revealed the same scenario of st. 5.

There are two interesting phenomena in our field study. The decrease of inorganic nutrient concentrations (INO_{70}) over tidal cycles seemed to be determined primarily by physical mixing (dilution) processes. Biological uptake via phytoplankton did occur but constituted <1% of the nutrient flux (~60 mmolN m^{-2} h^{-1}). This low uptake was verified by using the changes of $IChl_{Ze}$ concentrations and the maximal IPP_{Ze}. In the tidal study, we observed phytoplankton biomass doubled from 5 to 12 mgChl m^{-2} in 9 hrs, but the maximal Chl-a concentrations never exceeded 0.30 μgChl/L, which is very close to the values recorded in the adjacent oligotrophic Taiwan Strait (Shiah et al., 2000). In many upwelling systems, an increase of Chl-a concentrations >1.0 μgChl l^{-1} is not uncommon (e.g. Dudgale & Wilkerson, 1989 and citations therein). There are 3 possibilities for this. Firstly, the low N:P molar ratio (N:P = 12.7) suggested that phytoplankton growth and thus its biomass accumulation might be N-limited during the late relaxation period. Unfortunately we did not have evidence for this deduction. Secondly, zooplankton grazing if catch up quickly with the algal cycle, might prevent the accumulation of or even reduce algal biomass. We

though this possibility is low. During the 2nd (and the 1st, too) upwelled period, $IChl_{Ze}$ dropped abruptly from 10.6 to 6.7 mgChl m^{-2} in 2 hrs, which equals to a reduction rate of 18%Ch-a h^{-1} (i.e. [10.6-6.7]/[10.6 x 2]). Zooplankton grazing rates of the study area varied <0.1% ~ 2.0% Chl-a/h with a mean of 1.0% Chl-a/h. (Dr. Hwang JS, Inst. Mar. Biol. Natl. Taiwan Ocean Univ., unpublished data). Therefore, grazing alone can't account for such reduction of $IChl_{Ze}$. After pooling the data of sts. 5 and 7, we found significant linear positive and negative relationship of $IChl_{Ze}$ vs. euphotic zone averaged temperatures (21.6~24.9 ^{o}C, r = +0.92, n = 32, p< 0.001) and $IChl_{Ze}$ vs. euphotic zone averaged salinities (34.49~34.54 psu, r = -0.91, n = 32, p< 0.001), respectively. This indicates the temporal and spatial patterns of $IChl_{Ze}$ might be strongly determined by conservative mixing

The $IChl_{Ze}$ recorded during the 2 late relaxation periods (Fig. 8A) did not change much and always maintained values >9 mgChl m^{-2}. As argued above, we ascribed this unvaried $IChl_{Ze}$ during the relaxation periods more to the reduction of Pμ than zooplankton grazing. These indicate that the magnitude of physical mixing is probably more important in determining the temporal and spatial patterns of phytoplankton biomass at short time scales. That is, Chl-a is diluted during upwelled period and starts to grow when the water column becomes more stable during relaxation period. When nutrients were depleted afterwards, phytoplankton growth (turnover) rate begins to decrease abruptly and results in unvaried Chl-a concentrations. The 2nd cycle repeats again when next upwelling event occurs. More importantly, the residence time (<1 day) of the upwelled plume within the Bay ([Li, 1987 #1899]) was shorter than that of phytoplankton turnover time (1.3~3.7 d, Fig. 8B), indicating the lack of physical mechanism for massive accumulation of algal biomass.

Bacterial biomass, production and turnover rate values of this study fall within the ranges reported by other coral reefs studies (Ferrier-Pages et al., 2001; Torreton et al., 2002 and citations therein). The IBP_{Ze}/IPP_{Ze} (i.e. BP/PP) ratios did not varied much with a mean and a standard deviation of 5.2 ±0.9% (n = 7). These ratios were low when compared with the global average of 25% (Ducklow 1999). Torreton (1999) showed that the BP/PP ratios (~8%) recorded in the Great Astrolable Reef lagoon in Fiji were also vary low. Assuming a growth efficiency of 6.6% for reef bacteria (Torreton 1999), the *in situ* particulate primary production barely meets bacteria carbon demand in our system. This indicates that non-phytoplankton sources of dissolved organic matter (i.e. DOM) might be important in supporting bacterial carbon demand. One of the non-algal DOM sources may come from the benthic system (e.g. coral exudates and others, Ferrier-Pages et al., 2000 and citations therein).

Our results showed that heterotrophic processes were tightly coupled with phytoplankton activities and $IPOC_{Ze}$ (Table 3) but not algal biomass. The positive relationship found between bacterial rate parameters (production and turnover rate) vs. phytoplankton rate parameters has been traditionally cited as an evidence of bottom-up (organic substrate supply) control (Cole et al., 1988). Recent studies, on the other hand, suggested that this positive relationship might be induced by co-variation, particularly in warm and oligotrophic systems where NH_4^+ availability might limit bacterial and algal growth simultaneously (Shiah et al., 2001, 2003 and citations therein). The results of the enrichment experiments offered convincing evidence that bacterial growth was organic C-limited and the positive relationships among bacterial and phytoplankton rate parameters can be explained as bottom-up control. In fact, organic C-limitation on bacterial growth in reef systems has been reported (Ferrier-Pages et al., 2000; Torreton et al., 2000). Bimonthly enriched experiments performed afterwards also showed that for most time of the year, bacterial growth were C-limited (Shiah & Lin, unpublished data). We did not measured NH_4^+ concentrations during the cruise, but can reasonable deduce that the upwelling might bring NH_4^+up to the surface as shown by other upwelling studies (e.g. Dudgale & Wilkerson, 1989). Therefore, it was not surprise to see organic C-limitation on bacterial growth and tight couplings for bacterial rate parameters on phytoplankton rate parameters and $IPOC_{Ze}$ in a reef system during upwelling period.

Overall, this study offered evidence showing the sequential changes of chemical, auto- and heterotrophic processes in a coral reef system during 2 upwelling events over a time scale of hrs~days. Such sequential changes in phytoplankton activity and biomass can be explained by the “conveyor-belt” theory. Unlike other upwelling systems, phytoplankton biomass (i.e. Chl-a) were extremely low with copious supply of inorganic nutrients periodically in the Nan-Wan Bay reef system. This HNLC (High Nutrients and Low Chlorophyll) phenomenon seems can be ascribed to the short residence time (and quick dilution) of water mass within the Bay. In an upwelling system with abundant supply of inorganic nutrients, organic carbon limitation on bacterial growth can be expected, as shown by our enrichment experiments. In current days, most field studies are conducted in a way to cover longer time scales (seasonal to inter-annual) and larger spatial scales (several hundred Km to basin). Studying at shorter time scale (hrs to days) variations can be helpful in providing more insightful mechanistic information since it is in the range of planktoners’ turnover time.

Acknowledgements

LTER-Kenting project contribution paper #0003. This research was supported by the

NSC-Taiwan grant # 90-2621-B-002-009-A10. We would like to thank the crew of the *Ocean Researcher I* for cruise assistance.