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Trophic Cascading of Medusae on the Relationships between Copepods and Diatoms in a Subtropical Coastal Ecosystem

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ABSTRACT

To investigate the spatial and temporal variation of phytoplankton and copepods, eight seasonal cruises (January 2005 ~ October 2006) were conducted in a subtropical coast site that encompassed 19 sampling stations. The results indicated that the temperature (18.4 - 29.7 C) varied more than 10 C seasonally, while nutrient concentrations (nitrate: 0.4 - 6.3 M, phosphate: 0.1 - 0.8 M, and silicate 2.1 - 12.1 M) were inversely correlated with temperature. Diatoms (2792 - 1602437 cells m^{-3}) constituted > 90% of the phytoplankton assemblages and dinoflagellates (226 - 10029 cells m^{-3}) represented only ~10% of the algae biomass. Copepod abundance (8 - 1031 ind. m^{-3}) varied positively with that of diatom and temperature. The relative abundance of *Temora* spp. (1 - 712 ind. m^{-3}) varied from < 2% in winter to > 69% in summer; that of *Paracalanus* spp. (0.1 - 176 ind. m^{-3}) were > 25% in spring and autumn and *Calanus* spp. (0.5 - 24 ind. m^{-3}) dominated in winter and spring, but accounted for only ~10% of the total copepods. Both diatom density and copepod abundance were positively correlated with temperature, indicating these two plankton groups were left bottom-up control. The copepod abundance positively co-varied with diatoms in 2005, but not in 2006. Further season-to-season analysis showed that the diatom vs. copepod ratios changed positively only when the medusa abundance changed greatly (> 40-fold) between consecutive seasons. During periods when the medusa abundance varied less than 10-fold between seasons, there is no relationship between the ratios and the medusa abundance. This study suggests that the stability of the medusa abundance from season to season could be important in regulating the ecological linkage between diatoms and their predators – copepods.

Key words: Copepods, Phytoplankton, Cascading effect, Eutrophic, Temperature control

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1. INTRODUCTION

Copepods are the most dominant and most widely distributed mesozooplankton (size > 200 m) in marine ecosystems. They can graze on phytoplankton and microzooplankton (size < 200 m, e.g., protozoan), and play important roles in planktonic trophodynamics and organic carbon cycling (Calbet 2001; Calbet and Saiz 2005). Since herbivorous copepods are the major predator of phytoplankton, intuitively one may expect a certain statistical relationship between their abundances on different temporal and/or spatial scales (Davis 1987; Runge 1988; Cushing 1989; McLaren et al. 1989; Gislason and Astthorsson 1995).

Copepods that graze on phytoplankton have been studied extensively in estuaries and coastal systems (Bautista and Harris 1992; Dagg 1995; Sautour et al. 1996; Hwang et al. 1998; Sautour and Castel 1999; Froneman 2000, 2001; Liu and Dagg 2003). Several studies of copepod have been conducted at the sampling site of this study (i.e., the Tan-Shui estuary), emphasizing the seasonal variation of species composition (Hsieh and Chiu 1997; Hwang et al. 2006; Dur et al. 2007), physical effects (monsoon and the mixing of water masses) and the effect of pollution (Fang et al. 2006) on the spatial and temporal pattern. However, the spatial and temporal variation of copepods and their rela-

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tionships with food sources (phytoplankton) and predators (medusae) at the Tan-Shui estuary have seldom been explored.

In the natural environment, copepods are also subjected to intensive predation pressure. Macrozooplankton medusae (or jellyfishes) are their most common predators (Matsakis and Conover 1991; Purcell 1992; Schneider and Behrends 1994; Olesen 1995; Nielsen et al. 1997). The cascading theory states that in a system with more than 3 trophic levels, the temporal variations of trophic levels 1 and 3 will be much alike with each other. Many studies have demonstrated this theory in marine systems, showing that jellyfish may cause a shift in the trophic structure of the pelagic community as a result of trophic cascading (Behrends and Schneider 1995; Schneider and Behrends 1998; Stibor et al. 2003). The aforementioned studies have addressed the cascading effects on temporal scales, while their potential effects on the spatial variability of lower trophic levels have seldom been emphasized. However, the applicability of this theory to eutrophic coastal and estuarine systems has not been demonstrated until recently.

A total of eight cruises were conducted in 2005 and 2006 in a subtropical eutrophic estuary. The collected alga, copepod and, physical and chemical data were analyzed to improve our understanding of the tropho-dynamics among copepods, medusae and algae in a subtropical estuary.

2. MATERIAL AND METHODS

2.1 Study Site and Sampling

Samples were collected from eight cruises conducted from January 2005 to October 2006. A total of 19 sampling stations were occupied outside the mouth of the Tan-Shui River (Fig. 1). A CTD-Rosette assembly (General Oceanics) equipped with 20-l Go-Flo bottles was employed to record temperature and salinity as well as to collect water samples. The chemical and biological variables described below were all derived from the surface (2 m below surface) water samples.

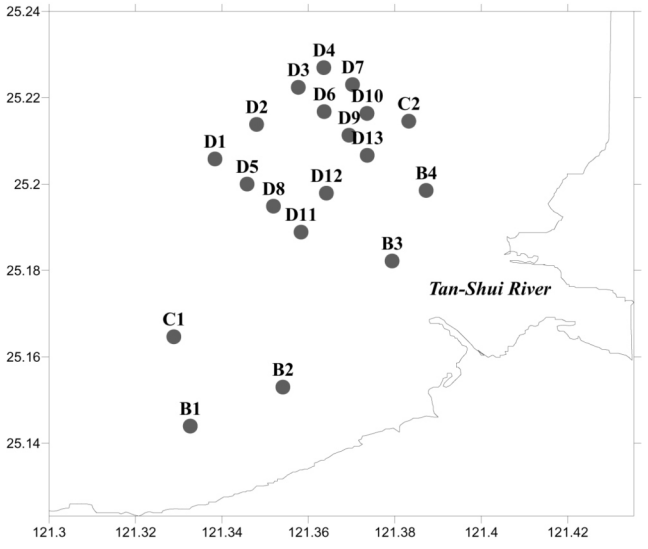

Fig. 1. Map of the 19 sampling stations outside the Tan-Shui River.

2.2 Inorganic Nutrients and Chlorophyll Concentrations

Water samples for the determination of nutrient concentration were placed in 100 ml polypropylene bottles, frozen instantly in liquid nitrogen, and stored in a freezer. Nutrients were analyzed with a self-designed flow injection analyzer (Strickland and Parsons 1972; Gong et al. 1992). Nitrate was reduced to nitrite with cadmium wires activated with a copper sulfate solution, and the nitrite was converted to pink azo dye for colorimetric determination. Concentrations of phosphate and silicate were measured using the Molybdenum blue and the silicomolybdenum blue methods (Strickland and Parsons 1972; Pai et al. 1990), respectively.

2.3 Diatom, Copepod and Medusa Abundance

To concentrate diatoms, a 500 ml water sample was processed by the Utermöhl method. Diatom species were identified and counted using an inverted epifluorescence microscope (Nikon-Tmd 300) at 200x or 400x. The details of the procedure can be found in Chiang and Taniguchi (1993). Diatom and dinoflagellate cells with sizes > 10 m were counted. A NORPAC net with a 0.45-m mouth and a 330- m mesh size was employed to collect the mesozooplankton. Collected samples were fixed with formaldehyde (final concentration is 5%). The species composition and abundance of the copepods and the medusae were counted under a microscope (Nikon, SMZ800). References for identification of copepod species were Chihara and Murano (1997) and Shih (2009).

3. RESULTS

3.1 Temperature, Salinity, and Nutrients

Temperature (18.5 - 29.7 C, Fig. 2a) varied seasonally with the lowest and highest values recorded in January and July, respectively. Spatially, temperature behaved homogeneously within each sampling period. Based on the annual temperature pattern, January, April, July, and October were defined as winter, spring, summer and autumn seasons respectively. Salinity (31.5 ~ 34.5 psu; Fig. 2c) also varied with seasonal temperature (Table 1). In some cases, salinity varied significantly among the stations in the same season. For example, spatial variance of the salinity was observed in July 2005, which might be due to higher river input. Silicate concentration varied ~15 fold (mean values 2.1 - 12.1 M; Fig. 2a) annually and showed a significant seasonal trend

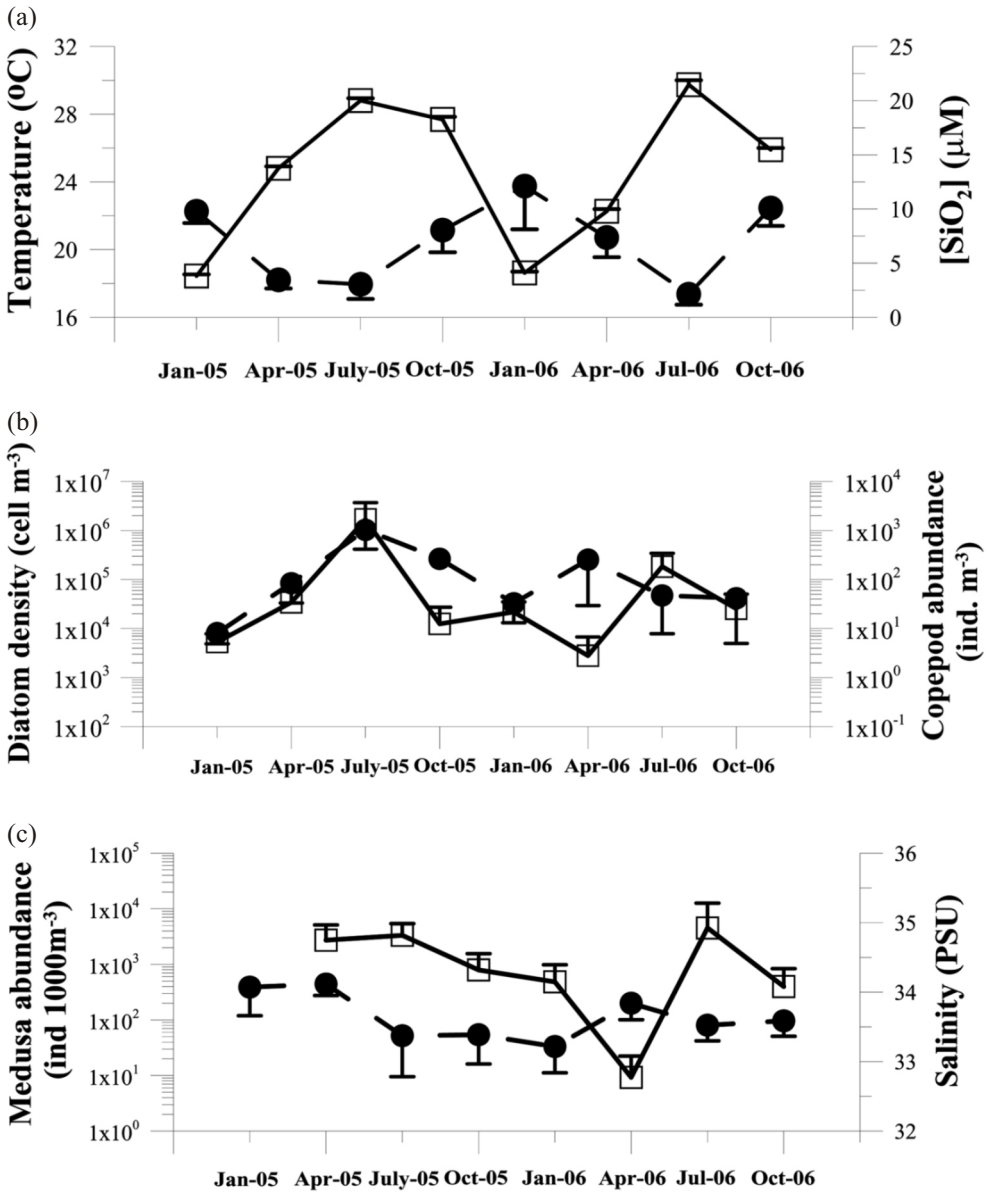

Fig. 2. Seasonal patterns of the mean values of (a) temperature (□) and silicate concentration (●), (b) Diatom density (□) and copepod abundance (●), (c) medusa abundance (□) and salinity (●) collected in 2005 and 2006. Vertical bars indicated standard deviation.

Table 1. Correlation matrix of measurements using (A) all data, (B) 2005, and (C) 2006; ns, not significant at p = 0.01 level, and dash lines, not analyzed.

Items	Units	Temperature	Salinity	Silicate	Diatoms	Copepods
Temperature	°C					
Salinity	PSU	ns				
Silicate	μM	-0.65	-0.31			
Diatoms	cells m^{-3}	+0.27	ns	-0.23		
copepods	inds. m^{-3}	+0.36	ns	-	+0.35	
Medusae	inds. 10^{-3} m^{-3}	+0.28	ns	-	ns	ns

(Table 1) with higher values in the winter and lower values in the summer in both years of the study. The temporal and spatial patterns of the other two major nutrients, namely nitrate (0.4 - 6.3 M) and phosphate (0.1 - 0.8 M), were similar to those of silicate. The correlation coefficients (i.e., r) for nitrate vs. silicate and phosphate vs. silicate were +0.83 (n = 152) and +0.72 (n = 152), respectively.

3.2 Temporal (Seasonal and Inter-Annual) Variations in Abundance of Plankton Groups

Phytoplankton was dominated (> 90% in abundance) by diatoms, with dinoflagellates (226 - 10029 cells m^{-3}) representing only < 10%. Thus, in the presentation and analysis below, we consider diatoms to be representative of the total phytoplankton. The abundance of diatoms (mean values, 2792 - 1602437 cells m^{-3}) basically varied with temperature (Table 1), but with some notable differences between the two years (Fig. 2b). In 2005, the diatom abundance was low in winter, increased in spring, peaked in summer and decreased in autumn. A similar pattern was observed in 2006, with the exception that diatom abundance in spring (2792 3926 cells m^{-3}) was three times lower than that in winter (9184 13795 cells m^{-3}). The second significant difference was inter-annual: the diatom abundance in July 2005 (1602437 2016246 cells m^{-3}) was at least 8X that in 2006, when the mean abundance was 183680 159811 cells m^{-3} (ANOVA, $p < 0.05$).

The species composition of copepods was defined. In winter, *Calanus sinicus*, *Undiluna vulgaris*, *Paracalanus parvus*, *Euchaeta concinna*, *Corycaeus affinis*, and *Acartia erythraea* were the dominant species. The dominant species in the spring were *Cosmocalanus darwini*, *Acrocalanus gibber*, *Paracalanus parvus*, *Temora turbinata*, *T discaudata*, *Corycaeus affinis*, *Onceae venusta*. *Temora turbinata* was the most dominant species (> 60% of abundance) in summer. *Acrocalanus gibber*, *Centropage furcatus*, *Paracalanus parvus*, *Temora turbinata*, and *Cosmocalanus darwini* were dominant in autumn. Copepod abundance (8 - 1031 ind. m^{-3}; Fig. 2b) exhibited significant seasonality and varied by more than two orders of magnitude. Their abundance correlated positively with the abundance of diatoms and the temperature (Table 1). Their inter-annual difference was also notable, as revealed by the fact that the mean abundance of copepods in July 2006 (47 40 ind. m^{-3}) was only 7% of that in July 2005 (ANOVA, $p < 0.05$). Overall, the three most abundant genera of copepods were *Temora*, *Paracalanus*, and *Calanus*. *Temora* spp. correlated positively with temperature ($r = +0.33$, $n = 152$, $p < 0.01$) and the diatoms (+0.40, $n = 152$, $p < 0.01$). The abundance of *Temora* spp. (1 - 712 ind. m^{-3}) was 70% of the copepod abundance in the summer, and was the most dominant copepods, representing > 50% of the total copepod abundance. *Paracalanus* spp. (0.1 - 176 ind. m^{-3}) also correlated positively with temperature ($r = +0.34$, $n = 152$, $p < 0.01$) but not with the abundance of diatoms. They represented > 25% of the total copepod abundance in spring and autumn. *Calanus* spp. were not significantly correlated with temperature or the abundance of diatoms. They were dominant in winter and spring, but accounted for only ~10% of total copepod abundance.

The mean medusa abundance (0 - 3811 10^{-3} inds. m^{-3}) changed more than three orders of magnitude during the investigation period (Fig. 2c). Medusa abundance varied positively with temperature (Table 1). It peaked in later spring and summer, decreasing thereafter to a minimum (9 13 10^{-3} inds. m^{-3}) during spring, 2006. A notable upsurge (> 400 fold) of medusa abundance was recorded from the spring to the summer (3811 7560 10^{-3} inds. m^{-3}) of 2006. Thereafter, the medusa abundance decreased again.

3.3 Spatial Variations of Plankton Groups

Spatial distribution of the abundance of diatoms and copepods revealed different relationships during the eight sampling periods. Datasets of the growing seasons, the summer and spring (Fig. 3), were used as illustrative examples. The remaining datasets are not shown here but will be included and analyzed in the next section. The distribution of copepods (Fig. 3e) almost followed that of diatoms (Fig. 3a) in spring, 2005. However, during the summer of 2005, the areas with high abundance of copepods (Fig. 3f) were within areas with a low density of diatoms (Fig. 3b), and *vice versa*. In spring 2006, high density diatoms (Fig. 3c) coalesced at the south of the study area while the copepods concentrated in the north-east. In the following summer, diatoms (Fig. 3d) aggregated in the south while their predators (Fig. 3h) accumulated in the north. Moreover, the abundance of *Temora* spp. was negatively correlated with diatoms ($r = +0.78$, $n = 13$, $p < 0.01$) and medusae ($r = +0.64$, $n = 13$, $p < 0.01$), such that the abundance of these three plankton groups was log-transformed. Similar results were obtained regarding the relationships of total copepods vs. diatoms and total copepods vs. medusae. Overall, the spatial patterns of copepods and phytoplankton during the growing seasons were in phase in 2005, but out of phase in 2006. The coupling and decoupling of copepods and phytoplankton, in terms of spatial distribution and seasonal pattern, may be affected by the distribution of the top predator, the medusae (Figs. 3i ~ l; see more below).

3.4 Tropho-Dynamics and Cascading Effects

Table 1 indicates that, overall, the temporal and spatial variation of the abundance of diatoms was positively correlated with that of copepods. Further analysis suggested that the predator-prey relationship was different inter-annually. Figure 4 revealed a significant correlation between diatom and copepod distributions only in 2005 ($r = +0.66$, $n = 76$,

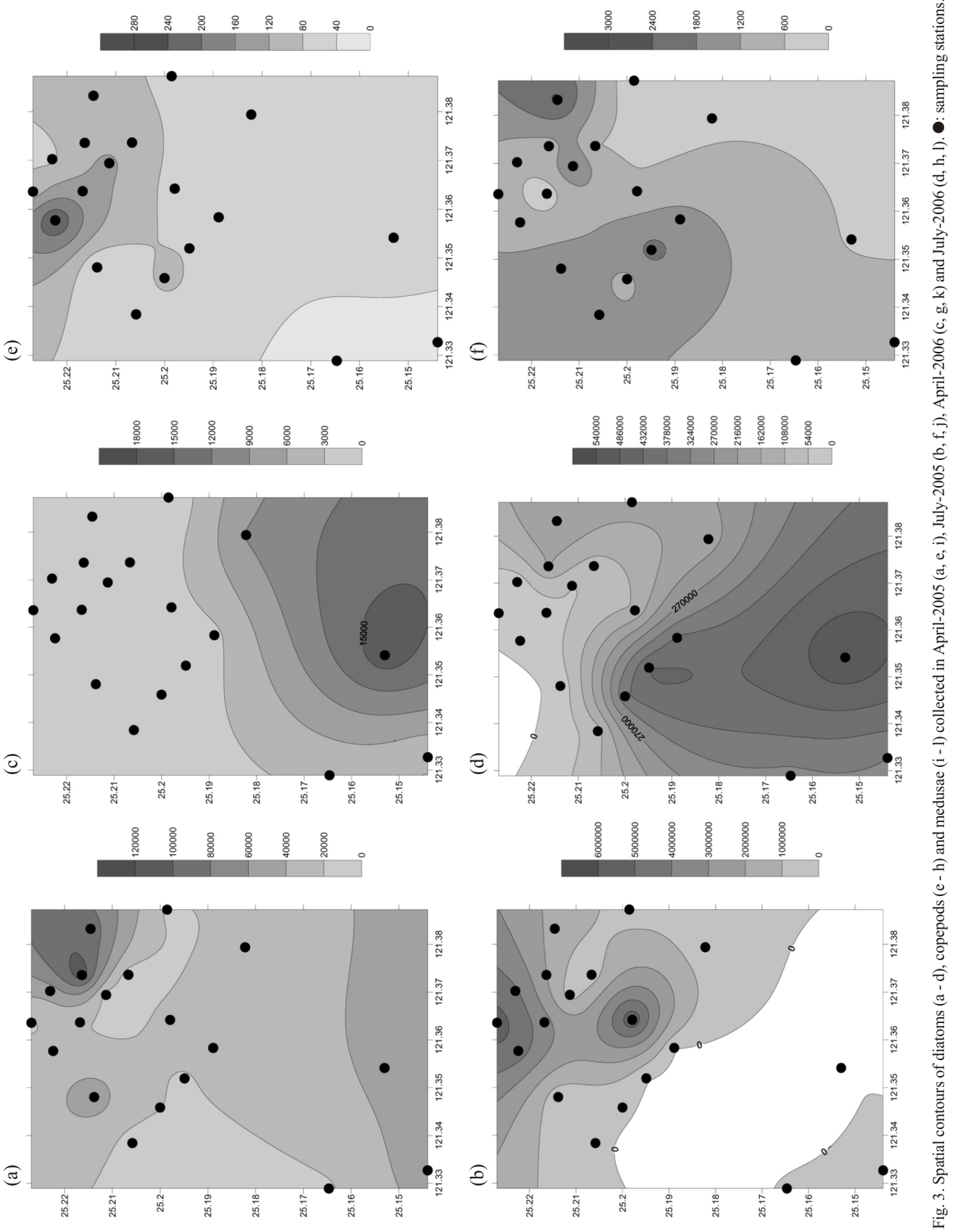

Fig. 3. Spatial contours of diatoms (a - d), copepods (e - h) and medusae (i - l) collected in April-2005 (a, e, i), July-2005 (b, f, j), April-2006 (c, g, k) and July-2006 (d, h, l). ●: sampling stations.

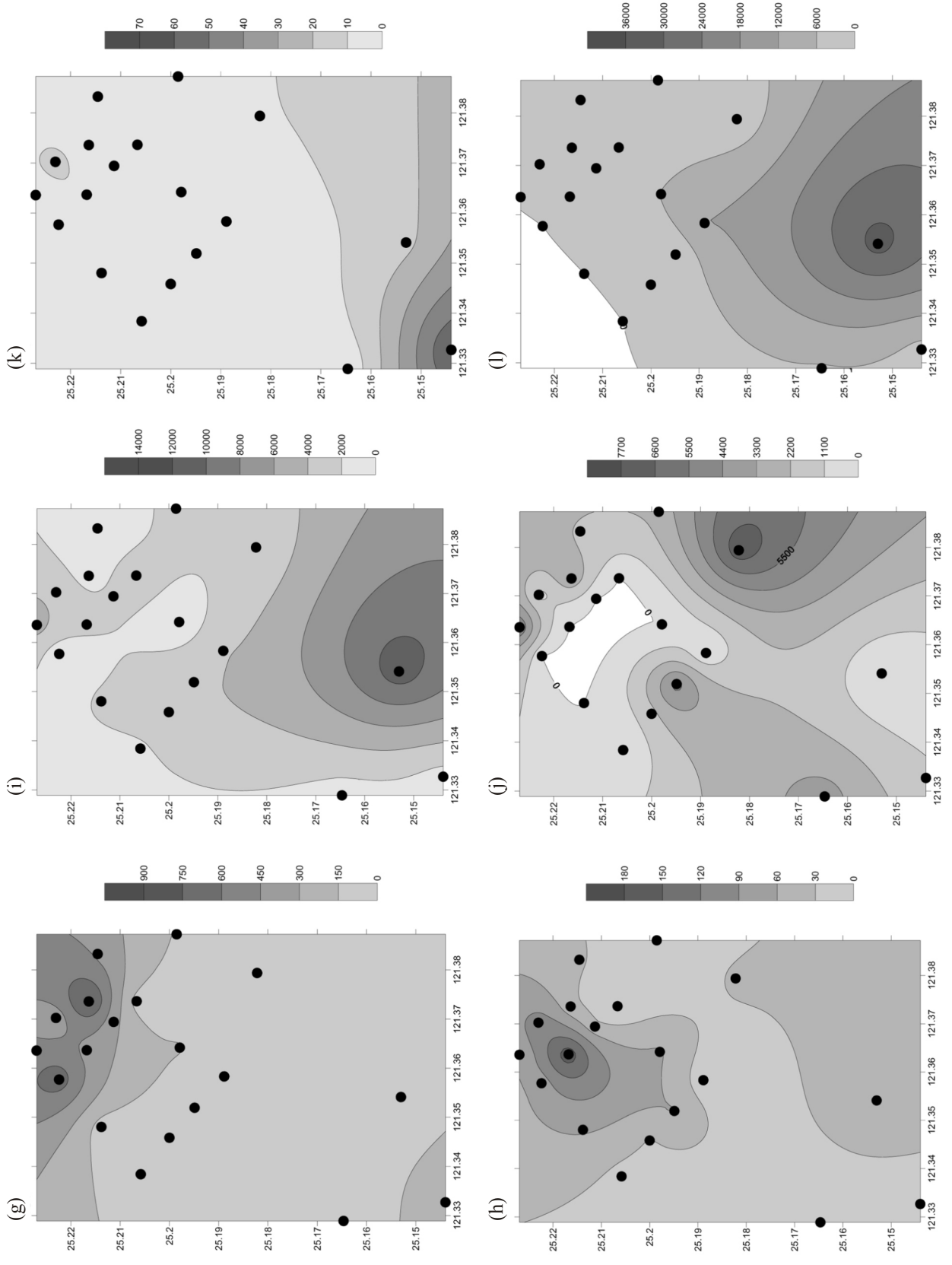

Fig. 3. (Continued)

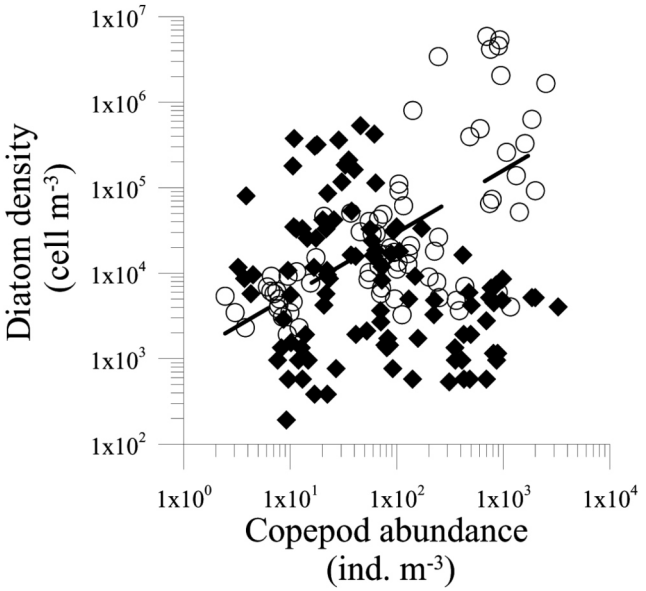

Fig. 4. A scatter plot of diatom abundance to copepod abundance using 2005 (solid circles) and 2006 (open diamonds) datasets. Dashed line indicated a regression of Ln(Y) = 1.30 (0.82) + 0.56 (0.08) Ln (X), n = 76, $r^2 = 0.44$, $p < 0.01$.

$p < 0.01$), but not in the consecutive year. The rate of increase of the net abundance due to temperature is compared with the rate of decrease of the net abundance of these two planktons during the shift-up (2005 winter ~ 2005 summer) and shift down (2005 summer ~ 2006 winter) phases. The results indicate that the temperature-normalized rates of increase all exceeded (46% for diatoms, 29% for copepods, and 35% for *Temora* spp.) the corresponding rates of decrease (Table 2).

The variation of medusa abundance seemed to regulate the seasonal and spatial relationships between copepods and diatoms (i.e., cascading effects). We calculated the ratios of diatoms to copepods (i.e., the ratios), and then plotted the ratios to medusae abundance. The initial results (Fig. 5) seemed to be quite random. However, individual (season by season) analysis indicates that during the periods medusae varied little (i.e., < 10-fold) between two consecutive seasons; no significant relationship existed between the ratios and the medusa abundance. Significant results appeared during the period of winter ~ summer 2006 (Fig. 2c) when the medusae varied greatly from one season to the next. In 2006, the medusa abundance decreased by a factor of ~43 from winter (383 480 10^{-3} inds. m^{-3}) to spring (9 13 10^{-3} inds. m^{-3}), and the ratios simultaneously decreased from 611 951 to 25 44 diatoms copepods^{-1}. As the medusae proliferated by a factor of ~411 from spring to summer (3811 7650 10^{-3} inds. m^{-3}), the ratios increased from 25 44 to 8591 9442 diatoms copepods^{-1}.

4. DISCUSSION AND CONCLUSIONS

The study area was a meso- to eutrophic system, as judged from high annual mean nitrate (3.7 2.3 M), phosphate (0.42 0.29 M) and silicate (7.0 4.0 M) concentrations. The climate in northern Taiwan can be regarded as wet in the summer and dry in the winter. In the summer, prevailing southwest monsoon and episodic typhoons are the major driving factors for high precipitation and, therefore, higher river discharge. Summer river discharge data in 2006 were not available from the Taiwan Water Resource Bureau since the monitor used to measure the flow rate malfunctioned for two months. Precipitation data were used alternatively in the discussion of the potential impacts of the river (source, Taiwan Weather Bureau).

The species identified in this work compare favorably with those in previous studies conducted in this estuary (Hsieh and Chiu 1997; Hwang et al. 2006). *Temora* spp. are very common herbivores in coastal ecosystems (Valentin et al. 1987; Ortner et al. 1989; Ianora and Poulet 1993; Nielsen et al. 1993, Gislason and Astthorsson 1995; Ragosta et al. 1995; Suárez-Morales and Gasca 1996). They are generally more abundant in warmer seasons (Mazzocchi and Ribera d'Alcalà 1995; Hsieh and Chiu 1997; Ribera d'Alcalà et al. 2004; Hwang et al. 2006). *Temora* spp. have a feeding preference for diatoms, particularly during the season of phytoplankton growth (Turner 1984). The result of an *in situ* feeding study shows that *Temora* spp. grazed 50% of the phytoplankton biomass (calculated by chlorophyll *a* concentration) per day in this estuary (Chung, unpublished data).

In natural environments, all living organism are well known to be subjected to physical, chemical and biological

Table 2. Slope values calculated from the linear regression of planktons' abundance vs. temperature during the shift-up and shift-down phases. See text for explanation.

Planktons	Units	Shift-up	Shift-down	Difference (%)***
Diatoms	$\times 10^3$ cells m^{-3} °C^{-1}	140 ± 38*	96 ± 38*	46
Copepods	inds. m^{-3} °C^{-1}	90 ± 13	70 ± 14	29
Temora sp.	inds. m^{-3} °C^{-1}	62 ± 12**	47 ± 13**	35

* and **: Significantly different from each other by ANCOVA test at 0.01 level.

***: Calculated as [(shift-up slope – shift-down slope) / shift-down slope] × 100%.

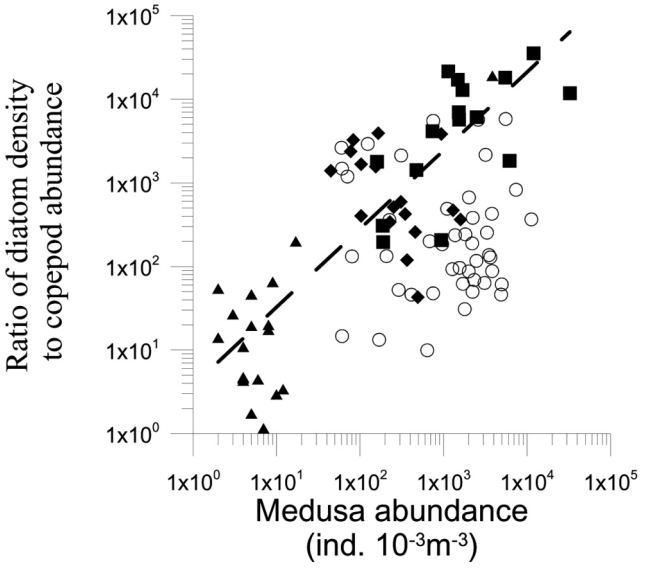

Fig. 5. A scatter plot of the ratio of diatom abundance to copepod abundance vs. medusa abundance. Symbols solid diamonds, solid triangles and solid squares represented winter, spring and summer 2006, respectively. Dashed line, Ln (Y) = 1.21 (0.48) + 0.95 (0.89) Ln (X) (n = 58, r^2 = 0.67, p < 0.01) from spring to summer 2006.

controls. An enhancement or reduction of biomass reflects the net result of these rate-limiting processes. The strong temperature dependence of diatoms and copepods (Table 1) indicates that their growth may be restricted more by interactions between temperature and top-down processes than by bottom-up control (nutrient and food supply) processes. Our argument for the temperature, but not substrate (or food) supply, control on plankton seasonality was based on the reasoning that temperature effects would not occur if their growth was limited by the food supply, since all living organisms feed on materials, but not on temperature (Shiah and Ducklow 1994). Previous studies have demonstrated that bottom-up control processes and biogeochemical processes in coastal and estuary system seldom control the growth of many planktons, including bacteria (Shiah et al. 2006), protozoans (Sherr and Sherr 2002) and copepods (Calbet 2001; Calbet and Saiz 2005).

The significant seasonal behavior of diatoms might also be affect by seasonal light intensity, which is in parallel to the change of temperature. A much lower diatom density was recorded in spring 2006 then that in spring 2005. In spring 2006, residual silicate concentration (7.4 1.8 M) was 3.9 M higher than in 2005 and temperature (22.3 C) was 2.5 C lower. Moreover, the daily light intensity (13.8 mEins m^{-2} d^{-1}) in April 2006 was 80% of that in 2006, and the densities of the copepods in 2006 (254 225 inds. m^{-3}) were three times higher than those of their counterparts in 2005 (84 51 inds. m^{-3}), supporting the conclusion that worse environmental conditions (lower temperature, lower light intensity and more grazers) did not favor the growth of diatoms, but led to a lower diatom abundance and higher ambient silicate concentrations in spring 2006. Moreover, the significant inter-annual difference (> 8X) of summer diatom abundance may result from of the variation in the precipitation. The total precipitation three weeks before July 2005 (101 mm) was 40% higher than that of July 2006, in which precipitation was 61 mm (data source, Central Weather Bureau of Taiwan). Greater river discharge that was caused by more precipitation may bring more nutrients into the study site. Those nutrients input might support more environmental carrying capacity in summer 2005, when diatom density was higher than that in 2006, despite the fact that copepod abundance was 20 times more in summer 2005 (1031 615 inds. m^{-3}) than that in 2006 (47 39 inds. m^{-3}).

Next to temperature effects, top-down control processes may be the secondary dominant factor in regulating the seasonal and temporal patterns of plankton. The results suggest that the relative importance of top-down control on phytoplankton abundance may be different in the shift-up and shift-down phases (Table 2). During the shift-up period, the increasing temperature (and light intensity) stimulated the growth of algae, and their growth rate must have exceeded the concurrent grazing rate to cause net accumulation of biomass. On the other hand, decreasing physical conditions might have inhibited algal growth during the shift-down period. Three possible explanations can be given. First, temperature stimulation (during the shift-up phase) may be more effective than temperature inhibition. Second, grazing pressure was less intense during the shift-down phase. Finally, the copepod grazing rate was reduced by lower temperature in the shift-down phase. The slopes in Table 2 were normalized by temperature, based on the assumption that physiological stimulating and inhibiting effects that were induced by temperature (or light intensity) were equal in both phases. Under this scenario, the lower grazing pressure in the shift-down phase plausibly explains the much slower decrease in the phytoplankton abundance during this period. Moreover, the decrease in the specific grazing rate caused by the decrease in temperature may also reduce grazing pressure. This suggestion is arguable because only one-cycle of analysis was conducted. However, the interpretation is reasonable since the same phenomenon occurred at the zooplankton level.

Many studies have demonstrated that medusae can cause a shift in the trophic structure of the pelagic community as a result of trophic cascading (Behrends and Schneider 1995; Schneider and Behrends 1998; Stibor et al. 2004 and citations therein). However, many of these published studies have addressed the effects of cascading effects on the temporal variability of lower trophic levels. The results demonstrate that medusa variability can strongly influence the spatial and temporal variations of the ecological relationship (i.e., the ratios) between diatoms and copepods. In an environment in which the abundance of top predators (trophic level 3, medusae) and thus their grazing pressures on trophic

level 2 (copepods) did not vary from season to season, such as in the cases of 2005, planktons of the lower two trophic levels may oscillate simultaneously under steady cascading control. In the sense of trophic cascading, one might say that the ecological relationships of the two lower trophic levels were free of the control exerted from trophic level 3. This fact may be one of the major reasons for the absence of a relationship between the ratios and the medusa abundance when the medusa abundance did not change significantly season by season. On the other hand, when the abundance of the top predators rapidly decreased or increased, their grazing pressure on trophic level 2 might have been significantly reduced or intensified such that a notable change of the ratios of the lower trophic levels was observed.

In conclusion, the dependence of phytoplankton and mesozooplankton abundances on temperature was strong in this area. Base on this dependency, bottom-up control may be weak, while top-down control is more important to the temporal and spatial variations of the planktons. The very large observed changes in medusa abundance that caused cascading effects affected not only temporally but also spatially on the relationship between diatoms and copepods. This huge change also affected copepod variation. A positive relationship between the lower two trophic levels occur when the abundance of the top predator varies insufficiently (i.e., < 10-fold), potentially yielding stable diatom to copepod ratios.

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