Journal of
Marine Science and Technology

Volume 21
Issue 7 *Vol 22, Supplemental*

Article 28

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Recommended Citation
Chao, Chien-Fu; Wang, Bo-Wei; Cheng, Chao-Hsiung; and Chiang, Kuo-Ping (2013) "THE DIEL DYNAMICS OF CILIATE COMMUNITY IN A TIDE-POOL," *Journal of Marine Science and Technology*: Vol. 21: Iss. 7, Article 28.
DOI: 10.6119/JMST-013-1220-11
Available at: https://jmstt.ntou.edu.tw/journal/vol21/iss7/28

Journal of Marine Science and Technology, Vol. 21, Suppl., pp. 216-222 (2013)
DOI: 10.6119/JMST-013-1220-11

THE DIEL DYNAMICS OF CILIATE COMMUNITY IN A TIDE-POOL

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Key words: ciliate, tide-pool, diel variation.

ABSTRACT

We investigated the diel cycle mechanism of a tide-pool ciliate community of the northeastern coast of Taiwan. The investigation was conducted on 17th-18th June (typical summer weather), and on 23th -24th July 2013 (10 days after a typhoon). In June, the tide-pool ecosystem was an independent and the excystment of ciliates in the tide-pool caused a dramatic increase in population abundance, as well as composition change. In July, there was no significant difference between the species composition in the tide-pool and that in the surrounding coastal water. However, the abundance of ciliates in the tide-pool was lower due to the inability of ciliates to adapt to the tide-pool environment. From these results, we infer that the excystment of ciliates plays an important role in the diel cycle of the ciliate population in a tide-pool.

I. INTRODUCTION

Intertidal zones are common throughout the world. Because of their isolation and the mixing created by the twice-daily tides, tide-pools are highly fluctuating and independent ecosystems (Johnson [17]). The tide-pool population survive within this extreme environment by adopting a specialized form of succession. Due to the ease of sampling and investigation, tide-pools often act as model systems for population studies (Johnson [17]), Raffaelli and Hawkins [23]).

In past studies protozoans have been found to be the dominant species in tide-pool environments (Johnson [17]), Raffaelli and Hawkins [23]). Protozoans have a high growth rate and a short generation time, on the order of hours to days. Therefore, they are useful as models to investigate population dynamics, including the effects of disturbance or environmental pressure, as well as cyclical behavior (Holyoak [15]). A central in tide-pool research is whether the organisms present there represent a resident community or are merely a reflection of the species found in adjacent coastal waters.

The importance of ciliates within aquatic environments resides in their roles as consumers of picoplankton and nanoplankton (Verity [30], Bernard and Rassoulzadegan [3], Berninger *et al.* [4], and Calbet and Landry [6]) and as prey for mesozooplankton (Broglio *et al.* [5], and Calbet and Saiz [7]). For these reasons, ciliates may constitute an important link between the microbial loop and higher trophic levels of the food chain (Gifford [13], Broglio *et al.* [5]). Many previous reports have indicated an ample abundance in tide-pools (Fauré-Fremiet [12], Jonsson [18], Montagnes *et al.* [20]). Montagnes *et al.* [20] demonstrated the cyclical behavior of ciliate Strombidium oculatum in a coastal tide-pool, with ciliate abundance quickly increasing when the tide-pool was isolated from the surrounding water, reaching a maximum abundance at 2~2.5 hrs and then decreasing rapidly thereafter. Ciliates excyst and grow rapidly during the period of low tide, and are then induced to form cysts at the beginning of the incursion of tide water. The specific live type will produce a special and independent ecosystem. For this reason, we used ciliates to describe the ecosystem in the tide-pool. The study area was affected by a strong typhoon, "Soulik", on 12th-13th July, with average gusts of 29.3 m s^{-1} and a maximum gust of 50 m s^{-1}. We collected samples on 23th -24th July, 10 days after the typhoon, to observe the "little islands" ecosystems reset by external force. In addition, we collected samples on 17th-18th June, when typical summer weather prevailed.

II. MATERIALS AND METHODS

Our study site was located at an intertidal zone in northern Taiwan (Fig. 1). Samples were collected on June 17-18, and July 23-24, 2013 in a tide-pool measuring about 2 m × 1 m × 0.4m (length × width × depth). Sampling was done every 30 minutes from the time the tidal-pool was isolated from the

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Paper submitted 11/20/13; revised 12/08/13; accepted 12/20/13. Author for correspondence: Kuo-Ping Chiang (e-mail: kpchiang@mail.ntou.edu.tw).

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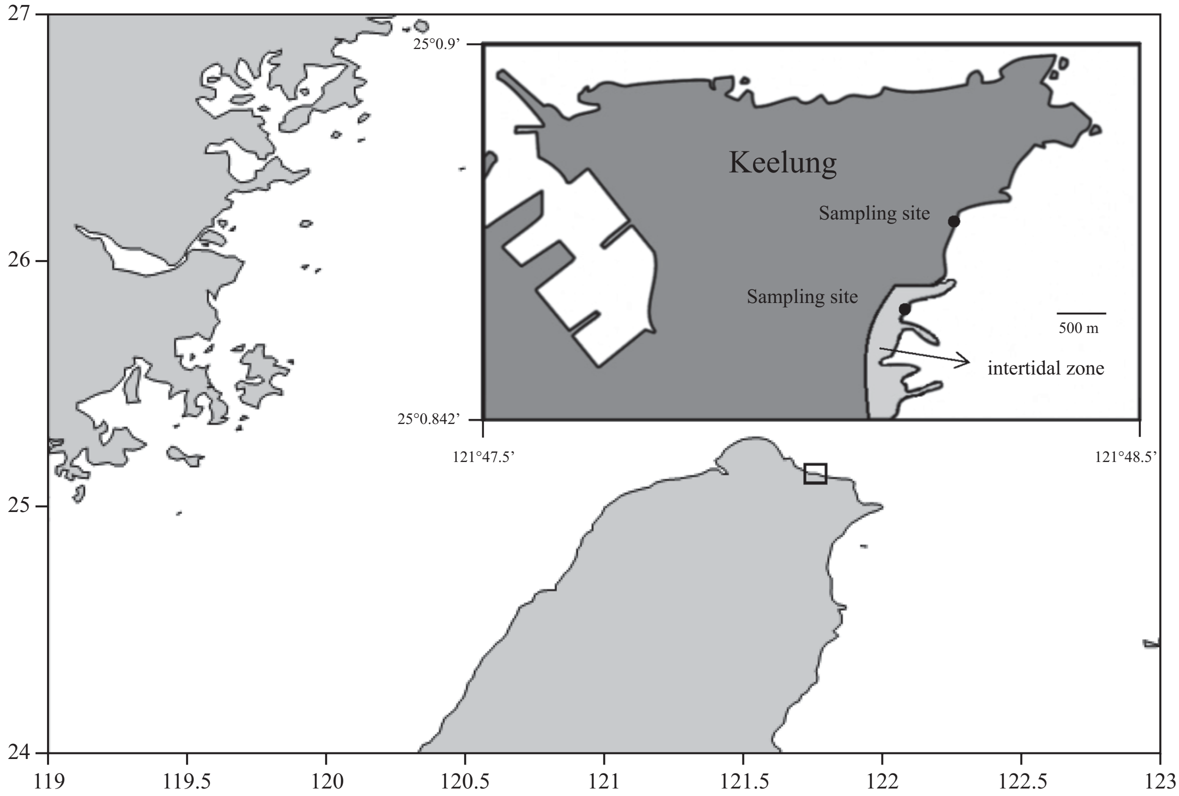

Fig. 1. Location of sampling sites in the coastal waters of the western subtropical Pacific, Keelung, north coast of Taiwan.

surrounding water to the time it was flooded by the intrusion of water at the beginning of the next high tide. In addition, we also collected surface sea water every hour from the sea-dike near the intertidal zone. There were two daytime low tides (7:30 to 12:00 on June 18 and 12:30 to 18:00 on July 23) and two at night (19:30 to 22:30 on June 17, and 1:30 to 4:30 on July 24). Temperature and salinity were measured with a mercury thermometer and a portable salinity meter (Consort C561). To count ciliates 500 ml water samples were fixed with Lugol's (2% final concentration of v/v), while for bacteria and nanoflagellates 50 ml water samples were fixed with glutaraldehyde (final concentration 1%) (Christaki *et al.* [9], Sanders *et al.* [26]).

Ciliate cells were concentrated in 100 ml water samples by the Utermöhl method (Hasle [14]) and were identified and counted using an inverted epifluorescence microscope (Nikon-Tmd 300) at 200× or 400×. Based on cell shape, lorica and collar appearance, the ciliates were categorized into five categories, namely *Strombidium* spp., *Strobilidium* spp., *Mesodinium* spp., Totonia, and tintinnids. Dividing ciliate cells were recorded and, the frequency of dividing cells (FDC) was calculated and the growth rate inferred (Carrick and Fahnenstiel [8]).

For bacteria and nanoflagellate enumerations, quantities of 1-2 ml and 20 ml respectively were filtered onto black Nuclepore filters of pore size 0.2 μm for bacteria or 0.8 μm for nanoflagellates. Samples were stained with DAPI (4',6-diamidino-2-phenylindole) at a final concentration of 1 μg ml^{-1} (Porter and Feig [22]). Pigmented and heterotrophic nanoflagellates (PNF and HNF) were enumerated according to the presence or absence of chlorophyll auto fluorescence using a separate filter set optimized for chlorophyll or DAPI under a 1000× epifluorescence microscope (Nikon-Optiphot-2). Bacteria and HNF were identified by their blue fluorescence under ultraviolet (UV) illumination, while synechococcus spp. and PNF were identified by their orange and red autofluorescence under blue light excitation. To obtain reliable estimates of abundance we counted 30 and 50 fields of view for bacteria and nanoflagellates, respectively.

All statistical operations, including correlation analysis, Pearson's chi-squared test (x^2) and T-test, were performed using SPSS (version 13).

III. RESULTS

Temperature and salinity show a similar diel variation pattern in June and July (Fig. 2), with higher temperatures occurring during the day and no significant difference between tide-pool and coastal surface sea water. In June, the temperature ranges for tide-pool and coastal water were 19.9 to 30.6°C and 19.3 to 29.8°C respectively (Fig. 2A, B). The corresponding figures for July were 20.5 to 35.2°C and 21 to 32.3°C (Fig. 2C, D).

In the tide-pool, salinity increased with time from the

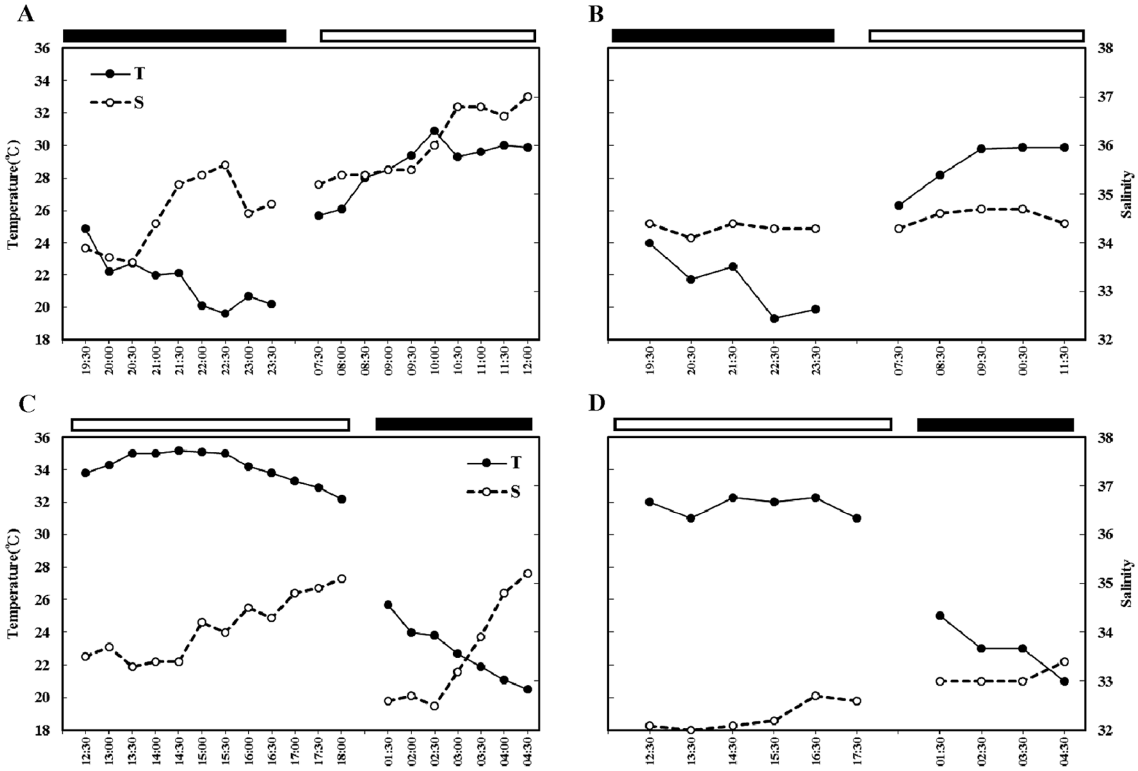

Fig. 2. Temporal variations in water temperature (°C) and salinity in June tide-pool (A), June coastal water (B), July tide-pool (C), July coastal water (D). Solid bar means day, hollow bar means night.

period of low tide, and was higher in the daytime than at night. Day/Night values for June were 35.2 to 37, and 33.6 to 35.6, respectively. For July the corresponding figures were 33.3 to 35.1, and 32.5 to 35.2. In coastal water, the salinity ranged from 34.1 to 34.7 in June and from 32 to 33.4 in July, with non-significant diel variation. (Fig. 2).

For each low-tide, there was a significant difference in the mean abundance of ciliates between tide-pool and coastal water (T-test $p < 0.05$). In addition, a noticeable diel variation was observed in both ecosystems. In June, the total ciliate abundance in the tide-pool, ranged from 140 to 830 L^{-1}, with an average of 189 L^{-1} at night, and a significantly higher average of 430 L^{-1} during the day (T-test $p < 0.05$). (Fig. 3A). In contrast, the abundance in coastal water ranged from 30 to 100 L^{-1} during the day, with an average of 44 L^{-1} ,and from 200 to 730 L^{-1} at night, with a significantly higher average of 458 L^{-1} (T-test , $p < 0.05$) (Fig. 3B). We found an FDC of 2.44 to 5.88 % in the initial tide-pool stage during the daytime.

There was a different pattern in June and July than that in the daytime in the tide-pool. Total ciliate abundance ranged from 10 to 100 L^{-1} during the day (average of 35 L^{-1}), and from 160 to 740 L^{-1} at night (average of 291 L^{-1}). The nighttime abundance was significantly higher than that in the daytime (T-test, $p < 0.05$) (Fig. 3C). In coastal water, total abundance ranged from 100 to 730 L^{-1} during the day (average of 310 L^{-1}), and from 1140 to 2140 L^{-1} at night (average of 1707 L^{-1}), the same trend as observed in June (Fig. 3D).

The dominant species in the ciliate communities in both tide-pool and coastal water were *Strobilidium*, *Strombidium*, and *Mesodinum*. A x^2 test revealed a revealed a significant difference in spatial composition between the two ecosystems (tide-pool and coastal water) (x^2 test $p < 0.05$ in day) in daytime in June, but no significant difference in July ($p > 0.05$). These variations indicate that the tide-pool and coastal water communities were independent during the daytime in June. In contrast, the tide-pool ecosystem in July was not isolated from the surrounding ecosystem, and the ciliate composition in the two ecosystems showed a similar composition (x^2 test $p > 0.05$).

In June, bacteria abundance was 1.42 to 11.14 × 10^6 cells ml^{-1} at night, and 1.43 to 4.8 × 106 cells ml^{-1} during the day in the tide-pool (Fig. 4A), and 0.56 to 1.06 × 10^6 cells ml^{-1} at night, and 0.78 to 0.97 × 10^6 cells ml^{-1} during the day in coastal water (Fig. 4B). In July, the corresponding tide-pool/coastal water figures were 2.55 - 5.46 × 10^6 cells ml^{-1} (day), and 0.56 - 0.98 × 10^6 cells ml^{-1} (night) (Fig. 4C), and 0.23 - 0.69 × 10^6 cells ml^{-1} (day), and 0.53 - 0.74 × 10^6 cells ml^{-1} (night) (Fig. 4D).

In June, the abundance of *synechococcus* in the tide-pool ranged from 1.17 to 1.82 × 10^4 cells ml^{-1} at night, and from 0.49 to 1.14 × 10^4 cells ml^{-1} during the day. In coastal water, the respective figures were 1.47 to 2.64 × 10^4 cells ml^{-1}, and 0.35 to 0.93 × 10^4 cells ml^{-1}. In July, abundance in the tide-pool ranged from 0.58 to 3.38 × 10^4 cells ml^{-1} during the

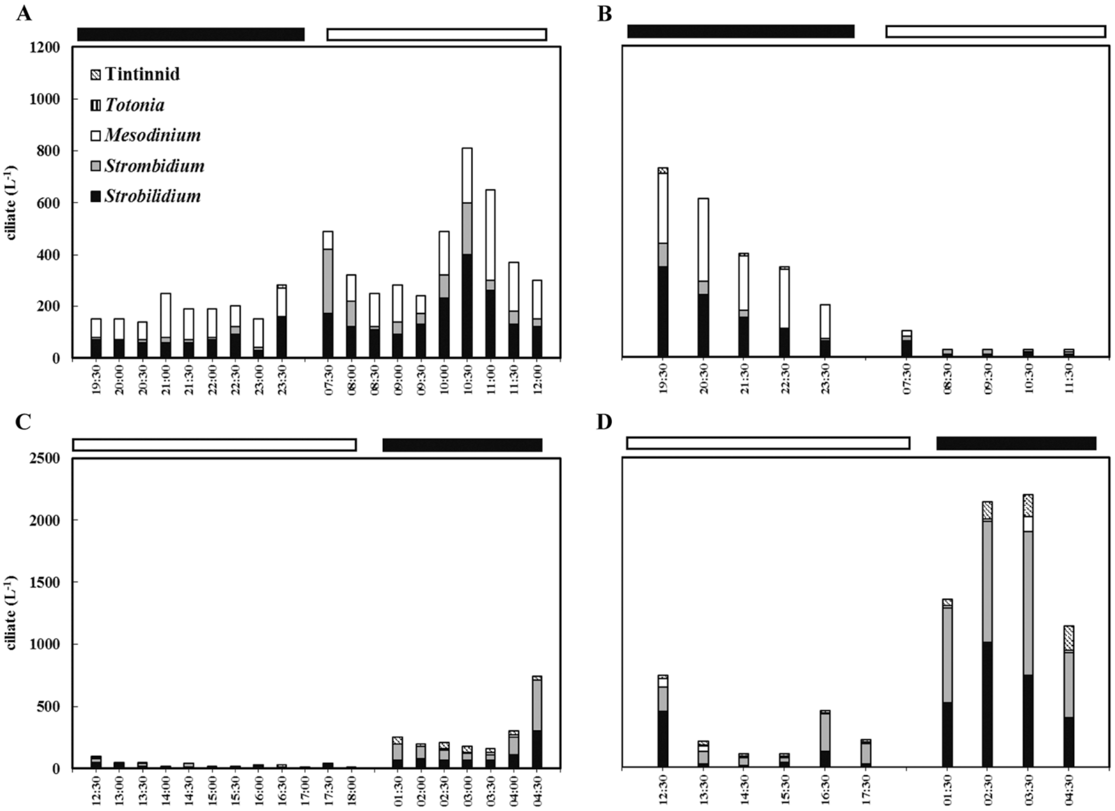

Fig. 3. Temporal variations in ciliate abundance (cells L^{-1}). See Fig. 2 depiction for A, B, C, D.

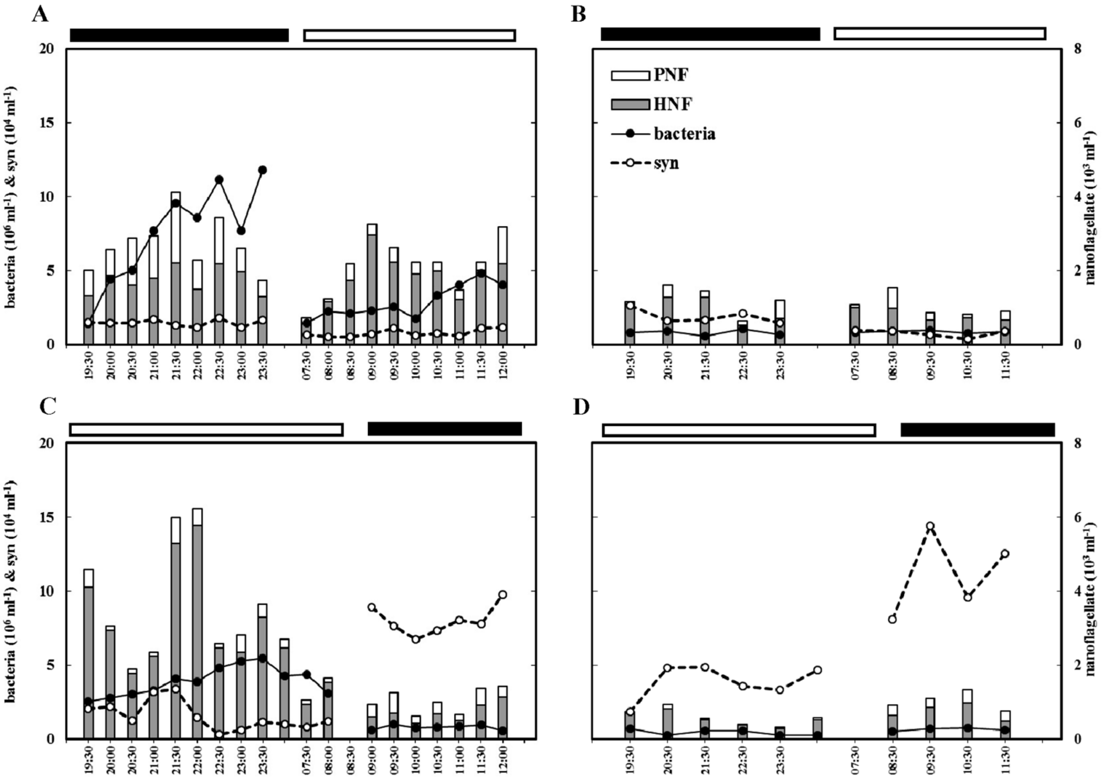

Fig. 4. Temporal variations in bacteria (bac, × 10^6 cells ml^{-1}), *synechococcus* (syn, × 10^4 cells ml^{-1}), pigmented and heterotrophic nanoflagellate (PNF and HNF × 10^3 cells ml^{-1}) . See Fig. 2 depiction for A, B, C, D.

day, and from 6.75 to 9.77 × 10^4 cells ml^{-1} at night. In coastal water, the respective figures were 1.82 to 4.84 × 10^4 cells ml^{-1} at night, and 8.06 to 14.42 × 10^4 cells ml^{-1} during the day (Fig. 4). In both ecosystems, nighttime abundance was significantly higher than daytime abundance ($p < 0.05$).

In June, HNF abundance ranged from 0.56 to 2.96 × 10^3 cells ml^{-1} in the tide-pool, and from 0.51 to 1.27 × 10^3 cells ml^{-1} in coastal water. The corresponding figures for July were 0.41 to 5.75 × 10^3 cells ml^{-1}, and 0.28 to 0.97 × 10^3 cells ml^{-1}. In June, PNF abundance ranged from 0.43 to 1.91 × 10^3 cells ml^{-1} in the tide-pool, and from 0.07 - 0.54 × 10^3 cells ml^{-1} in coastal water). The corresponding figures for July were 0.12 - 0.55 × 10^3 cells ml^{-1}, and 0.01 to 0.35 × 10^3 cells ml^{-1} (Fig. 4). PNF and HNF abundance did not differ between day and night in either ecosystem ($p > 0.05$).

IV. DISCUSSION

Sea water in tide-pools originates from the surrounding coastal water and then becomes isolated. Therefore the ciliate composition in a tide-pool ecosystem should be different from that in the surrounding coastal ecosystem. Montagnes *et al.* [20] found a clear diel cycle in a tide-pool ecosystem, with a significantly higher ciliate abundance during the day than at night. They assumed that the excystment process played a key role, with the daytime population increasing due to the growth of vegetable cells and excystment, and a decrease in abundance in the late stage of daytime low-tide following an increase in cysts. They also assumed that ciliates did not actively grow and excystment process, and affected by environmental pressures, the ciliate population decreased dramatically during the nighttime. In our study a similar diel cycle was observed in June, while a reversed diel pattern occurred in July. To compare the ciliate composition of the tide-pool with the surrounding coastal water, revealed a significant difference during the daytime in June, but no significant difference for the other three low-tide periods. Moreover, there was a significant difference in the mean abundance of ciliates between tide-pool and coastal water in each low-tide period (*T*-test $p < 0.05$). From these results, we inferred that the tide-pool ciliate community was independent from coastal water in June, both day and night. Though there was no significant difference in ciliate composition at night, there was a significant difference in mean abundance (T-test) and the pattern (stable in the tide-pool and decreased in coastal water) was found. We believe the observed temporal variation in ciliate abundance and composition in the tide-pool ecosystem can be explained by the following scenario. A rugged and highly fluctuating nighttime environment results in very low population density. With the arrival of daytime low-tide, excystment causes the ciliate population to dramatically increase. A growth of vegetable ciliate may also play a role in the increase of the ciliate population.

The temporal variation in FDC of ciliate showed a high proportion of dividing cells (about 5.8 %) in the initial stage of tide-pool. This supports the belief that vegetable cell growth contributed to the increase in the tide-pool ciliate population. If we assume that Td = 1 hr , FDC was 5.8% and the abundance was 250 L^{-1} at 9:30, then the abundance should grow to 264.5 L^{-1} (250 × (1+5.8%)/1 = 264.5) after one hour. In fact, this value is much lower than the observed ciliate abundance at 10:30 (830 L^{-1}). This indicates that vegetable cell growth is only part of the story. The daytime ciliate community in the tide-pool became dominated by *Strombidium* spp.. Many previous reports have demonstrated that most ciliate excystment species are members of *Strombidium* spp. (Kim and Taniguchi [19], Ichinomiya *et al.* [16], Agatha *et al.* [2]). Therefore, our results support the view of Montagnes *et al.* [20] that it is the excystment process, rather than the growth of vegetable ciliate that controls the ciliate population dynamic within a tide-pool. Our July sampling date occurred 10 days after typhoon "Soulik". We hypothesized that the high rainfall and tide would have completely scoured off the ciliate cyst from the tide-pool, so that there would be no ciliate excystment occurring within the isolated ecosystem. There was no significant difference in species composition between the tide-pool and the surrounding coastal water. However, the abundance of ciliates in the tide-pool was lower than in the coastal water (T-test $p < 0.05$). From these results, we know that the tide-pool ecosystem was not affected by ciliate excystment. The ciliates were brought into the tide-pool from the surrounding coastal water, and were unable to adapt to the environmental conditions there, resulting in a decrease in abundance for each ciliate species over time. This phenomenon may also support the theory of "island biogeography", whereby a pioneer species which moves to a new, but unsuitable, habitat will become extinguished after a short time. From our results, we infer that excystment plays an important role in the diel cycle of the ciliate population in a tide-pool.

A further significant diel cycle was observed in the northeastern coastal waters of Taiwan. Within an 8 hr daytime period (17:30 to 1:30) a phenomenal growth rate of 5.58 d^{-1} was noted, with ciliate abundance increasing from 210 L^{-1} to 1350 L^{-1}. Generally, marine ciliate growth rates range from 0 to 1.4 d^{-1} (Carrick and Fahnenstiel [8], Strom *et al.* [27], Adrian *et al.* [1]). As for freshwater ciliate, Weisse *et al.* [31] reported a higher growth rate of 4.71 d^{-1} for Bromeliothrix metopoides) in a culture experiment.

No adequate explanation could be found regarding the mechanism of the diel cycle of the ciliate community. In our study, ciliate abundance correlated positively with prey abundance (bacteria and synechococcus) (Table 1), suggesting that diel variations of prey abundance may be the cause. Just such a diel cycle of prey-predator has been used to describe the diel dynamic between picoplankton and nanoflagellate (Tsai *et al.* [28, 29]). Our study samples produced a large abundance of zooplankton consisting of copepods and crustacean larvae (data no show). Wu *et al.* [32] have demonstrated that the grazing behavior of microzooplankton differs from day to night, feeding on ciliate and dinoflagellate during the day, and

Table 1. Correlation analysis. Positive correlation (+), Negative correlation(-), marked (*) = $p < 0.01$, unmarked = $p < 0.05$.

June					
tide-pool	+T*	+S*	-syn*	-PHF*	
day					
night	+bac				
coastal water	+syn				
day	-T				
night					
July					
tide-pool	+T*	+bac*	-syn*		
day					
night	+syn	+HNF			
coastal water	-T*	+bac	+syn*	+HNF	+PNF*
day	-syn				
night	+HNF				

diatom at night. The top-down control of predators may therefore be another factor in the diel cyle of the ciliate population. Many previous studies have indicated that ciliates exhibit vertical migration to the surface during the daytime (Dale [10], Dawidowicz *et al*. [11], Pérez *et al*. [21], Rollwagen-Bollens *et al*. [24], Rossberg and Wickham [25]). This vertical migration may also explain the phenomenal daytime increase of the ciliate population.

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