Ecological response of lower trophic levels to episodic typhoons in temperate coastal waters

温帯沿岸域における台風に対する低次栄養段階生物の生態学的応答

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SYNOPSIS

近年の地球温暖化や気候変動に伴い、台風の強度が増加しており、水圏生態系における生物地球化学サイクルへの影響が懸念されている。本研究では、温帯沿岸域である相模湾真鶴港（水深 5m）および真鶴沖合定点（水深 120m）において、台風通過に伴う物理化学環境の変動と低次栄養段階生物群集の応答を研究した。真鶴港では 2005 年台風 11 号*Mawar*、2008 年台風 13 号*Sinlaku*、2009 年台風 9 号*Etau*、2010 年台風 9 号*Malou*通過後に、沖合定点では 2010 年台風 9 号*Malou*通過後に毎日サンプリングを行った。台風通過後、塩分が低下し、各種栄養塩濃度が増加した。*Sinlaku*、*Etau*、*Malou*では陸水の流入及び底泥の再懸濁、*Mawar*ではそれらに加えて湧昇によって栄養塩が負荷された。細菌生産は台風通過直後に極大を示し、一次生産と比較して 1.5 倍の値を示した。一方、一次生産は台風通過 3~5 日後に極大を示し、その極大時には細菌生産の 10 倍の値を示した。このことから、台風通過後は流入してくる異地性の栄養塩や有機物を利用して細菌生産が卓越した後、一次生産が卓越することが明らかとなった。植物プランクトン生物量は台風通過 4~6 日後に極大を示した。植物プランクトン群集は、台風通過直後には渦鞭毛藻の比較的高い優占度が見られたが、その後植物プランクトン生物量の増加とともに珪藻の優占へと遷移した。珪藻群集の中では*Mawar*では*Skeletonema* spp.が、*Sinlaku*、*Etau*、*Malou*では*Chaetoceros* spp.が優占し、これらの優占度はN/P比とそれぞれ負および正の有意な関係を示した。すなわち、植物プランクトンの遷移は台風通過後のN/P比が異なる栄養塩源の相対的貢献度に制御されていることが示唆された。次に、海洋環境への台風の鉛直方向への影響を明らかにするため、沖合定点において鉛直観測を実施した。植物プランクトンは通過 4~5 日後に顕著な増加を示し、同時に有光層以深においても比較的高濃度の植物プランクトン生物量が見られたことから、有光層で生産された植物プランクトンの速やかな沈降または移流が起こったと考えられる。また、有光層以深では細菌数及びNH_4濃度の顕著な増加が見られ、有光層で生産された植物プランクトンを起点として、素早い細菌活動が進行していたことを明らかにした。

Key words: Typhoon, Sagami Bay, Temperate coastal waters, Primary production, Bacterial production, N/P ratio, *Skeletonema*, *Chaetoceros*, Dinoflagellates

INTRODUCTION

Phytoplankton and bacteria are at the base of aquatic food webs. Their abundance and growth, as well as biogeochemistry, can be influenced by regular seasonal variations of biotic and abiotic factors, and irregularly and strongly influenced by climatic and anthropogenic perturbations in coastal and estuarine waters. However, biogeochemical and food web changes induced by these perturbations are complex, and our knowledge of how coastal and estuarine waters are influenced by different types of perturbations remains rudimentary. Climate change and global warming may lead to intensification of typhoons (including tropical cyclones and hurricanes) and the impact of typhoons on oceanic biogeochemistry may also be augmented (*e.g.* Kunkel et al. 2013). Understanding the effect of typhoons on phytoplankton and bacteria is necessary to predict the relationship between climate change and coastal ecosystems in the future.

In oceanic and coastal regions, typhoon passages induce physical disturbances such as upwelling, vertical mixing, terrestrial runoff and sediment resuspension, which supplies nutrients to the euphotic layer (*e.g.* Chung et al. 2012). The nutrient loading generally causes significant increases in primary production (PP) and bacterial production (BP) (*e.g.* Shiah et al. 2000). In addition, some prior studies have shown phytoplankton species succession and diatoms, such as *Skeletonema* spp., *Chaetoceros* spp. and *Nitzschia* spp., dominating phytoplankton communities after typhoon passages (*e.g.* Chen et al. 2009). Phytoplankton succession is known to be linked to and regulated by variability of nutrients. The nutrient environment after the passage of typhoons may vary depending on the relative contributions of nutrient sources, and each source has inherent unique nutrient ratios (*e.g.* Howarth 1988). However the succession mechanism of phytoplankton communities and nutrient stoichiometry after typhoon passage are still not well understood.

Storm-associated winds have the potential of completely mixing shallow coastal waters (<20-50 m) down to the sediment surface, where sediment resuspension will be one of the major nutrient sources besides terrestrial runoff and upwelling. BP was enhanced by sediment resuspension accompanied by typhoon passage in North Carolina (Fogel et al. 1999). In addition, sediment resuspension caused a dramatic short-term (a day) increase in BP in a mesocosm experiment (Chróst & Riemann 1994). Although it is foreseeable that BP and bacterial abundance (BA) might exhibit a short-term variation, little is known about the short-term evolution of BP and BA accompanied by typhoon passage. Since phytoplankton bloom occurred in 3 to 6 days after the typhoon passage (*e.g.* Tsuchiya et al. 2013b), BP may be rapidly enhanced by such perturbations and became dominant before phytoplankton bloom occurs at inshore waters.

After the storm-induced runoff, dinoflagellates often dominated the phytoplankton community in coastal regions (*e.g.* Hoover et al. 2006). The runoff might contribute to formation of shallow pycnocline layer with rich nutrients at the surface, and then dinoflagellates might accumulate in the layer using their swimming ability (Donaghay & Osborn 1997). After the dominance of dinoflagellates, diatoms became dominant (*e.g.* Zeeman et al. 1985). However, the vertical distribution and bloom formation process of diatoms and dinoflagellates after the passage of typhoon are still relatively unknown.

Contribution of the increased PP to annual PP has primarily been estimated in tropical and subtropical regions. In South China Sea, PP resulting from a typhoon contributed >2–4% to the annual new production, which is supported by nutrient inputs from outside the euphotic zone (Lin et al. 2003). Given an annual average of fourteen typhoons passing over the South China Sea, the contribution of typhoons to the South China Sea's annual primary production may be as much as 20–30%. Although typhoons are episodic events, the effect of a typhoon on PP is significant, and should be considered to estimate annual PP. Quantitative estimates of PP contributions to the annual PP during typhoons are still limited in coastal waters.

Fates of increased phytoplankton after the passage of typhoon have received increased attention in recent years. Prior studies suggested that high grazing pressure by micro- and mesozooplankton on phytoplankton (*e.g.* Zhou et al. 2011). Increase in fecal pellets (Chung et al. 2012) can accelerate sinking of phytoplankton from euphotic zone to deeper waters (Turner 2002). Typhoon events caused phytoplankton bloom and enhanced particulate organic carbon (POC) flux up to 1.7-fold higher than that of non-typhoon period (Hung et al. 2010). In addition, river runoff transports large amount of terrigenous POC. These phenomena such as grazing and sinking of phytoplankton and POC might affect chemical-biological processes below the euphotic zone. Among them, nutrient regeneration caused by grazing and microbial decomposition of organic matter might be progressed below the euphotic zone. However, difficulty of *in situ* sampling after the passage of typhoon have not let us shed a light on the short-temporal variations of chemical-biological processes below the euphotic zone.

The present study examined the response of phytoplankton and bacteria to the passage of typhoons in the coastal waters of Sagami Bay by conducting a time-series observations during the passage of typhoon *Mawar* (T0511), *Sinlaku* (T0813), *Etau* (T0909) and *Malou* (T1009). The specific objectives of the study were (1) to elucidate couplings between BP and PP, (2) to quantify contribution of PP enhanced by typhoon passage to annual PP, (3) to clarify a relationship between phytoplankton assemblage and nutrient stoichiometry determined by relative contribution of nutrient sources after the passage of typhoons, (Study 1) and (4) to reveal the bloom formation process and the fate after the passage of typhoon (Study 2).

MATERIALS AND METHODS

In Study 1, daily samplings after the passage of four typhoons (*Mawar* in 2005, *Sinlaku* in 2008, *Etau* in 2009 and *Malou* in 2010) were conducted at an inshore station, Manazuru Port (Sta. A, 5 m depth, 35º 08.9' N, 139º 09.1' E) in Sagami Bay. In Study 2, daily and vertical sampling after the passage of *Malou* in 2010 was conducted at a fixed offshore station (Sta. M, 120 m depth, 35º 09.0' N, 139º 10.5' E) using the R.V. "*Tachibana*" of the Manazuru Marine Laboratory, Yokohama National University.

Study 1. Responses of phytoplankton and bacteria to the passage of typhoons at inshore waters in Sagami Bay, Japan

Mawar occurred near Ogasawara Islands in southern Japan as a tropical depression on 20 August 2005, and passed through Sagami Bay on 26 August 2005. *Sinlaku* occurred in the Philippine Sea on 8 September 2008, and approached Sagami Bay on 20 September 2008. *Etau* occurred in Southern Japan as a tropical depression on 8 August 2009, and approached Sagami Bay on 11 August 2009. *Malou* occurred in the East of the Philippine Sea as a tropical depression on 3 September 2010. It passed over the East China Sea, Tsushima Straits and Japan Sea, and then made landfall from Japan Sea and approached Sagami Bay on 8 September 2010.

The sampling periods were from 25 August to 7 September in 2005 during *Mawar*, from 21 to 27 September in 2008 during *Sinlaku*, from 10 to 18 August in 2009 during *Etau*, and from 8 to 15 September in 2010 during *Malou*. In this study, we defined the day when each typhoon passed Sagami Bay as Day 0. Surface seawater was collected to measure water temperature, salinity, nutrients [NO_2+NO_3, NH_4, PO_4 and $Si(OH)_4$], POC, chlorophyll *a* (chl *a*), pheopigment, PP, phytoplankton assemblage, phytoplankton carbon biomass (PC), BA and BP. PP was measured during *Mawar* and *Malou*, and NH_4 and BP were measured during *Malou*.

Wind speed and wind direction were obtained from the Japan Meteorological Agency at the Ajiro Office (35º 02.7' N, 139º 05.5' E), and precipitation data were obtained at the Odawara Office (35º 16.6' N, 139º 09.3' E). Both are located less than 15 km away from our sampling site.

Study 2. Vertical and temporal variations of phytoplankton, and microbial processes below the euphotic zone after the passage of typhoon at offshore waters in Sagami Bay, Japan

Daily sampling was carried out from 9 to 13 September in 2010 (from Day 1 to Day 5) at Sta. M. Seawater sample was from 0, 10, 20, 30, 40, 60 and 100 m depths to measure water temperature, salinity, nutrients, POC, chl *a*, pheopigment, PP, phytoplankton assemblage, BA and BP. PP and BP were measured at the surface. The diffuse attenuation coefficient (K_d) for downwelling irradiance of photosynthetically available radiance (PAR) was determined, and 1% attenuation depth estimated from the K_d was defined as the "euphotic depth".

RESULTS AND DISCUSSION

Study 1. Responses of phytoplankton and bacteria to the passage of typhoons at inshore waters in Sagami Bay, Japan

Immediately after the passages of typhoon, salinity decreased and nutrient concentrations increased. The surge of nutrients might be attributable to terrestrial runoff and sediment resuspension during *Sinlaku, Etau* and *Malou*, and upwelling in addition these sources during *Mawar*. During *Mawar*, nutrient concentrations kept relatively high levels until Day 4, while during other three typhoons nutrients were loaded once and decreased rapidly. The long-lasting high nutrients might be due to the influx of upwelled water, which resulted in relatively low N/P ratio during *Mawar*. In addition, PO_4 concentrations during *Sinlaku, Etau* and *Malou* were significantly lower than *Mawar* (Tukey-Kramer test, $p < 0.05$).

During *Malou*, primary production (PP) showed relatively low values of 131 ± 64 mg m^{-3} d^{-1} from Day 1 to Day 3, increased from Day 4, and then reached a maximum of 554 ± 32 mg m^{-3} d^{-1} on Day 5. Bacterial production (BP) showed relatively high values of 114 ± 21 and 132 ± 14 mg C m^{-3} d^{-1} on Day 1 and Day 2, respectively. BP showed 79 ± 21 mg C m^{-3} d^{-1} from Day 3 to Day 8. The ratio of BP to PP (BP/PP ratio) showed a maximum of 1.5 on Day 1, and then decreased to 0.1 on Day 5 (Fig. 1), which suggests that dominant biological production rapidly changed from BP to PP after the passage of *Malou*. Assuming a bacterial grow growth efficiency (GGE) of 0.5, BP/PP ratios of >0.5 indicates that daily bacterial carbon demand (=BP / GGE) exceeded daily primary production. The high BP just after the passage of *Malou* might be largely supported by allochthonous substrates, *e.g.* from sediment resuspension.

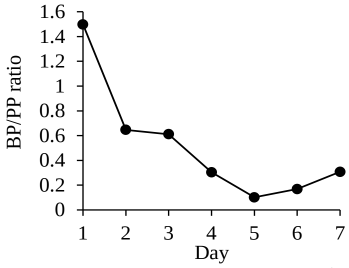

Fig. 1 Temporal variation in ratio of bacterial production to primary production (BP/PP ratio) during *Malou* at the surface of Sta. A

PP/Chl *a* ratios from Day 1 to Day 9 during *Mawar* (131 ± 29 mg C [mg chl *a*]$^{-1}$ d^{-1}) and from Day 1 to Day 7 during *Malou* (97 ± 45 mg C [mg chl *a*]$^{-1}$ d^{-1}) were significantly higher than the mean PP/Chl *a* ratio, 40 ± 28 mg C [mg chl *a*]$^{-1}$ d^{-1}, observed in August and September in Sagami Bay (Student's t-test, $p < 0.01$) reported by Sugawara et al. (2003). The results suggest that the passage of typhoons enhanced primary productivities for 9 days during *Mawar* and for 7 days during *Malou*. When the PP are integrated during the enhanced periods, the integrated PP are 2.10×10^3 mg C m^{-3} for 9 days and 2.07×10^3 mg C m^{-3} for 7 days, respectively, which accounts for 7.1-9.1% of the annual primary production in the upper waters of Sagami Bay (annual PP were derived from Satoh et al. 2000, Sugawara et al. 2003 and Ara & Hiromi 2009). Approximately three typhoons on average approach Sagami Bay annually (Japan Meteorological Agency), which implied that PP in the upper waters of Sagami Bay might be enhanced in the range of 21.3-27.3% of the annual PP. The present study verified that episodic events such as typhoons could make large contributions to annual PP in temperate coastal regions.

Relatively high proportions of dinoflagellates, such as *Ceratium* spp., *Dinophysis* spp., *Protoperidinium* spp. and *Gymnodinium* spp., were observed just after the passage of typhoons. These results agreed with prior studies conducted after the episodic events (*e.g.* Zeeman 1985, Hoover et al. 2006). Typhoon-driven runoff may contribute to the formation of low salinity and nutrient-rich fresh water layer at the surface, as suggested by Satoh et al. (2000). In the present study, influxes of runoff and sunny days after the passage of typhoon might have formed a sharp pycnocline and increased vertical stratification. Dinoflagellate cells could concentrate into such a layer due to their swimming behavior (Donaghay & Osborn 1997). Dinoflagellates are better adapted to utilize high-nutrient concentrations under low-turbulence conditions than other phytoplankton groups (Hoover et al. 2006). Further, dinoflagellates have been known to utilize organic substrates for nutrition (Zeeman 1985). Thus, these physical and physiological interactions might make the concentrated layer of dinoflagellates just after the passage of typhoons.

Dominant phytoplankton taxa shifted from dinoflagellates to diatoms with increases in chl *a* and PC. There was a significantly positive relationship between total PC and diatom proportions ([Diatom proportion] = 0.084 * ln[Total biomass] + 0.31; $r = 0.39$, $n = 33$, $p < 0.05$). The dominant diatom species were *Skeletonema* spp. after *Mawar*, and *Chaetoceros* spp. after *Sinlaku, Etau* and *Malou*. There were significant relationships between the two species and the N/P ratio ($p < 0.05$, Fig. 2), suggesting that *Skeletonema* spp. dominated under the condition of lower N/P ratio and *Chaetoceros* spp. dominated under the condition of higher N/P ratio. Roden & O'Mahony (1984) conducted an outdoor experiment in an enclosure and reported that *Skeletonema* spp. favor low N/P ratios and are dominant when the N/P ratio is less than 30. On the other hand, *Chaetoceros* spp. are not phosphorus limited when the N/P ratio is more than 30. In a prior study, alkaline phosphatase activity of *Chaetoceros affinis* was higher than that of *Skeletonema costatum*, especially under high N/P ratio (Møller et al. 1975). Those previous studies support that *Chaetoceros* spp. could dominate under higher N/P ratios, in other words, lower PO_4 concentrations. This was confirmed from the results of the present study during four different typhoons.

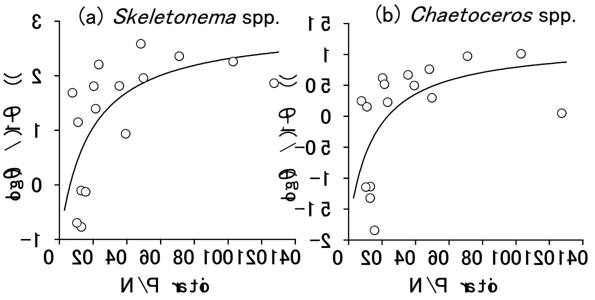

Fig. 2 Relationships between (a) *Skeletonema* spp. and (b) *Chaetoceros* spp., and N/P ratio. (a) θ = 1 – dominance of *Skeletonema* spp., $\log(\theta/(1-\theta)) = 3.94 \times [N/P] / ([N/P] + 17.8) - 1.03$ ($r = 0.653$, $n = 16$, $p < 0.05$). (b) θ = dominance of *Chaetoceros* spp., $\log(\theta/(1-\theta)) = 3.00 \times [N/P] / ([N/P] + 15.4) - 1.81$ ($r = 0.603$, $n = 16$, $p < 0.05$)

In the present study, contribution of nutrient sources was different between *Mawar* and the other three typhoons; upwelling and terrestrial runoff were likely the dominant nutrient sources in *Mawar*, and terrestrial runoff was the dominant nutrient source in *Sinlaku*, *Etau* and *Malou*. Terrestrial waters supply a large amount of nitrogen to coastal regions (*e.g.* Fujiki et al. 2004), which results in higher N/P ratios compared to that of deep water (*e.g.* Kamatani et al. 2000). In addition, relatively high PO_4 concentration lasted until Day 4 during *Mawar* when upwelling was considered as one of the major nutrient sources. The results of the present study suggest that the proportional contribution of nutrient sources, which determines nutrient stoichiometry, is an important factor in controlling phytoplankton community succession after the passage of typhoons.

Study 2. Vertical and temporal variations of phytoplankton, and microbial processes below the euphotic zone after the passage of typhoon at offshore waters in Sagami Bay, Japan

In order to examine vertical and temporal variations phytoplankton, and chemical-biological process below the euphotic zone, daily and vertical sampling was conducted after the passage of *Malo*u at Sta. M from Day 1 to Day 5.

The euphotic depth fluctuated from 16 m on Day 4 to 30 m on Day 5. After the passage of *Malou*, salinity decreased and reached a minimum of 23.7 on Day 2 at the surface. Thereafter salinity recovered to 33.9 at the surface on Day 5. Based on the results of water temperature and salinity, upwelling did not likely occur. Density σ_t at the surface were fluctuated between 14.5 on Day 2 and 21.4 on Day 5, and σ_t at 10 m depth showed values ranging between 22.0 and 22.1, which suggested that sharp pycnocline formed between the surface and 10 m depth. Nutrient concentrations increased with decrease in salinity at the surface, which suggested that terrestrial runoff might be a major nutrient source.

Dinoflagellate community was distributed generally at the surface (Fig. 3a). The biomass at the surface was 13.1 mg C m^{-3} on Day 1, increased to a maximum of 177 mg C m^{-3} on Day 4, dominated by *Prorocentrum* spp. and *Ceratium* spp. The result verified that dinoflagellate accumulated into the surface pycnocline layer and increased at the surface after the passage of typhoon. Diatom biomass showed 32.6 ± 7.4 mg C m^{-3} on average at 10 and 20 m depths from Day 1 to Day 2 (Fig. 3b). Thereafter, the diatom biomass showed maximums of 432 mg C m^{-3} at 10 m on Day 4 and 531 mg C m^{-3} at the surface on Day 5. *Chaetoceros* spp., *Cerataulina* spp. and *Rhizosolenia* spp. were dominant in the diatom bloom from Day 4. The diatom community also prevailed below the euphotic zone on Day 4 and Day 5. These results verified that dinoflagellates reflected swim strategy; diatoms reflected sink strategy after the passage of typhoon, as suggested by Smayda (1997).

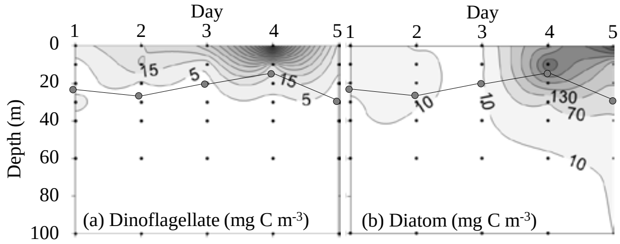

Fig. 3 Distributions of (a) diatom and (b) dinoflagellate at Sta. M. Solid lines indicate the euphotic depth (1%)

In terms of fate of phytoplankton after the passage of typhoon, previous studies suggested intensive grazing by micro- and mesozooplankton on phytoplankton (Hoover et al. 2006, Zhou et al. 2011, Chung et al. 2012). Pheopigments are known to be direct products of zooplankton grazing, and serve as a tag for herbivorous grazing (Shuman & Lorenzen 1975). In the present study, pheopigment concentrations increased and showed a maximum at 30 m on Day 5 at Sta. M accompanied by phytoplankton bloom, which suggests that possible zooplankton grazing pressure on phytoplankton might intensify. Integrated bacterial abundance in the euphotic zone and below the euphotic zone showed clear increasing trend at Sta. M, and reached maximums of 111 × 10^{12} cell m^{-2} below the euphotic zone on Day 4 and 150 × 10^{12} cell m^{-2} in the whole water column on Day 5 (Fig. 4a). Integrated NH_4 also increased and reached maximums of 50.6 mmol m^{-2} below the euphotic zone and 67.5 mmol m^{-2} in the whole water column on Day 5 (Fig. 4b). The results suggest that microbial process was activated and rapid regeneration of NH_4 occurred below the euphotic zone. There are significant positive correlations between bacterial abundance and pheopigment concentration ([BA] = 1.3 × [pheopigment] + 0.5; $n = 22$, $r = 0.78$, $p < 0.001$), and between bacterial abundance and NH_4 concentration ([BA] = 0.88 × [NH_4] + 0.67; $n = 22$, $r = 0.64$, $p < 0.01$) below the euphotic zone, whereas there was no significant correlation between pheopigment concentration and NH_4 concentration below the euphotic zone. These relationships suggests that bacterial activity was associated with zooplankton grazing, and bacteria was a mainly component to contribute to regeneration of NH_4.

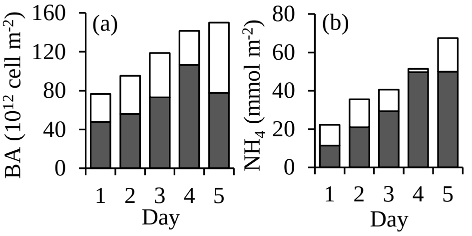

Fig. 4 Integrated (a) bacterial abundance (BA) and (b) NH_4 concentration above (open bar) and below (filled bar) the euphotic depth at Sta. M

SUMMARY

The present study clarified that after the passage of typhoons, (1) at the inshore station, dominant carbon production changed from BP to PP immediately, (2) typhoon-enhanced PP significantly contributed to annual PP in upper waters of Sagami Bay, (3) dominant phytoplankton taxa shifted from dinoflagellates to diatoms, and the dominant diatom species were controlled by the N/P ratios which might be determined by relative importance of nutrient sources, and (4) at the offshore station, dinoflagellates dominated at the surface just after the passage, and then diatoms became dominant in the whole water column, which verified swim strategy for dinoflagellates and sink strategy for diatoms. Accompanied by phytoplankton bloom, increase in pheopigment concentrations below the euphotic zone suggests possible grazing by zooplankton on phytoplankton. Below the euphotic zone, both of NH_4 concentrations and BA increased, and showed significant positive correlation between them, which suggested that bacterial NH_4 regeneration progressed. Therefore, episodic typhoons play an important and significant role to enhance biological productions, and the biochemical response within the water column is relatively fast after typhoon passage.

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