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Effects of typhoons on gelatinous carnivore zooplankton off Northern Taiwan

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Abstract: We examine the effect of typhoons, as potential drivers of nutrient pulse events, on gelatinous carnivore zooplankton. The period investigated spanned from 2007 to 2010, where seasonal abundance and taxonomic composition of the gelatinous zooplankton community was recorded off North Taiwan. Typhoon effects were assessed in the abundance, diversity and species richness of the gelatinous carnivore populations. Significant associations between typhoons and gelatinous carnivores were found in time delays varying from 3 to 25 days, but no association was identified for longer time intervals. Generally, a decrease in species richness occurred during the summer season, and this was accentuated in 2008, shortly after typhoons events. We hypothesize that typhoons might act as resource pulse triggers probably enhancing open niches for opportunistic carnivore zooplankton groups.

Résumé : *Effets des typhons sur le zooplancton carnivore gélatineux au large du nord de Taïwan.* Nous avons examiné les effets indirects des typhons sur l'abondance des carnivores gélatineux via l'enrichissement soudain de nutriments, de 2007 à 2010. Pendant cette période, nous avons quantifié l'abondance saisonnière et la composition taxonomique de la communauté des carnivores gélatineux au large du nord de Taiwan. Nous avons testé l'effet des typhons sur l'abondance, la diversité et la richesse spécifique des populations de ces organismes. Des relations significatives entre les typhons et les carnivores gélatineux ont été identifiées avec un délai entre 3 et 25 jours après le phénomène météorologique alors que, pour des délais plus importants, nous n'avons pas observé le même lien. Une diminution de la richesse spécifique généralement en période estivale a été identifiée, et celle-ci a été plus accentuée l'été et l'automne 2008, peu de temps après le passage de plusieurs typhons. Ces résultats suggèrent un effet non négligeable des typhons via l'enrichissement soudain de nutriments pouvant créer des nouvelles niches et bénéficier par la suite à des espèces opportunistes, telles que les carnivores gélatineux.

Keywords: Typhoon ● Gelatinous zooplankton ● Resource pulse

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Introduction

Resource pulses are large-magnitude and short-duration events of increased resource availability that can strongly affect ecosystems at different levels of ecological organisation (Yang et al., 2008). In the marine environment, resource pulses are closely related to the strength of atmospheric forcing, i.e. mixing effects of strong winds (Lin et al., 2003) or run-off after heavy precipitation events (Hoover et al., 2006). Compared to cold and temperate marine ecosystems, the response to nutrient pulses is faster in tropical environments, as optimum light and temperature conditions allow metabolically active communities. Therefore, there is a tight coupling indicated by alternating abundances in successive trophic levels and rapid increase (in the order of days-weeks) of carnivorous zooplankton (Hoover et al., 2006).

The coastal area off northern Taiwan is set in a subtropical environment, seasonally dependent on the monsoons and the interactions between the southward flowing coastal current of mainland China and the northward flowing Kuroshio Current (Tseng et al., 2008 & 2011; Hsiao et al., 2011a & b; Kâ & Hwang, 2011). Although typhoons considerably increase the primary productivity and the nutrient load in the upper layers of the otherwise oligotrophic Kuroshio Current (Chen et al., 2003; Chen et al., 2009), little is known on the effect in upper trophic levels. In this study, we examine the effect that typhoons exert on gelatinous carnivore zooplankton off northern Taiwan in terms of abundance, species richness and diversity.

Material and Methods

Gelatinous zooplankton was collected during the years 2007 to 2010 on the coast of Northeast Taiwan (Fig. 1). Sampling stations were located along five transects perpendicular to the coast at 250, 500, 1000, 2000 and 5000 m from the coastline (water depth < 105 m) (Fig. 1). Sampling tows were horizontal (between 5-10 m) in the surface layer using a typical Norpac zooplankton net (0.45 m mouth diameter, 333 µm mesh) with a Hydrobios flowmeter mounted at the centre of the mouth opening. Tows typically lasted 10 min at a constant speed of 2 knots, for preserving the integrity of the zooplankton sample. Samples were preserved in seawater with 5% buffered formalin for subsequent taxonomic identification. During identification, only organisms with complete nectocalyx were considered. In addition, colonial siphonophores were considered as one organism, counting only the anterior nectophore. We computed the species densities as number of individuals by cubic meter for each tow. The relative abundance (%) of each species was calculated as the proportion that the abundance the species represented from the total community abundance, and the occurrence rate (%) as the percentage of samples in which a species occur from the total numbers of sampling sites.

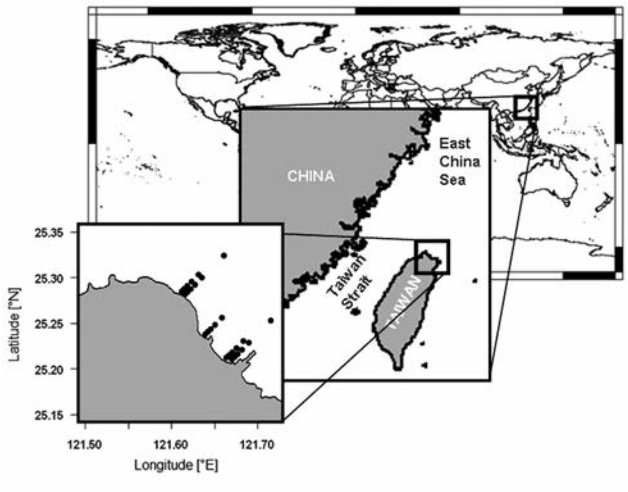

Figure 1. Location of the study site indicating the sampling points.

Figure 1. Localisation géographique de la zone d'étude des stations d'échantillonnage.

The record of typhoons affecting the North and North-East of Taiwan was obtained from the Taiwan Central Weather Bureau (http://cwb.gov.tw/V7/index.htm). Relative abundance was calculated for each sampling cruise. Seasonal anomalies in gelatinous zooplankton abundance were identified, by subtracting the seasonal average to each individual seasonal record. We used linear regression to determine the relation between the numbers of days elapsed since the previous typhoon and the abundance anomaly in a given season. The goodness of fit of the regression was evaluated with a Fisher test. Furthermore, we identified anomalies in temperature and salinity along the study period, to determine the possible effect of typhoons in these variables, and to discern if the effect was only noticeable until a certain distance from the coastline.

The dominant species, i.e. species whose abundance exceeded 50% of the total community abundance, were identified. The Shannon-Wiener diversity index was determined for the entire area in each sample cruise, and the species richness was also calculated.

Results and Discussion

For the period examined 11 typhoon events were recorded

Table 1. List of the typhoons affecting the study area between 2007 and 2010 and their main features. The sampling cruises undertaken during the same period are also listed, indicating the time elapsed between the end of the typhoon and the following sampling cruise, as well as the seasonally scaled abundance anomaly of the gelatinous zooplankton. Species which contributed in more than a 50% to the community abundance (by number) are also listed.

Tableau 1. Liste de typhons ayant un effet sur la zone d'étude entre 2007 et 2010. Les campagnes océanographiques sont indiquées, de même que le délai entre la fin des typhons et la période d'échantillonnage, et l'abondance saisonnière du zooplancton gélatineux standardisée. Les espèces dont l'abondance relative a été supérieure à 50% sont indiquées.

Year	Season	Typhoon Name	Impact Site (On Taiwan)	Intensity (Km)	Diameter Elapsed	Days Anomaly	Abundance Sp. (%)	Dominant
2007	Spring						+	
2007	Summer						-	
2007	Summer	WUTIP	East	Low	100	63		
2007	Summer	SEPAT	East	Strong	250	54		
2007	Summer	WIPHA	East-North	Medium	200	23		
2007	Autumn	KROSA	East-North	Strong	300	3		
2007	Autumn					↘	+	*Chelophyes contorta* (57.45%)
2008	Winter						+	
2008	Spring						-	
2008	Summer	KALMAEGI	East-North	Medium	120	14		
2008	Summer	FUNG-WONG	East	Medium	220	5		
2008	Summer					↘	+	*Chrysaora helvola* (93.13%)
2008	Summer	SINLAKU	East-North	Strong	250	39		
2008	Autumn	JANGMI	East-North	Strong	280	25		
2008	Autumn					↘	+	*Nausithoe punctata* (92.54%)
2009	Winter						-	
2009	Spring						+	*Nanomia bijuga* (68.02%)
2009	Summer						-	
2009	Summer	MORAKOT	East-North	Medium	250	65		
2009	Autumn					↘	-	
2010	Winter						-	
2010	Spring						+	
2010	Summer						-	
2010	Summer	NAMTHEUN	North	Low	80	82		
2010	Summer	FANAPI	East	Medium	200	63		
2010	Autumn					↘	-	

over North-East Taiwan and directly affected the study site (Table 1). The number of days elapsed between the typhoon and the following sampling cruise was highly variable, ranging between 3 and 82 days (Table 1). We found higher abundance, expressed as positive seasonally scaled anomalies in autumn 2007, and summer and autumn 2008 with an elapsed period since the previous typhoon ranging from 3 to 25 days (Table 1). However, in autumn 2009 and 2010 when the period elapsed between the typhoons and sampling cruise ranged between 63 and 82 days the abundance was negative (Table 1). The relation between the number of days elapsed since the last typhoon and the gelatinous zooplankton anomaly rendered negative and statistically significant (Fig. 2). These results suggest an enhanced bottom-up effect resulting from the nutrient input after a typhoon, likely producing a stepwise effect which increases the abundance of primary producers and zooplankton (Hoover et al., 2006). In fact, the copepod community shows generally low abundances in compliance with the low nutrient levels of surface waters (Hwang et al., 2004; Hsiao et al., 2011a & b; Kâ & Hwang, 2011; Tseng et al., 2011). The typhoon effects boost primary production, either through run-off inputs or vertical mixing, and might subsequently lead favourable conditions for the development of higher trophic groups, including copepods and gelatinous carnivore populations. The interplay between bottom-up and top-down effects could produce different outputs in the food web configuration depending on the initial conditions (Pitt et al., 2007) and the strength of the atmospheric-related nutrient pulse.

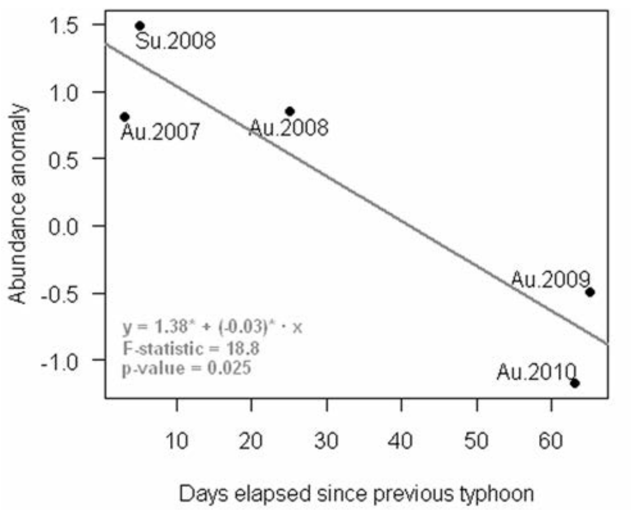

Figure 2. Abundance of the gelatinous zooplankton (anomalies) as a function of the days elapsed since the previous typhoon. Only cruise samplings immediately after the typhoon season, spring-summer, were considered. The trend is marked with a grey line, and statistics of the linear regression are also given (*: p-value < 0.05).

Figure 2. Abondance du zooplancton gélatineux (anomalies) en fonction des jours écoulés depuis le typhon précédent. Seules les campagnes d'échantillonnage faites immédiatement après la saison des typhons, printemps-été, ont été considérées. La tendance est indiquée par une ligne grise. Les statistiques de la régression linéaire sont aussi indiquées (*: p < 0,05).

Typhoon effects can typically be noticed in the temperature and salinity of the water mass by a generally slight increase in temperature before the typhoon and a steep decrease in temperature and salinity afterwards (Tsai et al., 2008). Since this effect might last only few days (Tsai et al., 2008) we were not able to record it during our sampling cruises (Fig. 3). However, the analysis of the temperature and salinity anomalies points out the homogeneity in environmental conditions in the study area during each sampling cruise (Fig. 3).

The gelatinous carnivore community amounted to 45 species pooling all sampling cruises. However, the relative contribution of each species to the community was highly variable (Table 2). Gelatinous zooplankton diversity seemed to be compromised by the resource pulse. We found that after those typhoons whose effects could be noted as a higher abundance, one species strongly dominated the community with abundances over 50% of the total for the sampling cruise (Table 1). These species were *Chelophyes contorta* (Lens & van Reimsdijk, 1908)*, Chrysaora helvola* (Brandt, 1838) and *Nausithoe punctata* (Kölliker, 1853). *Nanomia bijuga* (delle Chiaje, 1844) although not associated to the effects of any typhoon did also reach abundance exceeding 50% of the total community. To the best of our knowledge, no record exists to date of blooming events of the first three species. Hamner & Dawson (2009)

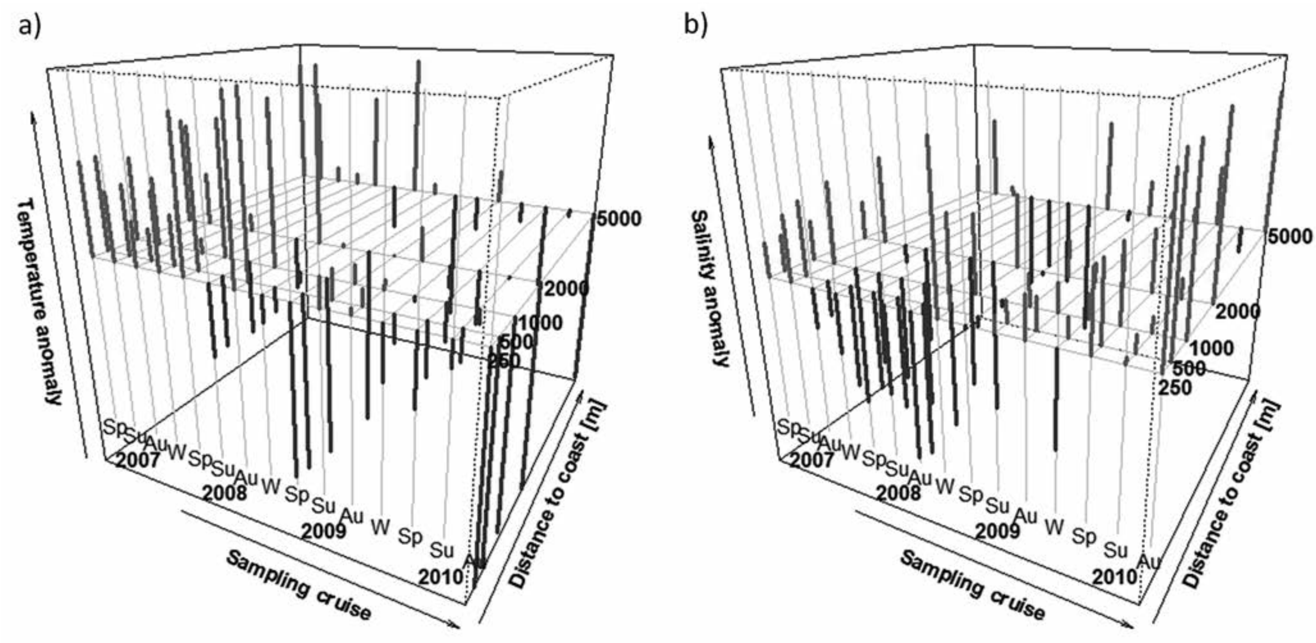

Figure 3. Temperature (a) and salinity (b) anomalies at the five stations distances to coast (250, 500, 1000, 2000 and 5000 m) in each sampling cruise.

Figure 3. Anomalies de température (a) et salinité (b) à cinq stations éloignées 250, 500, 1000, 2000 et 5000 m de la côte dans chaque campagne d'échantillonnage.

Table 2. List of species found in the study area, specifying: order, species, relative abundance (%) and occurrence rate (%).
Tableau 2. Liste d'espèces rencontrées dans la zone d'étude, en précisant : l'ordre, l'espèce, l'abondance relative (%) et la fréquence d'apparition (%).

Order	Species Name	Relative Abundance (%)	Occurrence Rate (%)
Anthoathecata	*Corymorpha bigelowi*	1.67	7.69
	Sarsia nipponica	0.08	1.37
	Hydractinia carnea	0.27	1.1
	Zanclea costata	0.04	0.27
Coronatae	*Nausithoe punctata*	2.94	2.47
Leptothecata	*Clytia folleata*	0.51	1.1
	Clytia hemisphaerica	0.15	0.55
	Obelia gracilis	0.62	0.82
	Obelia sp.	0.18	0.27
	Eirene brevistylis	0.01	0.27
	Eutima gentiana	0.16	1.1
	Eutima neucaledonia	0.37	1.37
	Laodicea undulata	4.65	6.59
	Eucheilota duodecimalis	0.07	1.37
Limnomedusae	*Gossea sp.*	0.04	0.27
Narcomedusae	*Solmudella bitentaculata*	0.59	2.75
Semaeostomeae	*Chrysaora helvola*	37.13	3.3
	Pelagia noctiluca	0.02	0.27
Siphonophorae	*Abyla trigona*	0.11	0.55
	Abylopsis eschscholtzi	0.03	0.27
	Abylopsis tetragona	2.62	7.14
	Aequorea parva	0.07	1.37
	Bassia bassensis	0.11	0.82
	Ceratocymba leuckarti	0.06	0.55
	Enneagonum hyalinum	0.06	0.27
	Agalma elegans	0.28	1.37
	Nanomia bijuga	11.54	6.59
	Chelophyes contorta	6.63	15.93
	Diphyes bojani	0.22	1.37
	Diphyes chamissonis	2.39	8.24
	Diphyes dispar	0.49	2.75
	Eudoxoides spiralis	0.03	0.27
	Lensia achilles	0.95	2.75
	Lensia conoidea	0.1	0.82
	Lensia multicristata	0.89	1.37
	Lensia subtilis	1.4	4.67
	Lensia subtiloides	3.88	10.16
	Muggiaea atlantica	4.47	4.4
	Sulculeolaria chuni	1.21	4.95
	Sulculeolaria monoica	0.02	0.27
	Sulculeolaria quadrivalvis	0.07	0.55
	Hippopodius hippopus	0.02	0.27
	Physophora hydrostatica	0.52	2.2
Trachymedusae	*Liriope tetraphylla*	0.64	2.75
	Aglaura hemistoma	11.73	19.78

deduced that species of the genera Nausithoe, as other coronates, do not bloom. *Chelophyes contorta* is an oceanic and relatively rare species (Palma & Silva, 2006). In the genera Chrysaora, *Chrysaora hysoscella* (Linné, 1766) was rarely observed in high numbers, and considered as not blooming species (Kogovsek et al., 2011). However, *Chrysaora quinquecirrha* (Desor, 1848) can produce blooms in temperate ecosystems associated to high temperatures and low salinities (Decker et al., 2007).

Controversy exists regarding the effect of nutrient pulses on species diversity. While in terrestrial environments resource pulses are thought to favour species coexistence by creating temporal niche opportunities (Chesson et al., 2004), in the pelagic environment, due to the higher turnover rates of plankton, climate driven resource pulses might initiate a succession where opportunistic organisms, like gelatinous carnivores, have the greatest advantage (Hoover et al., 2006). Although none of the dominant species in this study has been previously described as opportunistic, the massive proliferation they achieved after the typhoons, suggests that they might take advantage of environmental conditions and increased feeding resources. We did not find in the gelatinous community any relation between typhoons and species richness, however, a general decrease of species richness along the four years series arose from our study (Fig. 4). Species diversity strongly decreased in summer and autumn 2008, although the same response did not occur in autumn 2007 after the typhoon season (Fig. 4). A slight decrease in diversity is apparent during all summer seasons (Fig.4), but the effect of nutrient inputs from the summer typhoon season in this annual pattern is uncertain.

The temporal scale covered by this study, 15 cruises in the period 2007-2010, does not allow for a more comprehensive picture of the effects typhoons exert on the gelatinous zooplankton community off northern Taiwan. However, several hypotheses arose regarding the time that plankton food-web succession requires after resource pulse events, and its effects on species abundance, diversity and richness. This has importance implications as climate change is forecasted to increase the frequency and intensity of tropical storms in the near future (IPCC, 2007), hence, the frequency and intensity of the associated resource pulses in coastal areas of the tropics might also increase probably enhancing open niche for opportunistic carnivore zooplankton groups.

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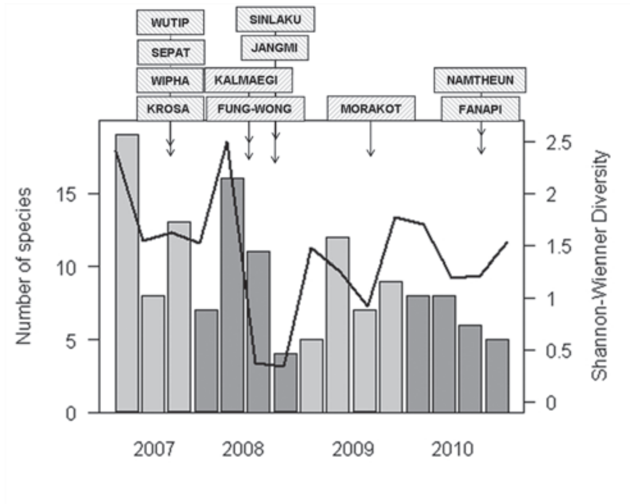

Figure 4. Species diversity (Shannon-Wiener Index) in each sampling cruise (black line) and species richness of the gelatinous zooplankton community during the study period (bars). The first bar corresponds to summer 2007 and the last one to winter 2010.

Figure 4. Diversité (Index de Shannon-Wiener, ligne continue) et richesse spécifique des carnivores gélatineux à chaque campagne (barres). La première barre indique l'été 2007 et la dernière l'hiver 2010.

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