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SHORT COMMUNICATION

Seasonal variability of the gelatinous carnivore zooplankton community in Northern Taiwan

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We investigated the gelatinous carnivore zooplankton community in the coastal waters of northeast Taiwan during the period 2007–2010. The community assemblage was composed of 45 species, of which only 14 appeared recurrent in Taiwanese waters. Although there was no clear seasonality, higher richness and abundances occurred in spring and autumn. Examination of potential physical drivers of coastal biomass accumulation did not show any link with water mass transport; instead, peak events were associated with typhoon disturbances, suggesting a potential resource pulse effect.

KEYWORDS: gelatinous zooplankton; wind-driven transport; tidal transport; seasonal variability; Northern Taiwan

The southern margin of the East China Sea is a complex environment dominated by coarse scale hydrographic patterns that include the Kuroshio Current and a mesoscale structure, “the cold dome” (Jan *et al.*, 2011; Shen *et al.*, 2011), related to upwelling from mid-Kuroshio waters north of Taiwan. Seasonal hydrographic variations in this area are paralleled by abundance and structural changes in crustacean zooplankton communities. Indeed, dominant species of these taxa are useful indicators of environmental fluctuations associated with regimes of dominant warm/cold water masses (Hwang *et al.*, 2006; Dur *et al.*, 2007). We may expect similar effects in other planktonic taxa, such as gelatinous carnivore zooplankton, whose abundance changes are strongly influenced by water mass transport reviewed by Graham *et al.* (Graham *et al.*, 2001). Gelatinous carnivore zooplankton are widely recognized as important predators of micro and mesozooplankton, fish eggs and fish larvae (Colin *et al.*, 2005), and can potentially alter pelagic food web dynamics. Therefore, it is important to understand the factors driving spatial and temporal patterns in this group for assessing linkages between zooplankton and primary producers, and ultimately matter fluxes through food web networks. In this study, we examined a 4-year field dataset of gelatinous carnivore zooplankton and explored their link with potential physical drivers of seasonal and inter-annual changes. The null hypothesis is that abundance changes result from water mass transport. Alternatively, we may expect that abundance peaks are driven by environmental changes coupled with rapid population growth.

The sampling design consisted of five coastal transects seasonally sampled from 2007 to 2010 in Northern Taiwan, and covering a total area of 70 km². Cross-shore transects were explored at sampling stations located at 250, 500, 1000 and 2000 m from the shoreline and two additional stations at 5000 m. At each station, temperature and salinity were measured using a conductivity–temperature–depth (CTD) device (SBE 911plus). Cnidarian samples were collected by horizontal tows in the subsurface layer (5–10 m depth), using a Norpac zooplankton net (45 cm mouth diameter, 333 µm mesh) towed for 10 min at a constant speed of 2 knots. The samples were preserved in seawater with 5% buffered formaldehyde immediately after collection. Siphonophores were counted as individuals if the anterior nectophore was present, while other gelatinous zooplankton were counted as individuals whenever the nectocalyx was present. Broken pieces were ignored during the identification.

We examined potential physical drivers that may yield coastal biomass accumulation over seasonal scales.

To do so, we used daily records of wind direction and speed, and tidal amplitude as potential drivers of inshore water mass transport. In addition, we used data of typhoons, which are known as drivers of nutrient pulse events that can trigger primary production potentially enhancing favourable conditions for zooplankton population growth (López-López *et al.*, 2012). Physical data were obtained from the Taiwan Central Weather Bureau <http://cwb.gov.tw/V7/index.htm>.

Changes in species abundance were assessed by means of the Heath’s population variability (PV) (Heath, 2006), which accounts for not normally distributed and rare events or large numbers of zeros in the dataset (Heath, 2006). In further analyses, only species present at more than eight sampling stations in at least 2 years were considered. We first identified clusters of samples based on their sea surface temperature (SST) and sea surface salinity (SSS) values. To do so, we scaled these variables and applied *k*-means clustering (Lloyd–Forgy algorithm, 100 iterations allowed) on the resulting matrix. The number of clusters was chosen as the one maximizing the within-cluster/between-cluster sums of squares while being representative of the main oceanographic regimes in the area. Subsequently, we identified associations between species and their preferred environmental conditions. A species was considered to be associated with one cluster when its occurrence within the cluster’s conditions was >80% of its total occurrence.

The potential effect of wind, as an underlying vector for gelatinous zooplankton transport into the study area, was evaluated using the surface Ekman transport. The seasonal variations in the Ekman transport were calculated using daily wind velocity at 10 m above the sea surface, as follows:

$$T_E = \frac{\tau}{f_{\text{Cor}}} [\text{kg m}^{-1} \text{ s}^{-1}]$$

where f_{Cor} is the Coriolis parameter and τ (kg m^{−1} s^{−2}) the wind stress over the sea surface. T was calculated using the following expression:

$$\tau = \rho_a \times C_D \times u_{10}^2 [\text{kg m}^{-1} \text{ s}^{-1}]$$

Given that wind speed did not surpass 33 m s^{−1}, we used a linear relation to compute the drag coefficient as follows:

$$C_D = (a + b \times u_{10}) \times 10^3$$

where $a = 0.60$ and $b = 0.07$ as determined in Yelland and Taylor (Yelland and Taylor, 1996).

Table I: Averaged abundance of gelatinous carnivore zooplankton with their standard error (SE) (individuals/1000 m³) and Heath's population variability of each species

Species	Average abundance \pm SE (ind./1000 m ³)	Heath's population variability
Anthoathecata		
Corymorphidae		
<i>Corymorpha bigelowi</i> (Maas, 1905)*	163 \pm 82	0.797
Corynidae		
<i>Sarsia nipponica</i> (Uchida, 1927)	3 \pm 2	1.000
Hydractiniidae		
<i>Hydractinia carnea</i> (M. Sars, 1846)	11 \pm 7	0.999
Zanclidae		
<i>Zanclaea costata</i> (Gegenbaur, 1857)	1 \pm 1	1.000
Coronatae		
Nausithoidae		
<i>Nausithoe punctata</i> (Kölliker, 1853)*	115 \pm 74	0.959
Leptothecata		
Campanulariidae		
<i>Clytia folleata</i> (McCrary, 1859)	20 \pm 11	1.000
<i>Clytia hemisphaerica</i> (Linnaeus, 1767)	6 \pm 5	0.992
<i>Obelia gracilis</i> (Linnaeus, 1758)	24 \pm 23	1.000
<i>Obelia</i> sp.	7 \pm 7	1.000
Eirenidae		
<i>Eirene brevistylis</i> (Huang & Xu, 1994)	1 \pm 1	1.000
<i>Eutima gentiana</i> (Haeckel, 1879)	5 \pm 3	1.000
<i>Eutima neucaledonia</i> (Uchida, 1964)	11 \pm 6	0.997
Laodiceidae		
<i>Laodicea undulata</i> (Forbes & Goodsir, 1853)*	104 \pm 38	0.893
Lovenellidae		
<i>Eucheilota duodecimalis</i> (A. Agassiz, 1862)	2 \pm 1	1.000
Narcomedusae		
Aeginidae		
<i>Solmudella bitentaculata</i> (Quoy & Gaimard, 1833)	22 \pm 10	0.953
Semaeostomeae		
Pelagiidae		
<i>Chrysaora helvola</i> (Brandt, 1838)*	1475 \pm 1335	1.000
<i>Pelagia noctiluca</i> (Forsskål, 1775)	1 \pm 1	1.000
Siphonophorae		
Abylidae		
<i>Abyla trigona</i> (Quoy & Gaimard, 1827)	4 \pm 3	0.982
<i>Abylopsis eschscholtzi</i> (Huxley, 1859)	1 \pm 1	1.000
<i>Abylopsis tetragona</i> (Otto, 1823)	97 \pm 40	0.943
<i>Aequorea parva</i> (Browne, 1905)	3 \pm 2	0.990

Continued

Table I: Continued

<i>Bassia bassensis</i> (Quoy & Gaimard, 1827)	44 \pm 40	0.997
<i>Ceratocym baleuckarti</i> (Huxley, 1859)	5 \pm 3	0.965
<i>Enneagonum hyalinum</i> (Quoy & Gaimard, 1827)	2 \pm 2	1.000
Agalmatidae		
<i>Agalma elegans</i> (Sars, 1846)	11 \pm 5	0.992
<i>Nanomia bijuga</i> (delle Chiaje, 1844)*	286 \pm 149	0.928
Diphyidae		
<i>Chelophyes contorta</i> (Lens & van Riemsdijk, 1908)*	201 \pm 66	0.858
<i>Diphyes bojani</i> (Eschscholtz, 1829)	15 \pm 8	0.984
<i>Diphyes chamissonis</i> (Huxley, 1859)	92 \pm 36	0.823
<i>Diphyes dispar</i> (Chamisso & Eysenhardt, 1821)	17 \pm 7	0.952
<i>Eudoxoides spiralis</i> (Bigelow, 1911)	1 \pm 1	1.000
<i>Lensia achilles</i> (Totton, 1941)	35 \pm 22	1.000
<i>Lensia conoidea</i> (Keferstein & Ehlers, 1860)	4 \pm 2	1.000
<i>Lensia multicristata</i> (Moser, 1925)	22 \pm 13	1.000
<i>Lensia subtilis</i> (Chun, 1886)	52 \pm 16	0.875
<i>Lensia subtiloides</i> (Lens & van Riemsdijk, 1908)*	144 \pm 41	0.940
<i>Muggiaea atlantica</i> (Cunningham, 1892)*	137 \pm 47	1.000
<i>Sulculeolaria chuni</i> (Lens & van Riemsdijk, 1908)*	115 \pm 44	0.864
<i>Sulculeolaria monoica</i> (Chun, 1888)	1 \pm 1	1.000
<i>Sulculeolaria quadrivalvis</i> (Blainville, 1834)	1 \pm 1	1.000
Hippopodiidae		
<i>Hippopodius hippopus</i> (Forskål, 1776)	1 \pm 1	1.000
<i>Vogtia glabra</i> (Bigelow, 1918)	2 \pm 2	0.989
Physophoridae		
<i>Physophora hydrostatica</i> (Forskål, 1775)	20 \pm 8	1.000
Trachymedusae		
Geryoniidae		
<i>Liriope tetraphylla</i> (Otto, 1823)	24 \pm 10	0.850
Rhopalonematidae		
<i>Aglaura hemistoma</i> (Péron & Le Sueur, 1809)*	405 \pm 86	0.686

Species name with * symbol are the 10 most abundant species.

Wind-driven transport in the study area may be hindered by strong meso- and macro-scale oceanographic structures (Jan *et al.*, 2011); however, the cyclonic component of Ekman transport can enhance winter upwelling in North-eastern Taiwan (Shen *et al.*, 2011) favouring surface transport to the Southeast along the coast. We used wind forcing data of a 15-day period prior to each sampling cruise for calculating the median Ekman transport and computed the number of days

with Southwest direction (responsible for the cyclonic transport to the Southeast along the coast) in the same fortnight. A multivariate linear model was used to assess the relationship between the direction and the strength of the surface transport in the abundance of carnivore gelatinous zooplankton at the easternmost transect of the study site, where accumulation was most likely to occur. Also, as tidal currents can be locally important in the study area (Hu, 2004), we assessed their potential link with the gelatinous carnivore assemblage by means of Pearson correlations between the tidal amplitude and the standardized abundance data at each sampling station, as for minimizing the effect of the coast morphology. Likewise, the effect on the gelatinous abundance of typhoons that occurred within the month preceding a sample cruise was assessed.

The gelatinous zooplankton community consisted of 45 species (Table I). Among the ten species with the highest total abundance, the scyphozoan *Chrysaora helvola* and the siphonophore *Muggiaea atlantica* had a PV of 1, as they appeared only during one of the sampling cruises (Table I). The second most abundant species, the hydrozoan *Aglaura hemistoma*, displayed the lowest Heath's PV (Table I), being thus the most recurrent species in the area.

Considering the distribution over the axis inshore—offshore, we observed that species occurring at >10 sampling stations during the study period were generally found all over the area. This prevented discrimination of species between coastal and open waters, as the low number of observations could produce an artefact distorting the species distribution. A total of 13 species were considered common, i.e. they occurred during at least two sampling years and more than eight sampling stations; all of these species were present in spring and eight of them occurred during the 4-year seasons (Fig. 1).

The *k*-means cluster analysis of SST and SSS yielded four clusters (cluster sum of squares/total sum of squares = 70.2%), mainly associated with different seasons. The first cluster with wide salinity variations and low temperature corresponded to winter samples and had no associated species. The second cluster was characterized by variable temperature but relatively high salinity values (34.06–35.37), mixed winter, autumn and spring samples; *Lensia subtiloides* occurred preferentially in these conditions (92%). The remaining two clusters corresponded to above-average temperatures (22.5–29.29°C). The third cluster was centred on average salinity conditions and mixed summer, autumn and spring samples; the species *Corymorpha bigelowi* and *Nausithoe punctata* occurred predominantly within this cluster (81 and 90%, respectively). The latter cluster

had relatively low salinities (28.90–33.35) and included only summer and autumn samples; the species *Laodicea undulata* was associated with this cluster (92%) (Fig. 2).

Gelatinous zooplankton showed higher abundances in spring and summer and lower in autumn and winter (Fig. 1). However, large abundance changes were observed during the 4 years (Fig. 1). The three sampling cruises possibly affected by the typhoons showed higher than average abundance (Fig. 1). Multivariate linear regression using as independent variables the Ekman transport and day of prevailing south-westerlies did not show a significant relationship with the abundance of gelatinous carnivore zooplankton (*F*-statistic: 0.161; *P*-value: 0.8543). Similarly, tidal amplitude did not have any measurable relationship with their abundance at any of the sampling stations ($r \leq 0.02$; $P > 0.1$).

Communities of siphonophores and hydromedusae similar to those identified in this work have already been described in waters surrounding Taiwan (Yu, 2006; Chang, 2008; Lin, 2010; Li *et al.*, 2012). Among the most common species, the great majority were cosmopolitan, such as the physonectae siphonophores *Agalma elegans* and *Nanomia bijuga*, the calycophorae *Abylopsis tetragona* and *Muggiaea atlantica* and the hydrozoan *Aglaura hemistoma* (Purcell, 1981; Lo and Biggs, 1996; Palma and Silva, 2006).

Small-sized gelatinous carnivore zooplankton typically drifts with currents accumulating in coastal areas during inshore transport (Kaneda *et al.*, 2007); however, we did not find evidence that the abundances recorded were related to tidal or to wind-driven transport. Instead, our results point towards other factors resulting in the observed abundance changes. The north of Taiwan is a crossroad of oceanic currents and several assemblages of crustacean zooplankton have been described as indicators for water masses (Hsieh *et al.*, 2004; Dur *et al.*, 2007). Concerning the gelatinous carnivore group, recent studies suggest an increase of siphonophore and hydromedusae abundance towards northern Taiwan (Yu, 2006; Lin, 2010). However, little is known in the region about particular gelatinous zooplankton species associated with a water mass, though this functional group potentially can be a useful indicator of hydrographic conditions (Palma and Silva, 2006) in the Southern Pacific. Among the Diphyidae siphonophores, *Chelophyes contorta* is representative of tropical water masses, while *Muggiaea atlantica* of temperate waters. *Muggiaea atlantica*, *Abylopsis tetragona* and *Agalma elegans* have been associated with the subantarctic waters flowing in the Southeast Pacific along the Chilean coast, but were not found in epipelagic waters within the subtropical gyre in the southern Pacific Ocean (Palma and Silva, 2006). All of these species were found in this

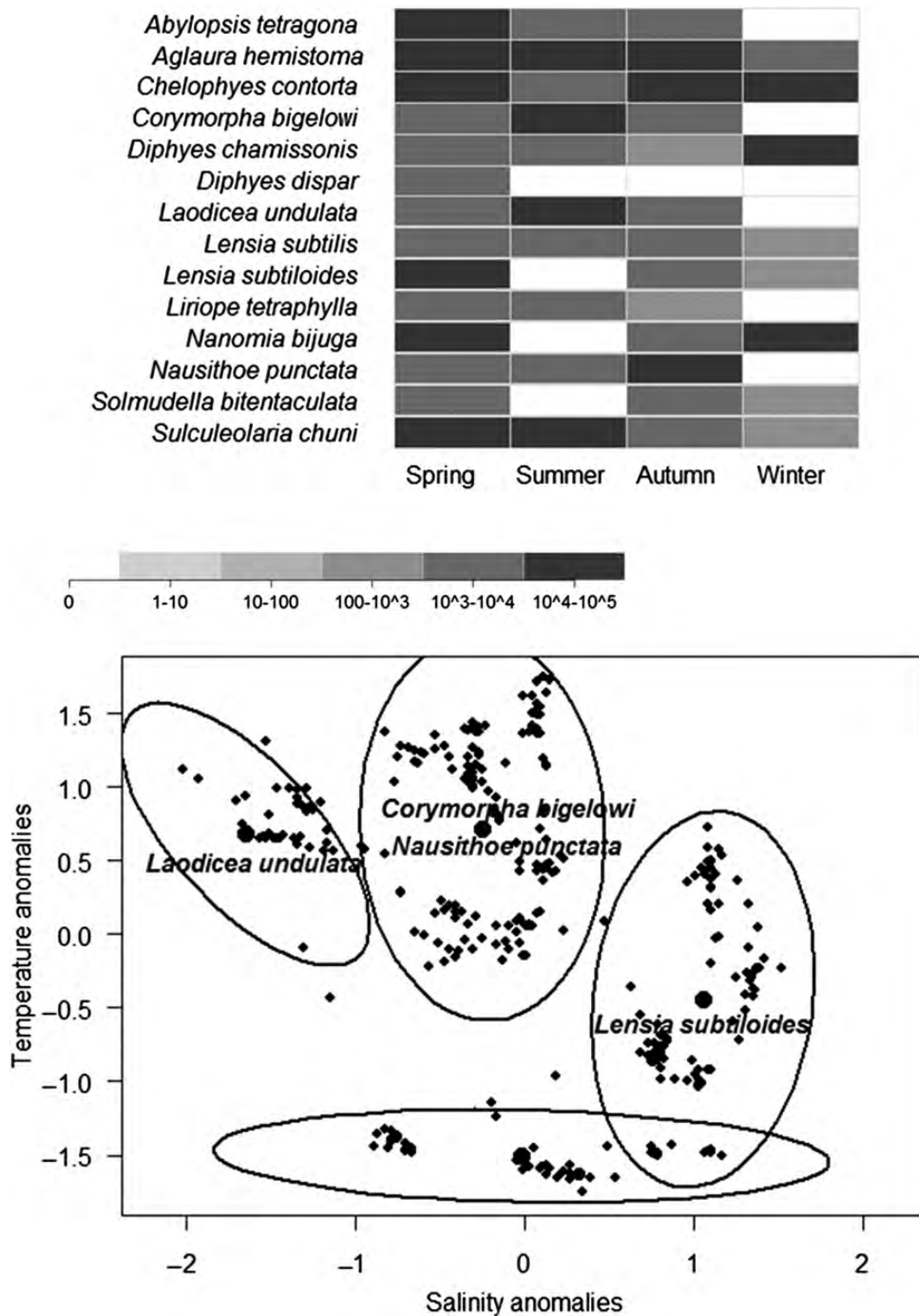


Fig. 1. Gelatinous carnivore resident species and abundance changes through the period 2007–2010 in the northern coastal area of Taiwan. Upper panel: seasonal abundance changes of resident gelatinous zooplankton species. Bottom panel: *k*-means clustering based on SST and SSS conditions found throughout the 4-year survey. Species whose abundance was >80% in a particular cluster are indicated in the corresponding cluster.

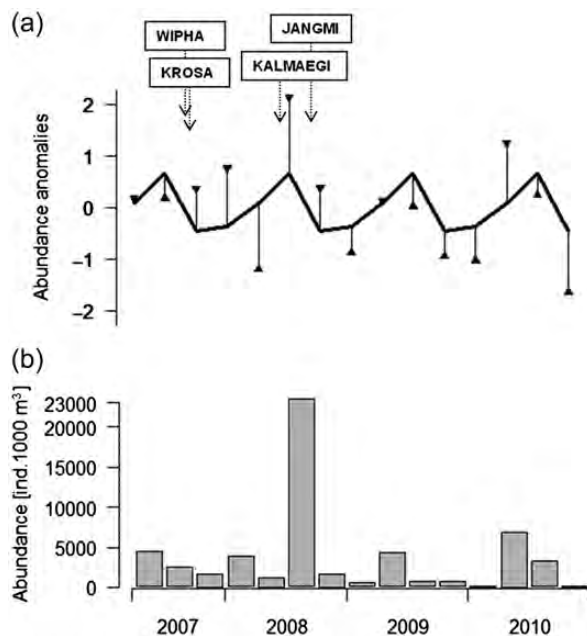


Fig. 2. (a) Seasonal anomalies of the gelatinous carnivore zooplankton community (solid line) and anomaly of each sampling cruise on the averaged seasonal value (vertical segments). The typhoons occurring in the month prior to a sampling cruise are indicated on top of the graphic. (b) Seasonal and inter-annual abundance changes (number of individuals/1000 m³) of gelatinous carnivore zooplankton during the period investigated.

study. We recorded *Abylopsis tetragona* associated with the higher temperature months from spring to autumn, contrasting with the observations by Palma and Silva (Palma and Silva, 2006). Moreover, our results identified some species associated with certain ranges of temperature and salinity. For instance, the hydrozoans *Corymorpha bigelowi* and *Nausithoe punctata* proliferated in warm water masses, while *Laodicea undulata* was associated with low salinities and *Lensia subtiloides* with the highest salinities.

Resources in the marine environment respond to seasonal cycles. We found recurring positive abundance anomalies in summer and negative ones during winter, consistent with the results of Li *et al.* (Li *et al.*, 2012). On top of the seasonal variability, several factors might contribute to the large variations in resource availability. Typhoons, for example, by enhancing terrestrial run-off, wind mixing and upwelling of deep Kuroshio waters yield higher phytoplankton production (Chen *et al.*, 2003, 2009). In tropical environments, the generally continuous stable temperature and light conditions make plankton communities able to respond quickly to nutrient enhancement triggered by typhoons through wind mixing and river run-off. Such response can rapidly permeate the plankton food web due to the rapid growth rates of plankton. Accordingly, we found

recurrent higher abundances of gelatinous carnivore zooplankton after such events, when a period <1 month elapsed between a typhoon and the following sampling cruise. Also, it is worth noticing that after typhoons some species proliferated exceptionally, thereby altering the structure of the gelatinous zooplankton assemblage through a decrease in diversity (López-López *et al.*, 2012). These results provide a first picture of the temporal changes of the small gelatinous carnivore zooplankton community, which showed high abundance variability due in part to frequent meteorological-driven resource pulse events. Our results suggest that typhoons may constitute a significant factor favouring sudden abundance peaks of small-sized gelatinous carnivore populations.

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REFERENCES

- Chang, W.-C. (2008) Spatiotemporal distribution of hydromedusae in relation to hydrography in the waters surrounding Taiwan. Master Thesis. National Sun Yat-Sen University, Department of Marine Biotechnology and Resources. 153 pp. (in Chinese with English abstract).
- Chen, A. C.-T., Liu, C.-T., Chuang, W.-S., Yang, Y.-J., Shiah, F.-K., Tang, T.-Y. and Chung, S.-W. (2003) Enhanced buoyancy and hence upwelling of subsurface Kuroshio waters after a typhoon in the southern East China Sea. *J. Mar. Sys.*, **42**, 65–79.
- Chen, Y.-L., Chen, H.-Y., Jan, S. and Tuo, S.-H. (2009) Phytoplankton productivity enhancement and assemblage change in the upstream Kuroshio after typhoon. *Mar. Ecol. Prog. Ser.*, **385**, 111–126.
- Colin, S. P., Costello, J. H., Graham, W. M. and Higgins, J. III (2005) Omnivory by the small cosmopolitan hydromedusa *Aglaura hemistoma*. *Limnol. Oceanogr.*, **50**, 1264–1268.

- Dur, G., Hwang, J.-S., Souissi, S., Tseng, L.-C., Wu, C.-H., Hsiao, S.-H. and Chen, Q.-C. (2007) An overview of the influence of hydrodynamics on the spatial and temporal patterns of calanoid copepod communities around Taiwan. *J. Plankton Res.*, **29**, 97–116.
- Graham, W. M., Pages, F. and Hammer, W. M. (2001) A physical context for gelatinous zooplankton aggregations: a review. *Hydrobiologia*, **451**, 199–212.
- Heath, J. P. (2006) Quantifying temporal variability in population abundances. *Oikos*, **115**, 573–581.
- Hsieh, C.-H., Chiu, T.-S. and Shih, C.-T. (2004) Copepod diversity and composition as indicators of the intrusion of the Kuroshio Branch Current into the northern Taiwan Strait in spring, 2000. *Zool. Stud.*, **43**, 393–403.
- Hu, J.-H. (2004) The coastal currents offshore the nuclear power plants at Northern Taiwan. *J. Mar. Sci. Technol.*, **12**, 355–363.
- Hwang, J.-S., Souissi, S., Tseng, L.-C., Seuront, L., Schmitt, F. G., Fang, L.-S., Peng, S.-H., Wu, C.-H., Hsiao, S.-H., Twan, W.-H., Wei, T.-P., Kumar, R., Fang, T.-H., Chen, Q.-C. and Wong, C. K. (2006) A 5-year study of the influence of the northeast and southwest monsoons on copepod assemblages in the boundary coastal waters between the East China Sea and the Taiwan Strait. *J. Plankton Res.*, **28**, 943–958.
- Jan, S., Chen, C.-C., Tsai, Y.-L., Yang, Y. J., Wang, J., Chern, C.-S., Gawarkiewicz, G., Lien, R.-C., Centurioni, L. and Kuo, J.-Y. (2011) Mean structure and variability of the cold dome Northeast of Taiwan. *Oceanography*, **24**, 101–109.
- Kaneda, A., Kohama, T., Kawamura, Y. and Takeoka, H. (2007) Periodicity in the accumulation of gelatinous zooplankton during the summer season in the coastal area of Iyo-Nada, Japan. *Limnol. Oceanogr.*, **52**, 707–715.
- Li, K. Z., Yin, J. Q., Huang, L. M. and Song, X. Y. (2012) Comparison of siphonophore distributions during the southwest and northeast monsoons on the northwest continental shelf of the South China Sea. *J. Plankton Res.*, **34**, 636–641.
- Lin, P.-C. (2010) Spatiotemporal distribution of hydromedusae in the water off Southern and Northern Taiwan. Master Thesis. National Sun Yat-Sen University, Department of Marine Biotechnology and Resources. 114 pp. (in Chinese with English abstract).
- Lo, W.-T. and Biggs, D. C. (1996) Temporal variability in the nighttime distribution of epipelagic siphonophores in the North Atlantic Ocean at Bermuda. *J. Plankton Res.*, **18**, 923–939.
- López-López, L., Molinero, J. C., Tseng, L.-C., Chen, Q.-C., Hwang, J.-W. and Hwang, J.-S. (2012) Effect of typhoons on gelatinous carnivore zooplankton off Northern Taiwan. *Cah. Biol. Mar.*, **53**, 349–355.
- Palma, S. and Silva, N. (2006) Epipelagic siphonophore assemblages associated with water masses along a transect between Chile and Easter Island (eastern South Pacific Ocean). *J. Plankton Res.*, **28**, 1143–1151.
- Purcell, J. E. (1981) Dietary composition and diel feeding patterns of epipelagic siphonophores. *Mar. Biol.*, **65**, 83–90.
- Shen, M.-L., Tseng, Y.-H. and Jan, S. (2011) The formation and dynamics of the cold-dome off northeastern Taiwan. *J. Mar. Sys.*, **86**, 10–27.
- Yelland, M. and Taylor, P. K. (1996) Wind stress measurements from the open ocean. *J. Phys. Oceanogr.*, **26**, 541–558.
- Yu, P.-W. (2006) Seasonal dynamics of siphonophores in the waters off southern and northern Taiwan. Master Thesis. National Sun Yat-Sen University, Department of Marine Biotechnology and Resources. 137 pp. (in Chinese with English abstract).