



Research papers

Jellyfish assemblages are related to interplay waters in the southern east China Sea

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ABSTRACT

Zooplankton communities are affected by spatial and temporal factors, as well as by general weather conditions, monsoons, and ocean currents. Present study examined the effects of typhoons, monsoons, and interplay waters on jellyfish assemblages in the complex hydrosystem in the coastal areas of the southern East China Sea. The species and composition of jellyfish and their seasonal succession in the coastal areas of northern Taiwan were investigated through 6 research cruises between October 2007 and January 2009. Among the samples obtained during these cruises, 23 jellyfish species from 2 classes, 7 orders, 13 families, and 19 genera were identified. The 3 most abundant jellyfish species were *Nausithoe punctata* (relative abundance, RA: 91.72%), *Aglaure hemistoma* (RA: 4.20%), and *Diphyes chamissonis* (RA: 1.13%). The species *A. hemistoma* exhibited the highest occurrence ratio (OR, 52.78%), and only this species was observed during all 6 research cruises. The abundance of *Corymorpha bigelowi* and *Lensia multicristata* correlated significantly and positively with seawater temperature, indicating that these species are brought to northeastern Taiwan by the warm Kuroshio Current. The formation of an *N. punctata* bloom yielded a density of 543.25 individuals/m⁻³ in October 2008, indicating that the jellyfish assemblage was influenced by a typhoon event and exhibited a clear pattern of seasonal succession. However, the interplay waters of the China Coastal Current and Kuroshio Current had a greater influence in shaping the jellyfish assemblage structure than did either typhoons or monsoons.

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1. Introduction

The structure of jellyfish assemblages is affected by various environmental factors, such as physical processes (Yoon et al., 2008) and changes in hydrographic conditions (Lo et al., 2008, 2014), including spatial (López-López et al., 2013), temporal changes (Li et al., 2012, 2013), monsoons (Hsieh et al., 2013; Lo et al., 2014), typhoons (López-López et al., 2012), and inter-annual variation in jellyfish abundance and quantifying. These inter-annual and long-term changes are also important issues (Lynam et al., 2011). Thus, the composition of jellyfish assemblages can be used to monitor the environment, specifically because their diversity is sensitive to changes in hydrological characteristics (Chen, 1992; Lo et al., 2008; Dong et al., 2010; López-López et al., 2012).

Jellyfishes belong to a taxon of zooplankton with the largest body size. The body of a jellyfish is predominantly water (> 95%)

with a low proportion of carbon (< 1%), enabling them to grow faster and larger than other species of zooplankton (Pitt et al., 2013). Because of their size, jellyfish play a crucial role in marine ecosystems in terms of transferring energy and material from small species of zooplankton to other species at the upper trophic level (Arai, 2005; Houghton et al., 2006). For example, larval fish (e.g., jack mackerel, *Trachurus japonicus*, Masuda et al., 2008), oceanic sea birds (e.g., gray-headed Albatross, *Thalassarche chrysostoma*, Catry et al., 2004), and sea turtles (e.g., leatherback turtle, *Dermochelys coriacea*, Houghton et al., 2006) are predators of jellyfish. Moreover, jellyfish consume fish roe and larvae, thus having a marked influence on fishery production and ecological structure (Greve, 1994; Yan et al., 2004; Brotz et al., 2012). In the East China Sea (ECS), jellyfish play a key role among zooplankton communities (Tseng et al., 2012a, 2012b). Several jellyfish species are an essential form of seafood with a high commodity value in China (Hsieh et al., 2001; Purcell et al., 2007). Recently, the abundance of giant jellyfish (Kawahara et al., 2006; Uye, 2008, 2010; Yoon et al., 2008) and macrojellyfish (Yan et al., 2004; Cheng et al., 2005) has increased in east Asian waters, including the ECS. Jellyfish blooms have caused considerable financial loss to fisheries (Yan et al.,

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2004; Uye, 2008; Dong et al., 2010; Nastav et al., 2013), as well as damage the fishing equipment (Yan et al., 2004; Brotz et al., 2012) and the water intakes of power plants situated in coastal areas (Henager et al., 1985; Masilamani et al., 2000). Jellyfishes are characteristically sensitive to environmental change (Cheng et al., 2005). Therefore, the dynamic of jellyfish assemblages serves as an indicator of the water masses movements (Cheng et al., 2005), global warming (Purcell et al., 2007; Richardson et al., 2009), and eutrophication (Mills, 2001; Liu and Diamond, 2005). Thus, monitoring changes in the structure of jellyfish assemblages is a critical issue worldwide.

The southern and southeastern ECS are complex hydrographic systems (Hwang et al., 2006; Tseng et al., 2013). Two major annual water currents influencing these areas are the China Coastal Current (CCC), which brings cool water from the Yellow Sea and the Bo-Hai Sea, and the Kuroshio Current (KC), which brings warm water from eastern Taiwan. The interplay between these 2 currents creates a dynamic environment supporting diverse marine biota in the southern ECS (Hwang et al., 2006; Chou et al., 2012; Tseng et al., 2013). Annually, the climatic influence of the northeast (NE) monsoon prevails during April–September, and that of the southwest (SW) monsoon prevails during October–March. Typhoons occur near Taiwan from June to September during the summer–autumn period. In the western Pacific Ocean, global warming has led to changes in the marine environment, and the frequency and power of typhoons in the area have increased (Xu et al., 2011). Thus, studying the effects of typhoons on zooplankton communities has gained importance. Previous studies have indicated that the southern ECS is a suitable area for evaluating how monsoons, typhoons, and interplay waters affect the zooplankton community.

Brotz et al. (2012) reported the population trends of jellyfish species and revealed a marked increase in the number of invasive jellyfish species in the region of the western Pacific Ocean. Currently, the effects of such complex environmental factors on jellyfish assemblages in the coastal areas of the southern ECS remain unclear. Therefore, present study was conducted to collect samples from different environments of the southern ECS to evaluate the effects of monsoons, typhoons, and interplay waters on the diversity and assemblage structure of jellyfish (major class Hydrozoa and Scyphozoa) to provide baseline data in northern Taiwan.

2. Material and methods

2.1. Study area and field sampling

Present study is the first to investigate the effects of the seasonal successions of jellyfish on the abundance and composition in northern Taiwan. Six sampling stations were selected: one in Shen-Aou Bay and 5 in Fan-Zai-Aou Bay in northeastern Taiwan, located near the southern edge of the ECS in the vicinity of Keelung City, Taiwan, between 25°07′–25°09′N and 121°48′–121°50′E (Table 1 and Fig. 1).

Six sampling cruises were conducted between October 2007

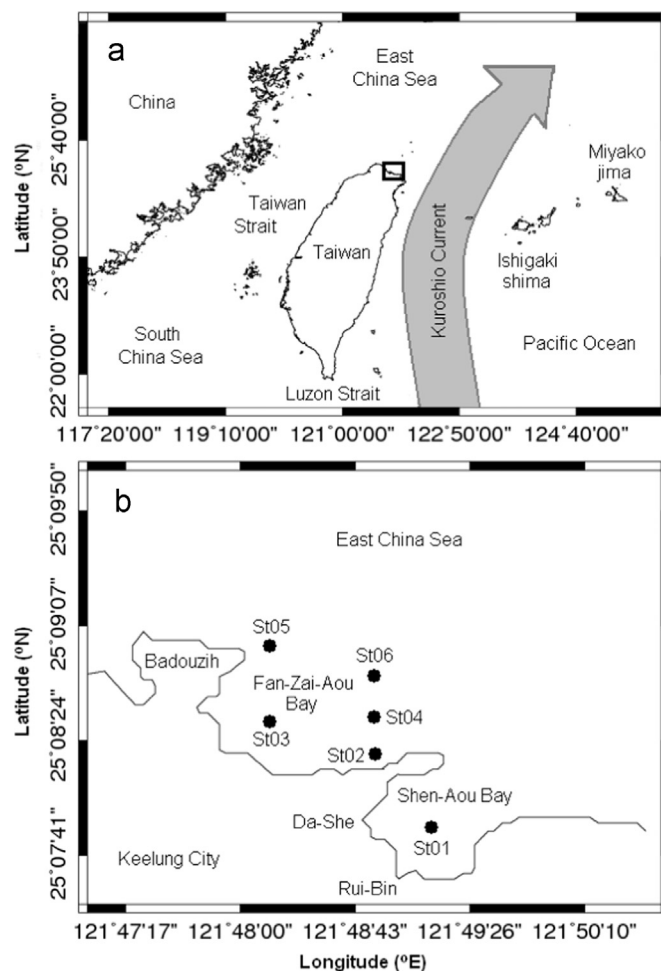


Fig. 1. Map of the research area (a) and location of the sampling stations (b) in Northeastern Taiwan and the Southern East China Sea from October 2007 to March 2009.

and March 2009. Prior to conducting the plankton tow, the on-board salinity and temperature were measured at all of the selected stations. Zooplankton samples were collected using surface net tows (0–5 m) with a standard North Pacific zooplankton net (mouth diameter 45 cm, length 1.8 m, and mesh size 333 μm) for approximately 10 min. at a vessel speed of 2 knots. A flowmeter (Hydrobios, Germany) mounted at the center of the net opening. Following on-board retrieval, the samples were immediately preserved in 5% buffered seawater formaldehyde solution.

2.2. Identification and enumeration of zooplankton

In the laboratory, a Folsom splitter was used to split the zooplankton samples into subsamples until each subsample contained approximately 300 specimens. Jellyfish were categorized and identified at the species level according to the keys proposed by Yamaji (1996) and Chihara and Murano (1997). The number of jellyfish belonging to each taxon was recorded as individuals/ m^{-3} (ind/ m^{-3}). A jellyfish (siphonophores) was included in the sample whenever its nectocalyx (anterior nectophore) was present. Jellyfish that were broken to pieces were ignored during the identification process.

2.3. Statistical analysis

To evaluate similar jellyfish distribution patterns, the data of 36 samples comprising 23 jellyfish species were analyzed using

Table 1
Location of the sampling stations of the 6 research cruises in Northern Taiwan.

| Station | Latitude ($^{\circ}$ N) | Longitude ($^{\circ}$ E) |
|---------|--------------------------|---------------------------|
| St01 | 25°7.44' | 121°49.18' |
| St02 | 25°8.15' | 121°49.27' |
| St03 | 25°8.70' | 121°48.45' |
| St04 | 25°8.14' | 121°49.33' |
| St05 | 25°8.43' | 121°48.24' |
| St06 | 25°8.22' | 121°49.30' |

nonmetric multidimensional scaling (NMDS) to elucidate the variations in assemblage composition and species diversity among the research cruises. In addition, among all of the samples, the 13 dominant jellyfish species with an OR greater than 5% (99.32% of all jellyfishes) were subjected to a cluster analysis to evaluate the relative similarities in the distribution patterns of jellyfishes for the study of water masses movement.

The species abundance in each sample was used as a reference to calculate Bray–Curtis similarities prior to conducting the NMDS and clustering analyses. The functional test proposed by Box and Cox (1964) was applied to transform the data before performing the clustering analysis. A λ value of 0.94 was used in the power transformation for the jellyfishes, and $\log(x+1)$ was applied as the logarithmic transform for calculating the individual densities of the jellyfish assemblages. The clustering analysis function in the Paleontological Statistics (PAST) software package was used to identify significant differences between the jellyfish assemblages (Hammer et al., 2001).

The Shannon–Wiener diversity index was used to evaluate the species diversity, and the Margalef richness and Pielou's evenness indices were used to estimate the community composition of each sample. The abundance data of the samples from different cruises and stations were treated as a set of replicates for the temporal and spatial analyses. To identify the differences in the abundance during different seasons and at different stations, one-way and 2-way analysis of variance (ANOVA) with post hoc Tukey's honest significant difference (HSD) tests were applied. In addition, Pearson's product-moment correlation was calculated to determine the correlation among jellyfish abundance, temperature, and salinity.

3. Results

3.1. Meteorological characteristics and weather

Fig. 2 shows a summary of the variations in the mean daily temperature, wind direction, and wind speed from September 1, 2007, to April 1, 2009. The meteorological data were collected using automatic monitoring equipment at the Central Weather Bureau of the Ministry of Transportation and Communications (Keelung City, Taiwan). The weather-monitoring station was located adjacent to the area of investigation, approximately 6.5 km from the sampling area. In total, 5 typhoons affected the sampling area during the investigation period: Wipha (September 17–19, 2007), Krosa (October 4–7, 2007), Kalmaegi (July 16–18, 2008), Sinlaku (September 11–16, 2008), and Jangmi (September 26–29, 2008) (Fig. 2a). The mean air temperature ranged from 9.9 °C (February 9, 2008) to 31.5 °C (August 21, 2008) during the period of September 1, 2007, to April 1, 2009. In general, lower air temperatures were recorded from January to March, whereas higher air temperatures were recorded from June to September (Fig. 2a).

Wind direction was used as a reference to determine the shift in monsoon seasons in the investigation area, as shown in Fig. 2b (0° indicates northerly winds, 90° indicates easterly winds, etc.). Hence, the SW monsoon transition can be seen to occur during early March and prevail from April to September, whereas the NE monsoon transition occurs in early October and prevails from mid-October to February (Fig. 2b). The mean wind speed varied from 0.5 (March 1, 2008) to 15.0 (October 6, 2007) m/s. Typhoons were associated with fast wind speeds in the sampling areas, with increased wind speeds observed during typhoons Krosa (15 m/s), Kalmaegi (10 m/s), Sinlaku (13.2 m/s), and Jangmi (11 m/s). The wind speed was slower during the SW monsoon period than during the NE monsoon period (Fig. 2c).

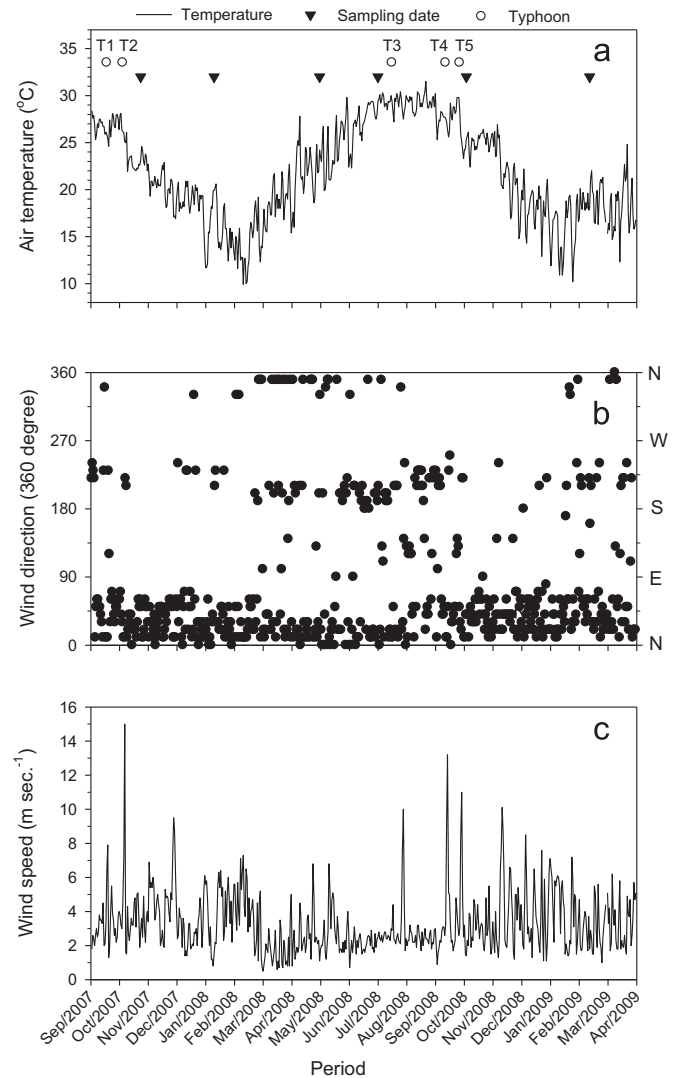


Fig. 2. Mean daily temperature, wind direction, and wind speed from September 2007 to April 2009. Data were recorded using automatic monitoring equipment located in Keelung City (adjacent to the investigation area). Air temperatures were higher in June–September and on the days of typhoon events, as well as on days of the research cruises (a). Changes in wind direction: 0° indicates a northerly wind, 90° indicates an easterly wind, 180° indicates a southerly wind, and 270° indicates a westerly wind (b). Changes in the wind speed (c). Typhoons: Wipha (T1), Krosa (T2), Kalmaegi (T3), Sinlaku (T4), and Jangmi (T5).

3.2. Hydrological structure

Satellite images of sea surface temperature (SST) in each sampling month were used to evaluate the interaction of various water masses in and around the study area (Fig. 3). The images indicate that the cold CCC water mass was influencing the study area from October to April (Fig. 3a and e). The CCC waters occupied the coastal areas of northern Taiwan during the NE monsoon season (Fig. 3b and f). The warm KC water mass from northeastern Taiwan intruded the study area; concurrently, the CCC water mass progressed to the northern area of Mainland China (Fig. 3c). The mean SST around Taiwan peaked at 30 °C during the SW monsoon (Fig. 3d).

The mean seawater temperature (Fig. 4a) and salinity (Fig. 4b) varied during each sampling cruise. The temperature variations revealed an obvious seasonal shift, as indicated by the decrease in seawater temperature in January 2008 and February 2009, whereas the seawater temperature began to increase in April. During the sampling period, the peak seawater temperature was

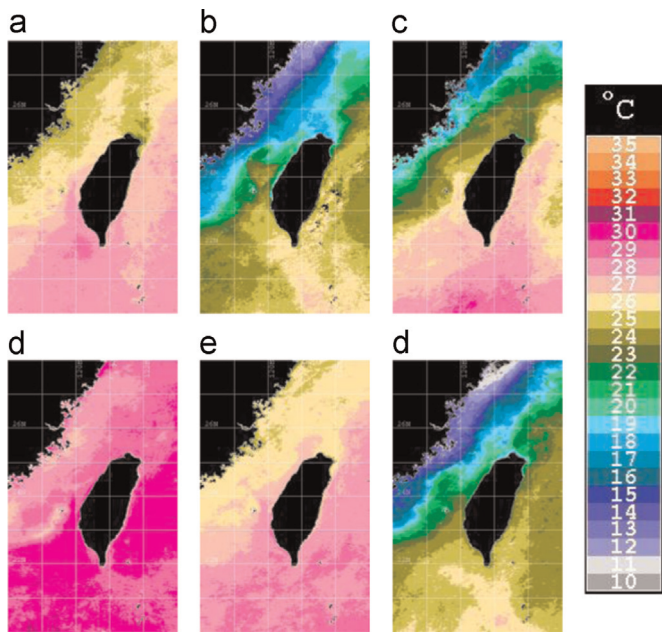


Fig. 3. The mean monthly data were derived from Advanced Very High Resolution Radiometer for sea surface temperatures (SST) during the investigation period. October 2007 (a), January 2008 (b), April 2008 (c), July 2008 (d), Oct/2008 (e), and February 2009 (f).

recorded in July 2008 (28.64 ± 0.14 °C) (mean \pm S.E.), and the lowest temperature was recorded in February 2009 (17.70 ± 0.13 °C) (Fig. 4a). The salinity was stable during the investigation period. The mean salinity values ranged between 33.72 ± 0.60 (October 2007) and 35.87 ± 0.29 (January 2008) (Fig. 4b). Similarly, the pH level was stable throughout the investigation period (Fig. 4c). The mean salinity values ranged between 8.07 ± 0.05 (January 2008) and 8.23 ± 0.05 (April 2008) (Fig. 4c).

The correlation between on-board seawater temperature and salinity during the 6 research cruises is depicted through the temperature–salinity (T–S) plots in Fig. 4d. A comparison between the CCC and the KC water masses indicated the environmental dynamic of the investigation area. The reference curves depicting the properties of the CCC and KC water masses were obtained from the Ocean Research Vessel I cruise CR-618 in July 2001. The T–S plots reveal the characteristics of the water masses in the Yangtze River estuary ($30^{\circ}30'N$, $123^{\circ}10'E$) and in the KC area ($25^{\circ}10'N$, $123^{\circ}10'E$). Characteristically, lower seawater temperatures and salinity levels indicated that the CCC introduced cold water into the study area. By contrast, the KC seawaters exhibited higher temperatures and salinity levels. Among the 6 research cruises, the properties of the water masses in July 2008, October 2007, and April 2008 were similar to those of KC water masses. During October 2008, the water masses of northern Taiwan exhibited characteristics similar to both the CCC and KC. A comparison of the corresponding T–S curves indicates that these water masses exhibited characteristics of the CCC in January 2008 and February 2009 (Fig. 4d).

3.3. Systematic inventory of jellyfish

Overall, the 36 samples comprised 23 jellyfish species belonging to 2 classes, 7 orders, 13 families, and 19 genera (Table 2). Most species belonged to the class Hydrozoa (91.3%, 21 species), with the remainder belonging to the class Scyphozoa (8.7%, 2 species). The species abundance and community composition among the 6 research cruises were dynamic, indicating seasonal successions

in the studied areas. During the investigation period, the 3 most abundant jellyfish species were *Nausithoe punctata* (relative abundance, RA: 91.72%), *Aglaurea hemistoma* (RA: 4.20%) and *Diphyes chamissonis* (RA: 1.13%). *N. punctata* revealed marked aggregation in the study area, with a peak density of 167.04 individuals/m³ in October 2008. Moreover, *A. hemistoma* exhibited the highest OR (52.78%), and this species alone was observed in all of the samples collected during the 6 research cruises.

Variation in the overall abundance and number of jellyfish species were recorded at each station during the 6 research cruises (Fig. 5a–f). In total, no jellyfish were observed in 8 of the 36 samples. The total density of the jellyfishes ranged from 0 to 543.25 individuals/m³ (St 5, October 2008). The highest number of identified species was 8 species per station (St 2, April 2008). The spatial distribution of jellyfishes without clear patterns in the investigated areas was evaluated: the mean total abundance, number of species (Fig. 5g), and indices of richness, diversity, and evenness (Fig. 5h) varied among each research cruise. The mean jellyfish density in most research cruises was less than 5 individuals/m³. The peak abundance was observed during October 2008 (167.25 ± 94.96 individuals/m³), although the lowest number of species was identified then (0.83 ± 0.4 species per station) (Fig. 5g). Similarly, among the 6 research cruises, the lowest richness (0.13 ± 0.07), diversity (0.009 ± 0.006), and evenness (0.038 ± 0.019) indices were observed in the samples collected during October 2008 (Fig. 5h).

3.4. Jellyfish assemblage structure

The relative rank abundance of the top-3 dominant jellyfish species from each cruise indicated seasonal succession (Fig. 6). In particular, the most dominant species of the Nausithoidae family, *N. punctata*, was observed only during October 2008, accounting for 99.88% of all instances. The second-most dominant species of the Rhopalonematidae family, *A. hemistoma*, was observed during all the 6 research cruises, with the highest proportion of *A. hemistoma* recorded during February 2009 (68.37%), followed by October 2007 (67.14%). *Laodicea undulata* (28.07%) and *Clytia hemisphaerica* (18.91%) were abundant in the samples collected during April 2009. *Corymorpha bigelowi* (16.89%) and *Lensia multicristata* (10.59%) were abundant in the samples collected during July 2008. In addition, *D. chamissonis* was abundant in the samples collected during October 2007 (31.41%), January 2008 (15.10%), and February 2009 (34.87%), when the CCC approached northern Taiwan. A few dominant opportunistic species included *Nanomia bijuga*, *Lensia subtilis*, *Hydractinia carnea*, and *Abylopsis tetragona*. The dynamic of the jellyfish assemblages indicated that the succession of these species was highly temporal (Fig. 6).

The NMDS results were derived the data of all 36 samples collected during the 6 research cruises (Fig. 7). Based on the collected samples, the assemblage composition of the jellyfish assemblages were similar, except for those collected during October 2008, indicating that the jellyfish assemblages were markedly affected by Typhoon Jangmi (Fig. 7). The correlation of abundance among the 13 most abundant species in each sample was evaluated using normalized Bray–Curtis distances. Moreover, the jellyfish species with similar distribution patterns were clustered, which revealed the extent of co-occurrence among these species (Fig. 8). The clustered samples and their hydrographic characterize of mean temperature and salinity levels associated with the jellyfish species indicated that certain jellyfishes inhabit various waters (Table 3).

The first assemblage (Group I-A) contained a single jellyfish species, *N. punctata*, which was observed in the samples collected during October 2008, characterized by low water temperature (22.1 ± 0.36 °C) and low salinity (34.4 ± 0.10) (‰) (Table 3). An

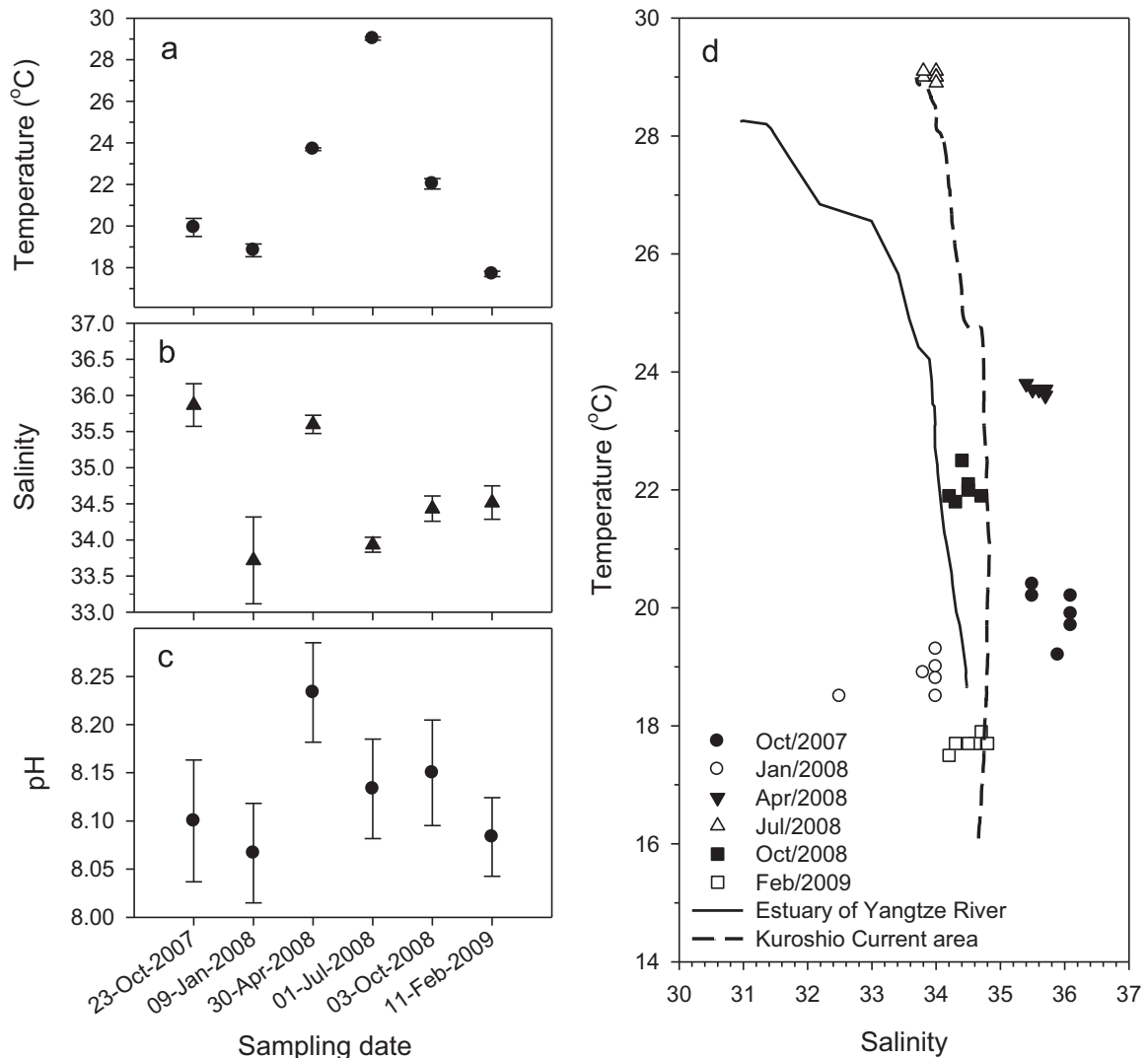


Fig. 4. Mean temperature (a), salinity (b), and pH (c) during the 6 research cruises. The temperature–salinity (T–S) plot reveals the distribution of the corresponding mean values of the samples collected from the 6 cruises. Two T–S curves of the Yangtze River estuary (30°30'N, 122°52'E) and the Kuroshio Current (25°10' N, 123°10'E) were recorded on the research vessel, Ocean Research 1, cruise 618, July 15–29, 2001 (d).

aggregation of this species was identified in a single research cruise (Table 2). The second assemblage (Group II-A) contained 5 jellyfish species, *Corymorpha bigelowi*, *Chelophyes contorta*, *D. chammisonis*, *L. subtilis* and *A. hemistoma*, which were identified in all of the samples from all 6 research cruises, indicating that they might belong to a native species of northeastern Taiwan. In particular, *A. hemistoma*, which had the highest OR (52.78%), was the only species identified in all of the sampling months (Table 2). The mean temperature and salinity associated with these 5 species was 21.9 ± 3.92 °C to 34.7 ± 0.97 (‰), respectively. The third assemblage (Group III-A) included 3 jellyfish species that were identified from the samples that were collected during the monsoon transition periods (October 2007 and April 2008). High salinity levels indicated that the KC waters had reached the sampling area (Fig. 4), indicating that these 3 species arrived with the KC waters. The mean temperature and salinity associated with these 3 species were 22.8 ± 1.69 °C and 35.7 ± 0.21 (‰), respectively (Table 3). The fourth assemblage (Group III-B) included 4 jellyfish species. Unlike the other 3 clusters, these 4 jellyfish species were collected during periods where the temperature salinity levels were at their highest; they were observed in the samples that were collected when the investigation area was influenced by the KC waters (Fig. 4). The mean temperature and salinity associated

with these 5 species was 23.8 ± 3.92 °C and 35.1 ± 0.7 (‰), respectively. A cluster analysis of these assemblages indicated that the jellyfish assemblages were affected by interplay waters. This phenomenon implies a substantial succession of the jellyfish assemblages in the waters of northeastern Taiwan (Fig. 8).

3.5. The effect of monsoons

Present study conducted 6 research cruises in all 4 seasons and in 2 monsoon periods. A taxonomic analysis revealed 12 jellyfish species during the NE monsoon (October–March) and 18 jellyfish species during the SW monsoon (April–September) (Table 2). Among these species, 5 of them were identified in the samples collected during the NE monsoon period alone: *H. carnea*, *D. chammisonis*, *L. subtilis*, *Sulculeolaria chuni*, and *N. punctata*. In addition, 11 species were identified in the samples collected during the SW monsoon period alone: *Hydractinia apicata*, *Aequorea australis*, *C. hemisphaerica*, *Eutima neucaledonia*, *Eutima variabilis*, *Diphyes dispar*, *L. multicristata*, *Lensia subtiloides*, *Muggiaea atlantica*, *Rhopalonema funerarium*, and *Pelagia noctiluca*. The remaining 7 species were detected in the samples collected during both monsoon periods (Table 2). Furthermore, a statistical analysis revealed that significantly more species were identified during the SW monsoon

Table 2
Mean density (individuals/m³), relative abundance (RA, %), and occurrence ratio (OR, %) of the jellyfishes during each season. Superscripts NE and SW respectively indicate the jellyfishes that were identified only during the northeast and southwest monsoon periods.

| Sampling time Total filtered water volume (m ³) | Oct/2007 178.69 | Jan/2008 376.74 | Apr/2008 192.04 | Jul/2008 94.14 | Oct/2008 177.49 | Feb/2009 250.21 | RA (%) | OR (%) | Mean \pm S.D. |
|---|--------------------|--------------------|--------------------|-------------------|--------------------|--------------------|--------|--------|--------------------|
| CLASS HYDROZOA | | | | | | | | | |
| Order Anthoathecata | | | | | | | | | |
| Family Corymorphidae | | | | | | | | | |
| <i>Corymorpha bigelowi</i> (Maas, 1905) | 0 | 0.12 | 0.05 | 0.54 | 0 | 0 | 0.39 | 11.11 | 0.12 \pm 0.42 |
| Family Hydractiniidae | | | | | | | | | |
| <i>Hydractinia apicata</i> Kramp, 1959 ^{SW} | 0 | 0 | 0.06 | 0 | 0 | 0 | 0.03 | 2.78 | 0.01 \pm 0.06 |
| <i>Hydractinia carnea</i> M. Sars, 1846 ^{NE} | 0 | 0 | 0 | 0 | 0.10 | 0 | 0.06 | 2.78 | 0.02 \pm 0.1 |
| Order Leptothecata | | | | | | | | | |
| Family Aequoreidae | | | | | | | | | |
| <i>Aequorea australis</i> Uchida, 1947 ^{SW} | 0 | 0 | 0.05 | 0 | 0 | 0 | 0.03 | 2.78 | 0.01 \pm 0.05 |
| Family Campanulariidae | | | | | | | | | |
| <i>Clytia hemisphaerica</i> (Linnaeus, 1767) ^{SW} | 0 | 0 | 0.49 | 0 | 0 | 0 | 0.27 | 2.78 | 0.08 \pm 0.49 |
| Family Eirenidae | | | | | | | | | |
| <i>Eutima neucaledonia</i> Uchida, 1964 ^{SW} | 0 | 0 | 0.06 | 0 | 0 | 0 | 0.03 | 2.78 | 0.01 \pm 0.06 |
| <i>Eutima variabilis</i> McCrady, 1859 ^{SW} | 0 | 0 | 0.09 | 0 | 0 | 0 | 0.05 | 2.78 | 0.01 \pm 0.09 |
| Family Laodiceidae | | | | | | | | | |
| <i>Laodicea undulata</i> (Forbes and Goodsir, 1853) | 0.01 | 0 | 0.73 | 0 | 0 | 0 | 0.41 | 16.67 | 0.12 \pm 0.33 |
| Order Narcomedusae | | | | | | | | | |
| Family Aeginidae | | | | | | | | | |
| <i>Solmudella bitentaculata</i> (Quoy and Gaimard, 1833) | 0.02 | 0 | 0.06 | 0.20 | 0 | 0 | 0.15 | 8.33 | 0.05 \pm 0.21 |
| Order Siphonophorae | | | | | | | | | |
| Family Abylidae | | | | | | | | | |
| <i>Abylopsis tetragona</i> Otto, 1823 | 0 | 0 | 0.05 | 0.14 | 0 | 0.08 | 0.15 | 8.33 | 0.04 \pm 0.16 |
| Family Agalmatidae | | | | | | | | | |
| <i>Nanomia bijuga</i> (Delle Chiaje, 1844) | 0.03 | 0 | 0.31 | 0 | 0 | 0 | 0.19 | 19.44 | 0.06 \pm 0.13 |
| Family Diphyidae | | | | | | | | | |
| <i>Chelophyes contorta</i> Lens and van Reimsdijk, 1908 | 0 | 0.22 | 0 | 0.24 | 0 | 0 | 0.25 | 5.56 | 0.08 \pm 0.32 |
| <i>Diphyes chamosonis</i> Huxley, 1859 ^{NE} | 1.28 | 0.61 | 0 | 0 | 0 | 0.17 | 1.13 | 22.22 | 0.34 \pm 1.11 |
| <i>Diphyes dispar</i> Chamosso and Eysenhardt, 1821 ^{SW} | 0 | 0 | 0.12 | 0.14 | 0 | 0 | 0.14 | 8.33 | 0.04 \pm 0.16 |
| <i>Lensia multicristata</i> (Moser, 1925) ^{SW} | 0 | 0 | 0 | 0.34 | 0 | 0 | 0.18 | 5.56 | 0.06 \pm 0.24 |
| <i>Lensia subtilis</i> (Chun, 1886) ^{NE} | 0 | 0.63 | 0 | 0 | 0 | 0 | 0.35 | 8.33 | 0.11 \pm 0.38 |
| <i>Lensia subtiloides</i> Lens and van Riemsdijk, 1908 ^{SW} | 0 | 0 | 0 | 0.24 | 0 | 0 | 0.13 | 2.78 | 0.04 \pm 0.24 |
| <i>Muggiaea atlantica</i> Cunningham, 1892 ^{SW} | 0 | 0 | 0.10 | 0 | 0 | 0 | 0.06 | 5.56 | 0.02 \pm 0.07 |
| <i>Sulculeolaria chuni</i> (Lens and van Riemsdijk, 1908) ^{NE} | 0 | 0 | 0 | 0 | 0 | 0.05 | 0.03 | 2.78 | 0.01 \pm 0.05 |
| Order Trachymedusae | | | | | | | | | |
| Family Rhopalonematidae | | | | | | | | | |
| <i>Aglaura hemistoma</i> Péron and Le Sueur, 1809 | 2.74 | 2.44 | 0.33 | 1.36 | 0.11 | 0.66 | 4.20 | 52.78 | 1.27 \pm 2.11 |
| <i>Rhopalonema funerarium</i> Vanhöffen, 1902 ^{SW} | 0 | 0 | 0.04 | 0 | 0 | 0 | 0.02 | 2.78 | 0.01 \pm 0.04 |
| CLASS SCYPHOZOA | | | | | | | | | |
| Order Coronatae | | | | | | | | | |
| Family Nausithoidae | | | | | | | | | |
| <i>Nausithoe punctata</i> Kölliker, 1853 ^{NE} | 0 | 0 | 0 | 0 | 167.04 | 0 | 91.72 | 8.33 | 27.84 \pm 108.22 |
| Order Semaestomeae | | | | | | | | | |
| Family Pelagiidae | | | | | | | | | |
| <i>Pelagia noctiluca</i> (Forsskål, 1775) ^{SW} | 0 | 0 | 0.06 | 0 | 0 | 0 | 0.03 | 2.78 | 0.01 \pm 0.06 |
| Total abundance | 4.08 | 4.03 | 2.61 | 3.18 | 167.25 | 0.96 | | | |

than during the NE monsoon period ($p=0.006$, $t=-3.0$, $df=26$, Student's t test), although no significant difference was observed in the total jellyfish abundance during both monsoon periods ($p=0.21$, $t=1.3$, $df=26$, Student's t test). These results indicated a marked difference in the jellyfish assemblage structure during the 2 monsoon periods investigated.

3.6. The effect of typhoon events

In present study, the research cruises conducted in October 2007 and 2008 collected zooplankton after the passage of a typhoon: The October 2007 cruise was conducted 16 days after passage of Typhoon Krosa, whereas the October 2008 cruise was conducted 4 days after passage of Typhoon Jangmi. Typically, the Shannon–Wiener diversity index exhibited a decrease after passage of a typhoon passage (Fig. 5). We identified 5 jellyfish species in the samples collected during October 2007 and 3 species in October 2008 (Table 2). Similar results found proportion of the

dominant species higher than 60%. Such as follows: *A. hemistoma* accounted for 67.14% of jellyfish species for October 2007, whereas *N. punctata* accounted for 99.88% of jellyfish species during October 2008 (Fig. 6).

3.7. Statistical analysis

Among all of the species, a positive correlation was observed between the abundance of *C. bigelowi* and *L. multicristata* and seawater temperature (Pearson's correlation, Table 4). Very few species exhibited changes in their density, which correlated significantly with salinity. Moreover, the abundance of *L. undulate* and *N. bijuga* correlated positively with salinity. By contrast, the abundance of *L. subtilis* correlated negatively with salinity (Table 4).

A 2-way ANOVA was performed to evaluate the individual and combined effects of each season and station on the total abundance and number of species (Table 5). No significant temporal

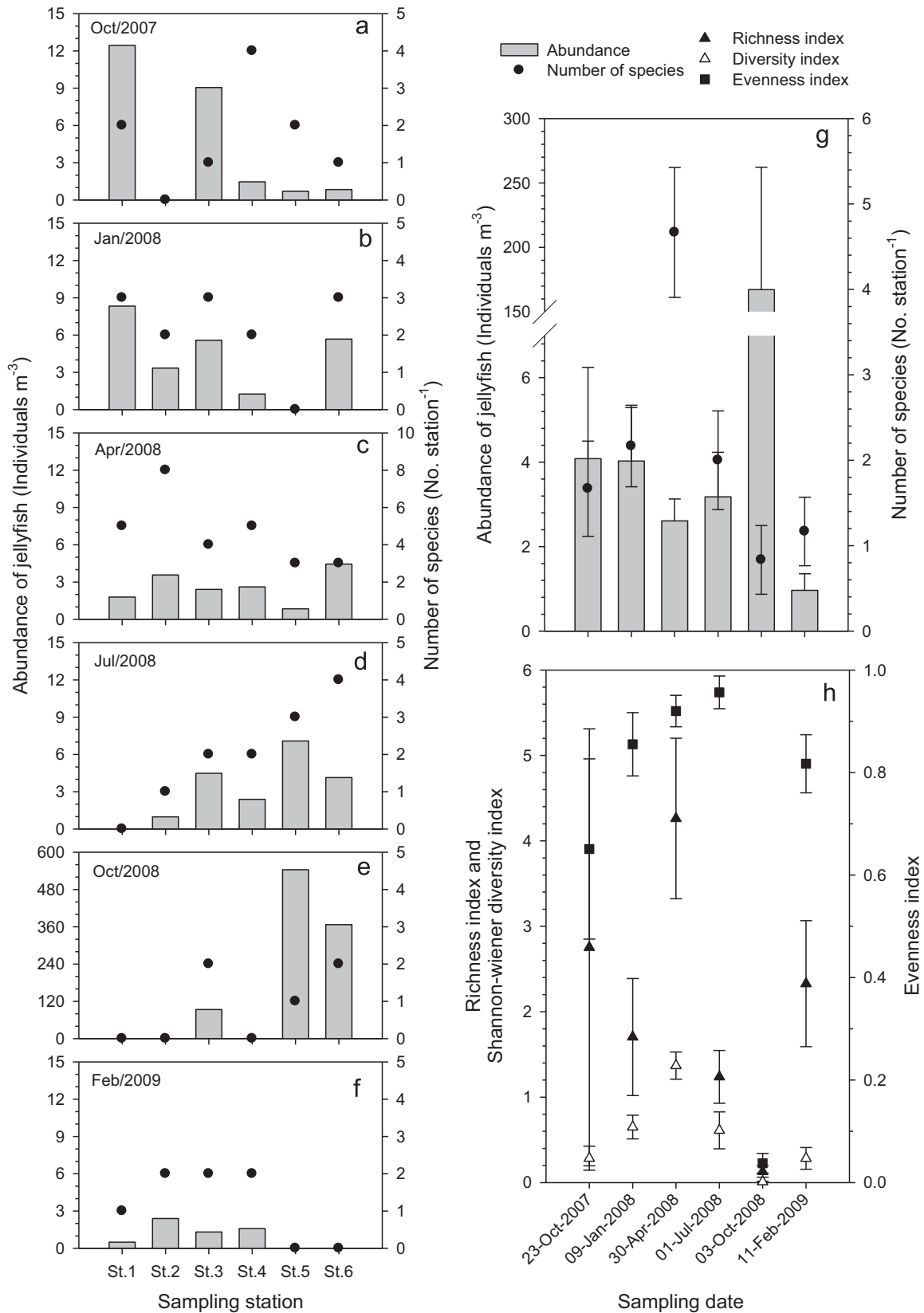


Fig. 5. Variations in species abundance and number at each station during the 6 research cruises (a)–(f). Variations in the mean (\pm standard deviation) jellyfish abundance and species number (g). The indices of richness, Shannon–Wiener diversity, and evenness (h) were obtained from the samples of each research cruise.

(season) and spatial (station) difference was observed in the overall jellyfish abundance ($p > 0.05$). By contrast, the results regarding the number of species revealed the significance of season

($p < 0.001$) and mixed effects ($p = 0.04$) regarding the variation in species diversity. No significant difference was observed in the number of species among the stations ($p > 0.05$) (Table 5).

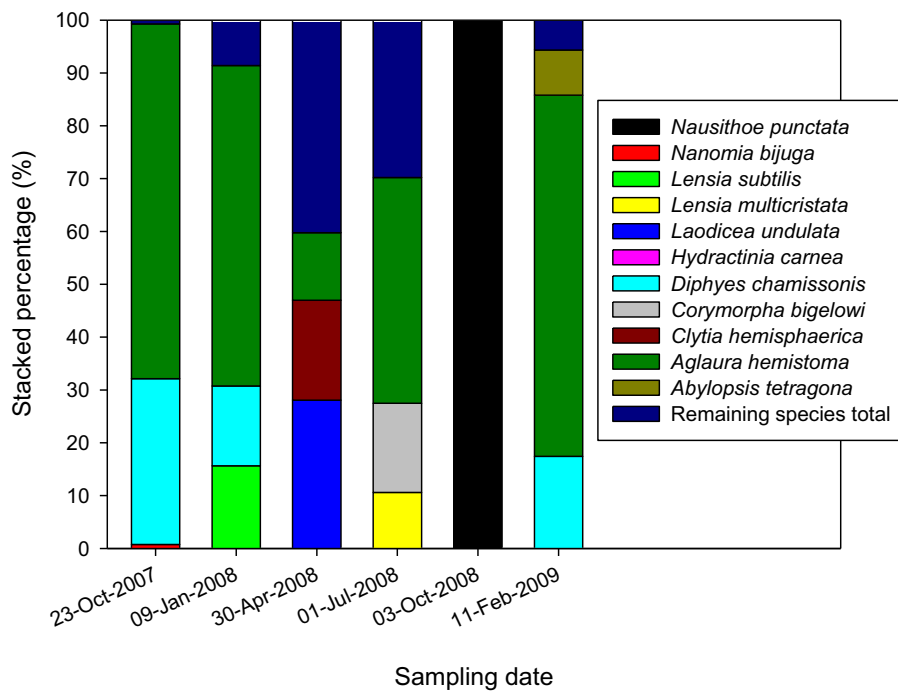


Fig. 6. Relative abundance (proportion) of the 3 most abundant jellyfish species during each research cruise.

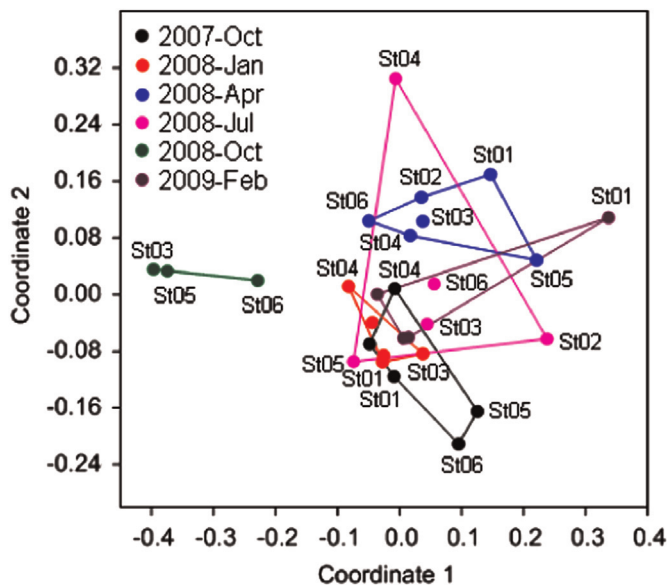


Fig. 7. Nonmetric multidimensional scaling (NMDS) of all jellyfish data from the 36 samples collected during the 6 research cruises.

4. Discussion

Numerous reports have indicated that jellyfish blooms are critical issues in coastal areas (Purcell et al., 2007; Richardson et al., 2009). Several environmental factors have been used to explain jellyfish blooms, including a decrease in the number of predators (Uye and Ueta, 2004), overfishing (Jackson et al., 2001; Pauly et al., 2009; Richardson et al., 2009), eutrophication (Mills, 2001; Liu and Diamond, 2005), hydrographic changes (Cheng et al., 2005), artificial constructions (Uye, 2008; Dong et al., 2010), global warming (Purcell et al., 2007; Richardson et al., 2009; Purcell, 2012), and climate change (Dong et al., 2010). A growing body of evidence has indicated that several human activities have increased the frequency of jellyfish blooms, including shipping,

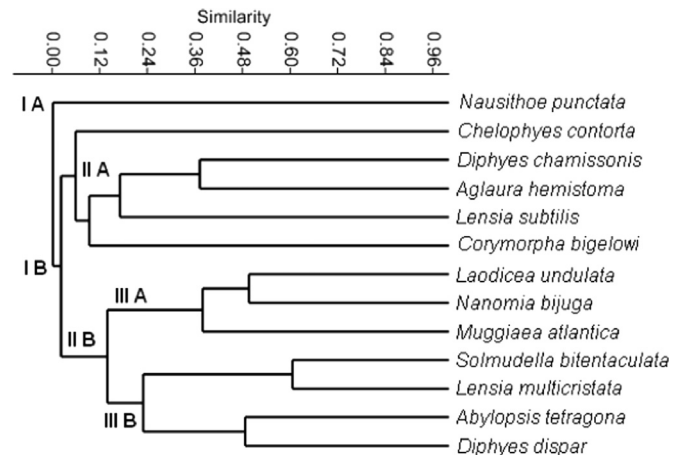


Fig. 8. Dendrogram of the 13 most abundant jellyfish species (comprising 99.32% of the total jellyfish samples); measured using Bray–Curtis distances, which reveals the degree of relative dissimilarity of distribution among the species in Northern Taiwan waters.

aquaculture, industrialization in and around coastal areas, and the outcomes of policies on coastal protection management (Duarte et al., 2013). These studies have reported that ocean sprawl could promote jellyfish blooms in coastal waters. However, the potential benefits of jellyfish to humans (e.g., in the development of medicinal drugs) (Ohta et al., 2009; Purcell et al., 2007) and their negative impacts on humans (e.g., stings by tentacle, injuries, and deaths) (Purcell and Arai, 2001; Gershwin et al., 2010) have been reported. Baseline data indicating the dynamic abundance and succession of jellyfish assemblages in coastal areas are essential for elucidating their ecological importance and value to humans (Brotz et al., 2012). Moreover, long-term monitoring on changes of zooplankton is valuable for understanding their thermal adaptation and response to climate changes (e.g., copepod) (Tseng et al., 2011c; Hinder et al., 2014), (e.g., jellyfish) (López-López et al., 2012, 2013). Keeping track on natural fluctuations of zooplankton as long as possible will be useful to evaluate the anthropogenic

Table 3

Cluster grouping samples, mean temperature, and mean salinity level according to jellyfish species (cluster grouping results, Fig. 8).

| Cluster group | Included samples (sample number) | Mean temperature (°C) | Mean salinity (‰) |
|---------------|--|-----------------------|-------------------|
| I A | Station 3, 5, 6 in Oct/2008 (3). | 22.1 ± 0.36 | 34.4 ± 0.10 |
| II A | Station 1, 3–6 in Oct/2007, station 1–4, 6 in Jan/2008, station 2–6 in Apr/2008, station 2–3, 5–6 in Jul/2008, station 6 in Oct/2008, station 2–4 in Feb/2009 (23) | 21.9 ± 3.92 | 34.7 ± 0.97 |
| III A | Station 4, 5 in Oct/2007, all samples of Apr/2008 (8) | 22.8 ± 1.69 | 35.7 ± 0.21 |
| III B | Station 4 in Oct/2007, station 2, 3, 4, 5 in Apr/2008, station 4, 6 in Jul/2008, station 1 in Feb/2009 (8) | 23.8 ± 3.92 | 35.1 ± 0.7 |

Table 4

Significant correlations among jellyfish species abundance, seawater temperature, and salinity in Northern Taiwan waters.

| Factor/species | r-Value | p-Value |
|-----------------------------|------------|---------|
| Temperature | | |
| <i>Corymorpha bigelowi</i> | 0.41 (*) | 0.030 |
| <i>Lensia multicristata</i> | 0.50 (**) | 0.007 |
| Salinity | | |
| <i>Laodicea undulata</i> | 0.46 (*) | 0.014 |
| <i>Nanomia bijuga</i> | 0.50 (**) | 0.007 |
| <i>Lensia subtilis</i> | −0.53 (**) | 0.004 |

* Correlation is significant at the 0.05 level (2-tailed).

** Correlation is significant at the 0.01 level (2-tailed).

Table 5

Two-way ANOVA results (total abundance and number of jellyfish species).

| Source of variations | df | Sum of squares | Mean squares | F value | p Value |
|----------------------|----|----------------|--------------|---------|---------|
| Abundance | | | | | |
| Season | 3 | 47279.15 | 15759.72 | 0.51 | 0.69 |
| Station | 5 | 21337.89 | 4267.58 | 0.14 | 0.98 |
| Season × Station | 12 | 50635.28 | 4219.61 | 0.14 | 1.00 |
| Number of species | | | | | |
| Season | 3 | 27.20 | 9.07 | 15.87 | < 0.001 |
| Station | 5 | 3.58 | 0.72 | 1.25 | 0.38 |
| Season × tation | 12 | 26.52 | 2.21 | 3.87 | 0.04 |

effects on marine ecosystem.

Previous studies have reported various numbers of jellyfish species in northern Taiwan according to the sampling location and period employed in those studies. In a 4-year study, López-López et al. (2013) identified 45 species in the surface water layer of coastal waters in northern Taiwan. A comparison between the jellyfish species identified in present study with those identified by López-López et al. (2013) revealed that the increased number of species was associated with the extent of temporal investigation. Lo et al. (2014) reported that *Chelophyes appendiculata*, *D. chammissonis*, *L. subtiloides*, *Bassia bassensis*, and *M. atlantica* were the most dominant siphonophore species in the waters near Taiwan. Present study also observed *D. chammissonis*, *L. subtiloides*, and *M. atlantica* in the investigation area. The findings reported by Lo et al. (2014) confirm the critical role of the KC water intrusions and CCC in influencing the jellyfish assemblage.

Several studies reported that generally the most serious factor which caused underestimation of zooplankton density and biodiversity is using inappropriate collection equipment, such as employing the improper mesh sizes net (Evans and Sell, 1985; Turner, 2004). Applying different mesh size net strongly influences the abundance of the copepod *Oithona* spp. (Hwang et al., 2007, 2010) and community structure of copepod (Tseng et al., 2011a) in the South China Sea. Present study uses the net with small opening (45 cm), which might cause the underestimation of the

abundance, species richness, and occurrence rate of large jellyfish.

4.1. Effects of interplay waters on jellyfish assemblage

Cheng et al. (2005) reported significant differences in macro-jellyfish assemblages between April and June 2004 in the northern ECS and Yellow Sea. Similarly, the jellyfish assemblages in the Taiwan Strait differed between January and July 2005 (Hsieh et al., 2013), as did those in the northern South China Sea (SCS) between summer and winter (Li et al., 2012, 2013). In present study, marked differences were observed regarding the diversity of species and abundance during each research cruise. These results indicated clear seasonal successions in the jellyfish assemblage. Mackie et al. (1987) reported that the siphonophore jellyfish assemblage exhibited seasonal succession, although this differed among the sampling years. Their results indicated that this was caused by distinct water characteristics of the CCC and KC. Similarly, present study identified significant differences in the composition of jellyfishes during the same sampling period over 3 years. The area investigated in present study was located close to the southeastern ECS, which is influenced by waters from both the CCC and KC. These 2 water masses contributed to transporting diverse marine creatures to the investigation area. Reportedly, these 2 water masses caused the seasonal succession of copepods (Chou et al., 2012) in northeastern Taiwan and that of jellyfish (López-López et al., 2012, 2013) in northern Taiwan.

Among the Diphyidae family, the 7 species *C. contorta*, *D. chammissonis*, *D. dispar*, *L. multicristata*, *L. subtilis*, *L. subtiloides*, and *S. chuni* have been observed in the areas of southwestern Taiwan that are continuously affected by the KC waters (Hung, 2002). In present study, most of the species were identified in the samples collected during April and July in 2008. The satellite images (Fig. 3) and T–S curves (Fig. 4) revealed that this period coincided with the period when the KC waters reached the investigation area. This might indicate that the occurrence of these species was related to KC transport or their preference for warm-water environments. Chang (2008) reported that water masses shape the hydromedusa assemblages, contribute to higher jellyfish abundance in CCC waters, and also contribute to the higher number and greater diversity of jellyfish species in KC waters. Lin (2010) studied hydromedusae in the waters near Taiwan and indicated that their spatiotemporal distribution was strongly affected by water masses and food availability. Furthermore, the seasonal hydrographic variations exhibited a greater influence on species richness in the waters off southern Taiwan (Lin, 2010).

Dong et al. (2010) reviewed scyphomedusae and identified 25 species in the ECS. Moreover, they identified a few scyphomedusae species that could cause blooms in the Chinese Seas. Huang and Lin (2012) provided images of scyphozoan jellyfish and identified 39 species in the waters adjacent to Mainland China. Present study identified 2 scyphozoan species, *N. punctata* and *P. noctiluca*, in the southern ECS. The species *N. punctata* was the dominant one during the sampling period, with a peak density of 543.25 individuals/m^{−3} at Station 5 in October 2008 (Fig. 5e). These 2 species have been identified in the waters adjacent to Mainland China (Huang and Lin, 2012). The species *N. punctata* is widely

distributed in the ECS and SCS, and also in Japanese, Australian, and Mediterranean waters (Liu, 2008; Hamner and Dawson, 2009; Hong and Lin, 2010). However, present study is the first to report *N. punctata* blooms in the ECS. The other species, *P. noctiluca*, was not abundant in present study. The species *P. noctiluca* has been sighted in the ECS and SCS, as well as in Japanese waters and the Pacific Ocean (Liu, 2008). Furthermore, this species has been frequently recorded in the past 20 years in the northern Adriatic Sea (Kogovšek et al., 2010). In our study, *P. noctiluca* was present only during the SW monsoon period.

Buecher (1999) reported that *A. tetragona* was the dominant species in the northwestern Mediterranean Sea, and it has typically been identified in samples throughout the year. In addition, the abundance of *A. tetragona* was reportedly higher during periods characterized by high salinity levels and seawater temperatures; by contrast, the abundance of this species is lower during winter. In present study, *A. tetragona* was identified in the samples collected during April 2008, July 2008, and February 2009. The RA was 0.15%, and the OR was 8.33%. Our cluster analysis results (Fig. 8) revealed that this species was grouped with other species that favored a wide range of seawater temperatures (23.8 ± 3.92 °C) and high salinity levels (35.1 ± 0.7) (Table 3). The results of present study are consistent with those reported by Buecher (1999), indicating that *A. tetragona* is a eurythermal and euryhaline species.

A. hemistoma exhibited the highest OR (52.78%) among all species observed in present study, and it was the only species that was identified in the samples collected during all 6 cruises. Chang (2008) reported that the abundance of *A. hemistoma* correlated positively with salinity. Liu (2008) reported the prevalence of this species in the ECS, SCS, as well as in the Pacific, Indian, and Atlantic Oceans. In addition, *A. hemistoma* was identified in abundance in Nanwan Bay in Taiwan (Hwang et al., 2003), in the waters around Taiwan (Chang, 2008), and as a dominant species in the waters off southern and northern Taiwan (Lin, 2010). Previous studies on *A. hemistoma* have indicated its high adaptability to diverse environments as well as its broad distribution. Present study confirmed that *A. hemistoma* is a domestic species in the waters near Taiwan, and it can adapt to various water environments, including the CCC and KC and the interplay waters of the CCC with KC.

4.2. Jellyfish assemblages in both monsoon periods

The east Asia monsoon system has a strong influence on the spatial and temporal distribution of zooplankton communities, specifically caused by the monsoon-driven CCC and KC interplay waters in the regions of the southern ECS. Several previous reports have revealed that the zooplankton community structure difference between the 2 monsoon periods in the regions of the southern ECS (Tseng et al., 2011b, 2012a; Chou et al., 2012). In present study, the jellyfish assemblages exhibited an obvious succession between the NE and SW monsoon periods; these results confirmed that the jellyfish assemblages is dynamic with the interplay of monsoon-driven water masses in northern Taiwan (López-López et al., 2012, 2013). Present study recorded the densities and ORs of the siphonophorae *N. bijuga*, *A. tetragona*, *D. chamosis* and *L. subtiloides*, which differed between the 2 monsoon periods. These species have been identified in the northern SCS (Li et al., 2012, 2013). By contrast, their abundance and occurrence, as identified in the samples collected during the summer and winter seasons, were unaffected by the monsoon-driven waters. The seawater temperature was higher in the northern SCS than in the southern ECS. These results might indicate that these species prefer a warm-water environment, and were thus uninfluenced by the monsoon transitions.

In the Taiwan Strait, the monsoon-driven waters have additional impacts on the distribution and assemblages of siphonophore jellyfishes (Hsieh et al., 2013; Lo et al., 2014). Li et al. (2012, 2013) reported spatial and temporal variations in the siphonophore community during the SW and NE monsoon periods in the northwest continental shelf of the SCS; in addition, they reported that the local coastal upwelling and surface ocean currents derived from the SW monsoon further enhanced the abundance and richness of the jellyfish assemblage, whereas the NE monsoon period forced the cold coastal current into the northwest continental shelf of the SCS, thereby reducing the density and number of species in the jellyfish assemblage. Present study confirmed that the species richness of the jellyfish assemblage was higher during the SW monsoon than during the NE monsoon. Previous studies in northern, western, and southern Taiwan waters have concluded that the CCC waters play a crucial role in transporting jellyfish from these cold waters to the waters of northern Taiwan, Taiwan Strait, and southeastern Mainland China (Li et al., 2012, 2013; López-López et al., 2012, 2013; Hsieh et al., 2013). Moreover, present study recognized that the jellyfish assemblages in northeastern Taiwan are strongly influenced by the interplay waters driven by the 2 seasonal monsoons.

4.3. Effects of typhoon on jellyfish assemblage

Climate change contributes to increases in SST through heat accumulation at the ocean surface; furthermore, changes in evaporation inherently cause changes in the frequency of precipitation, thereby increasing the magnitude of river discharge, which, in turn forms storms and typhoons. Climate change and typhoons markedly influence both ocean and coastal marine ecosystems (Ishizaka, 2010). Changes in rainfall affect river discharge, which, in turn, may lead to changes in the production of primary food sources and further alter the plankton biomass and composition in the coastal ocean. A growing body of evidence has demonstrated that climate change could affect waves, typhoons, and storm surges (Mase et al., 2013). Such complex processes create new and ephemeral environments that could change the dominant taxa or species in a marine ecosystem (Ishida et al., 2009). Present study observed jellyfish with the highest density (543.25 individuals/m⁻³, St 5) in October 2008 – 4 days after the passage of Typhoon Jangmi. In total, 3 species were identified in present cruise: *H. carnea*, *A. hemistoma*, and *N. punctata*. In particular, *N. punctata* was the dominant species among these jellyfishes (167.04 ± 232.54 individuals/m⁻³, 99.88%) in present cruise (October 2008). Thus, Typhoon Jangmi reduced the species diversity but markedly increased the abundance (Table 2 and Fig. 5). Incidentally, López-López et al. (2012) reported a marked increase in the abundance of *N. punctata* (92.54%) 25 days after the passage of Typhoon Jangmi in northern Taiwan. To date, few reports have discussed the changes in the jellyfish assemblage after typhoon passage because it is difficult to obtain samples during that period. López-López et al. (2012) reported an increase in jellyfish abundance after passage of a typhoon; moreover, they identified strong associations between typhoons and jellyfishes within 3–25 days of a typhoon event. Consistent with these results, present study identified the immediate and short-term effects of typhoons on coastal areas.

In conclusion, present report provides 3 key results: (i) the jellyfish species identified in northern Taiwan exhibit clear seasonal successions, similar to those of zooplankton in the waters off northern Taiwan; (ii) the jellyfish abundance and composition were influenced by typhoon events in northern Taiwan; and (iii) interplay waters play a vital role in shaping the jellyfish assemblage structure in northern Taiwan.

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References

- Arai, M.N., 2005. Predation on pelagic coelenterates: a review. *J. Mar. Biol. Assoc.* 85, 523–526.
- Box, G.E.P., Cox, D.R., 1964. An analysis of transformations (with discussion). *J. Roy. Stat. Soc. Ser. B* 26, 211–246.
- Brotz, L., Cheung, W.W.L., Kleisner, K., Pakhomov, E., Pauly, D., 2012. Increasing jellyfish populations: trends in large marine ecosystems. *Hydrobiologia* 690, 3–20.
- Buecher, E., 1999. Appearance of *Chelophyes appendiculata* and *Abylopsis tertagona* (Cnidaria, Siphonophora) in the Bay of Villefranche, northwestern Mediterranean. *J. Sea Res.* 41, 295–307.
- Catry, P., Phillips, R.A., Phalan, B., Silk, J.R.D., Croxall, J.P., 2004. Foraging strategies of grey-headed albatrosses *Thalassarche chrysostoma*: integration of movements, activity and feeding events. *Mar. Ecol. Prog. Ser.* 280, 261–273.
- Chang, W.-C., 2008. Spatiotemporal distribution of hydromedusae in relation to hydrography in the waters surrounding Taiwan. (M. Sc. thesis). Department of Marine Biotechnology and Resources, National Sun Yat-sen University, Kaohsiung, Taiwan (in Chinese with English abstract).
- Chen, Q.-C., 1992. Zooplankton of China seas (1). Science Press, Beijing, China, p. 87.
- Cheng, J.H., Ding, F.Y., Li, S.F., Yan, L.P., Ling, J.Z., Li, J.S., 2005. A study on the quantity distribution of macro-jellyfish and its relationship to seawater temperature and salinity in the East China Sea Region. *Acta Ecol. Sinica* 25, 440–445.
- Chihara, M., Murano, M., 1997. An illustrated guide to marine plankton in Japan. Tokyo University Press, Tokyo.
- Chou, C., Tseng, L.-C., Ou, C.-H., Chen, Q.-C., Hwang, J.S., 2012. Seasonal succession of planktonic copepods in bight environments of Northeastern Taiwan. *Zool. Stud.* 51, 1380–1396.
- Dong, Z.-J., Liu, D.-Y., Keesing, J.K., 2010. Jellyfish blooms in China: Dominant species, causes and consequences. *Mar. Pollut. Bull.* 60, 954–963.
- Duarte, C.M., Pitt, K.A., Lucas, C.H., Purcell, J.E., Uye, S.I., Robinson, K., Brotz, L., Decker, M.B., Sutherland, K.R., Malej, A., Madin, L., Mianzan, H., Gili, J.M., Fuentes, V., Atienza, D., Pagés, F., Breitburg, D., Malek, J., Graham, W.M., Condon, R.H., 2013. Is global ocean sprawl a cause of jellyfish blooms? *Front. Ecol. Environ.* 11, 91–97.
- Evans, M.S., Sell, D.W., 1985. Mesh size and collection characteristics of 50-cm diameter conical plankton nets. *Hydrobiologia* 122, 97–104.
- Gershwin, L.A., De Nardi, M., Winkel, K.D., Fenner, P.J., 2010. Marine stingers: review of an under-recognized global coastal management issue. *Coast. Manage.* 38, 22–41.
- Greve, W., 1994. The 1989 German Bight invasion of *Muggiaea atlantica*. *ICES J. Mar. Sci.* 51, 355–358.
- Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontol. Electron.* 4, 9.
- Hamner, W.M., Dawson, M.N., 2009. A review and synthesis on the systematics and evolution of jellyfish blooms: advantageous aggregations and adaptive assemblages. *Hydrobiologia* 616, 161–191.
- Henager, C.H., Daling, P.M., Jhonson, K.I., 1985. Factors that may intensify the safety consequences of biofouling, bivalve fouling of nuclear power plant service water system, NUREG/CR 4070, U.S. NRC, Washington, Washington, D.C.
- Hinder, S.L., Gravenor, M.B., Edwards, M., Ostle, C., Bodger, O.G., Lee, P.L., Walne, A.W., Hays, G.C., 2014. Multi-decadal range changes vs. thermal adaptation for north east Atlantic oceanic copepods in the face of climate change. *Glob. Change Biol.* 20, 140–146.
- Hong, H., Lin, L., 2010. Study on the fauna of the Scyphomedusae in the China Sea. *J. Jimei Univ. (Nat. Sci.)* 15, 18–24 (in Chinese).
- Houghton, J.D.R., Doyle, T.K., Wilson, M.W., Davenport, J., Hays, G.C., 2006. Jellyfish aggregations and leatherback turtle foraging patterns in a temperate coastal environment. *Ecology* 87, 1967–1972.
- Hsieh, Y.H.P., Leong, F.M., Rudloe, J., 2001. Jellyfish as food. *Hydrobiologia* 451, 11–17.
- Hsieh, H.-Y., Yu, S.-F., Lo, W.-T., 2013. Influence of monsoon-driven hydrographic features on siphonophore assemblages in the Taiwan Strait, western North Pacific Ocean. *Mar. Freshw. Res.* 64, 348–358.
- Huang, Z., Lin, M., 2012. An illustrated guide to species in China's Seas (volume 3)-Animalia (1): Porifera Cnidaria Platyhelminthes Nemertinea Nematoda; Acanthocephala Rotifera Gastrotricha Kinorhyncha Priapulida Annelida; Sipuncula Echiura. The living species and their illustrations in China's Seas (Part II). China Ocean Press, Beijing, China (in Chinese).
- Hung, Y.-P., 2002. Seasonal distribution of Siphonophores in Tapeng Bay and Kaoping coastal waters, Southwestern Taiwan. (M. Sc. thesis). Department of Marine Biotechnology and Resources, National Sun Yat-sen University Kaohsiung, Taiwan (in Chinese with English abstract).
- Hwang, J.-S., Kumar, R., Dahms, H.-U., Tseng, L.-C., Chen, Q.-C., 2007. Mesh-size affects abundance estimates of *Oithona* spp. (Copepoda, Cyclopoida). *Crustaceana* 80, 827–837.
- Hwang, J.-S., Kumar, R., Dahms, H.-U., Tseng, L.-C., Chen, Q.-C., 2010. Interannual, seasonal, and diurnal variation in vertical and horizontal distribution patterns of 6 *Oithona* spp. (Copepoda: Cyclopoida) in the South China Sea. *Zool. Stud.* 49, 220–229.
- 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., 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.
- Hwang, J.-S., Zhang, J.-B., Lian, G.-S., 2003. Species composition and abundance distribution of Hydromedusae in late autumn and early winter from Nanwan Bay of Taiwan, China. *J. Oceanogr. Taiw. Strait* 4, 437–444.
- Ishida, H., Watanabe, Y.W., Ishizaka, J., Nakano, T., Nagai, N., Watanabe, Y., Shimamoto, A., Maeda, N., Magi, M., 2009. Possibility of recent changes in vertical distribution and size composition of chlorophyll-*a* in the western North Pacific region. *J. Oceanogr.* 65, 179–186.
- Ishizaka, J., 2010. Climate change and marine ecosystem. *Int. Arch. Photogr. Remote Sens. Spat. Inf. Sci., Kyoto Japan* 38, 23–24.
- Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, K.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M. J., Warner, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293, 629–637.
- Kawahara, M., Uye, S.I., Ohtsu, K., Iizumi, H., 2006. Unusual population explosion of the giant jellyfish *Nemopilema nomurai* (Scyphozoa: Rhizostomeae) in East Asian waters. *Mar. Ecol.-Prog. Ser.* 307, 161–173.
- Kogovšek, T., Bogunović, B., Malej, A., 2010. Recurrence of bloom-forming scyphomedusae: wavelet analysis of 200-years time series. *Hydrobiologia* 645, 81–96.
- Li, K.Z., Yin, J.Q., Huang, L.M., Lian, S.-M., Zhang, J.L., 2013. Spatio-temporal variations in the siphonophore community of the northern South China Sea. *Chinese J. Oceanol. Limnol.* 31, 312–326.
- Li, K.Z., Yin, J.Q., Huang, L.M., 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. (M. Sc. thesis). Department of Marine Biotechnology and Resources, National Sun Yat-sen University, Kaohsiung, Taiwan (in Chinese with English abstract).
- Liu, R., 2008. Checklist of Marine Biota of China Seas. Science Press, Academia Sinica, Beijing (in Chinese).
- Liu, J., Diamond, J., 2005. China's environment in a globalizing world. *Nature* 435, 1179–1186.
- Lo, W.-T., Purcell, J.E., Hung, J.-J., Su, H.-M., Hsu, P.-K., 2008. Enhancement of jellyfish (*Aurelia aurita*) populations by extensive aquaculture rafts in a coastal lagoon in Taiwan. *ICES J. Mar. Sci.* 65, 453–461.
- Lo, W.-T., Yu, S.-F., Hsieh, H.-Y., 2014. Hydrographic processes driven by seasonal monsoon system affect siphonophore assemblages in tropical-subtropical waters (Western North Pacific Ocean). *PLoS One* 9, e100085.
- López-López, L., Molinero, J.C., Tseng, L.-C., Chen, Q.-C., Hwang, J.-S., 2012. Effects of typhoons on gelatinous carnivore zooplankton off Northern Taiwan. *Cah. Biol. Mar.* 53, 349–355.
- López-López, L., Molinero, J.C., Tseng, L.-C., Chen, Q.-C., Hwang, J.-S., 2013. Seasonal variability of the gelatinous carnivore zooplankton community in Northern Taiwan. *J. Plankton Res.* 35, 677–683.
- Lynam, C.P., Lilley, M.K.S., Bastian, T., Doyle, T.K., Beggs, S.E., Hays, G.C., 2011. Have jellyfish in the Irish Sea benefited from climate change and overfishing? *Glob. Change Biol.* 17, 767–782.
- Mackie, G.O., Pugh, P.R., Purcell, J.E., 1987. Siphonophore Biology. In: Blaxter, J.H.S., Southward, A.J. (Eds.), *Advances in Marine Biology*, 24. Academic Press Inc., (London) Ltd, pp. 97–262.
- Mase, H., Mori, N., Yasuda, T., 2013. Climate change effects on waves, typhoons and storm surges. *J. Disaster Res.* 8, 145–146.
- Masilamani, J.G., Jesudoss, K.S., Nandakumar, K., Satpathy, K.K., Nair, K.V.K., Azariah, J., 2000. Jellyfish ingress: a threat to smooth operation of coastal power plants. *Curr. Sci.* 79, 567–569.
- Masuda, R., Yamashita, Y., Matsuyama, M., 2008. Jack mackerel *Trachurus japonicus* juveniles use jellyfish for predator avoidance and as a prey collector. *Fish. Sci.* 74, 276–284.
- Mills, C.E., 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? *Hydrobiologia* 451, 55–68.
- Nastav, B., Malej, M., Malej Jr, A., Malej, A., 2013. Is it possible to determine the economic impact of jellyfish outbreaks on fisheries? A case study – Slovenia. *Medit. Mar. Sci.* 14, 214–223.
- Ohta, N., Sato, M., Ushida, K., Kokubo, M., Baba, T., Taniguchi, K., Urai, M., Kihira, K.,

- Mochida, H.-K., 2009. Jellyfish mucin may have potential disease-modifying effects on osteoarthritis. *BMC Biotechnol.* 9, 98.
- Pauly, D., Graham, W., Libralato, S., Morissette, L., Palomares, M.L.D., 2009. Jellyfish in ecosystems, online databases, and ecosystem models. *Hydrobiologia* 616, 67–85.
- Pitt, K.A., Duarte, C.M., Lucas, C.H., Sutherland, K.R., Condon, R.H., Mianzan, H., Purcell, J.E., Robinson, K.L., Uye, S.I., 2013. Jellyfish body plans provide allometric advantages beyond low carbon content. *PLoS One* 8, e72683.
- Purcell, J.E., 2012. Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. *Annu. Rev. Mar. Sci.* 4, 209–235.
- Purcell, J.E., Arai, M.N., 2001. Interactions of pelagic cnidarians and ctenophores with fish: a review. *Hydrobiologia* 451, 27–44.
- Purcell, J.E., Uye, S.I., Lo, W.-T., 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Mar. Ecol.-Prog. Ser.* 350, 153–174.
- Richardson, A.J., Bakun, A., Hays, G.C., Gibbons, M.J., 2009. The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends Ecol. Evol.* 24, 312–322.
- Tseng, L.-C., Dahms, H.U., Chen, Q.-C., Hwang, J.-S., 2012a. Mesozooplankton and copepod community structures in the southern East China Sea: the status during the monsoonal transition period in September. *Helv. Mar. Res.* 66, 621–634.
- Tseng, L.-C., Dahms, H.U., Kumar, R., Chen, Q.-C., Hwang, J.-S., 2012b. Autumn community structure in the shallow mixed layer of the subtropical South China Sea reveals a peculiar copepod and zooplankton assemblage. *J. Nat. Hist.* 47, 667–683.
- Tseng, L.-C., Hung, J.-J., Chen, Q.-C., Hwang, J.-S., 2013. Seasonality of the copepod assemblages associated with interplay waters off northeastern Taiwan. *Helv. Mar. Res.* 67, 507–520.
- Tseng, L.-C., Dahms, H.-U., Hung, J.-J., Chen, Q.-C., Hwang, J.-S., 2011a. Can different mesh sizes affect the results of copepod community studies? *J. Exp. Mar. Biol. Ecol.* 398, 47–55.
- Tseng, L.-C., Kumar, R., Chen, Q.-C., Hwang, J.-S., 2011b. Summer distribution of *Noctiluca scintillans* and mesozooplankton in the Western and Southern East China Sea prior to the Three Gorges Dam operation. *Hydrobiologia* 666, 239–256.
- Tseng, L.-C., Kumar, R., Chen, Q.-C., Hwang, J.-S., 2011c. Faunal shift between two copepod congeners (*Temora discaudata* and *T. turbinata*) in the vicinity of two nuclear power plants in southern East China Sea: spatiotemporal patterns of population trajectories over a decade. *Hydrobiologia* 666, 301–315.
- Turner, J.T., 2004. The importance of small planktonic copepods and their roles in pelagic marine food webs. *Zool. Stud.* 43, 255–266.
- Uye, S.I., 2008. Blooms of the giant jellyfish *Nemopilema nomurai*: a threat to the fisheries sustainability of the East Asian marginal seas. *Plankton Benthos Res.* 3, 125–131.
- Uye, S.I., 2010. Jellyfish blooms in East Asian coastal seas: loss of productive ecosystem. In: *Proceedings of the International Symposium on Integrated Coastal Management for Marine Biodiversity in Asia*, pp. 16–19.
- Uye, S.I., Ueta, Y., 2004. Recent increase of jellyfish populations and their nuisance to fisheries in the Inland Sea of Japan. *Bull. Jpn. Soc. Fish. Oceanogr.* 68, 9–19 (in Japanese with English abstract).
- Xu, X., Lu, C., Xu, H., Chen, L., 2011. A possible mechanism responsible for exceptional rainfall over Taiwan from Typhoon Morakot. *Atmos. Sci. Lett.* 12, 294–299.
- Yamaji, I., 1996. *Illustrations of the marine plankton of Japan*. 4th Printing. Hoi-kushu Publ. Co., Osaka, Japan.
- Yan, L.P., Li, S.F., Ding, F.Y., 2004. The preliminary studies on the dynamics of macro-jellyfish resources and their relationship with fisheries in the East China Sea and Yellow Sea. *Mar. Fish* 26, 9–12.
- Yoon, W.D., Yang, J.-Y., Shim, M.B., Kang, H.-K., 2008. Physical processes influencing the occurrence of the giant jellyfish *Nemopilema nomurai* (Scyphozoa: Rhizostomeae) around Jeju Island, Korea. *J. Plankton Res.* 30, 251–260.