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Succession of Monsoons and Water Mass Influences on Euphausiid Assemblages in the Waters Around Taiwan, Western North Pacific Ocean

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Ren-Jye Hsieh, Hung-Yen Hsieh, and Wen-Tseng Lo (2016) This study took advantage of the zooplankton samples collected by the Fisheries Research Institute that implemented Taiwan Cooperative Oceanic Fisheries Investigation, the first large scale hydrographic and plankton survey around Taiwan Island. The aim of the study was to elucidate the spatial and temporal distribution patterns of euphausiids and their correlations with the hydrographic features during the southwesterly (summer) and northeasterly (winter) monsoons in 2004. A total of 35 taxa of euphausiids belonging to 6 genera and 1 family were recognized from our studied samples. The five predominant species were *Pseudeuphausia lalifrons*, *Stylocheiron* sp., *Stylocheiron suhmii*, *Euphausia pacifica* and *Stylocheiron carinatum*, together comprising 54.6% of the total euphausiid catch. Abundance, species richness and species diversity of euphausiids were significantly higher in summer than in winter. Cluster analysis revealed two station groups during both seasons. Higher abundance and lower species richness generally were observed in waters west of Taiwan where the China Coastal Current prevails, and a reverse condition was found in the waters east of Taiwan where the Kuroshio Current dominates. The distribution patterns in abundance and species assemblages were closely correlated with the hydrographic conditions, and well linked with the abundance of zooplankton and chlorophyll *a* concentration. Euphausiid assemblage showed clear seasonal variations. The succession of water mass induced by monsoon apparently affects the distribution patterns of euphausiids in the study area.

Key words: Euphausiid, Distribution, Monsoon, Water mass, Taiwan.

BACKGROUND

Taiwan is a subtropical island that locates in the western North Pacific Ocean. Waters surrounding Taiwan are very complex and mainly affected by the interactions of three water masses, namely the Kuroshio Current (KC), China Coastal Current (CCC), and the South China Sea Surface Current (SCSSC) (Jan et al. 2002). The KC is characterized by high temperature, high salinity and low nutrient concentration, and is derived from the North Equatorial Current, which flows westerly to the east coast of the Philippines, and then turn north along the east coast of Taiwan all year-round (Nitani 1972; Tang et al. 1999; Hsiao et al. 2011; Kâ and Hwang 2011). The main axes of KC swing to the right and left seasonally, getting closer to the east coast of Taiwan during winter season when the northeasterly monsoon (NEM) prevails (Wang and Chern 1989). In late spring and summer, NEM is replaced by the southwesterly monsoon (SWM), the main axes of KC is then moving outwards of Taiwan. When the KC flows northward through northeastern Taiwan into the East China Sea (ECS) continental shelf waters, due to the Earth's rotation, this originally flows northward and then turns northeast and finally flows into the ECS along the eastern coast of Japan. However, a small part of the water mass may keep the original direction, flowing towards the continental shelf waters of the

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ECS, and mixing with the ECS, this way forming a complex hydrological environment (Liu and Pai 1987).

The changes of water masses west of Taiwan are more complex than those of eastern Taiwan. In winter, the prevailing NEM will bring the CCC flowing southward along the China coast and entering the northern or central Taiwan Strait (TS). Meanwhile, the Kuroshio Branch Current (KBC) invades the northern part of South China Sea by passing through the Luzon Strait and southwestern TS and Penghu Channel. When KBC and CCC are flowing through the central Strait, affected by the NEM and Yuen-Chang Ridge that hinder its progress. This causes a frontal confrontation in the central Strait (Liang et al. 2003; Hwang et al. 2006). Thus, the north of the TS is entrenched by the CCC, while in the south it is entrenched by the KBC, where it produces an upwelling (Jan et al. 1998, 2002, 2006, 2010) near the Penghu Islands. In spring, the NEM decreases and the SWM rises gradually which makes the KBC in the south of Taiwan to pull northwards, while the bottom water shifts to the northern TS by crossing the Yun Chang Ridge. When the SWM is prevailing during summer, CCC completely evacuates from the north of the Strait, the KBC hindered by the SCSSC brought by SWM, evacuates from south of TS and is replaced by the SCSSC (Fang 1982; Hu et al. 2000; Jan et al. 2006). When SCSSC, enhanced by SWM, flows into the TS and comes across the Yun Chang Ridge, the South China Sea bottom water may turn to the west, while surface water may bypass the Yun Chang Ridge flowing northward along the western coast of Taiwan (Jan et al. 1994). In autumn, the SWM decreases and again the NEM is formed, CCC flows into the northern TS, the SCSSC gets weakened due to a decreasing SWM and evacuates southward to the south of the TS. In winter, KBC flows into the TS replacing the SCSSC, and forms a distinctive seasonal succession of water masses in the TS (Jan et al. 2002, 2006). All of these complex hydrological features in the waters around Taiwan apparently influence the distribution patterns of marine zooplankton and other organisms (Hu et al. 2000, 2003; Lo et al. 2004a, 2004b, 2010; Hwang and Wong 2005; Hsieh et al. 2005, 2012, 2013; Hu et al. 2010; Liao et al. 2013).

Euphausiids are common and usually form patchness in both neritic and oceanic waters. They feed primarily on phytoplankton, zooplankton and detrital materials, and themselves also serve as an important food source for many marine fishes, thus, playing an important role in the matter and energy flux of marine ecosystem (Brodeur and Pearcy 1992; Robinson 2000; Tanasichuk 2002). The distribution patterns of euphausiids are influenced by physical factors such as light intensity, water temperature, salinity, and seasonal changes in water masses (Mauchline and Fisher 1969), and by biotic factors such as the availability and quality of food sources, predation pressure, and reproductive strategy (Youngbluth 1975, Bollens et al. 1992, Gibbons 1993, Tarling et al. 1999).

In the past two decades, many scholars have successively been engaged in euphausiid research in the adjacent waters of Taiwan (Chen and Zhang 1983; Cai 1989; Wang et al. 2003; Xu and Chen 2005; Xu and Li 2005), especially in the Yellow Sea, ECS, the west coast of TS and South China Sea. For example, Taki's studies (Taki 2006, 2007, 2010) in northeastern Japan Sea found that the biomass and abundance of *Euphausia pacifica* were higher in the northern latitude and during the daytime. Furthermore, he also found that during the period from spawning to growth, the euphausiid abundance and Chl *a* concentration is closely related, showing that the phytoplankton is the key factor as the main food source during their growth. Brinton (1975) engaged of research of euphausiid distribution in the water surrounding Taiwan during 1959-1976, and recorded 19 species in 6 genera, with the abundance in the waters of western Taiwan higher than that of the eastern coast; meanwhile, the upwelling zone has the highest abundance. Xu and Chen (2005) studied in the ECS and found that the different dominant species of euphausiids appear in different seasons and water masses. For example, *Euphausia pacifica* appears only in cold water mass of winter and spring, and *Euphausia nana*, *Pseudeuphausia sinica* and *Pseudeuphausia latifrons* appears in warm water areas in summer.

In recent years zooplankton was studied intensively in the waters around Taiwan. For example, in the coastal waters and estuaries of Taiwan, Tzeng et al. (2002) found that succession of monsoons could affect the assemblage structure and seasonal distribution patterns of fish larvae in Taiwan's western coastal estuaries, and it is associated with water temperature and salinity. The authors also found that the species diversity is generally higher in spring and autumn than in winter, and higher in the south of the estuaries than in the north. Hsieh et al. (2005) also found that the abundance, structure, and distribution of planktonic copepods and larval fish assemblage varied with temperature, salinity and upwelling in the Taiwan Strait. When the SWM prevails in summer, the SCSSC invades the northern Strait with increasing temperature and increased abundance of these organisms. When the NEM induced southward CCC in winter the waters become colder and more turbulent, and the abundance of organisms is reduced, whereas the upwelling area generally shows a higher abundance of plankton. Lo et al. (2004a, b) found that in the southeastern TS, the distribution of copepods was associated with the hydrological environment, particularly in the upwelling area south of Penghu Islands where highest copepod abundance and species richness was observed. Lo et al. (2010) and Hwang and Wong (2005) proposed that both water mass succession and upwelling caused by seasonal monsoon-driven currents affect the composition and abundance distribution of fish larvae. Many copepod related studies were also conducted, such as in estuarine areas (Dahms et al. 2012), coastal waters (Tseng et al. 2011), adjacent waters of nuclear power plants (Tseng et al. 2011), harbors and embayment environments (Chang et al. 2010), hydrothermal vents (Kâ and Hwang 2011), and lagoons (Hsu et al. 2008). By contrast, euphausiid research is relatively lacking in this area.

The present study used zooplankton samples obtained by the Taiwan Cooperative Oceanic Fisheries Investigation (TaiCOFI) conducted by the Taiwan Fisheries Research Institute. This is the first survey of plankton and hydrographic features at large-scale (21~26°N, 118~123°E) in the waters around Taiwan. The main purpose of TaiCOFI is to establish a long-term hydrographic and biological database and to construct a numerical model for fishery forecasts. Our investigation on spatial distribution of euphausiids during the NEM and SWM seasons in waters around Taiwan is aiming at possible influences of hydrological features driven by seasonal monsoons on distributional patterns of euphausiid assemblages.

MATERIALS AND METHODS

This study was conducted at 62 stations in the waters surrounding Taiwan during two cruises of the Fishery Researcher I (FRI-200402 and FRI-200408) in winter (February, NEM) and summer (August, SWM) of 2004 (Fig. 1). At each station, temperature and salinity were measured with

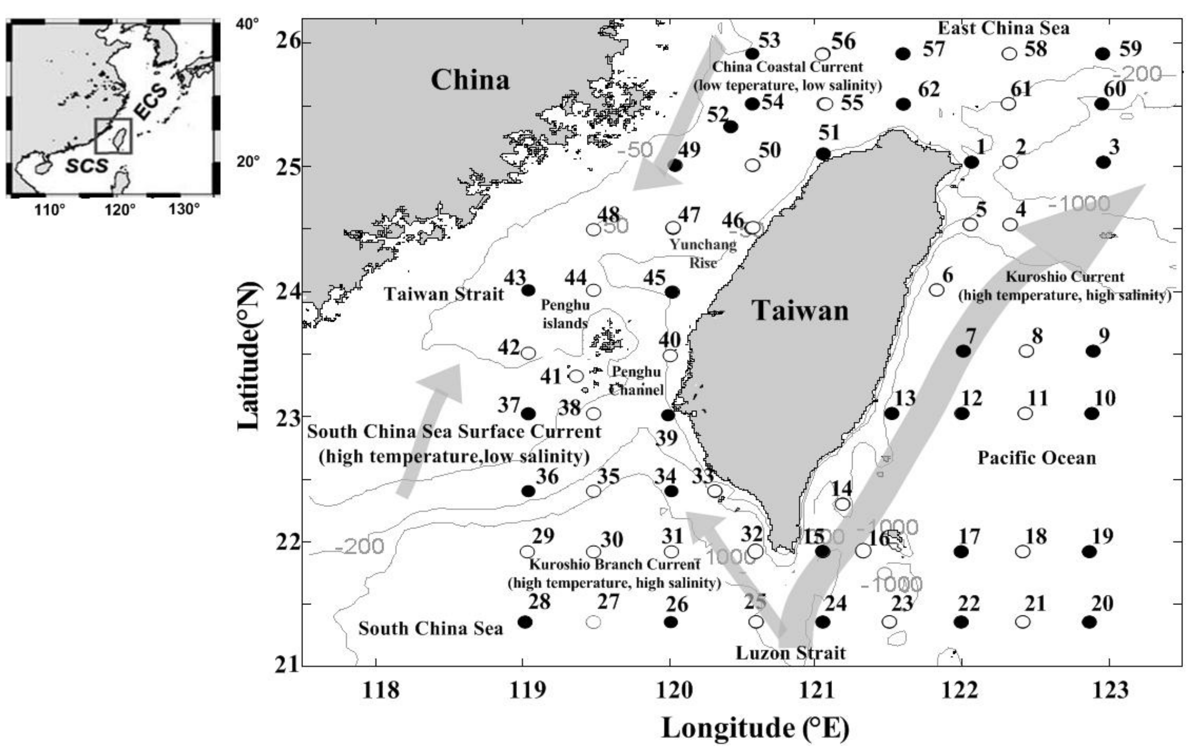

Fig. 1. Station locations and current states in waters around Taiwan in February and August of 2004. Gray circle: stations with CTD data only; black circles: stations with both CTD and euphausiid samples.

a SeaBird CTD from the sea surface to 200 m depth (or 10 m above the bottom at stations of < 200 m depth). Seawater samples for Chl *a* concentration measurements were obtained with Go-Flo bottles at 6 depths (5, 25, 50, 75, 100 and 150 m). Seawater samples were immediately filtered through Whatman GF/F filter papers, which were then put in vials containing 10 ml of 90% aqueous acetone and left for 24 hours in a dark refrigerator for full extraction. The sample vials were then shaken and centrifuged, and the fluorescence was measured by a fluorescence spectrophotometer (Hitachi model F-2000, Japan) before and after acidification with 10% hydrochloric acid. Then, equations (Strickland and Parsons 1972) were used to calculate Chl *a* concentrations. The contours of temperature, salinity and Chl *a* concentration of each season were drawn by graphics software Sufer 7.0. Measurements at 10 m were used to reduce the disturbances of surface water caused by wind. Temperature-Salinity (T-S) graphs were drawn by using the measurements of temperature and salinity from surface water to 200 m depth. Hydrographic features and water masses of various stations surrounding Taiwan were classified according to Sawara and Hanzawa (1979). Sea surface water current velocity and direction (data from the ocean data bank of the National Center for Ocean Research, Taiwan) in Taiwanese waters during winter and summer were obtained to see large-scale hydrographic patterns in this study area (Fig. 2). And, images of sea surface temperature (SST) during winter and summer cruises of 2004 from the advanced very-high-resolution radiometer (AVHRR) satellite of the National Oceanic and Atmospheric Administration (NOAA) were also used (Fig. 3).

Zooplankton samples were collected at 30 of the 62 hydrographic stations using an ORI net (mouth opening: 1.6 m; mesh size: 330 μm). A flow-meter (Hydro-Bios) was fixed in the mouth opening to estimate the volume of filtered water. The net was towed vertically from 200 m (or 10 m above the bottom at stations of < 200 m in depth) to the surface at a speed of 1 m/s. Zooplankton samples were then immediately preserved on board in 5% borax-buffered formalin seawater. In the laboratory, euphausiid specimens were sorted, counted, and identified to species level if possible, under a dissecting microscope. Identification of euphausiid species was made according to Baker et al. (1990) and Chihara and Murano (1997).

Euphausiid abundances were standardized as the number of individuals/100 m^3. Shannon diversity index (H') (Shannon and Weaver 1963) was used to calculate the species diversity. An analysis of variance (ANOVA) was applied to test if biological and hydrographic variables significantly differed between seasons (NEM vs. SWM) and locations (station groups) using statistical software SPSS 10.0 (Dunn and Clark 1974). Cluster analysis (Everitt 1974) was performed to evaluate the similarity of hydrographic conditions among stations, and the distribution of station groups were then delineated on a map to visualize its relationship with hydrographic conditions. Multidimensional scaling (MDS) (Kruskal and Wish

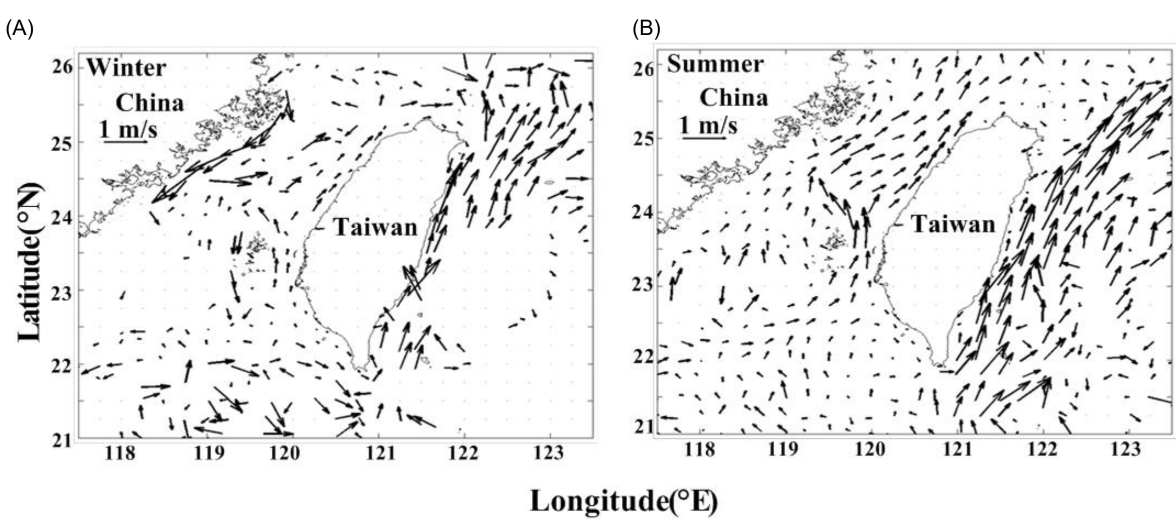

Fig. 2. The water current in waters around Taiwan in February and August of 2004. The velocity of water current is 1 m/s; the direction of the water current (A, B) are arrow. Data were obtained from the ocean databank of the National Center for Ocean Research, Taiwan.

1978) was used to examine the seasonal and spatial variations of the euphausiid community structure. Multiple regressions with a forward stepwise method were applied to analyze relationships between euphausiid abundances and hydrographic variables.

RESULTS

Hydrography

Hydrographic features of Taiwanese waters are complex and have clear seasonal variations. Maps of large scale water currents (Fig. 2) and satellite images of sea surface temperature (Fig. 3) revealed that the CCC flowed southward along the mainland China coast into northern and even central parts of the TS and formed a clear northeast to southwest front in TS during winter, while the SCSSC flowed northward by SWM into TS and dominated in the TS during summer. In the east of Taiwan, the KC always flowed northwardly along the east coast of Taiwan. Its main flow was always closer to the coast in winter due to the NEM, and the current was stronger during summer. The average water temperature of the waters surrounding Taiwan was significantly lower in winter (22.6 ± 0.10°C (SE)) than in summer (28.9 ± 0.03°C (SE)) (one-way ANOVA; $p < 0.001$) (Table 1). The contours of water temperature showed a clear front in the TS and a gradual increase from the northwest to the southeast of the TS (Fig. 4). The highest temperature in winter was found at Station 21 (26.4°C) in the KC area and the lowest at Station 52 (15.1°C) within the CCC zone. During summer SWM, the water temperature of Taiwanese waters was generally warmer, over 28°C, with the exception in the center of TS near the Penghu islands where temperatures were below 28°C. In the waters of eastern and southern Taiwan, the water temperature was generally > 29.2°C (Fig. 4). Mean Chl *a* concentrations were higher in winter than in summer, but did not show significant differences between seasons (Table 1). Salinities were generally higher in the waters southeast of Taiwan than in the waters northwest of Taiwan during both seasons, and usually formed a salinity front between water masses in the TS. For instance, a clear salinity front was observed in the western TS in winter, and fronts were also found in the waters southwest and northeast of Taiwan during summer (Fig. 4). Higher Chl *a* concentrations were generally observed in the TS if compared with KC area in the east of Taiwan. The highest Chl *a* concentration was generally found in the frontal areas of the TS and the upwelling zone nearby Penghu Island, the lowest values

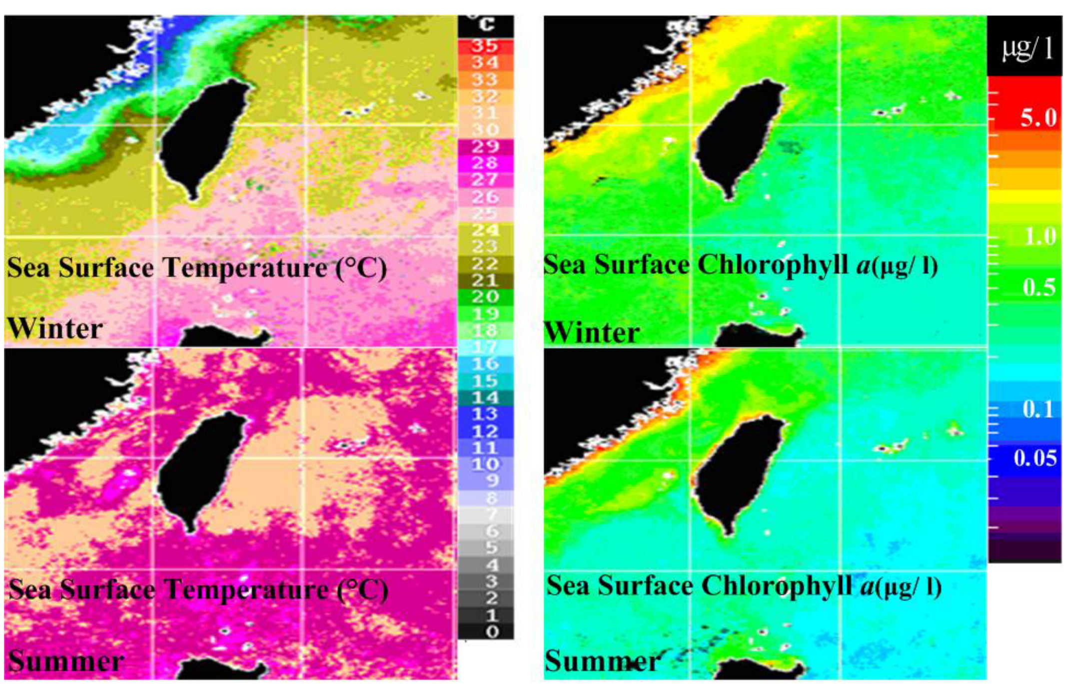

Fig. 3. Satellite images of sea surface temperature and chlorophyll *a* around Taiwan in 2004. Data were obtained from the ocean data bank of the National Center for Ocean Research, Taiwan.

were consistently found in the KC area during both seasons (Fig. 4).

According to the results of our cluster analysis based on hydrological data, we found that the water masses around Taiwan can clearly be divided into two groups during both seasons: namely A1 and A2 in winter (Fig. 5) and B1 and B2 in summer (Fig. 6), respectively. In winter, Group A1 (black dot) included 36 stations, which were mostly located in the waters east and south of Taiwan which were dominated by KC and SCSSC. According to the T-S diagram, we found that the group A1 was characterized by higher temperature and salinity, and was mainly influenced by the KC, SCSSC, and ECS mixed waters. Group A2 (white dot) comprised 26 stations, which were mainly located in the waters west and northwest of Taiwan. The T-S diagram showed that the waters around group A2 is with lower temperature and salinity and is mainly influenced by the CCC (Fig. 5). In summer, Group B1 (white dot) contained 25 stations, which were distributed in the waters west and north of Taiwan. The T-S diagram showed that the warmer and higher saline waters of group B1, are mainly coming from the KC, SCSSC, and ECS Mixed Water. Group B2 (black dot) included 37 stations, which were located in the waters east and south of Taiwan. The T-S diagram showed that the waters of group B2, with higher temperature and salinity, mainly came from the KC and SCSSC (Fig. 6).

Abundance and composition of euphausiids

The abundance, species richness and species diversity of euphausiids showed significant spatial and seasonal variations in the waters around Taiwan. The average abundance and species richness of euphausiids in summer were significantly higher than in winter, but no significant difference was observed in species diversity (Table 1). Spatial distribution pattern of euphausiids was similar in both seasons, the abundance of euphausiids was generally higher in the waters off northern and western Taiwan, while the species richness and diversity of euphausiids were more diverse in the waters off eastern and southern Taiwan where the KC and SCSSC dominated during both seasons (Fig. 7).

In total, 35 taxa of euphausiids (including 5 unidentified taxa of euphausiids), belonging to 1 family and 6 genera, were identified in this study. The 5 predominant euphausiid taxa were *Pseudeuphausia lalifrons*, *Stylocheiron* sp., *Stylocheiron suhmii*, *Euphausia pacifica* and *Stylocheiron carinatum*. Among them, *P. lalifrons* and *Stylocheiron* sp. were the 2 most abundant species, with the relative abundance of 19.2% and 13.0%, respectively. In winter, 28 taxa of euphausiids were identified. The 5 predominant euphausiid taxa were *E. pacifica*, *Stylocheiron* sp., *S. carinatum*, *S. affine*, and *Euphausia hemigibba*. These 5 predominant euphausiids occupied 62.4% of the total euphausiid catch. *E. pacifica* and *Stylocheiron* sp. were most dominant, with a relative abundance of 35.6% and 9.8%, respectively (Table 1). In summer, 31 taxa of euphausiids were found. The 5 most abundant taxa were *P. lalifrons*, *Stylocheiron* sp., *S. suhmii*, *S. carinatum*, and *S. affine*. These 5 predominant

Table 1. Hydrographic variables, average abundances, RA, species richness and species diversity of euphausiids in 2004

Winter		Summer		Overall	
Species	Mean ± SE (RA%)	Species	Mean ± SE (RA%)	Species	Mean ± SE (RA%)
Euphausia pacifica	25.7 ± 1.6 (35.6%)	*Pseudeuphausia lalifrons*	56.9 ± 3.4 (24.6%)	*Pseudeuphausia lalifrons*	29.1 ± 2.6 (19.2%)
Stylocheiron sp.	7.1 ± 0.3 (9.8%)	*Stylocheiron* sp.	32.3 ± 1.1 (14.0%)	*Stylocheiron* sp.	19.7 ± 0.9 (13.0%)
Stylocheiron carinatum	6.0 ± 0.7 (8.3%)	*Stylocheiron suhmii*	24.7 ± 0.9 (10.7%)	*Stylocheiron suhmii*	13.6 ± 0.7 (9.0%)
Stylocheiron affine	3.7 ± 0.2 (5.1%)	*Stylocheiron carinatum*	8.9 ± 0.5 (3.8%)	*Euphausia pacifica*	12.8 ± 1.2 (8.5%)
Euphausia hemigibba	2.6 ± 0.1 (3.6%)	*Stylocheiron affine*	6.8 ± 0.3 (2.9%)	*Stylocheiron carinatum*	7.4 ± 0.6 (4.9%)
Abundance	72.2 ± 2.4	Abundance	230.75 ± 6.50***	Abundance	151.5 ± 5.5
Species richness (Total)	9.0 ± 0.1 (28)	Species richness (Total)	12.37 ± 0.15* (31)	Species richness (Total)	11.0 ± 0.1 (35)
Species diversity	1.8 ± 0.01	Species diversity	1.94 ± 0.01	Species diversity	1.9 ± 0.02
Temperature (°C)	22.6 ± 0.10	Temperature (°C)	28.9 ± 0.03***		
Salinity	34.3 ± 0.02	Salinity	34.2 ± 0.01		
Chlorophll *a* (μg/l)	0.17 ± 0.01	Chlorophll *a* (μg/l)	0.09 ± 0.00		

RA, relative abundance; Asterisks indicate a significant difference between seasons according to an ANOVA at *$p < 0.05$, **$p < 0.01$, and ***$p < 0.001$.

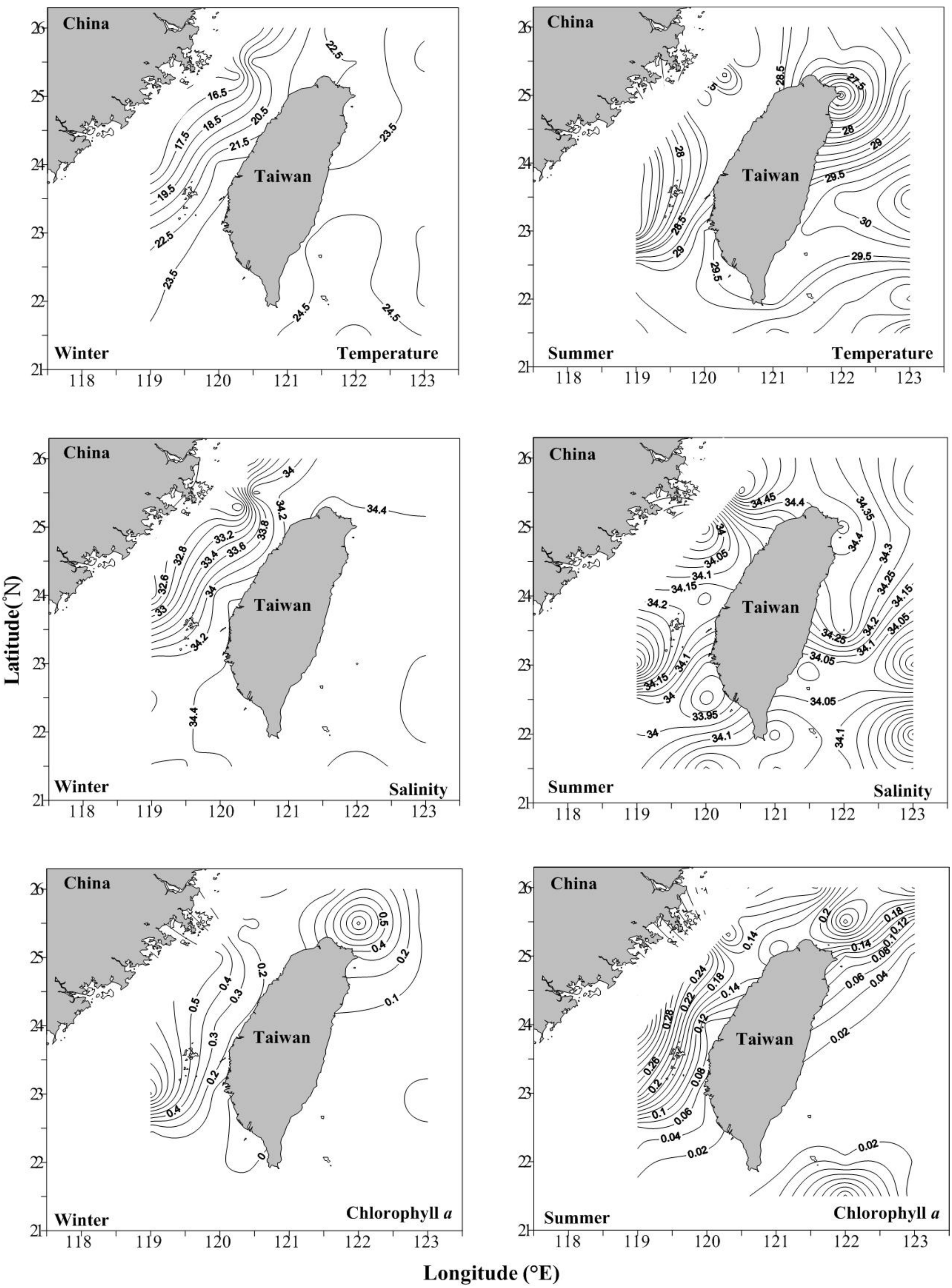

Fig. 4. Temperature (°C), salinity and chlorophyll *a* contours in waters around Taiwan in February and August of 2004. The distribution of temperature (°C), salinity and chlorophyll *a* in surface waters.

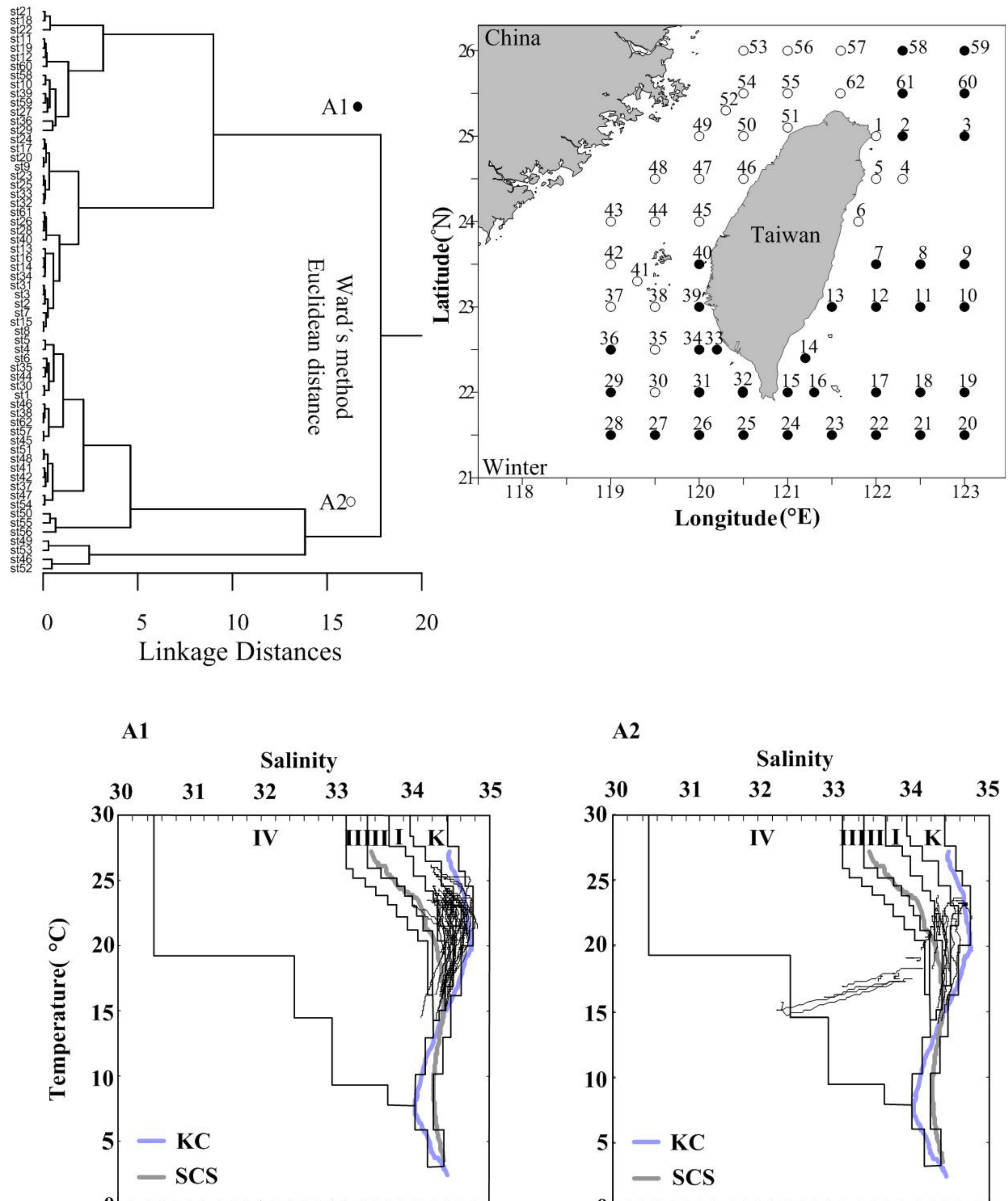

Fig. 5. Dendrogram of station groups in waters around Taiwan in February of 2004. Cluster analysis based on hydrographic data; temperature and salinity at a depth of 1-20 m; K: Kuroshio Current, I: East China Sea Mixed Water, II: Yellow Sea Mixed Water, III: The Kuroshio Edge of Mixed Water, IV: East China Sea Coastal Water, KC: Kuroshio Current, SCS: South China Sea Surface Current.

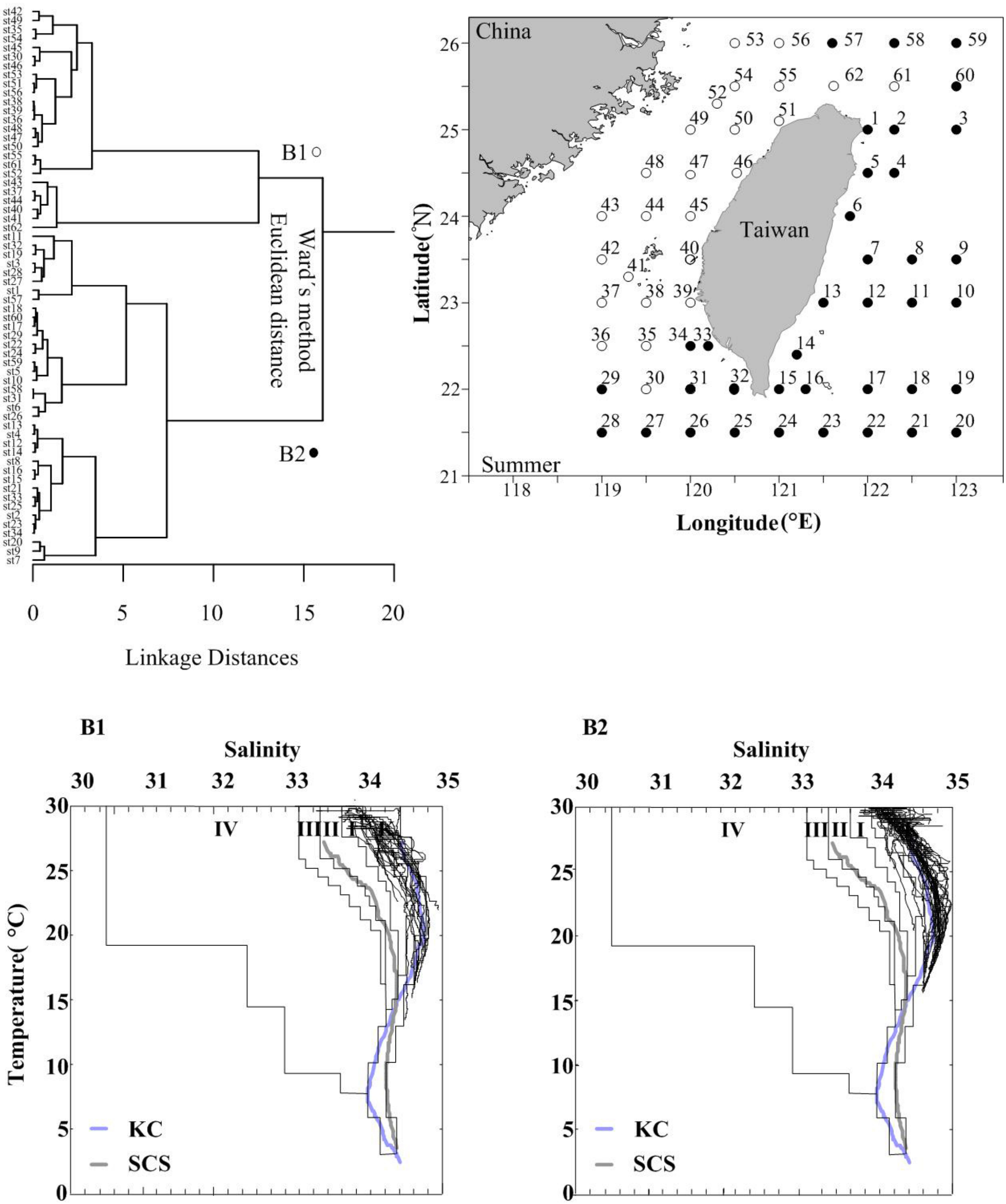

Fig. 6. Dendrogram of station groups in waters around Taiwan in August 2004. Cluster analysis based on hydrographic data; temperature and salinity at a depth of 1-20 m; K: Kuroshio Current, I: East China Sea Mixed Water, II: Yellow Sea Mixed Water, III: The Kuroshio Edge of Mixed Water, IV: East China Sea Coastal Water, KC: Kuroshio Current, SCS: South China Sea Surface Current.

euphausiids comprised 56% of the total euphausiid abundance. *P. lalifrons* and *Stylocheiron* sp. were most abundant, with the relative abundance of 24.6% and 14.0%, respectively. Among these dominant taxa, *Stylocheiron* sp., *S. carinatum* and *S. affine* were common in both seasons but with a higher abundance in summer. *E. pacifica* and *P. lalifrons* appeared to perform a clear seasonal succession (Table 1). In that, *E. pacifica* occurred only in winter, with high abundance in the waters west and north of Taiwan, while *P. lalifrons* was abundant in summer and in the waters north of the TS (Fig. 8).

Euphausiid assemblages related to water masses

According to the results of the hydrographic station groups (from Figs. 5, 6), Station group of A1 in winter are mainly in the waters east and south of Taiwan that are dominated by KC and SCSSC, while station group A2 mostly in the

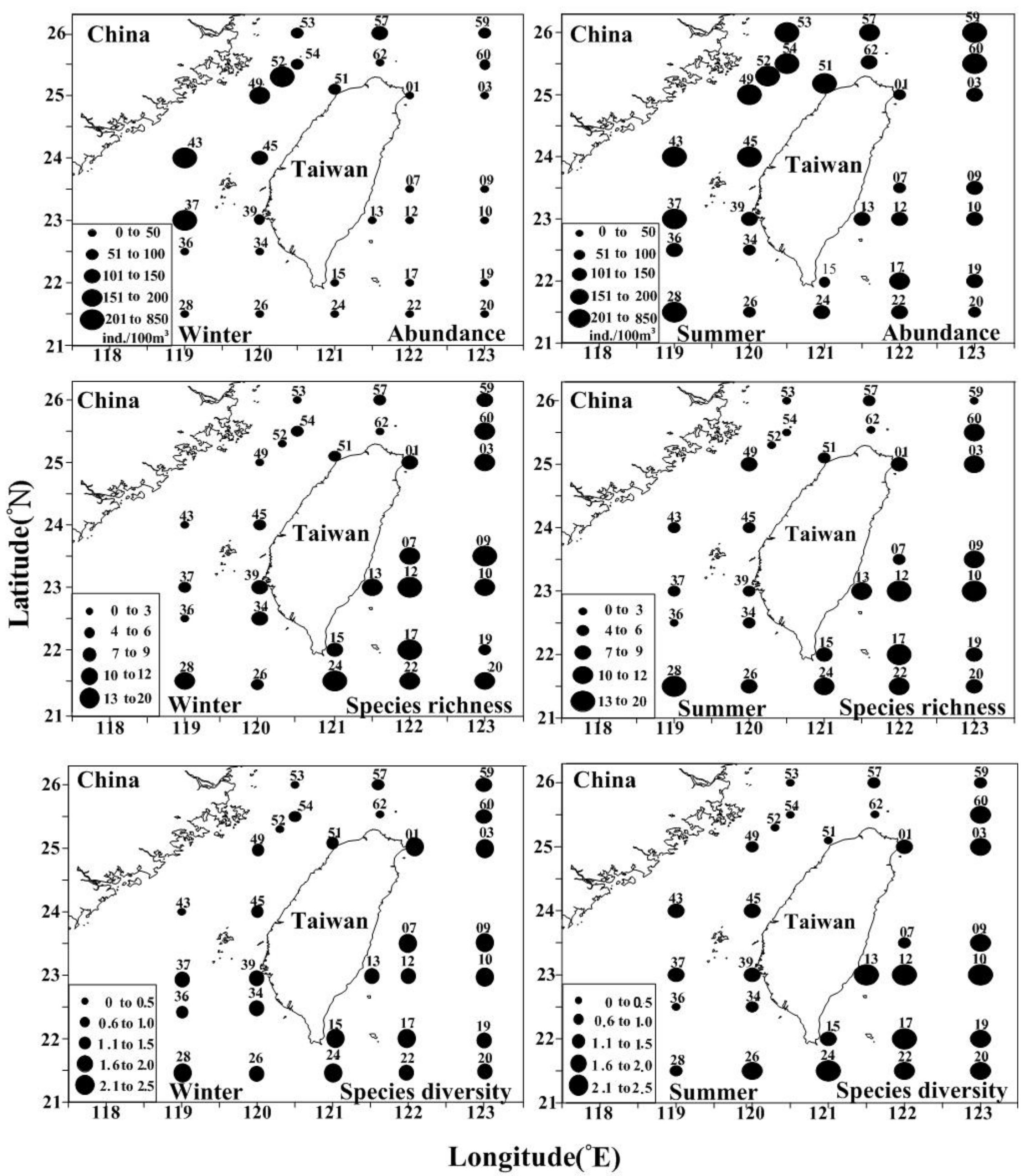

Fig. 7. Abundance, species richness and species diversity of euphausiids in waters around Taiwan in February and August of 2004.

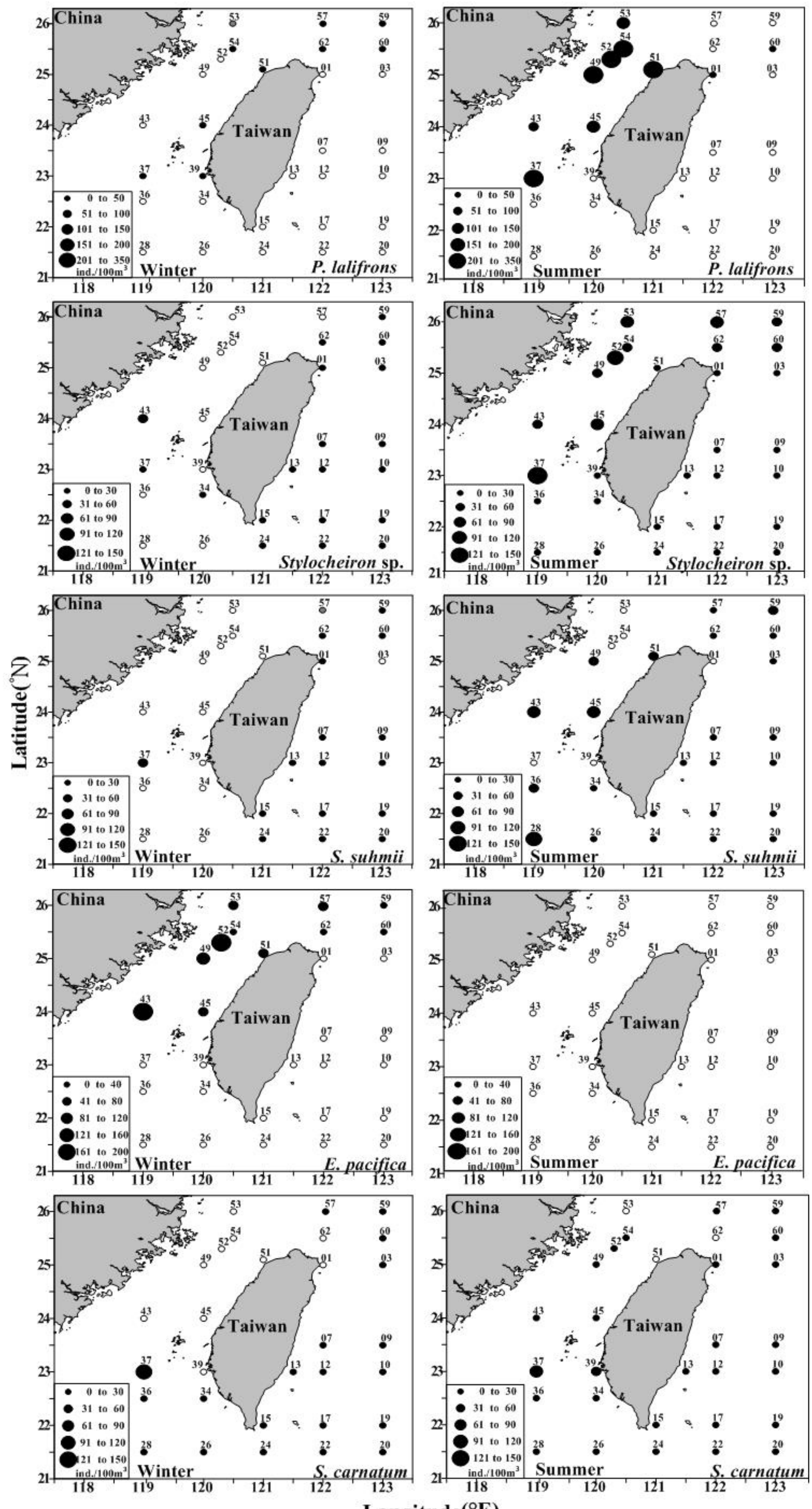

Fig. 8. The distribution of 5 predominant euphausiid species in waters around Taiwan in February and August 2004.

waters west and northwest of Taiwan where mainly influenced by the CCC. *Stylocheiron* sp. was dominant in station group A1, with an average and relative abundance of 9.4 ± 1.9 ind./100 m^3 and 25.4%, respectively. Other dominant euphausiid species included *Stylocheiron affine*, *Stylocheiron carinatum*, *Euphausia recurva*, and *Stylocheiron suhmii*, which provided 33.2% of the total euphausiid abundance (Table 2). The euphausiid species of station group A1 were basically subtropical and tropical species and their abundance was generally low (Table 2, Fig. 5). The 5 predominant euphausiid taxa in station group A2 were *Euphausia pacifica*, *S. carinatum*, *Euphausia hemigibba*, *S. suhmii*, and *Euphausia mutica*, together comprising 68.4% of the total euphausiid catch. Among them, *E. pacifica* was the most dominant, with an average and relative abundance of 68.1 ± 5.2ind./100 m^3 and 51.3%, respectively (Table 2). The euphausiid species in the Group A2 mostly belonged to temperate, subtropical and tropical species, and had higher abundances than that of the group A1 (Table 2, Fig. 5).

Station group of B1 in summer was mainly located in the TS (Fig. 6). The top 5 dominant species of station group B1 were *Pseudeuphausia lalifrons*, *Stylocheiron* sp., *Stylocheiron suhmii*, *Stylocheiron carinatum* and *Thysanopoda tricuspidata*, together comprising 64.5% of the total euphausiid abundance (Table 2). Among them, *P. lalifrons* was the most abundant, with average abundance and relative abundance of 150.4 ± 11.3 ind./100 m^3 and 37.2%, respectively. Station group of B2 distributed mainly in the waters of eastern and southern Taiwan and were dorminated by KC and SCSSC (Fig. 6). The 5 predominant species were *S. suhmii*, *Stylocheiron* sp., *Stylocheiron affine*, *Euphausia sanzoi*, and

Table 2. Mean abundance (mean ± SE, ind./100 m^3) and relative abundance (R.A., %) of 5 predominant euphausiids and environmental variables of each station group in winter (Feb) and Summer (Aug) of 2004. (Station groups from Figs. 4-5)

Winter A1 st3,7,9,10,12,13,15,17,19,20,22,24,26,28,34,36,39,59,60		Summer B1 St36,37,39,43,45,49,51,52,53,54,62	
Species	Mean ± SE (RA%)	Species	Mean ± SE (RA%)
Stylocheiron sp.	9.4 ± 1.9 (25.4%)	*Pseudeuphausia lalifrons*	150.4 ± 11.3 (37.2%)
Stylocheiron affine	5.8 ± 1.7 (15.7%)	*Stylocheiron* sp.	59.0 ± 3.6 (14.6%)
Stylocheiron carinatum	3.0 ± 0.7 (8.2%)	*Stylocheiron suhmii*	27.1 ± 2.9 (6.7%)
Euphausia recurva	1.8 ± 0.6 (4.8%)	*Stylocheiron carinatum*	16.2 ± 2.1 (4.0%)
Stylocheiron suhmii	1.7 ± 0.5 (4.5%)	*Thysanopoda tricuspidata*	8.2 ± 1.7 (2.0%)
Total Euphausia	37.2 ± 1.0	Total Euphausia	404.0 ± 20.7
Species richness	11.8 ± 0.7	Species richness	8.0 ± 0.7
Species diversity	2.1 ± 0.1	Species diversity	1.6 ± 0.1
Temperature (°C)	24.2 ± 0.2	Temperature (°C)	28.4 ± 0.3
Salinity	34.4 ± 0.03	Salinity	34.3 ± 0.1
Chlorophyll *a* (μg/l)	0.02 ± 0.01	Chlorophyll *a* (μg/l)	0.06 ± 0.01
Winter A2 st1,37,43,45,49,51,52,53,54,57,62		Summer B2 st1,3,7,9,10,12,13,15,17,19,20,22,24,26,28,34,57,59,60	
Species	Mean ± SE (RA%)	Species	Mean ± SE (RA%)
Euphausia pacifica	68.1 ± 5.2 (51.3%)	*Stylocheiron suhmii*	23.4 ± 1.3 (17.9%)
Stylocheiron carinatum	11.1 ± 3.3 (8.4%)	*Stylocheiron* sp.	16.8 ± 0.9 (12.9%)
Euphausia hemigibba	4.2 ± 0.3 (3.2%)	*Stylocheiron affine*	6.4 ± 0.3 (4.9%)
Stylocheiron suhmii	3.7 ± 1.1 (2.8%)	*Euphausia sanzoi*	5.4 ± 0.2 (4.2%)
Euphausia mutica	3.6 ± 0.7 (2.7%)	*Stylocheiron carinatum*	4.6 ± 0.1 (3.5%)
Total Euphausia	132.7 ± 7.7	Total Euphausia	130.4 ± 3.1
Species richness	6.1 ± 0.7	Species richness	14.9 ± 0.8
Species diversity	1.3 ± 0.1	Species diversity	2.2 ± 0.1
Temperature (°C)	19.9 ± 0.9	Temperature (°C)	29.1 ± 0.2
Salinity	33.7 ± 0.3	Salinity	34.2 ± 0.1
Chlorophyll *a* (μg/l)	0.14 ± 0.04	Chlorophyll *a* (μg/l)	0.03 ± 0.01

S. carinatum, together occupied 43.4% of the total euphausiid catch (Table 2). Among them, *S. suhmii* was the most dominant, with average and relative abundances of 23.4 ± 1.3 ind./100 m^3 and 17.9%, respectively. Euphausiids found in both station groups in summer were mostly belonging to subtropical and tropical species. Station group B1 had a higher euphausiid abundance but lower species richness and diversity than that of station group B2.

The results of the MDS analysis indicated that euphausiid assemblages showed some variations between season and areas (Fig. 9), particularly the neritic assemblage in the waters west of Taiwan, which exhibited a clear difference between seasons and had larger variation among stations than that of the oceanic assemblage in the waters east of Taiwan.

Relationships between euphausiids and hydrographic variables

Results of a multiple regression analysis (Table 3) showed that, except *Euphausia pacifica* ($p < 0.001$), most euphausiid species showed significantly positive correlations with temperature. Moreover, *E. pacifica* ($p < 0.001$) and *Stylocheiron suhmii* ($p < 0.05$) showed a significantly negative correlation with salinity, though species diversity ($p < 0.05$) was positively correlated with salinity. *Stylocheiron carinatum* ($p < 0.001$), and total abundance ($p < 0.05$) showed a significantly positive correlation with Chl *a* concentrations, but the species richness ($p < 0.05$) was negatively correlated.

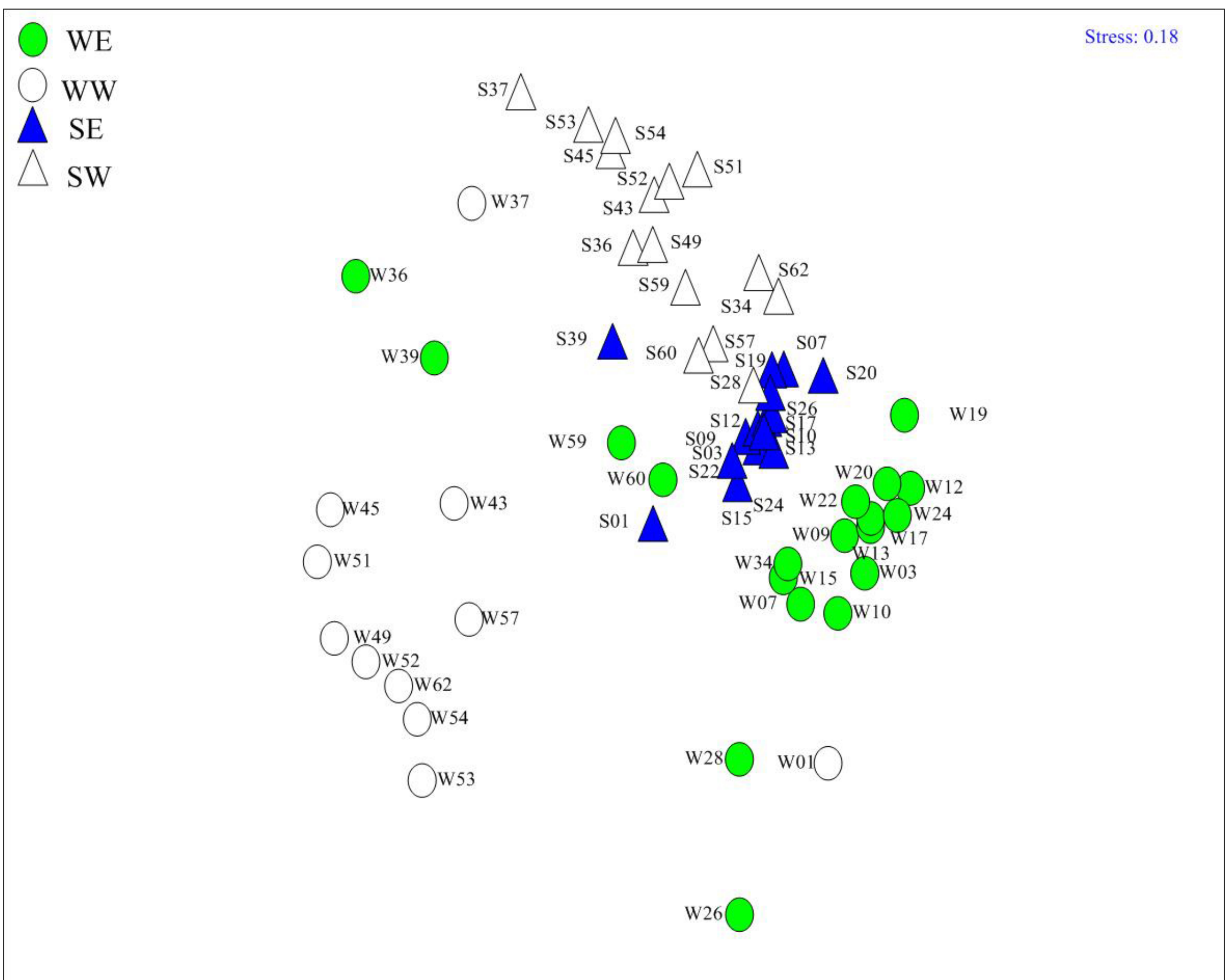

Fig. 9. Multidimensional scaling (MDS) analysis of euphausiid assemblages in the waters around Taiwan in February and August of 2004. WE: Winter East (Oceanic, > 200 m depth), WW: Winter West (Neritic, < 200 m depth), SE: Summer East, SW: Summer West.

DISCUSSION

Effects of seasonal monsoons on hydrographic conditions

Hydrographic conditions in the waters around Taiwan are commonly affected by seasonal monsoons and bathymetric topography, and showed apparent seasonal and spatial variation (Jan et al. 2002, 2006). During the winter season, the prevailing NEM forces the CCC southward along the China coast towards the northern or central TS, resulting in colder and less saline waters in the northwest of Taiwan (Figs. 4-6), while in the waters of eastern Taiwan, the warm and salty KC pulls northwards the whole year, and the KBC may flow through the Luzon Strait and invades the southwest of the TS and the Penghu Channel (Jan et al. 2002, 2006). When KBC and CCC flows through the central TS, it was usually blocked by the Yuen-Chang Ridge, forming a northeast-southwest front in the central TS (Fig. 4). A similar phenomenon can also be observed from satellite images of the SST and Chl *a*, particularly during the winter season (Fig. 3). Furthermore, higher Chl *a* concentrations are commonly observed in the waters near the Penghu Islands during both seasons (Fig. 3).

When KBC or SCSSC flows northward along the southwest coast of Taiwan into the TS, it confronts the narrower Penghu channel and shallower shelf, the KBC may become faster and more turbulent, and finally gets impeded by the Yuen-Chang Ridge. The deeper and colder subsurface water then rises and turns northwestward to the south of the Penghu Islands and forms an upwelling in this area (Wang and Chern 1988; Jan et al. 2010). This topographic upwelling enriches nutrient loads, increases primary production and higher zooplankton abundances that were found in this study (Figs. 7, 10) and by Hong et al. (2011). In summer, the prevailing SWM urges the warm and lower-salinity SCSSC flowing northwards into the TS, replacing the KBC, and dominating the summer hydrography in the TS. Compared to waters west of Taiwan, the hydrographic situation in waters east of Taiwan is much simpler and is dominated by a warm and highly saline KC year-round (Fig. 4). These hydrographic conditions in waters surrounding Taiwan can be observed from satellite images of the SST during the sampling period (Fig. 3), and are consistent with previous studies on the KC and ECS (Wang and Chern 1988; Chern et al. 1990; Liu et al. 1992) and on the TS (Jan et al. 2002, 2006).

Chlorophyll *a* concentration in our study were lower in the waters east and south of Taiwan, and higher in the waters of the northern TS, particularly along the coasts of mainland China and northwestern Taiwan. Our northern stations were located in the southern ECS where the KC flows through the area northeast of Taiwan. When the KC intrudes into the ESC shelf area, a cold dome develops at the shelf break and forms a transitional zone between the ECS and the KC (Chern and Wang 1990). This transitional zone is characterized by an upwelling of nutrient-rich subsurface water to the surface and generally is highly productive (Wong et al. 1991). Similar phenomena were also observed in this study and adjacent area, such as high concentrations of Chl *a* (Chen 1992), phytoplankton (Chen 1992), copepod (Shih and Chiu 1998), siphonophores (Lo et al. 2013), and thaliaceans (Liao et al. 2013). High phytoplankton biomass and primary

Table 3. Results of the stepwise regression and partial correlation coefficient (*R*) evaluating the relationships of the abundances of the five predominant euphausiid species and environmental variables in waters around Taiwan in winter and summer 2004 are evaluated

Species	*R* for *T*	*R* fo *S*	*R* for *C*	Predictive equation
Pseudeuphausia lalifrons (PL)	0.305*	0.005	0.175	PL = 6.176T
Stylocheiron sp. (Ss)	0.377*	-0.029	0.148	Ss = 2.758T
Stylocheiron suhmii (SS)	0.622***	-0.273*	0.239	SS = 3.661T - 12.63S
Euphausia pacifica (EP)	-0.478***	-0.573***	0.033	EP = -4.418T - 41.64S + 1549.01
Stylocheiron carinatum (SC)	0.169	0.144	0.550***	SC = 137.17 Chl *a*
Total Euphausiacea (TT)	0.455**	-0.249	0.324*	TE = 19.75T + 732.10 Chl *a*
Species richness (SN)	0.435**	0.007	-0.254*	SN = 0.50T - 15.28 Chl *a*
Species diversity (SD)	0.306*	0.259*	-0.217	SD = 0.04T + 0.27S - 8.16

**p* < 0.05, ***p* < 0.01, ****p* < 0.001; ns, not significant; *T*, temperature; *S*, salinity; *C*, chlorophyll *a*.

production was also recorded at the shelf break near the Gulf Stream associated with upwelling of subsurface water (Checkley et al. 1988). Thus, both food source and hydrographic condition are important factors affecting the distribution patterns of marine organisms (Rodríguez et al. 1999; Okazaki et al. 2002; Reese et al. 2005; Hsieh et al. 2010).

Water mass shifts affecting the distribution of euphausiids

Marine plankton is strongly affected by mesoscale hydrographic features, such as fronts and eddies (Rodríguez et al. 1999; Okazaki et al. 2002). Fronts and eddies act as mechanisms for the enrichment, concentration and retention of nutrients, thereby contributing to an increase in biological production and larval survival (Bakun 1996). In the study, the mean abundance and species richness of euphausiids showed clear seasonal and spatial changes, with higher values in summer than in winter, and a higher abundance with lower species richness in the waters west of Taiwan than in the waters east of Taiwan (Table 1, Fig. 7). This phenomenon has been suggested by several previous studies in the same area, such as studies on siphonophores (Lo et al. 2013), thaliaceans (Liao et al. 2013), and fish larvae (Su et al. 2011).

The KC is an oceanic current with a more stable environment for plankton than that of the CCC, which is subject to disturbance and nutrient enrichment from rivers or other terrestrial inputs, and, therefore, the reason why euphausiids were commonly abundant in the neritic waters dominated by the CCC in this study. Generally, diversity was higher in the waters east and southwest of Taiwan which are affected by the KC and KBC and lower in the waters north of Taiwan and the northwestern TS where the CCC prevails, particularly in winter. Our results clearly indicate that the abundance and species richness of euphausiids generally increased with temperature, and is closely related with their planktonic food (Table 3). Some environmental factors, such as predator and hydrological conditions, may also represent important factors influencing the distribution pattern of euphausiids and other zooplankton (Xu and Chen 2005; Hwang and Wong 2005; Lo et al. 2010; Liao et al. 2013). For instance, Gibbons et al. (1995) found a lower species diversity of euphausiids in the waters south of South Africa than in the waters east and west of South Africa due to the interacting influence of the Indian Ocean, the Atlantic Ocean and the South Water Masses. Li et al. (2012) studied siphonophores in the South China Sea, and proposed that local coastal upwelling and surface ocean currents driven by the southwesterly monsoon in summer enhanced the species richness and abundance of siphonophores. In winter, however, the northeasterly monsoon pushed the cold coastal waters into this area, and resulted in low species richness and abundance. Liao et al. (2013) also mentioned that the distribution in abundance and size fractions of thaliaceans in Taiwanese waters are affected by the seasonal successions of water masses, food sources, and their other ecological preferenda.

Such preferenda may include their physiological and ecological traits. The most dominant euphausiid, *Pseudeuphausia lalifrons*, belongs to the group of tropical and subtropical coastal species, which is mainly distributed in the intercepting adjacent waters of the CCC and the KC in winter. *P. lalifrons* occurs in the upper 100 m water depth in night and shows diel vertical migration (Mauchlin and Fisher 1969; Chihara and Murano 1997). *P. latifrons* is also a dominant euphausiid in the Tsushima Strait, Japan and spreads with the KC to the waters of the ECS, the south of the Yellow Sea towards the southeast of Japan (Hong et al. 2011). The optimum temperature of the distribution of *P. lalifrons* was reported to be around 25°C (Xu 2007). In the present study, *P. lalifrons* occurred mainly in the northern and western waters of Taiwan. The abundance of *P. lalifrons* was significantly positive correlated with temperature. In winter, the CCC intruded into the TS and caused low temperature and low salinity of the seawater, which is not suitable for *P. lalifrons*. This result was consistent with the study of Xu and Li (2005) who found that the abundance of *P. lalifrons* increased with temperature in the ECS.

The second, third and fifth dominant species of euphausiids (*Stylocheiron* sp., *Stylocheiron suhmii* and *Stylocheiron carinatum*) were widespread and warm-water species, which were common in the Pacific, Atlantic, Indian Oceans and the ECS (Brinton 1962). The optimum temperature and salinity in PSU for the above three euphausiids species are > 25°C and < 34, respectively (Xu 2007). In winter, during the intrusion of the CCC, the three species of euphausiids were rare in the waters west of Taiwan and occurred mainly in the waters southwest and east of Taiwan where the KC and KBC dominated (Fig. 8). In contrast, in summer the surface seawater temperatures around Taiwan were > 28°C and the three euphausiid species were abundant in the waters around Taiwan. This phenomenon was revealed by multiple regression analysis, where the abundances of *Stylocheiron* sp. and *S. suhmii* showed significant positive correlations with seawater temperature (Table 3).

The fourth dominant species of *Euphausia pacifica* likes to live in low temperature waters (Brinton 1962; Xu 2007). The optimum temperature for *E. pacifica* was reported to be below 15°C (Xu 2007). *Euphausia pacifica* occurs in the upper 100 m water layer at night, then migrates to deeper water layers during daytime (Brinton 1967; Endo and Yamano 2006). According to the studies of Anon (1977), Zhang (1991), Wang et al. (2003), Xu (2007), Sun et al. (2011) and Taki (2006, 2007, 2010), *E. pacifica* is the dominant species in the Yellow Sea and ECS. The spatial distribution of *E. pacifica* was influenced primarily by seawater temperature and the adults seems to prefer cold water (Sun et al. 2011). When surface temperature was over 20°C during summer and autumn seasons, *E. pacifica* was mainly found in the Yellow Sea Bottom Cold Water where the temperature below the thermocline was 8-10°C. Furthermore, Xu and Li (2005) also found that the abundance of *E. pacifica* decreased with increasing temperature in the ECS. In this study, *E. pacifica* was only recorded in winter and was abundant in the waters west and north of Taiwan (Fig. 8). The results of multiple regression analysis showed that the abundance of *E. pacifica* was negatively correlated with seawater temperature (Table 3). Thus, we speculated that *E. pacifica* may be transported from the ECS to the TS by the CCC in winter.

CONCLUSIONS

In summary, euphausiid assemblages showed clear seasonal and spatial variations in the waters around Taiwan that were closely associated with prevailing hydrographic processes, particularly in the TS neritic waters west of Taiwan. The monsoon-driven succession of CCC, KBC, and SCSSC water masses play an important role in the distribution of euphausiids. The availability of food and their own ecological preferences also interactively influenced the spatio-temporal patterns of euphausiids. This study, therefore, expanded our understanding of the distribution patterns of euphausiid assemblages in the waters around Taiwan and provided good evidence for their responses to hydrological conditions and interactions among monsoon-driven water masses.

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