

Monsoon-Driven Succession of Copepod Assemblages in Coastal Waters of the Northeastern Taiwan Strait

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Monsoon-driven succession of copepod assemblages in coastal waters of the northeastern Taiwan Strait. *Zoological Studies* 47(1): 46-60. Monsoon winds (a southwesterly (SW) monsoon during summer and a northeasterly (NE) monsoon during winter) were shown to play pivotal roles in shaping species richness and diversity of planktonic organisms in the water masses of the Taiwan Strait (TS). We investigated monsoon-related variations in copepod assemblages in the northeastern TS from Aug. 1998 to May 1999 on 4 research cruises. Our data provide basic information for the biological monitoring of the TS, using improved index measurements. In total, 36 copepod species belonging to 21 genera and 14 families were identified. The abundance of Calanoida showed a negative correlation with salinity ($r = -0.381$, $p = 0.011$, Pearson's product moment correlation) and a positive correlation with temperature ($r = 0.662$, $p < 0.001$, Pearson's product moment correlation). Application of the indicator value index proposed by Dufrêne and Legendre indicated that cold-water species become dominant in this region only when the NE monsoon weakens and retracts from the southern part of the TS. Regardless of the seasonal succession, the calanoid copepod, *Acrocalanus gibber*, was the dominant species with a mean density of 3868 individuals (ind)/1000 m³ (with a relative abundance of 36.5%), followed by *Acartia erythraea* with a mean density of 1874 ind/1000 m³ (17.7%), and by *Labidocera euchaeta* with a mean density of 1178 ind/1000 m³ (11.1%). Four copepod communities were distinguished prior to the advent of the NE and SW monsoonal winds and during the peak periods of the respective monsoons. Our results also reveal the influence of the Kuroshio Branch Current in the study area on copepod assemblages, with temporal successions being determined by the SW and NE monsoonal winds.

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Key words: Copepod assemblages, Taiwan Strait, Monsoon, Kuroshio Branch Current.

The Taiwan Strait (TS) is a relatively shallow (with an average depth of 60 m), 350 km long, and 180 km wide channel between the island of Taiwan and the southeastern Chinese coast, connecting the 2 marginal seas of the western Pacific, the East China Sea (ECS) in the north and the South China Sea (SCS) in the south. In the TS, there is a congruence of 3 different water masses: the ECS, SCS, and the water masses representing the Kuroshio Current of the western North Pacific (Jan et al. 1998 2002, Jan and Chao 2003, Tseng and Shen 2003). Three current systems, the China Coastal Current (CCC), South China

Sea Warm Current (SCSWC), and Kuroshio Branch Current (KBC), as well as river runoff from continental China in the west and from the island of Taiwan in the east influence the hydrographic conditions in the TS (Hsieh and Chiu 2002, Jan et al. 2002, Liang et al. 2003). Such hydrographic conditions also affect the zooplankton community compositions in the TS (Hsieh and Chiu 2002, Hwang et al. 2003 2006, Hsieh et al. 2004, Lo et al. 2004). Wind patterns in this region are determined by the typical East Asian monsoon that is from the northeast (NE) during winter (Oct.-Mar.) and from the southwest (SW) during summer

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(May-Aug.).

During the NE monsoon, the CCC with low temperatures, low salinities, and high nutrient levels moves southwards (Liang et al. 2003, Liu et al. 2003, Tseng and Shen 2003) driving zooplankton from the Bohai Sea, the Yellow Sea, and the ECS towards the TS (Wang and Chern 1988 1989, Chen 1992, Chiu and Chen 1998, Lo et al. 2004, Hwang and Wong 2005). Cold-water copepod species such as *Calanus sinicus* and *Paracalanus parvus* are common in the TS and in coastal waters of southern China during winter (Hwang and Wong 2005).

Throughout the year, the warm, highly saline, and nutrient-poor Kuroshio Branch Current (KBC) (Chu 1971, Jan et al. 2002, Tseng and Shen 2003) intrudes into the TS through the northern SCS and along the coast of southwestern Taiwan (Wang and Chern 1988 1989, Shaw 1989, Liang et al. 2003). However, during the prevailing NE monsoon period, the southerly flowing CCC compels and drives the KBC into the TS through the Penghu Channel (Wang and Chern 1988, Jan et al. 2002). At the same time, the northerly flowing KBC stagnates because of the southerly flowing CCC near the Penghu Channel, south of the Changyun Ridge in the southeastern TS (Wang and Chern 1988, Jan et al. 2002, Hsieh et al. 2004). In spring when the NE monsoon weakens, the KBC moves northward along the local isobaths

into the northern part of the TS. Conversely, under the prevailing winds of the SW monsoon (May-Aug.), the SCSWC with intermediate temperatures, salinities, and nutrient levels intrudes into the TS and moves northward together with the KBC that transports plankton from the northern SCS.

The hydrographic properties of this part of the Taiwan Strait are mainly influenced by the NE and SW monsoons. The influence of cold water masses disappears during summer with increasing strength of the SW monsoon as water masses from the northern part of the SCS enter the TS and influence the hydrography around the west coast of Taiwan, and Guangdong and Fujian Provinces, China (Jan et al. 1998 2002, Liang et al. 2003).

In view of their dependence on water mass movements, planktonic organisms provide an appropriate model for an ecological study of plankton community structures and their temporal dynamics (Sommer 1989, Goldblatt et al. 1999, Paffenhöfer and Flagg 2002, Bonnet and Frid 2004) since their abundances and compositions are affected by several properties of water masses (Boucher et al. 1987, Lopes et al. 1999, Hwang and Wong 2005). This also holds for copepods that are major components of marine zooplankton and play a central role in the transfer of nutrients and energy through marine food webs (Poulet and Williams 1991, Williams et al. 1994, Kjørboe

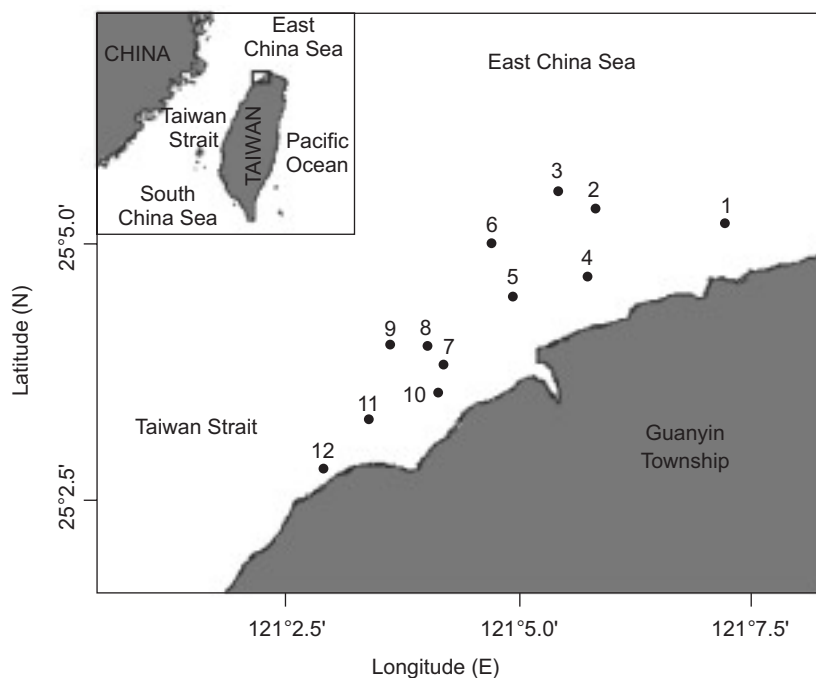


Fig. 1. Map of sampling stations in the northeastern Taiwan Strait.

1997). Considering monsoon-driven intrusions of different water masses being characteristic for the warm temperate, subtropical, and tropical regions of the TS, discernible successional patterns of copepod communities can be expected on seasonal scales. Previous studies of planktonic copepods in the TS were mainly confined to single region cruises without examining larger-scale seasonal shifts (Shih and Chiu 1998, Hwang et al. 2000 2003, Hsieh and Chiu 2002, Lo et al. 2004). Such sporadic analyses of copepod assemblages reveal differential species compositions and patterns of dominance (Hsieh and Chiu 2002, Hwang et al. 2003, Lan et al. 2004, Lo et al. 2004).

Previous studies indicated that during the NE monsoon period, intrusions of cold water masses influence species assemblages in Chinese coastal waters to the south of Fujian Province, in Hong Kong, and even in waters of Hainan I. (Hwang and Wong 2005) after passing through the northeastern region of the TS (Wang and Chern 1988 1989, Jan et al. 2002). Furthermore, under the influence of the SW monsoon, the SCSWC moves northwards towards the study area together with the KBC (Liang et al. 2003, Tseng and Shen 2003). In this study we hypothesized that the SW monsoon brings along neritic copepod species, whereas the KBC brings oceanic copepod species to the study area. It is further hypothesized that the cold-water species become dominant in this region only when the NE monsoon weakens and retracts from the southern part of the TS.

Table 1. Abbreviations used

Abbreviations	Original text
CCC	China Coastal Current
ECS	East China Sea
KBC	Kuroshio Branch Current
KC	Kuroshio Current
NE and SW monsoons	northeasterly and southwesterly monsoons
SCS	South China Sea
SCSWC	South China Sea Warm Current
TS	Taiwan Strait
<i>Acr. gibber</i>	<i>Acrocalanus gibber</i>
<i>Acr. gracilis</i>	<i>Acrocalanus gracilis</i>
<i>Can. pauper</i>	<i>Canthocalanus pauper</i>
<i>Cen. tenuiremis</i>	<i>Centropages tenuiremis</i>
<i>Cor. affinis</i>	<i>Corycaeus affinis</i>
<i>Cor. andrewsi</i>	<i>Corycaeus andrewsi</i>
<i>Onc. venusta</i>	<i>Oncaea venusta</i>
<i>Par. aculeatus</i>	<i>Paracalanus aculeatus</i>
<i>Par. parvus</i>	<i>Paracalanus parvus</i>

To date, no time-series study has been conducted to investigate monsoon-driven changes in copepods in the main channel of the TS except that by Hwang et al. (2006), who studied boundary waters between the TS and ECS. With the lack of year-round copepod surveys from specific areas of the TS, the possible impacts that monsoonal winds have on copepod community compositions remain largely unknown (see Hwang et al. 2006).

In order to investigate how monsoonal winds influence copepod abundances and community compositions, we examined relatively shallow (at depths of < 20 m in the presence of a thermocline at < 20 m (Jan et al. 1998 2002)) northeastern coastal waters of the TS in the vicinity of Guanyin Township, Taiwan.

MATERIAL AND METHODS

Our sampling stations were located at 25°2.5'-25°5.7'N and 121°2.5'-121°7.5'E, about 25 km south of the northeastern boundary between the coastal waters of the TS and ECS (Danshuei Estuary) (Fig. 1). Research cruises were conducted 4 times in Aug., (before the onset of the NE monsoon), in Dec. (when the NE monsoon prevails), in Mar. (when the NE monsoon begins to wane), and in May (when the SW monsoon prevails) in 1998 and 1999. Zooplankton were collected at 12 stations by surface tows (at 0-5 m in depth) using a standard North Pacific zooplankton net (with a mouth diameter of 45 cm and a mesh size of 333 µm), with a Hydrobios flow meter mounted in the center of the net opening. Samples were immediately preserved onboard with seawater containing 5% buffered formaldehyde. Prior to plankton sampling, the salinity and temperature were measured onboard using a Seabird CTD instrument. In the laboratory, samples were split with a Folsom splitter until the subsample contained ≤ 500 specimens. Copepods were sorted and identified to species level using the keys of Chen and Zhang (1965), Chen et al. (1974), Huys and Boxshall (1991), and Chihara and Murano (1997). Original revisional references were consulted if required. Abbreviations are provided in table 1.

Statistical analyses

In order to evaluate the patterns of copepod distribution, species densities from different samples were analyzed by multivariate analyses of

copepod species which had an occurrence frequency of > 5%. In order to reduce higher heteroscedasticity observed in the original species abundance data, a transformation power ($\lambda = 0.97483$) was generated by regression coefficients that were estimated by maximizing the log likelihood function (Box and Cox 1964). Accordingly, a non-metric cluster analysis was used in conjunction with Bray-Curtis similarity indices after logarithmic transformations ($\log(X+1)$) of copepod abundance data. Significant levels of differences between seasons for the respective copepod assemblages were obtained using ANOSIM and SIMPER software from the PRIMER software package (vers. IV; Clarke and Warwick 1994).

Species characterizing each cluster were further identified using the indicator value index (*IndVal*) proposed by Dufrêne and Legendre (1997). This index is obtained by multiplying the product of 2 independently computed values by 100:

$$IndVal(j,s) = 100SP(j,s)FI(j,s) \dots \dots \dots (1)$$

where (*SP*_{*j,s*}) is the specificity, and (*FI*_{*j,s*}) is the fidelity of a species (*s*) toward a group of samples (*j*), and these are calculated by:

$$SP(j,s) = \frac{NI(j,s)}{\sum NI(s)} ; FI(j,s) = \frac{NS(j,s)}{\sum NS(s)} \dots \dots \dots (2)$$

where *NI* (*j,s*) is the mean abundance of species *s* across samples pertaining to *j*, $\sum NI$ (*s*) is the sum of the mean abundances of species *s*

within the various groups in the partition, *NS* (*j,s*) is the number of samples in *j* where species *s* is present, and $\sum NS$ (*s*) is the total number of samples in that group. The specificity of a species for a group is greatest if a particular species is found only in a particular group, whereas the fidelity of a species to a group is greatest if the species is present in all samples of the group considered. In order to evaluate copepod assemblages for the entire sampling period, indicator species were separately analyzed for each sampling cruise.

The Shannon-Wiener diversity index was used to analyze species diversity, and Pielou's evenness was used to measure the relative abundances of species in each season. To identify differences in copepod abundances among cruises, one-way analysis of variance (ANOVA) with post hoc Tukey's honest significant difference test was applied. To estimate relationships between copepod abundances with temperature and salinity, Pearson's product moment correlation was applied.

RESULTS

Over the study period, the surface water temperature ranged from 19.5°C in Dec. to 28°C in August, whereas salinity followed an opposite trend with a maximum value of 34.4 practical salinity units (psu) in Dec. and a minimum of 33.91 psu

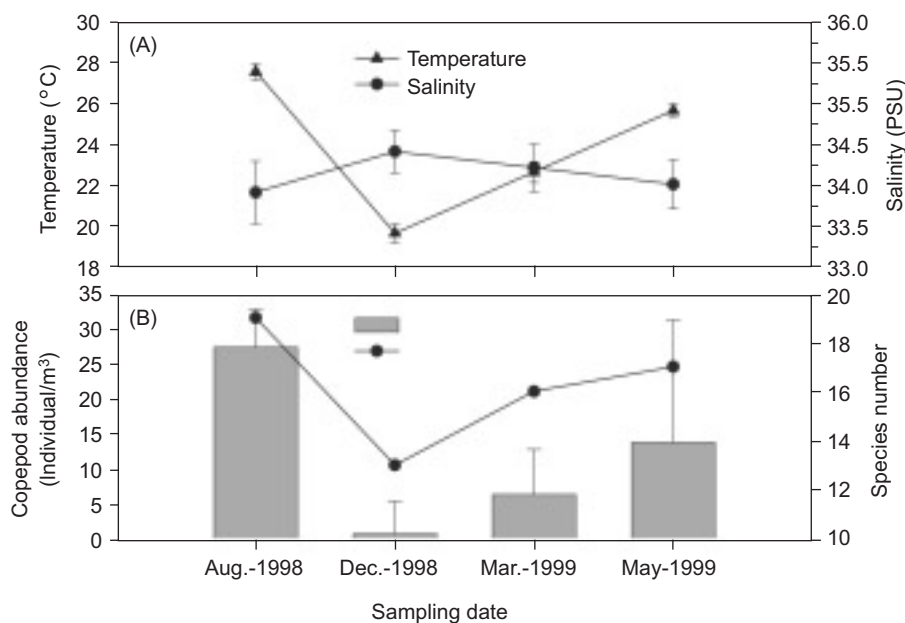


Fig. 2. Average values (mean \pm SD) of (A) sea water salinity, temperature, (B) copepod abundance, and number of species recorded in the northeastern Taiwan Strait during each sampling season.

Table 2. Copepod species, average density (individuals /1000 m³), relative abundance (RA, %), occurrence frequency (OR, %), Shannon-Wiener diversity index (H'), and Pielou's evenness (J') recorded during each season. Copepod abundances were significantly correlated with temperature (at the * 95% and ** 99% confidence levels)

Sampling time	Aug. 1998	Dec. 1998	Mar. 1999	May 1999				
Total water filtered (m ³)	602.3	867.1	1152.7	889.3				
Average copepod density (ind. /1000 m ³)	27285 ± 5487	710 ± 460	6294 ± 6453	13691 ± 17466				
Shannon diversity Index (H')	1.07 ± 0.16	1.21 ± 0.36	1.41 ± 0.19	1.07 ± 0.28				
Species richness	0.82 ± 0.26	0.65 ± 0.22	0.78 ± 0.16	0.56 ± 0.22				
Pielou's evenness	0.50 ± 0.11	0.75 ± 0.15	0.73 ± 0.11	0.62 ± 0.15				
					RA (%)	OR (%)	Mean	SD
CALANOIDA								
ACARTIIDAE								
<i>Acartia erythroa</i> Giesbrecht, 1889 **	10282.75	16.33	0	0	17.67	22.73	1874.05	4601.66
CALANIDAE								
<i>Calanus sinicus</i> Brodsky, 1962	0	0	131.33	0	0.34	15.91	35.82	112.13
<i>Canthocalanus pauper</i> Giesbrecht, 1888	0	14.58	100.08	70.50	0.48	29.55	50.50	118.92
<i>Nannocalanus minor</i> Claus, 1863	0	0	3.00	0	0.01	4.55	0.82	3.80
<i>Undinula vulgaris</i> Dana, 1849	0	2.50	4.42	0	0.02	6.82	1.89	7.36
CANDACIIDAE								
<i>Candacia catula</i> Giesbrecht, 1889	0	2.67	0	0	0.01	2.27	0.73	4.82
CENTROPAGIDAE								
<i>Centropages furcatus</i> Dana, 1849	2.88	0	0	0	< 0.01	2.27	0.52	3.47
<i>Centropages orsinii</i> Giesbrecht, 1889 *	440.25	0	0	1.83	0.76	20.45	80.55	303.42
<i>Centropages tenuiremis</i> Thompson and Scott, 1903	0	0	110.58	3509.33	9.31	40.91	987.25	3321.69
EUCALANIDAE								
<i>Subeucalanus subcrassus</i> Giesbrecht, 1888	3.50	14.08	17.00	22.50	0.14	20.45	15.25	48.53
LUCICUTIIDAE								
<i>Lucicutia flavicornis</i> Claus, 1863 *	10.75	0	0	0	0.02	6.82	1.95	7.31
METRIDICIDAE								
<i>Pleuromamma abdominalis</i> Lubbock, 1856	0	0	0	28.92	0.07	2.27	7.89	52.31
PARACALANIDAE								
<i>Acrocalanus gibber</i> Giesbrecht, 1888 **	12294.00	372.92	907.83	4704.92	36.47	90.91	3867.73	5372.59
<i>Acrocalanus gracilis</i> Giesbrecht, 1888	0	38.67	686.83	437.50	2.99	40.91	317.18	701.94
<i>Paracalanus aculeatus</i> Giesbrecht, 1888	0	0	168.50	0	0.43	6.82	45.95	198.08
<i>Paracalanus crassirostris</i> Dahl, 1893	0	0	0	25.42	0.07	2.27	6.93	45.98
<i>Paracalanus parvus</i> Claus, 1863	2.88	151.58	3162.33	0	8.53	54.55	904.32	2335.12
PONTELLIDAE								
<i>Calanopia elliptica</i> Dana, 1849 *	7.13	0	0	0	0.01	4.55	1.30	6.01
<i>Labidocera bipinnata</i> Tanaka, 1936 **	3114.00	0	0	43.00	5.45	25.00	577.91	1438.38
<i>Labidocera euchaeta</i> Giesbrecht, 1889	8.75	0	37.67	4276.75	11.11	31.82	1178.25	5029.82
<i>Labidocera minuta</i> Giesbrecht, 1889	2.63	0	0	1.83	0.01	4.55	0.98	4.53
<i>Pontellina plumata</i> Dana, 1849	0	0	0	20.67	0.05	2.27	5.64	37.39
<i>Pontellopsis tenuicauda</i> Giesbrecht, 1889 *	55.75	0	0	0	0.10	13.64	10.14	30.14
<i>Pontellopsis yamadae</i> Mori, 1937	0	4.83	0	124.33	0.33	15.91	35.23	112.66
TEMORIDAE								
<i>Temora discaudata</i> Giesbrecht, 1889	0	0	0	32.83	0.08	6.82	8.95	49.34
<i>Temora turbinata</i> Dana, 1849	156.38	0	267.17	179.67	1.42	45.45	150.30	350.66
TORTANIDAE								
<i>Tortanus gracilis</i> Brady, 1883 **	789.75	0	0	0	1.35	18.18	143.59	395.67
CYCLOPOIDA								
OITHONIDAE								
<i>Oithona rigida</i> Giesbrecht, 1896	9.38	0	0	0	0.02	4.55	1.70	8.16
POECILOSTOMATOIDA								
CORYCAEIDAE								
<i>Corycaeus andrewsi</i> Farran, 1911	79.25	13.58	0	0	0.17	18.18	18.11	62.44
<i>Corycaeus crassiusculus</i> Dana, 1849	0	2.67	0	0	0.01	2.27	0.73	4.82
<i>Corycaeus pumilus</i> M. Dahl, 1912	0	10.83	1.42	2.33	0.04	9.09	3.98	16.95
<i>Corycaeus affinis</i> McMurrich, 1916	0	0	647.25	0	1.66	27.27	176.52	485.19
<i>Corycaeus gibbulus</i> Giesbrecht, 1891 **	14.38	0	1.92	0	0.03	9.09	3.14	11.31
<i>Corycaeus longistylis</i> Dana, 1849	3.50	0	0	0	0.01	2.27	0.64	4.22
ONCAEIDAE								
<i>Oncaea mediterranea</i> Claus, 1863 *	7.13	0	0	0	0.01	4.55	1.30	6.01
<i>Oncaea venusta</i> Philippi, 1843	0	64.67	47.08	208.50	0.82	52.27	87.34	182.10

in Aug. (Fig. 2A). Warming of the sea surface began in Mar. (Fig. 2A), and the temperature recorded in August was $< 27.5^{\circ}\text{C}$. Comparisons of Aug. and Dec. variations in seawater temperatures were highly significant (Mann-Whitney U -test $p < 0.005$; Fig. 2A), whereas surface water salinity varied widely among sampling stations and showed no clear seasonal variation. Figure 3 shows variations in average daily (monitored and recorded each hour) temperatures, wind direction, and wind speed from automatic monitoring equipment at Shinwu Township of the Central Weather Bureau, Ministry of Transportation and Communications, Taiwan. Shinwu Township is located

adjacent to Guanyin Township, close to the area of investigation, and the weather monitoring station was about 10 km away from our sampling area. The average temperature varied from 19.5 to 28°C . Lower air temperatures were recorded from Jan. to Mar. in winter, and higher temperatures from June to Sept. in summer (Figs. 2A, 3A).

Monsoon-induced changes in air temperatures are shown in figure 3A and 3B (0° means wind coming from the north, 90° means wind from the east, etc.). Hence, the NE monsoon prevails from mid-Aug. to mid-Mar., and the SW monsoon prevails from mid-Mar. to mid-Aug. The average wind speed varied from 0.1 to 6.7 m/s, with a high-

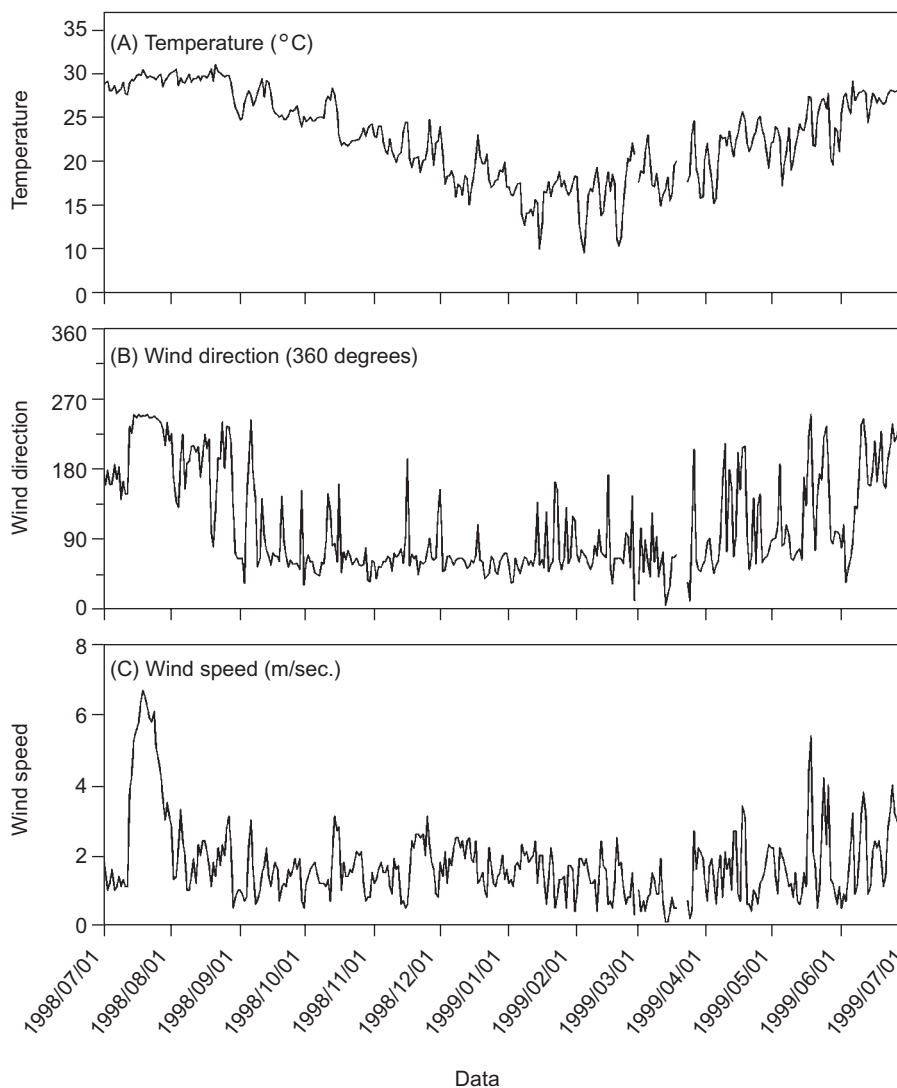


Fig. 3. Average daily temperature, wind direction, and wind speed from automatic monitoring equipment in Shinwu Township adjacent to Guanyin Township. (A) Lower temperatures were evident from Jan. to Mar. and higher temperatures from June to Sept. (B) Changes in wind direction: 0° degree means a northerly wind, 90° means an easterly wind, 180° means a southerly wind, and 270° means a westerly wind. (C) Changes in wind speed.

er wind speed recorded in July when the southwesterly monsoon prevails. Wind speed values did not exceed 4 m/s from Aug. 1998 to May 1999 (Fig. 3C). Figure 4 demonstrates the monsoonal effects of water masses through respective satellite images of monthly average sea-surface temperatures (SSTs) derived from averaged hourly recordings (AVHRRs) in the area of investigation off the northwestern coast of Taiwan. Integrating all information, it can be inferred that higher temperatures and wind speeds prevail during the SW monsoon. The NE monsoon provides an opposite regime with lower temperatures and wind speeds.

In total, 36 copepod species representing 3 orders, 14 families, and 21 genera were identified (Table 2). The mean copepod abundance was highest in Aug. and lowest in Dec. (Fig. 2B). The diversity followed opposite trends as the lowest values (1.07) of the Shannon-Wiener diversity index were recorded in Aug. and May and the highest (1.41) in Mar. (Table 2). Log values of total copepod abundances and that of Calanoida showed a significantly positive correlation ($r^2 = 0.56$; $p < 0.001$, Fig. 5) with surface water temperature. Calanoid abundance showed a negative correlation with salinity ($r = -0.381$; $p = 0.011$, Pearson's product moment correlation) and a positive correlation with temperature ($r = 0.560$; $p < 0.001$; Pearson's product moment correlation). The dominant species in our sample (with a relative abundance of 36.5%) was *Acrocalanus gibber* which occurred in > 90% of samples, followed by *Acartia erythraea* (17.7%) and *Labidocera euchaeta* (11.1%). The abundance of *Acr. gibber* was positively correlated ($r = 0.71$; $p = 0.001$, Pearson's product moment correlation) with surface water temperature and negatively with salinity

($r = -0.431$; $p = 0.003$, Table 2). The highest copepod density (27,285 individuals (ind)/1000 m³) was recorded in Aug. 1998, and the lowest (710 ind/1000 m³) in Dec. 1998 (one-way ANOVA, $p < 0.02$, Fig. 2B; Table 2). Only the single species of *Acr. gibber* with the highest occurrence frequency (90.9%) could be identified in most samples. For instance, *Paracalanus parvus* and *Oncaea venusta* occurred in < 50% of samples, however, with respective relative abundances of 8.5% and 0.82%. The 4 dominant copepod species had contrasting abundance and occurrence frequency patterns (Fig. 6).

At the highest grouping level, the Bray-Curtis cluster analysis revealed strong seasonal variations in copepod community structures (Fig. 7). The copepod abundance and diversity recorded in the Guanyin region of the Taiwan Strait in Aug. 1998 (summer) were separately clustered from those recorded in Dec., Mar., and May. The 2nd hierarchical level distinguished samples recorded in May (cluster IIA; Fig. 7). Samples collected in Aug. were characterized by the dominance of *Acr. gibber* followed by *Aca. erythraea*. Index values for species occurring in > 50% of samples of each cluster are given in table 3. The contributions of *Acr. gibber* and *Aca. erythraea* to the similarity of the Aug. samples were 48.9% and 36.9%, respectively (SIMPER analysis). Figure 8 shows the relative abundances of the 5 most indicative copepod species identified for each cluster in figure 5. Furthermore, the spatial distributions of copepod abundances during each season in the northeastern region of the TS adjacent to Guanyin Township, Taiwan are demonstrated in figure 9.

Acrocalanus gibber was the most dominant species in cluster IIA followed by *Lab. euchaeta*,

Table 3. Indicator species and index values (%) for each cluster identified by the Bray-Curtis cluster analysis (Fig. 5)

Cluster level	Indicator species
IA	<i>Acrocalanus gibber</i> (45.06%), <i>Acartia erythraea</i> (37.69%), <i>Tortanus gracilis</i> (2.89%), and <i>Centropages orsinii</i> (1.61%)
IIA	<i>Acr. gibber</i> (34.37%), <i>Labidocera euchaeta</i> (28.64%), <i>Cen. tenuiremis</i> (21.357%), and <i>Oncaea venusta</i> (1.14%)
IIIA	<i>Acr. gibber</i> (52.53%), <i>Par. parvus</i> (21.35%), <i>Onc. venusta</i> (7.59%), <i>Acr. gracilis</i> (2.72%), <i>Cor. andrewsi</i> (0.64%), <i>Subeucalanus subcrassus</i> (0.83%), and <i>Canthocalanus pauper</i> (0.68%)
IIIB	<i>Par. parvus</i> (46.05%), <i>Cor. affinis</i> (10.28%), <i>Acr. gibber</i> (9.61%), <i>Acr. gracilis</i> (8.18%), <i>Temora turbinata</i> (3.18%), <i>Calanus sinicus</i> (1.22%), <i>Can. pauper</i> (0.79%), <i>Cen. tenuiremis</i> (1.17%), <i>Par. aculeatus</i> (0.67%), <i>Onc. venusta</i> (0.25%)

Centropages tenuiremis, and *Oncaea venusta*. *Onc. venusta* was found in > 75% of samples, albeit at lower densities with a relative abundance of 1.52% (Fig. 8). Cluster IIB was restricted to win-

ter (Dec.) and early spring (Mar.) samples. The 3rd hierarchical level separated Dec. samples (cluster IIIA) from those collected in Mar. (cluster IIIB). In cluster IIIA, *Acr. gibber* was followed by

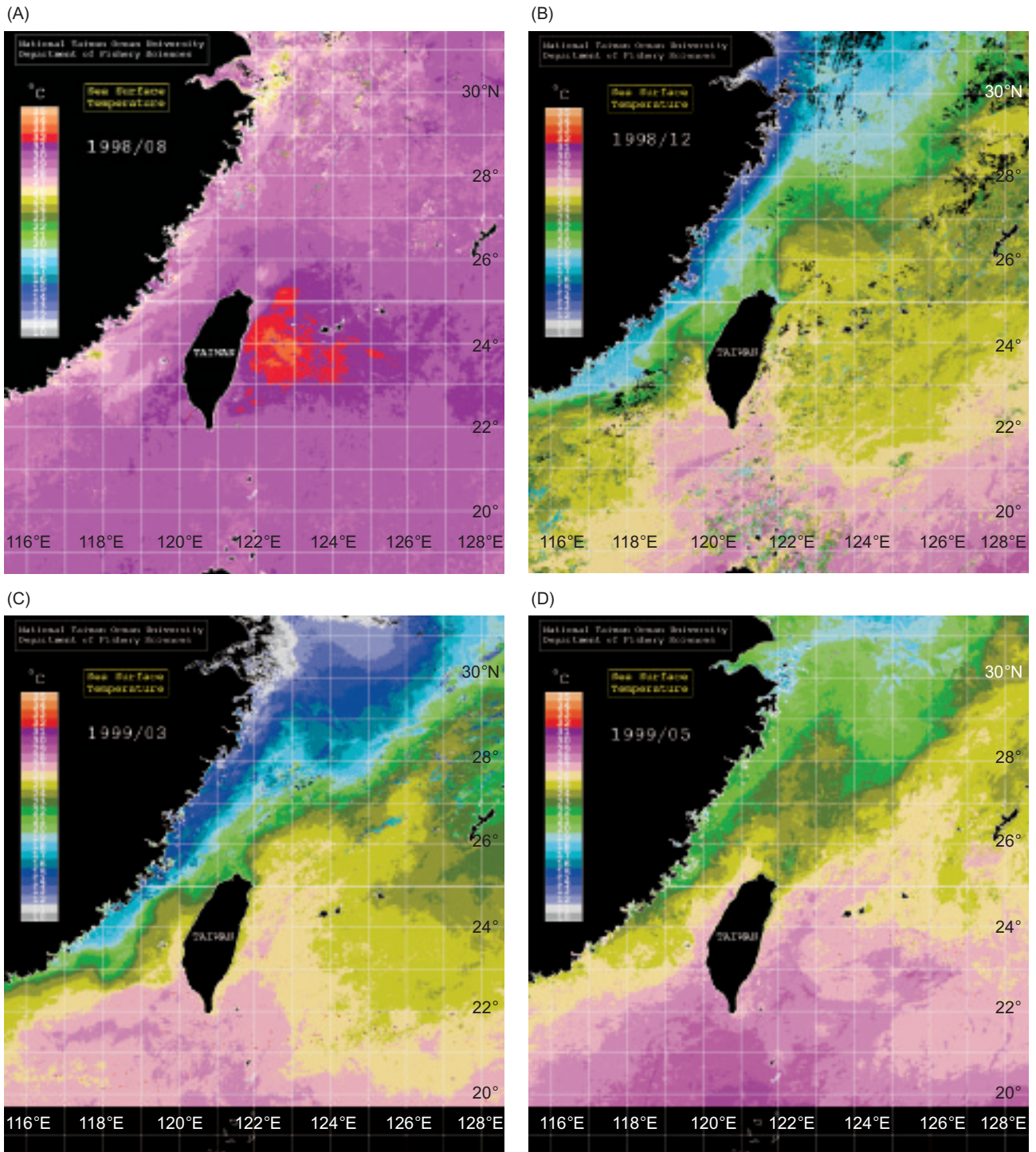


Fig. 4. Monthly average sea-surface temperatures (SSTs) derived from averaged hourly recordings (AVHRRs) for (A) Aug. 1998, (B) Dec. 1998, (C) Mar. 1999, and (D) May 1999. The white circle shows the area of investigation in the northwestern part of Taiwan.

Par. parvus and *Onc. venusta*. *Acrocalanus gibber* and *Par. parvus* occurred in all samples, whereas *Onc. venusta* occurred in > 80% of samples. Cluster IIIB was dominated by *Par. parvus* with an occurrence frequency of 91.7%, followed by *Acr. gibber* and *Aca. gracilis*. All samples collected in Mar. contained the small species *Corycaeus affinis*, however, at lower abundances (with a relative abundance of 10.3%; Fig. 8).

Spatial variations in copepod compositions (Table 2) and abundances were not obvious in Aug. samples, whereas in Mar. and May samples, the most offshore stations showed higher copepod densities and clustered separately from those collected at onshore stations (Fig. 9).

DISCUSSION

As this study was intended to demarcate monsoon-driven changes in copepod abundances and community structures in the northeastern part of the TS, 2 aspects were specifically targeted: were there any indications of copepod community structure changes prior to the advent of the NE and SW monsoon winds?; and were there any changes during the prevailing period of either of

the monsoonal winds?

The southeastern region of the TS (including the Pescadore Archipelago (Penghu)) is perennially influenced by the KBC (Jan et al. 2002, Jan and Chao 2003, Liang et al. 2003) and SCSWC (Shaw 1989, Liang et al. 2003). A higher abundance of copepods in the southeastern part of the TS can thus be explained by the combined effects of both

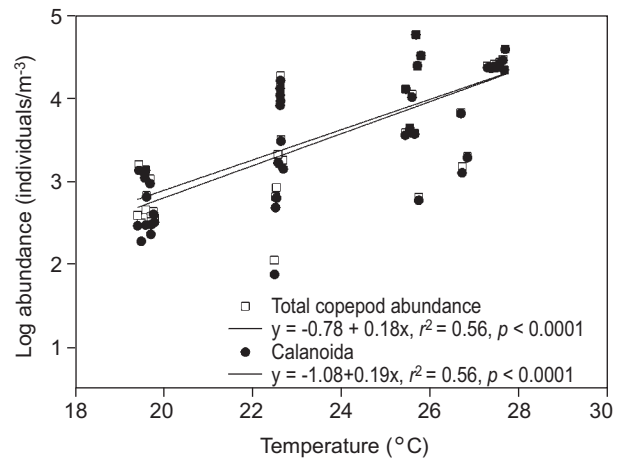


Fig. 5. Correlations (Pearson's product moment correlation) of total copepod and calanoid copepod abundances with temperature.

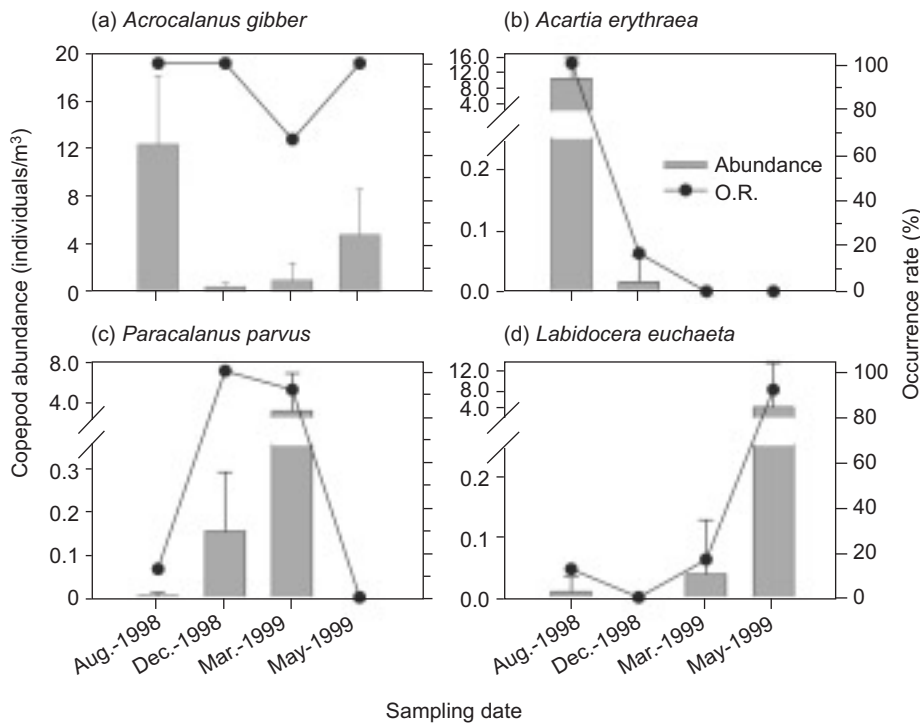


Fig. 6. Seasonal variations in average (mean ± SD) abundances and frequencies of occurrence of 3 numerically dominant copepod species in coastal waters of the Taiwan Strait adjacent to Guanyin Township.

currents (Hwang et al. 2003, Lo et al. 2004). In the southeastern TS, the deep Penghu Channel guides the intruding water masses, as the north edge of the channel is bordered by the Changyun Ridge which partially blocks water transport along the eastern side of the TS (Jan et al., 2002). Furthermore, the SW monsoonal winds, the main northward driving force in the TS, were much weaker near our sampling stations (Jan et al. 2002), which also reduces the intrusion of copepods from the southern portion of the TS.

Copepod abundances along the Guanyin coastal area recorded prior to the onset of the NE monsoon and after the waning of the SW monsoon (in Aug.) were higher, and the indicative species were *Acr. gibber*, *Aca. erythraea*, *Tortanus gracilis*, and *Cen. orsinii*. These are warm-water species found in the TS during summer (Hsieh and Chiu 2002, Lo et al. 2004) that are perennially present in the SCS and KBC (Lo et al. 2001, Chen 1992). The absence of winter species as indicators of the CCC in Dec. and the dominance of *Acr. gibber* are

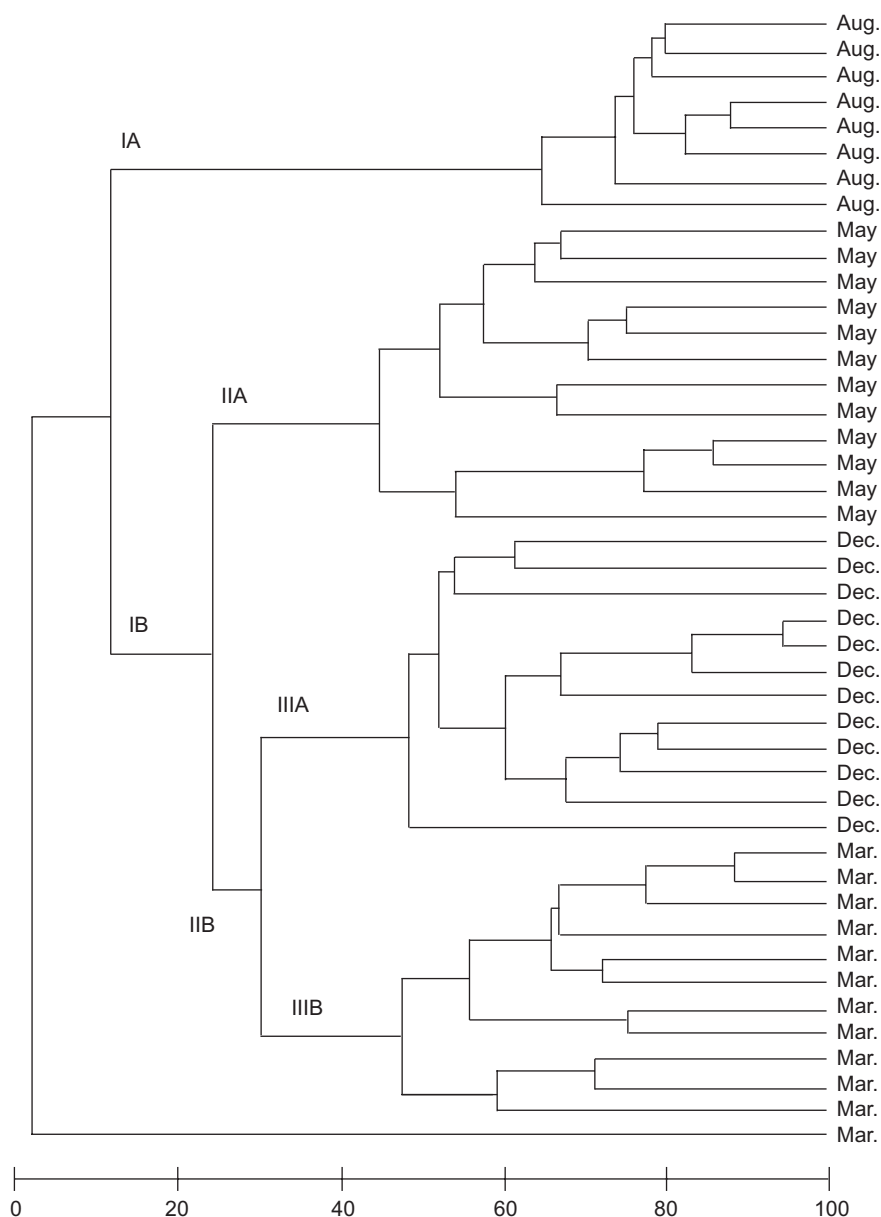


Fig. 7. Clustering dendrogram of different samples (seasons) using Bray-Curtis similarity and clustering strategy of flexible links in the northeastern region of the Taiwan Strait adjacent to Guanyin Township, Taiwan. The dendrogram is scaled by the percent of information remaining.

interpreted as a cessation of the effect of the NE monsoon bringing copepods from the CCC to this region. A few species, e.g., *Par. parvus* which shows an affinity for relatively colder temperatures (Peterson et al. 2002, Hsieh et al. 2004), appeared in Dec. Tropical species are highly abundant, occur perennially in coastal waters, and exhibit noticeable seasonal variations in abundances (Takahashi and Hirakawa 2001, Hwang et al. 2006). *Paracalanus parvus* is a subtropical neritic species, which is generally found in association with coastal warm-water species (Peterson et al. 2002).

In winter, during the peak period of the NE monsoon, a stagnation of the KBC due to southerly flowing water masses of the CCC (Jan et al. 2002) near the Penghu Channel (Shih and Chiu 1998) limits the transport of planktonic copepods from the SCS and KBC waters to the Guanyin area. It should be noted that the main route of the CCC in the northern part of the TS is along the Chinese coast, bypassing the eastern part, which comprised the present study area (Liang et al. 2003, Liu et al. 2003, Tseng and Shen 2003). During the NE monsoon period, intrusions of cold-water masses influence species assemblages in Chinese coastal waters to the south of Fujian, in Hong Kong, and even in waters of Hainan I. (Chen 1992, Chiu and Chen 1998, Lo et al., 2004, Hwang and Wong 2005). Our study area showed relative-

ly low copepod abundances and diversities in Dec., the peak period of the NE monsoon. During the NE monsoon, the CCC deviates from the ECS and passes through the western part of the TS (Jan et al. 2002, Liang et al. 2003). Hence, there is only a slight chance of transport of copepods from the ECS to our study area. High water turbidities were noted during all sampling campaigns. During the waning of the NE monsoon in early Mar., the most indicative species recorded (cluster IIIB) were *Par. parvus*, *Cor. affinis*, *Temora turbinata*, and *Calanus sinicus*. These species are consistently found along the northern coast of Taiwan during winter and spring (Hsieh and Chiu 2002, Hwang et al. 2006, Shih and Chiu 1998, Shih and Young 1995). All species of the cluster except *Tem. turbinata* show an affinity to warm temperate conditions (Chen 1992, Chen and Zhang 1965, Takahashi and Hirakawa 2001). For example, *Par. parvus* is a dominant species in the coastal waters off China, *Cal. sinicus* is confined to the western marginal seas of the North Pacific, and dominant in the Bohai Sea, Yellow Sea, and the ECS, whereas *Cor. (Ditrichocorycaeus) affinis* is abundant in coastal waters of the Yellow Sea (Chen and Zhang 1965, Chen et al. 1974, Chen 1992, Hwang and Wong 2005). From our study, we supposed that *Cal. sinicus*, *Cor. affinis*, and *Par. parvus* follow the retracting CCC, whereas warm-water species in this region are driven by the

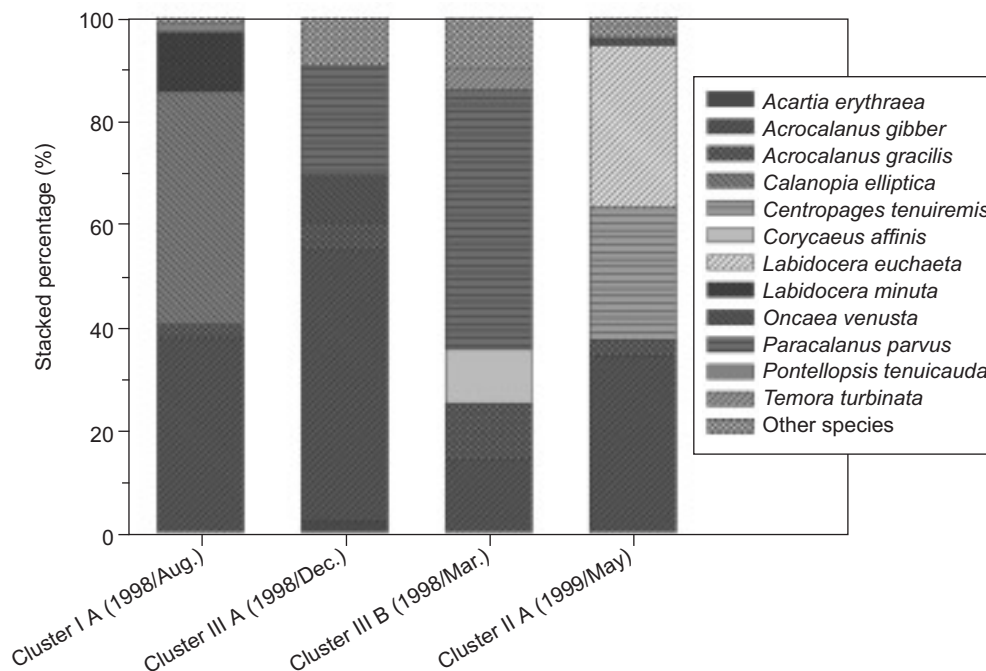


Fig. 8. Relative abundances of the 5 most indicative copepod species identified for each cluster in figure 5.

KBC and SCSWC. Our samples collected during the SW monsoon (in May) were represented by *Cen. tenuiremis*, *Acr. gibber*, *Lab. euchaeta*, and *Onc. venusta*, which are a combination of oceanic and neritic species (Chen 1992, Chen and Zhang 1965, Chen et al. 1974, Noda et al. 1998). Under the influence of the SW monsoon, the SCSWC moves northwards towards our study area together with the KBC (Liang et al. 2003, Tseng and Shen 2003). We supposed, accordingly, that the SW monsoon brings neritic copepod species, whereas the KBC brings oceanic copepod species to the study area. This hypothesis was further supported by the fact that an earlier study by Hsieh and Chiu

(2002) recorded no oceanic species in water masses sampled from coastal regions of China. However, those authors reported oceanic species in samples collected from the eastern part of the TS.

It should be noted that overall copepod abundances recorded in the present study area are an order of magnitude lower than those recorded at the northeastern tip of the TS in the boundary waters between the TS and ECS (Hwang et al. 2006) as well as in the waters around the Pescadores (Hwang et al. 2003, Lo et al. 2004). It should be further considered that extensive construction and development work were going on in Guanyin Township along the coast facing the TS.

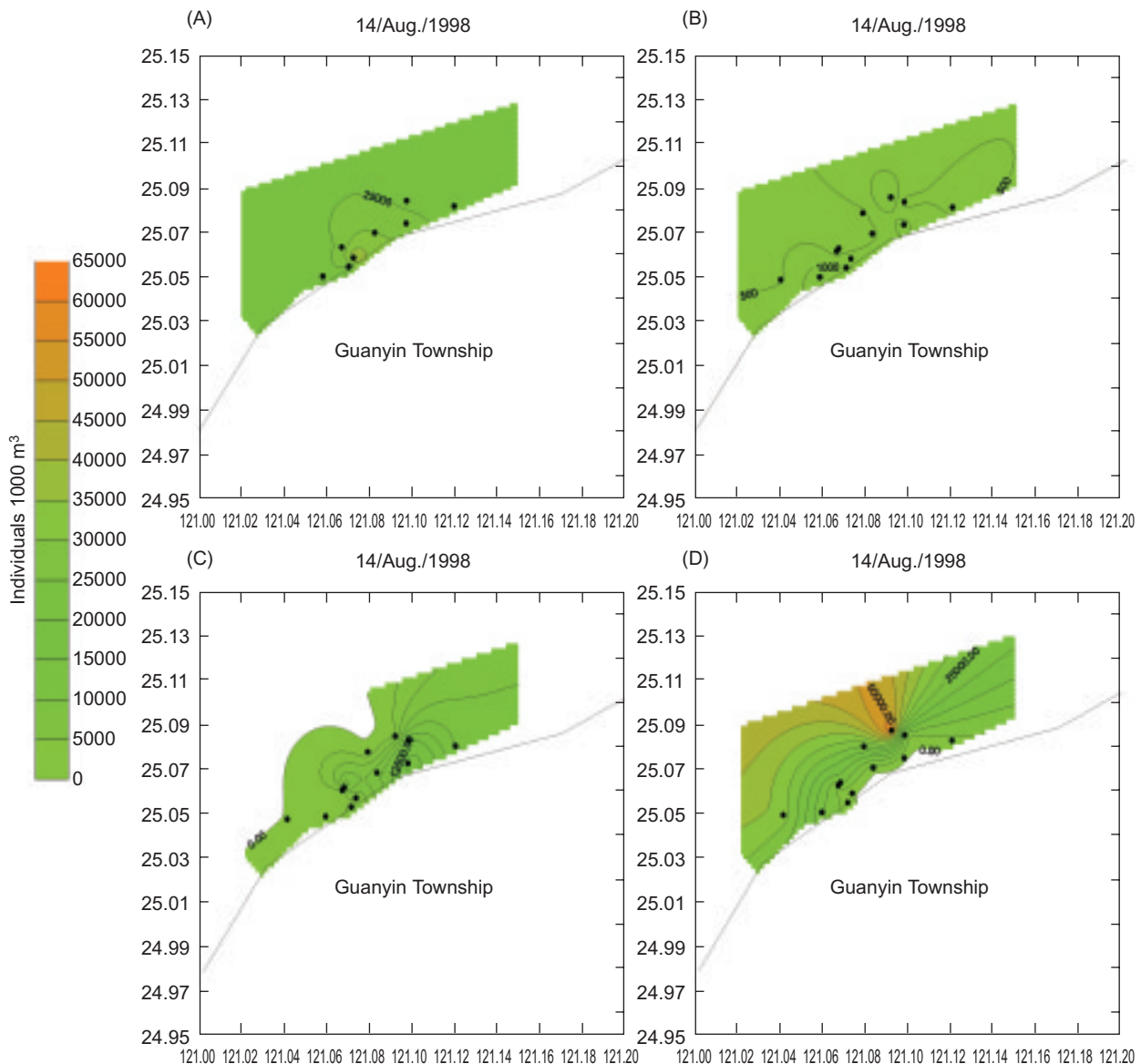


Fig. 9. Spatial distributions of copepod abundances during each season in the northeastern region of the Taiwan Strait adjacent to Guanyin Township, Taiwan.

Strong tidal currents and visibly higher turbidity due to land runoff and resuspension of sediments from sandy bottoms may have also contributed to low copepod abundances.

The northeastern boundary waters of the TS sampled in our earlier studies (Hwang et al. 2004 2006) consisted of estuarine water masses of the Danshuei River, where increased diversity and density of copepods were explained by nutrient inputs from fresh water and secondarily treated sewage water (Tseng 1975 1976, Hwang et al. 2006). Similar results were obtained in estuarine waters in other parts of the globe (Carlsson et al. 1995, Dalal and Goswami 2001, Tan et al. 2004, Thor et al. 2005). Higher copepod abundances in the study area during spring until Aug. can be attributed to the transport of copepods from the southern portion of the TS. In addition, when the NE monsoon weakens, the KBC begins flowing from the Changyun Ridge, driving copepods towards the present sampling stations, also producing higher abundances of copepods in the study area. The seasonal succession recorded here, therefore, supports our hypothesis that the northeastern region of the TS is mainly influenced by the constant effect of the KBC, and by monsoon-influenced changes in the hydrographical regimes in the area.

Variations in copepod abundances and community compositions at the seasonal scale recorded during the present study conceivably reflect the influences of different water masses driven by monsoonal winds.

Significant differences in copepod species compositions and abundances among water masses of the northern (Hsieh et al. 2004, Lan et al. 2004, Hwang et al. 2006) and southern parts (Hwang et al. 2003, Lo et al. 2004) of the TS were previously reported. Stations in the vicinity of Guanyin Township selected for this study are associated with the KBC. A significantly positive correlation between copepod abundances and temperatures can be explained by the influence of KC species in this region. Lower temperatures and lower copepod abundances in winter are caused by stagnation of KBC waters due to a counter-current effect of the CCC during the peak period of the NE monsoon. Higher copepod abundances in Kuroshio waters were previously reported (Liu et al. 1988, Hwang et al. 2000, Hsiao et al. 2004, Hsieh et al. 2004). It should be emphasized that most of the common copepod species found in the present study except *Par. parvus*, *Cor. affinis*, and *Cal. sinicus* belong to warmer-water species

according to ecological classifications proposed by Hirakawa et al. (1990) and Takahashi and Hirakawa (2001).

Index values of several copepod species reflect the dominance of cold-water species in this region only when the NE monsoon weakens and retracts from the southern part of the TS. Our data provide basic information for biological monitoring of the TS, using indicator species and improved index values. The present study strengthens the role of copepods as indicators of water mass intrusions, as these taxa have successfully been used in earlier studies (Peterson and Keister 2003, Bonnet and Frid 2004, Hsieh et al. 2004).

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