COMMUNITY STRUCTURE OF PLANKTONIC COPEPODS IN I-LAN BAY AND THE ADJACENT KUROSHIO WATERS OFF NORTHEASTERN TAIWAN

BY

CHUN-YEIN LEE[1,4]), CHANG-TAI SHIH[2]) and CHIEN-CHUNG HSU[3])

[1]) Marine Fisheries Division, Fisheries Research Institute, 199 Hou-Ih Road, Keelung 20246, Taiwan

[2]) Department of Environmental Biology and Fisheries Science, National Taiwan Ocean University, Keelung 20248, Taiwan

[3]) Institute of Oceanography, National Taiwan University, Taipei 10617, Taiwan

ABSTRACT

Our knowledge on seasonal fluctuation of the planktonic copepods in the waters off northeastern Taiwan is limited. To estimate whether the regional fishery production is at a reasonable level or not, the study of marine copepods could be necessary. Plankton samples for copepod studies were collected by a ring trawl net with 335 μm mesh size at five fixed stations along a transect extending eastward from I-Lan Bay to about 40 nautical miles (approx. 72 km) offshore, in 2004. A total of 137 species of copepods belonging to 4 orders, 25 families, and 53 genera were identified. Twenty-six dominant species contributed to the main components of seasonal abundance of the copepod community. Four of these, i.e., *Cosmocalanus darwini*, *Clausocalanus minor*, *Oithona plumifera*, and *Oncaea venusta*, were the most widely distributed species that occurred at all stations in each season. The principal results have shown that copepod abundance was higher in the continental shelf waters and lower in the Kuroshio waters, but the number of species was higher in the Kuroshio waters than that on the continental shelf, except in autumn. Apparent seasonal fluctuations in the composition of dominant species were observed by replacement rates at all stations. Geographical variation in distributional associations of the copepod community occurred over a seasonal scale, and the intermediate region was mainly influenced by the Kuroshio Current. *Calanus sinicus* might be considered an indicator species for the intrusion of eddy waters from the East China Sea into I-Lan Bay and its adjacent waters.

RÉSUMÉ

Notre connaissance des fluctuations saisonnières des copépodes planctoniques dans les eaux au large du nord-est de Taiwan est limitée. Afin d'estimer si la production régionale des pêches se situe à un niveau raisonnable, l'étude des copépodes marins pourrait s'avérer nécessaire. Des échantillons de plancton destinés aux études de copépodes ont été récoltés à l'aide d'un filet à plancton de 335 μm

[4]) Corresponding author; e-mail: cylee@mail.tfrin.gov.tw

Also available online: www.brill.nl/cr

de vide de maille sur 5 stations fixes sur un transect s'étendant vers l'est, de I-Lan Bay jusqu'à environ 40 miles nautiques (environ 72 km) au large, en 2004. Un total de 137 espèces de copépodes appartenant à 4 ordres, 25 familles, et 53 genres ont été identifiées. Vingt-six espèces dominantes constituaient les éléments principaux de l'abondance saisonnière de la communauté de copépodes. Quatre d'entre elles, *Cosmocalanus darwini*, *Clausocalanus minor*, *Oithona plumifera* et *Oncaea venusta*, étaient les plus largement réparties, présentes dans toutes les stations à chaque saison. Les principaux résultats ont montré que l'abondance des copépodes était supérieure dans les eaux du plateau continental, et inférieure dans les eaux du Kuroshio, mais le nombre d'espèces était plus élevé dans les eaux du Kuroshio que sur le plateau continental, sauf en automne. Les fluctuations saisonnières apparentes de la composition des espèces dominantes ont été observées par des taux de remplacement à toutes les stations. La variation géographique des associations de distribution dans la communauté de copépodes existe à l'échelle de la saison, et la région intermédiaire est principalement influencée par le courant du Kuroshio. *Calanus sinicus* peut être considérée comme une espèce indicatrice de l'intrusion de courants venant de la mer de Chine orientale dans la baie de I-Lan et ses eaux adjacentes.

INTRODUCTION

Marine planktonic copepod communities comprise an incredibly wide diversity of species that form the basis of food webs (Huys & Boxshall, 1991). Their grazing plays a key role in the recycling of all biogenic elements in the oceans. For, the abundance of copepods can dramatically affect the structure of oceanic food webs because of their controllable regulation of the material and energy fluxes. The role of copepods as secondary producers in marine ecosystems makes their potential influence on fishery resources critical. However, copepod communities may change in response to unusual hydrographic conditions. This has been the primary reason why researchers have attempted to determine how hydrographic factors affect the seasonal and/or long-term community dynamics of copepods (Clark et al., 2003). Seasonal fluctuations of abundance and distribution in planktonic copepods are highly related to the hydrographic characteristics of the marine environment (Yang et al., 1999a, b). Certain copepod species are also known to be indicators of water masses and oceanic currents.

Coastal and inshore fisheries are two of the most important domestic economic activities in Taiwan. The fishery production from the northeastern waters off Taiwan, especially the landings from the surrounding waters of Kuei-Shan Island, is not only abundant but sustainable throughout the year (Jean, 1987; Lee et al., 1996). To maintain these fisheries at a reasonable level, a long-term investigation and monitoring of planktonic copepods, information on which with regard to seasonal fluctuation has not been established before, could be one measure of major importance.

The primary objectives of this research are to illustrate the relationship between copepod distribution and hydrographic factors, especially the Kuroshio Current

(Nitani, 1972), in the waters of our study area, and to monitor the faunas of marine planktonic copepods in I-Lan Bay and its adjacent waters off northeastern Taiwan. The present study is able to present some preliminary information on these important organisms and their seasonal community dynamics, such as species composition, abundance, distributional pattern, parameters of biodiversity, community structure, and other issues of biological oceanography.

MATERIAL AND METHODS

The R/V "Hai-Chien" of the Fisheries Research Institute was commissioned to conduct the seasonal sampling surveys in 2004. Plankton samples were collected by vertical hauls at a speed of 0.5 m/s with a ring trawl net (1 m in mouth diameter, 335 μm mesh size, with a flowmeter mounted at the center of the mouth) at five fixed stations along a latitudinal transect extending from I-Lan Bay eastward to about 40 nautical miles (approx. 72 km) offshore (fig. 1). Samples were immediately fixed in 5% formalin-seawater solution. Detailed information of sampling dates, starting time of hauls, and sampling depths is available (table I).

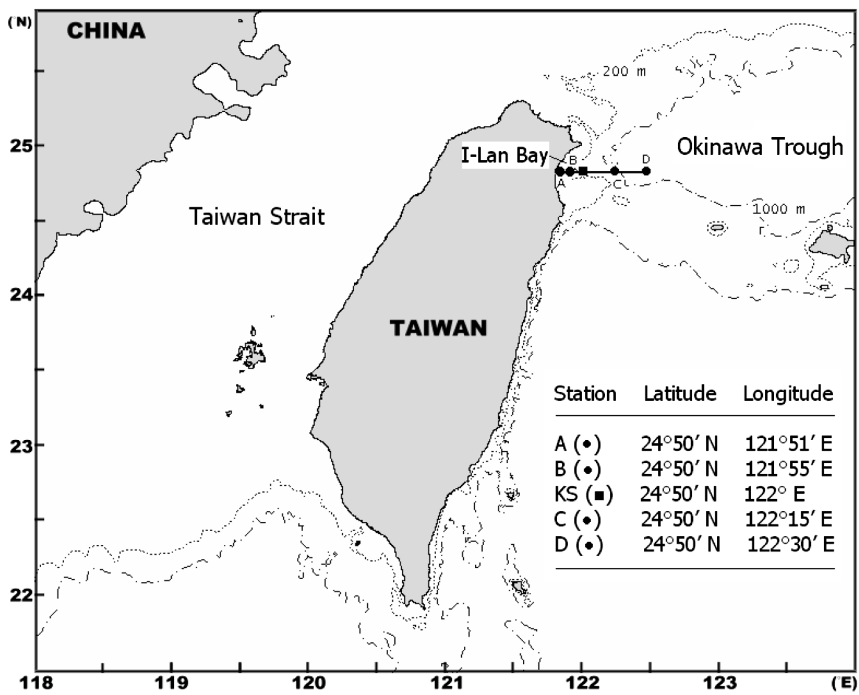

Fig. 1. The position of sampling stations along a transect extending eastward from I-Lan Bay to 40 nautical miles (approx. 72 km) offshore.

TABLE I
Sampling dates (mm/dd) and starting time of hauls (hh:mm) of the collections of planktonic copepods at the various stations by vertical hauls with a ring trawl net in 2004

Station	A	B	KS	C	D
Sampling depth (m)	65	130	200	200	200
Winter	i/08	i/08	i/08	i/07	i/07
	13:01	12:03	14:00	16:05	14:18
Spring	iv/21	iv/21	iv/21	iv/20	iv/20
	12:24	13:06	14:00	16:44	14:41
Summer	vii/23	vii/23	vii/23	vii/22	vii/22
	11:24	12:06	14:10	17:58	16:05
Autumn	x/22	x/22	x/22	x/21	x/21
	11:30	12:15	14:15	17:55	15:49

The transect, located at the southern margin of the Okinawa Trough (Lee & Hu, 1998; Yu & Song, 2000) passes through different water masses and over various water depths from stations A (75 m) and B (140 m) on the continental shelf, via station KS (280 m, approx. 5.4 km east of Kuei-Shan Island) on the continental slope, to stations C (1,066 m) and D (over 2,000 m, actual depth was beyond the range of the sonar equipment on the "Hai-Chien"). The hydrographic data, mainly temperature and salinity of the sea water, were taken simultaneously by a CTD (Conductivity-Temperature-Depth) device (SBE 19, Sea-Bird Electronics, Inc.) at each station in all seasons. The depth of the CTD measurements was set at 70, 135, 250, 500, and 500 m to the surface at stations A, B, KS, C, and D respectively, except in spring at station D, where we measured from 700 m to surface in order to test the new wire connected with the CTD.

In the laboratory, all samples were preserved in 70% alcohol. Each sample was repeatedly divided by a Folsom splitter until the subsample contained about 300-500 copepods (Shih & Chiu, 1998), then these copepods were identified to species level where possible, and the abundance of each species was recorded. Grice (1962), Chen & Zhang (1965), Chen et al. (1974), Chihara & Murano (1997), and Mauchline (1998) were the general references for identification. Species compositions were compared among stations using the Shannon-Wiener index of species diversity, the Margalef index of species richness, the Pielou index of species evenness, and the Jaccard coefficient of similarity between two communities where the stations were clustered on the basis of their similarity indices using the Unweighted Pair Group Method of Averages (UPGMA; Kang & Hong, 1995).

For comparison of the dynamic values with other studies of the regions adjacent to this study, the following formulae were used (Yang et al., 1999b):

$$Y_i = (N_i/N) \times f_i$$

$$R = (a + b - 2c)/(a + b - c) \times 100\%$$

Where Y_i is the dominance of species i, N_i is the number of individuals of species i at all stations, N is the number of individuals of all species at all stations, f_i is the frequency of station that species i occurs. A species with a Y value $\geqq 0.02$ is defined as a dominant species. R is the seasonal replacement rate of dominant species, a and b are the numbers of dominant species occurring in two adjoining seasons respectively, and c is the number of dominant species common to both.

RESULTS

Hydrographic characteristics

Two types of water masses are readily recognized by their seasonal temperature-salinity diagrams throughout the year (fig. 2). Stations A and B, which have lower and narrower ranges in temperature and salinity, are characterized as shelf waters. Stations C and D are characterized as Kuroshio waters by exhibiting a temperature-salinity curve intermediate between that of the South China Sea and that of the western Philippine Sea waters (Lee & Hu, 1998). Station KS has similar properties but with wider ranges of temperature than those at station B in all seasons.

The higher temperature was found in the upper water layer at all stations, with an extreme of about 29°C at stations C and D in summer. The seasonal hydrographic patterns of stations A, B, and KS were found to fluctuate considerably, but those at stations C and D were relatively stable.

Species composition

A total of 137 species of copepods belonging to 4 orders, 25 families, and 53 genera was identified (table II). There were 94 species of Calanoida, 7 species of Cyclopoida, 1 species of Harpacticoida, and 35 species of Poecilostomatoida. Fifty-two of these were common in all seasons, and four species, i.e., *Cosmocalanus darwini* (Lubbock, 1860), *Clausocalanus minor* Sewell, 1929, *Oithona plumifera* Baird, 1843, and *Oncaea venusta* Philipp, 1843, were the most widely distributed species that occurred at all stations in each season. In contrast, 33 species showed only a single appearance throughout the year, and there were 5, 6, 8, 8, and 6 species at stations A, B, KS, C, and D, respectively, including five uncertain species, respectively, in each of the genera *Ctenocalanus*, *Neoscolecithrix*, *Scaphocalanus*, *Scolecithricella*, and *Tharybis*.

TABLE II

List of planktonic copepods collected in the study area. Species in boldface denote the dominant species, and those with an asterisk are the single-appearance species

CALANOIDA

ACARTIDAE
Acartia danae Giesbrecht, 1889
***Acartia negligens* Dana, 1849**

AETIDEIDAE
Aetideus acutus Farran, 1929
Aetideus giesbrechti Cleve, 1904 *
Aetideus truncatus Bradford, 1971 *
Bradyidius angustus Tanaka, 1957 *
Gaetanus minor Farran, 1905
Undeuchaeta incisa Esterly, 1911 *

AUGAPTILIDAE
Haloptilus longicornis (Claus, 1863)
Haloptilus spiniceps (Giesbrecht, 1893)

CALANIDAE
Calanoides philippinensis Kitou & Tanaka, 1969 *
***Calanus sinicus* Brodsky, 1962**
***Canthocalanus pauper* (Giesbrecht, 1888)**
***Cosmocalanus darwini* (Lubbock, 1860)**
Mesocalanus lighti (Bowman, 1955) *
***Nannocalanus minor* (Claus, 1863)**
Neocalanus gracilis (Dana, 1849)
***Undinula vulgaris* (Dana, 1849)**

CALOCALANIDAE
Calocalanus pavo (Dana, 1849)
Calocalanus plumulosus (Claus, 1863)

CANDACIIDAE
Candacia catula (Giesbrecht, 1889)
Candacia curta (Dana, 1849)
Candacia ethiopica (Dana, 1849)
Candacia longimana (Claus, 1863)
Paracandacia bispinosa (Claus, 1863)
Paracandacia simplex (Giesbrecht, 1888)
***Paracandacia truncata* (Dana, 1849)**

CENTROPAGIDAE
Centropages calaninus (Dana, 1849)
Centropages elongatus Giesbrecht, 1896
Centropages furcatus (Dana, 1849)
Centropages gracilis (Dana, 1849)
Centropages longicornis Mori, 1932 *

CLAUSOCALANIDAE
***Clausocalanus arcuicornis* (Dana, 1849)**
Clausocalanus brevipes Frost & Fleminger, 1968 *
***Clausocalanus farrani* Sewell, 1929**
***Clausocalanus furcatus* (Brady, 1883)**
***Clausocalanus mastigophorus* (Claus, 1863)**
***Clausocalanus minor* Sewell, 1929**
Clausocalanus parapergens Frost & Fleminger, 1968
Clausocalanus pergens Farran, 1926
Ctenocalanus vanus Giesbrecht, 1888
Ctenocalanus sp. *

EUCALANIDAE
Eucalanus hyalinus (Claus, 1866) *
Pareucalanus attenuatus (Dana, 1849)
Rhincalanus cornutus (Dana, 1849)
Rhincalanus nasutus Giesbrecht, 1888
Subeucalanus crassus (Giesbrecht, 1888)
Subeucalanus mucronatus (Giesbrecht, 1888)
***Subeucalanus subcrassus* (Giesbrecht, 1888)**
Subeucalanus subtenuis (Giesbrecht, 1888)

EUCHAETIDAE
Euchaeta concinna (Dana, 1849)
Euchaeta indica Wolfenden, 1905
Euchaeta longicornis Giesbrecht, 1888
Euchaeta plana Mori, 1937
Euchaeta rimana Bradford, 1973

HETERORHABDIDAE
Heterorhabdus papilliger (Claus, 1863)

LUCICUTIIDAE
***Lucicutia flavicornis* (Claus, 1863)**
Lucicutia gaussae Grice, 1963 *

MECYNOCERIDAE
Mecynocera clausi Thompson, 1888

METRIDINIDAE
Pleuromamma abdominalis (Lubbock, 1856)
Pleuromamma borealis (Dahl, 1893)
Pleuromamma gracilis (Claus, 1863)
Pleuromamma robusta (Dahl, 1893)
Pleuromamma xiphias (Giesbrecht, 1889)

PARACALANIDAE
***Acrocalanus gibber* Giesbrecht, 1888**
***Acrocalanus gracilis* Giesbrecht, 1888**
Acrocalanus longicornis Giesbrecht, 1888 *
Acrocalanus monachus Giesbrecht, 1888 *
Bestiolina similis (Sewell, 1914) *

TABLE II
(continued)

***Paracalanus aculeatus* Giesbrecht, 1888**
***Paracalanus parvus* (Claus, 1863)**

PHAENNIDAE
Phaenna spinifera Claus, 1863 *

PONTELLIDAE
Calanopia elliptica (Dana, 1849)
Calanopia minor A. Scott, 1902
Labidocera acuta (Dana, 1849)
Pontellina plumata (Dana, 1849)

SCOLECITRICHIDAE
Neoscolecithrix sp. *
Scaphocalanus sp. *
Scolecithricella ctenopus (Giesbrecht, 1888)
Scolecithricella dentata (Giesbrecht, 1893)
Scolecithricella minor (Brady, 1883)
Scolecithricella vittata (Giesbrecht, 1893)
Scolecithricella sp. *
Scolecithrix bradyi (Giesbrecht, 1888)
Scolecithrix danae (Lubbock, 1856)
Scolecithrix nicobarica Sewell, 1929
Scottocalanus securifrons (T. Scott, 1893) *
Scottocalanus sedatus Farran, 1936

TEMORIDAE
Temora discaudata (Giesbrecht, 1889)
Temora stylifera (Dana, 1849)
***Temora turbinata* (Dana, 1849)**
Temoropia mayumbaensis T. Scott, 1894

THARYBIDAE
Tharybis sp. *
Undinella spinifera Tanaka, 1960 *

CYCLOPOIDA
OITHONIDAE
Oithona atlantica Farran, 1908 *
Oithona fallax Farran, 1913
Oithona longispina Nishida, 1977 *
Oithona nana Giesbrecht, 1893 *
***Oithona plumifera* Baird, 1843**
Oithona robusta Giesbrecht, 1891 *
***Oithona setigera* (Dana, 1849)**

HARPACITICOIDA
MIRACIIDAE
Macrosetella gracilis (Dana, 1848)

POECILOSTOMATOIDA
CORYCAEIDAE
Corycaeus (Agetus) flaccus Giesbrecht, 1891
Corycaeus (Agetus) limbatus Brady, 1883
Corycaeus (Agetus) typicus (Kroyer, 1849)
***Corycaeus (Corycaeus) clausi* F. Dahl, 1894**
Corycaeus (Corycaeus) crassiusculus Dana, 1849
***Corycaeus (Corycaeus) speciosus* Dana, 1849**
Corycaeus (Corycaeus) vitreus Dana, 1849 *
Corycaeus (Ditrichocorycaeus) affinis McMurrich, 1916
Corycaeus (Ditrichocorycaeus) andrewsi Farran, 1911
Corycaeus (Ditrichocorycaeus) asiaticus F. Dahl, 1894
Corycaeus (Ditrichocorycaeus) dahli Tanaka, 1957
Corycaeus (Onychocorycaeus) agilis Dana, 1849
***Corycaeus (Onychocorycaeus) catus* F. Dahl, 1894**
Corycaeus (Onychocorycaeus) pacificus M. Dahl, 1912
Corycaeus (Onychocorycaeus) pumilus M. Dahl, 1912 *
Corycaeus (Urocorycaeus) furcifer Claus, 1863
Corycaeus (Urocorycaeus) longistylis Dana, 1849
Farranula carinata (Giesbrecht, 1891)
Farranula concinna (Dana, 1849)
***Farranula gibbula* (Giesbrecht, 1891)**
Farranula sp.1
Farranula sp.2
Farranula sp.3

ONCAEIDAE
Lubbockia squillimana Claus, 1863 *
Oncaea conifera Giesbrecht, 1891
Oncaea media Giesbrecht, 1891
Oncaea mediterranea Claus, 1863
Oncaea minuta Giesbrecht, 1893 *
***Oncaea venusta* Philippi, 1843**

SAPPHIRINIDAE
Copilia lata Giesbrecht, 1891 *
Copilia mediterranea (Claus, 1863) *
Copilia mirabilis Dana, 1849
Copilia recta Giesbrecht, 1891 *
Sapphirina metallina Dana, 1849 *
Sapphirina stellata Giesbrecht, 1891

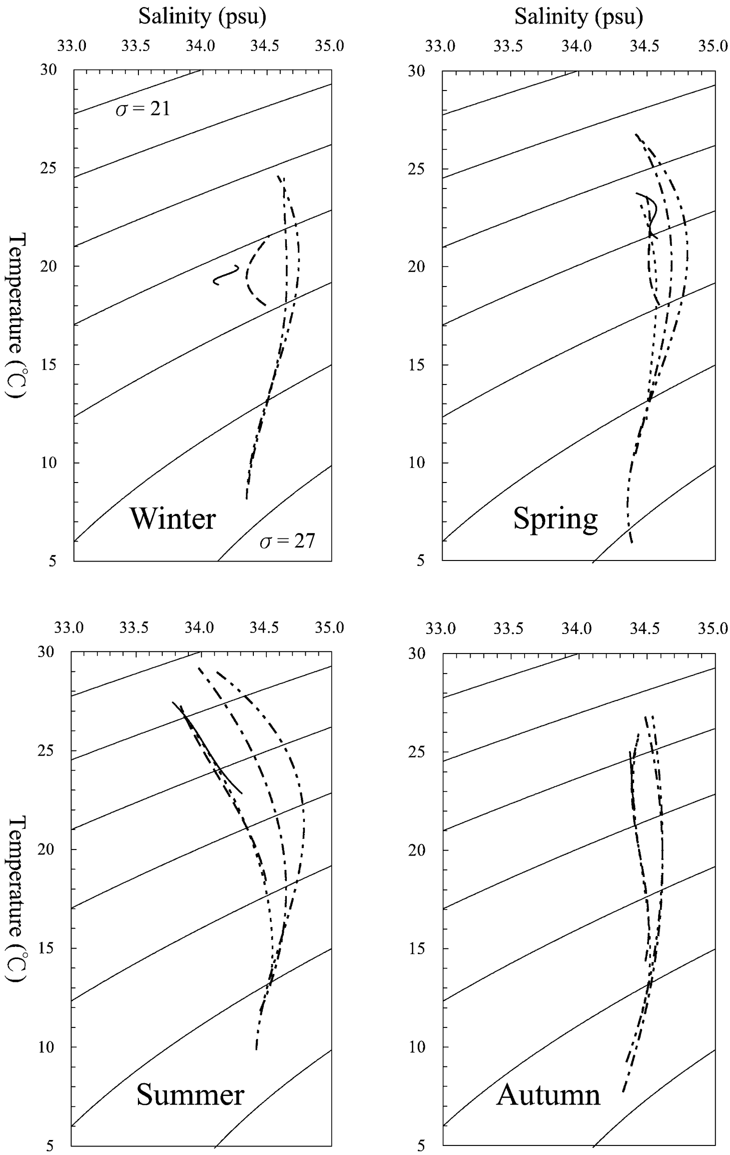

Fig. 2. Seasonal temperature-salinity diagrams at stations A (——), B (– –), KS (· · · ·), C (– · –), and D (– · · –) in 2004.

Abundance and the dominant species

Seasonal fluctuations of the abundance of planktonic copepods distributed in the study area were noted. The greatest abundance occurred at station A with an average of 999 ± 372 ind./m^3 and a highest value of 1,334 ind./m^3 in spring (fig. 3).

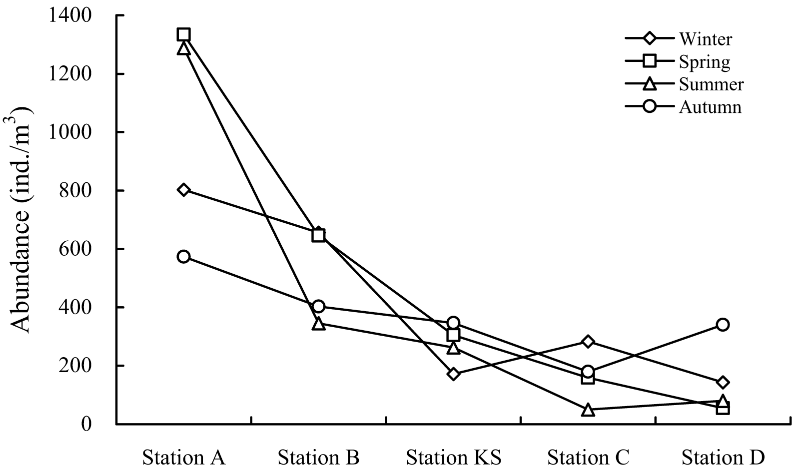

Fig. 3. Seasonal fluctuations of abundance of planktonic copepods collected at the various stations in 2004.

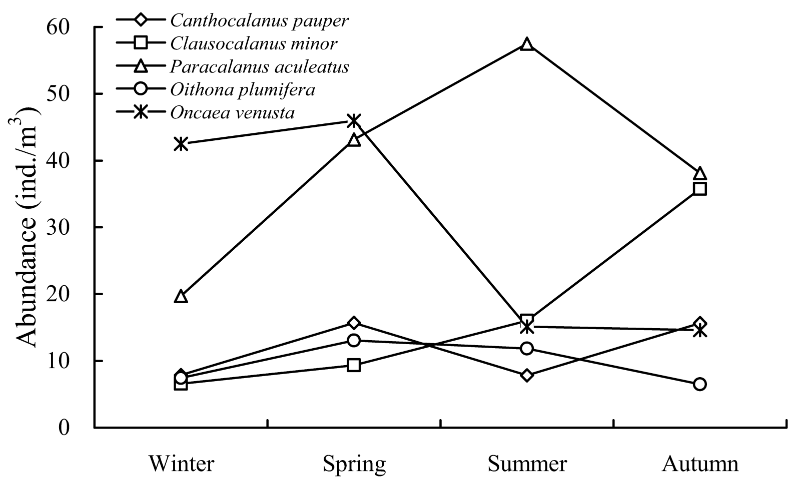

Fig. 4. Seasonal fluctuations of abundance of the five dominant species occurring in all seasons, as collected in 2004.

By contrast, the abundance in Kuroshio waters, i.e., at stations C and D, was at lower levels than that in the shelf waters.

There were 26 dominant species that contributed to the main components of seasonal abundance of copepods (table III). Five of these, i.e., *Canthocalanus pauper* (Giesbrecht, 1888), *Clausocalanus minor*, *Paracalanus aculeatus* Giesbrecht, 1888, *Oithona plumifera*, and *Oncaea venusta*, were the dominant species that occurred in all seasons (fig. 4). Ten species, which usually were less abundant, only occurred in a single season.

TABLE III

The seasonal dominance (Y) and abundance (X, ind./m^3) of dominant species of planktonic copepods; # denotes Y < 0.02 and / denotes species was not found

Dominant species	Winter		Spring		Summer		Autumn	
	Y	X	Y	X	Y	X	Y	X
Canthocalanus pauper (Giesbrecht, 1888)	0.0352	7.88	0.0228	15.70	0.0245	7.84	0.0517	15.63
Clausocalanus minor Sewell, 1929	0.0241	6.57	0.0371	9.36	0.0612	16.01	0.1238	35.77
Paracalanus aculeatus Giesbrecht, 1888	0.0528	19.72	0.0684	43.15	0.1365	57.50	0.1198	38.13
Oithona plumifera Baird, 1843	0.0221	7.42	0.0376	13.05	0.0472	11.87	0.0216	6.50
Oncaea venusta Philippi, 1843	0.1205	42.47	0.0816	45.96	0.0481	15.12	0.0517	14.62
Calanus sinicus Brodsky, 1962	0.1088	51.71	0.3127	127.50	#		0.0229	6.04
Nannocalanus minor (Claus, 1863)	0.0313	12.00	0.0201	13.55	#		0.0419	12.83
Clausocalanus furcatus (Brady, 1883)	0.0489	21.94	0.0360	9.95	#		0.0347	11.20
Lucicutia flavicornis (Claus, 1863)	0.0248	6.42	#		0.0219	2.19	0.0269	6.60
Temora turbinata (Dana, 1849)	0.0261	11.79	0.0488	9.81	0.1216	72.66	#	
Acartia negligens Dana, 1849	0.0391	13.97	#		#		0.0367	10.60
Cosmocalanus darwini (Lubbock, 1860)	0.0599	25.00	0.0212	12.39	#		#	
Undinula vulgaris (Dana, 1849)	#		#		0.0656	36.82	0.0203	6.27
Clausocalanus farrani Sewell, 1929	0.0228	11.81	#		#		0.0301	8.73
Acrocalanus gibber Giesbrecht, 1888	#		#		0.0481	9.55	0.0432	12.63
Oithona setigera (Dana, 1849)	0.0215	4.55	#		0.0210	9.05	#	
Paracandacia truncata (Dana, 1849)	0.0208	4.00	/		#		#	
Clausocalanus arcuicornis (Dana, 1849)	#		#		#		0.0236	6.41
Clausocalanus mastigophorus (Claus, 1863)	0.0261	3.72	#		#		#	
Subeucalanus subcrassus (Giesbrecht, 1888)	#		#		0.0420	19.78	#	
Acrocalanus gracilis Giesbrecht, 1888	#		#		0.0306	7.51	#	
Paracalanus parvus (Claus, 1863)	#		0.0477	33.54	/		#	
Corycaeus (Corycaeus) clausi F. Dahl, 1894	0.0208	8.87	#		/		#	
Corycaeus (Corycaeus) speciosus Dana, 1849	#		#		#		0.0262	7.22
Corycaeus (Onychocorycaeus) catus F. Dahl, 1894	0.0248	14.37	#		#		#	
Farranula gibbula (Giesbrecht, 1891)	#		#		#		0.0203	6.04
Numbers of species	18		11		12		16	

TABLE IV
The numerical percentages summed (%) of dominant species (Y ≧ 0.02) of planktonic copepods in the seasonal collections at the various stations in 2004

Station	A	B	KS	C	D
Winter	75.7	65.6	35.6	43.1	45.7
Spring	67.2	61.0	67.0	43.0	46.1
Summer	69.2	61.3	61.5	56.7	53.0
Autumn	49.2	57.4	68.4	49.4	57.7

None of the dominant species was the most abundant in all seasons. Actually, the supremacy of these dominant species fluctuated seasonally. According to the replacement rates between two adjoining seasons, the highest value was 64.7% observed during the spring-summer interchange, and the lowest was 47.4% observed during the winter-spring interchange. Potential changes in dominance and numerical percentage were examined at the various sampling stations, showing the dominant copepod faunas of the shelf region had relatively higher numerical percentages (49.2-75.7%) than those in the Kuroshio region (43.0-57.7%) (table IV).

Biodiversity parameters

According to the seasonal variations in four important indices of copepod species diversity at each station (fig. 5), the number of species tended to have an increasing trend from coastal waters to the open sea, except for an irregular condition in autumn. The total number of species in each season was between 77 and 101. The geographical fluctuation pattern of species richness of the copepod fauna, expressed by the Margalef index, was similar to that of the number of species. The other two indices of copepod diversity, the Shannon-Wiener index and the Pielou index, which ranged from 3.03 at station B in spring to 5.16 at station D in summer, and from 0.57 at station B in spring to 0.91 at station D in summer, respectively, presented another, similar geographical pattern with relatively lower values at stations B and KS in spring.

Distributional association

The cluster analysis of season-station associations based on the Jaccard coefficient shows the degree of similarity in the geographical distribution of the copepod faunas in the study area (fig. 6). Stations A and B, as well as C and D, respectively, were grouped together first in each season, and were then grouped into two major faunal areas, i.e., the shelf fauna and the Kuroshio fauna. In other words, among-station similarity variations were significantly greater than within-season, implying the similarity of station-to-station variation in distributional associations occurred

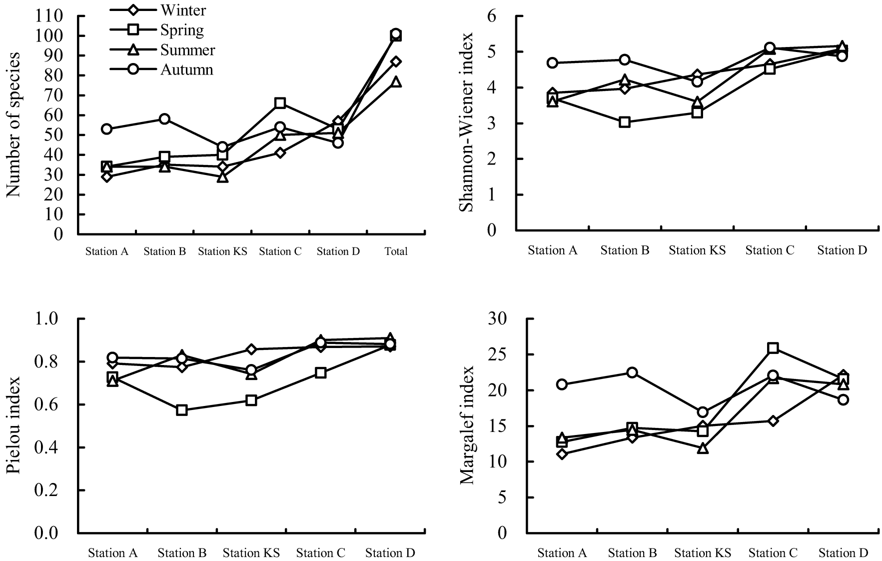

Fig. 5. Number of species, Shannon-Wiener index, Pielou index, and Margalef index of planktonic copepods collected at the various stations in the four seasons of 2004.

over a seasonal scale. Station KS exhibited a feature intermediate between the two faunal areas, showing a more similar association with the shelf fauna during summer and autumn.

Biological oceanography

Calanus sinicus Brodsky, 1962, was one of the dominant species (table III), and reached in spring the maximal Y value of 0.31, among all species throughout the year. Its geographical distribution pattern of seasonal abundance clearly fluctuated (fig. 7). High abundances occurred in the shelf region during winter and spring, with extreme values of 239 and 255 ind./m^3 at stations A and B in spring. No *C. sinicus* were found at these two stations in summer, but there were a few individuals in autumn. Although there were some individuals at stations KS and C in all seasons, *C. sinicus* never occurred at station D.

The season-to-season as well as the station-to-station fluctuations of the *C. sinicus* population took place in a particular pattern that might be concerned with the oceanographic environment in the study region. An additional description of biological oceanography, mainly on the comparison of the countercurrent observed on the inshore side of the Kuroshio northeastern of Taiwan, will be further explored in the Discussion.

DISCUSSION

Aetideus truncatus Bradford, 1971, with a single female found at station C in autumn, is new to the western Pacific Ocean (Markhaseva, 1996). Seven species only occurred at stations C and D, four of these, i.e., *Gaetanus minor* Farran, 1905, *Haloptilus longcornis* (Claus, 1863), *Pareucalanus attenuatus* (Dana, 1849), and *Scolecithricella dentata* (Giesbrecht, 1893), are Kuroshio warm-water species according to Chihara & Murano (1997); another species, *Candacia longimana* (Claus, 1863), is classified as a deep-water species of the Kuroshio by Huang et al. (2000); and the remaining two species, *C. ethiopica* (Dana, 1849) and *Pontellina plumata* (Dana, 1849), are also warm-water species distributed in the epipelagic zone of the oceans around the world (Chihara & Murano, 1997).

Although the total number of species in the present study was lower than the 223 in the 200-0 m collections of the northern waters off Taiwan reported by Yang et al. (1999b), the percentage of the number of common species for all seasons, 37.9%, was higher than the 31.8% in Yang et al. (1999b), who collected samples in a much wider region boxed roughly by the coordinates 24°40′N to 27°50′N and 120°40′E to 125°00′E. A similar result of 32.7% to a total of 226 species was recorded by Xu et al. (2004), who investigated the pelagic copepods in the East China Sea (23°30′N to 33°00′N and 118°30′E to 128°00′E). The number of dominant species in the present study, however, was higher than the 13 in Yang et al. (1999b) and the 17 in Xu et al. (2004), but the compositions of all of these three studies fluctuated in a seasonal pattern. The replacement rates in this study ranged from 47.4 to 64.7%, and were lower than the 66.7 to 88.9% in Xu et al. (2004), and had narrower ranges than the 36.4 to 75.0% in Yang et al. (1999b). However, six species, including *Calanus sinicus*, *Cosmocalanus darwini*, *Nannocalanus minor* (Claus, 1863), *Undinula vulgaris* (Dana, 1849), *Acrocalanus gibber* Giesbrecht, 1888, and *Temora turbinata* (Dana, 1849), were common in the waters investigated by these three studies. Five species belonging to the genus *Clausocalanus* were among the most numerous dominant species in the present study. This conformed to the opinion that the species of *Clausocalanus* often dominate numerically in the epipelagic zone of temperate to tropical oceans (Frost & Fleminger, 1968; Chihara & Murano, 1997).

The abundance of copepods varies greatly in the coastal and shelf regions of the world (Mauchline, 1998). For instance, the average annual abundance ranged from 150 to 2,000 ind./m^3 of a 53 m water column sampled vertically by a 200 μm meshed net in the North Sea (Roff et al., 1988). Fluctuations of average seasonal abundance in this study ranged from 999 $\pm$ 372 ind./m^3 at station A to 155 $\pm$ 129 ind./m^3 at station D, and thus, apparently, showed a decreasing trend seaward. This trend is probably due to the high levels of nutrients carried by the freshwater runoff that, therefore, enriches the shelf waters (Lalli & Parsons, 2000). A similar trend is found in Meng et al. (1996), Yang et al. (1999a), and Xu et al. (2003). On the other hand, general fluctuations in number of species at the various stations indicated an increasing trend seaward (fig. 5, ranging from 29 to 66), and was thus in conformation with the result (ranging from 21 to 64) of Shih & Chiu (1998). Furthermore, 84.4% (65 out of 77) of the calanoid species collected from Kuroshio waters (stations C and/or D) were common to the species in the 200-0 m samples collected with the same net from Kuroshio waters off eastern Taiwan (the upstream section of this study) in Hsiao et al. (2004), implying a small annual variation in calanoid species composition in these waters.

The relatively low values of the Shannon-Wiener index as well as of the Pielou index at stations B and KS in spring, were clearly due to the presence of a large amount of *Calanus sinicus* (39.5% and 40.4% of numerical abundance at each station, respectively). A similar phenomenon was observed in Yang et al. (1999b) at their station S1-4 in spring and their stations S2-4 and S2-5 in autumn, caused by the most dominant species, *Temora turbinata* (e.g., 35% of numerical abundance at S1-4). However, copepod diversity generally exhibited an increasing trend from coastal waters to the open sea, and conformed to the results of Kang & Hong (1995), Shih & Chiu (1998), and Yang et al. (1999b). The most stable seasonal variation of copepod diversity was observed at station D, e.g., numbers of species varied within a narrow range from 46 to 57 and the Shannon-Wiener indices varied from 4.87 to 5.16 (fig. 5). This was due to the relatively homogeneous hydrographic conditions throughout the year (fig. 2). The annual peak in numbers of species at stations A and B in autumn was probably also due to the hydrographic conditions being relatively similar to those of the Kuroshio waters, where usually more species are found.

Kang & Hong (1995) reported from Korean waters four major clusters of oceanic warm-water calanoid copepods, which were grouped on the basis of Jaccard's similarity index. The seasonal distributional variation of each cluster was closely related to the strength of the Tsushima Current. They, therefore, suggested that the regime of the Tsushima Current might be traced by examining the biological characteristics of the copepods in these waters. Similarly, two major faunal areas recognized by cluster analysis in the present study also illustrate a geographical distribution of the copepod community influenced by the Kuroshio Current. The station KS was shown to have a closer association with the shelf fauna during summer and autumn, but with the Kuroshio fauna during winter and spring (fig. 6). It coincided with the results of hydrographic surveys in Chern & Wang (1994) and Lee & Hu (1998), who indicated that the Kuroshio axis moved toward the shelf during winter and shifted further offshore during summer.

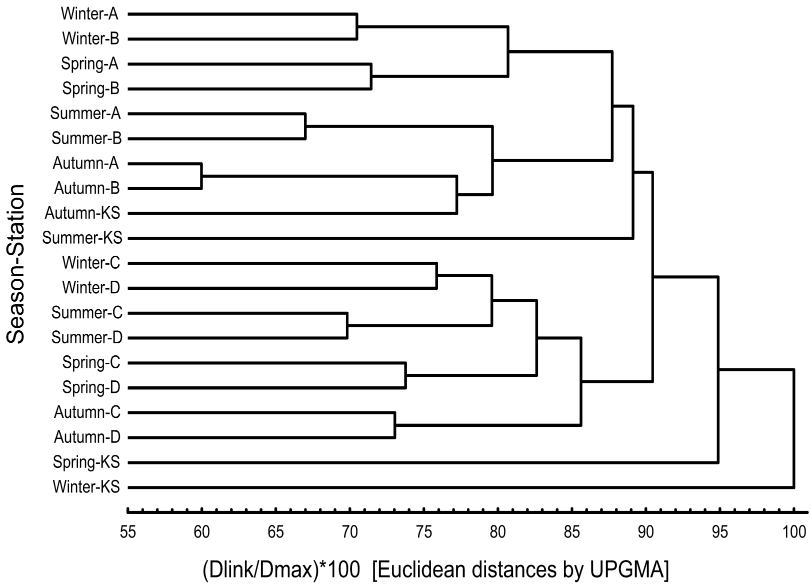

Fig. 6. Dendrogram of season-station associations based on the Jaccard coefficient using UPGMA, and showing the degree of relative dissimilarity in copepod faunas between seasons-stations.

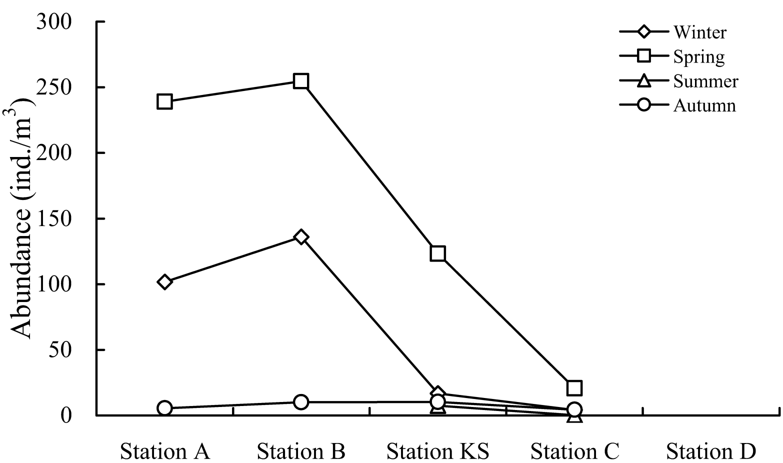

Fig. 7. Seasonal fluctuations in the abundance of *Calanus sinicus* Brodsky, 1962 at the various stations in 2004.

Calanus sinicus is one of the key species in the Yellow Sea and East China Sea, comprising about 85% of the total zooplankton biomass in the Yellow Sea in spring (Liu et al., 2003). All stages of *C. sinicus* can be found throughout the year, and the peak of abundance usually occurs in spring in response to the rising water temperature and richer food supply (Chang & Sun, 2001; Wang et al., 2002; Xu et al., 2004). A recent systematic investigation on seasonal fluctuation of horizontal distribution of this widely distributed species in the East China Sea by Xu et al. (2004) has shown that there was a certain area of high abundance in the southern region during winter; a sharp increase in abundance during spring and reaching its peak during summer, but mainly concentrated in the northern region where the water temperature was relatively lower; the abundance decreased to a low level throughout the southern region during autumn. The seasonal fluctuation pattern of *C. sinicus* abundance in the present study closely matched that in the southern region of the East China Sea in Xu et al. (2004), especially the great abundance at stations A and B during winter and spring, and no specimen was found during summer. The fairly steady countercurrent on the inshore side of the Kuroshio off northeastern Taiwan observed by Chuang et al. (1993) is supposed to be a transporting current for this non-resident population in I-Lan Bay. That is, *C. sinicus* could be an indicator species of the countercurrent of Kuroshio, which is a continuation of remote origin, rubs the slope, spills over the shelf edge, and then feeds back to the ocean in the northeastern waters of Taiwan (Chuang et al., 1993). Furthermore, the upper thermal range for reproduction of *C. sinicus* is about 23°C, whence the population can not be maintained in the warm Kuroshio Current, except at great depths (Uye, 2000). This is why this species prospered in the shelf region where the water temperature was ideal in winter and spring (fig. 2), but was lethally high in the whole water column during summer. A previous study by Shih & Chiu (1998) indicated the only small numbers of *C. sinicus* that were just expatriates at the Kuroshio stations (just downstream of our study), while the other stations in the southern East China Sea were dominant. The individuals found at station C were probably also expatriates that inhabited the deeper water, where the temperature was still suitable.

ACKNOWLEDGEMENTS

This study was supported by a research grant, 93AS-9.1.1-AI-A4(2), from the Council of Agriculture, R.O.C. We thank Captain Wang and the crew of R/V "Hai-Chien", who helped us collect the samples and the hydrographic data. Mr. S. H. Wu and Mr. Y. M. Chen of the Marine Fisheries Division, Fisheries Research Institute, are thanked for handling the pre-processing modules of CTD data.

REFERENCES

CHANG, F. & S. SUN, 2001. Review on the ecology of the planktonic copepod *Calanus sinicus*. Mar. Sci., **25** (11): 16-19.

CHEN, Q. C. & S. Z. ZHANG, 1965. The planktonic copepods of the Yellow Sea and the East China Sea, I. Calanoida. Stud. mar. Sinica, **7**: 20-131, pls. 1-52.

CHEN, Q. C., S. Z. ZHANG & C. S. ZHU, 1974. On planktonic copepods of the Yellow Sea and the East China Sea, II. Cyclopoida and Harpacticoida. Stud. mar. Sinica., **9**: 27-76, pls. 1-24.

CHERN, C. S. & J. WANG, 1994. Influence of the seasonal thermocline on the intrusion of Kuroshio across the continental shelf northeast of Taiwan. Journ. Oceanogr., **50**: 691-711.

CHIHARA, M. & M. MURANO, 1997. An illustrated guide to marine plankton in Japan: 649-1004. (Tokai Univ. Press, Tokyo).

CHUANG, W. S., H. W. LI, T. Y. TANG & C. K. WU, 1993. Observations of the countercurrent on the inshore side of the Kuroshio northeast of Taiwan. Journ. Oceanogr., **49**: 581-592.

CLARK, R. A., C. L. J. FRID & K. R. NICHOLAS, 2003. Long-term, predation-based control of a central-west North Sea zooplankton community. ICES Journ. mar. Sci., **60**: 187-197.

FROST, B. & A. FLEMINGER, 1968. A revision of the genus *Clausocalanus* (Copepoda: Calanoida) with remarks on distributional patterns in diagnostic characters. Bull. Scripps Inst. Oceanogr., Univ. California, San Diego, **12**: 1-235.

GRICE, G. D., 1962. Calanoid copepods from equatorial waters of the Pacific Ocean. Fish. Bull., U.S., **61**: 171-246.

HSIAO, S. H., C. Y. LEE, C. T. SHIH & J. S. HWANG, 2004. Calanoid copepods of the Kuroshio Current east of Taiwan, with notes on the presence of *Calanus jashnovi* Huslemann, 1994. Zool. Stud., **43** (2): 323-331.

HUANG, F. P., F. MENG, D. Y. LIU & J. SUN, 2000. Distribution of Copepoda in the Kuroshio region in the northern East China Sea. Journ. Oceanogr. Huanghai Bohai Seas, **18** (3): 61-65.

HUYS, R. & G. A. BOXSHALL, 1991. Copepod evolution: 1-468. (The Ray Society, London).

JEAN, C. T., 1987. Survey on demersal fish resources of baby trawl fishery at Dah-Shi. Bull. Taiwan Fish. Res. Inst., **43**: 129-142.

KANG, Y. S. & S. Y. HONG, 1995. Occurrences of oceanic warm-water calanoid copepods and their relationship to hydrographic conditions in Korean waters. Bull. Plankt. Soc. Japan, **42** (1): 29-41.

LALLI, C. M. & T. R. PARSONS, 2000. Biological oceanography: an introduction (2nd ed.): 209-213. (Butterworth-Heinemann, Oxford).

LEE, D. A., S. H. WU, I. C. LIAO & H. P. YU, 1996. On three species of commercially important sergestid shrimps (Decapoda: Sergestidae) in the coastal waters of Taiwan. Journ. Taiwan Fish. Res., **4** (1): 1-19.

LEE, I. H. & J. H. HU, 1998. The relation between the I-Lan bight water and the shelf water northeast of Taiwan. Acta oceanogr. Taiwanica, **37** (1): 89-103.

LIU, G. M., S. SUN, H. WANG, Y. ZHANG, B. YANG & P. JI, 2003. Abundance of *Calanus sinicus* across the tidal front in the Yellow Sea, China. Fish. Oceanogr., **12** (4-5): 291-298.

MARKHASEVA, E. L., 1996. Calanoid copepods of the family Aetideidae of the world: 1-331. (Ocean. Zool. Inst. Russian Acad. Sci., St. Petersburg).

MAUCHLINE, J., 1998. The biology of calanoid copepods. Advances in Marine Biology, **33**: 65-97. (Academic Press, San Diego).

MENG, F., S. Q. CHEN & B. L. WU, 1996. Distribution of biomass of zooplankton in the Kuroshio area of the East China Sea. Acta oceanol. Sinica, **15** (3): 365-376.

NITANI, H., 1972. Beginning of the Kuroshio. In: H. STOMMEL & K. YOSHIDA (eds.), Kuroshio — its physical aspects: 129-163. (Univ. Tokyo Press, Tokyo).

ROFF, J. C., K. MIDDLEBROOK & F. EVANS, 1988. Long-term variability in North Sea zooplankton off the Northumberland coast: productivity of small copepods and analysis of trophic interactions. Journ. mar. biol. Assoc. U.K., **68**: 143-164.

SHIH, C. T. & T. S. CHIU, 1998. Copepod diversity in the water masses of the southern East China Sea north of Taiwan. Journ. mar. Syst., **15**: 533-542.

UYE, S., 2000. Why does *Calanus sinicus* prosper in the shelf ecosystem of the northwest Pacific Ocean? ICES Journ. mar. Sci., **57** (6): 1850-1855.

WANG, R., H. Y. ZHANG, K. WANG & T. ZUO, 2002. Function performed by small copepods in marine ecosystem. Oceanol. Limnol. Sinica, **33** (5): 453-460.

XU, Z. L., X. S. CUI & W. Z. CHEN, 2004. Species composition and dominant species study on pelagic copepods in the East China Sea. Journ. Fish. China, **28** (1): 35-40.

XU, Z. L., M. JIANG, M. CHAO, Y. L. WANG, Q. YUAN & Y. Q. CHEN, 2003. Quantitative distribution of pelagic copepods in the East China Sea. Journ. Fish. China, **27** (3): 258-264.

YANG, G. M., D. H. HE, C. S. WANG, Y. T. MIAO & H. H. YU, 1999a. Study on the biological oceanographic characteristics of planktonic copepods in the waters north of Taiwan, I. Abundance distribution. Acta oceanol. Sinica, **21** (4): 78-86.

— —, — —, — —, — — & — —, 1999b. Study on the biological oceanography characteristics of planktonic copepods in the waters north of Taiwan, II. Community characteristics. Acta oceanol. Sinica, **21** (6): 72-80.

YU, H. S. & G. S. SONG, 2000. Physiographic and geologic frameworks of the shelf-slope region off northeastern Taiwan. Acta oceanogr. Taiwanica, **38**: 1-22.

First received 2 May 2006.
Final version accepted 2 June 2006.