Zoological Studies **43**(2): 464-474 (2004)

Zoological Studies

Seasonal Distribution of Copepods in Tapong Bay, Southwestern Taiwan

Wen-Tseng Lo[1,*], Chia-Lu Chung[1] and Chang-tai Shih[2,3]

[1]*Department of Marine Resources, National Sun Yat-Sen University, Kaohsiung, Taiwan 804, R.O.C.*
[2]*Taiwan Fisheries Research Institute, Keelung, Taiwan 202, R.O.C.*
[3]*Canadian Museum of Nature, Ottawa, K1P 6P4 Canada*

(Accepted March 16, 2004)

Wen-Tseng Lo, Chia-Lu Chung and Chang-tai Shih (2004) Seasonal distribution of copepods in the Tapong Bay, southwestern Taiwan. *Zoological Studies* **43**(2): 464-474. Seasonal distribution of planktonic copepods was investigated at 3 stations, S (southern), C (central), and N (northern), in Tapong Bay, southwestern Taiwan, during the 2-yr period from July 1999 to June 2001. The numerical abundance of small-sized (at 100~330 μm) zooplankton was about 7 times that of the large-sized (at > 330 μm). Calanoid copepods were dominant in both groups, numerically comprising 77.6% and 89.1% of the total, respectively. Other common taxa differed between the 2 groups: cyclopoid copepods, copepod nauplii, and barnacle nauplii were greater in the small-sized group; while cladocerans, ephyrae, and crab zoea were common in the large-sized group. Among the copepods, 35 species were recognized, and 16 taxa were identified to family or genus level; copepodites and nauplii were numerically dominant. The 6 most-common copepod taxa were nauplii; unidentified copepodites of the Paracalanidae, Oithonidae, and Acartiidae; *Acartia tsuensis*; and *Parvocalanus crassirostris*. *Acartia tsuensis*, and *P. crassirostris* belong to small-sized species and were common in fishponds and coastal waters, respectively. The overall annual mean abundance, species number, and diversity of copepods were consistently higher at stn. N and lower at stn. C. Each station was characterized by different dominant taxa and seasonal distribution patterns. Paracalanidae copepodites and *P. crassirostris* were common at stn. N and exhibited higher abundances in autumn; copepod nauplii and copepodites of the Oithonidae dominated at stn. C but without significant seasonal changes; while *A. tsuensis* was the most abundant species at stn. S with a peak abundance in summer. Using cluster analysis, 3 sampling groups and 4 copepod assemblages were defined and are discussed herein. The multiple biotic and abiotic factors, such as food sources, predation pressure from medusae, and the hydrographical complexity, may interactively influence the spatial and seasonal distribution of copepods in the bay. http://www.sinica.edu.tw/zool/zoolstud/43.2/464.pdf

Key words: Copepod composition, Seasonal distribution, Tapong Bay.

Copepods are usually the dominant group in zooplankton communities; they feed primarily on phytoplankton and serve as secondary producers in marine ecosystems. In the last few decades, the importance of planktonic copepods in marine food web dynamics has become a relevant issue, particularly the feeding impact on phytoplankton and the contribution to organic matter fluxes by these crustaceans (Miller et al. 1991, Dam et al. 1994, Landry et al. 1994). Copepods are also consumed by other marine organisms of higher trophic levels; thus, their distribution may also directly affect the dynamics of fishery resources in the ocean. The distribution and succession of copepods are influenced by environmental factors, especially in estuaries, bays, and lagoons (Castel and Courties 1982, Ferrari et al. 1985).

Very few studies focused on copepods in the waters surrounding Taiwan before the 1980s, except those by Tan (1967) and Tseng (1972). Several aspects of the ecology of copepods have recently been studied, including behavior (Hwang and Turner 1995), co-occurrence with ichthyoplankton (Cheng 1998, Hsieh and Chiu 2002),

*To whom correspondence and reprint requests should be addressed. Tel: 886-7-5252000 ext. 5050. Fax: 886-7-5255020. E-mail: lowen@mail.nsysu.edu.tw

diversity and water masses (Shih and Chiu 1998), grazing rates (Hwang et al. 1998, Wong et al. 1998), and estuarine and coastal distributions (Hsieh and Chiu 1998, Lo et al. 2001). These studies, except that of Lo et al. (2001), were mainly conducted in the waters off northern Taiwan.

The present work is part of a multidisciplinary oceanographic study on the Land-Ocean Interaction Coastal Zone (LOICZ) in Taiwan. The overall aim of the LOICZ project is to determine and predict the effects of natural and anthropogenic activities on changes in ecological environments in the Kaoping coastal zone and in Tapong Bay of southwestern Taiwan. Our study site focused on Tapong Bay, a semi-enclosed subtropical lagoon with a total area of around 5.3 km^2. The depth of the bay ranges from 1 m near the tidal inlet in the north to 6 m in the inner bay, with an average depth of 2.2 m. The water exchange between Tapong Bay and the Taiwan Strait, primarily driven by a semi-diurnal tide, is characterized as a poorly flushed condition due to the presence of only 1 tidal inlet (0.5 km wide). The bay is characterized by very high primary productivity with significant spatial and temporal variabilities that generally increase in the inner Bay compared to those in the outer bay, particularly when nutrient inputs occur through the Linpan Dike in summer (Su 2002). The impacts of human activities on the bay are apparent due to the surrounding drainages from urban areas and fishponds, and particularly the extensive aquatic farming of hanging oysters and caged fish within the bay itself; these therefore usually significantly influence the distribution patterns of organisms in the bay. In this study, we report on the succession of the copepod community in Tapong Bay through 2 annual cycles. We compared the data obtained by 2 NorPac nets fitted with mesh sizes adequate for the collection of meso- and microzooplankton. Results are discussed in relation to seasonal changes in temperature, salinity, and the concentration of chlorophyll *a*.

MATERIALS AND METHODS

Zooplankton samples were taken monthly at 3 stations in Tapong Bay, southwestern Taiwan (Fig. 1) from July 1999 to June 2001. Samples were collected using 2 NorPac nets with a 100 and 330 μm mesh, respectively; a flowmeter was mounted at the center of the mouth opening. Two nets were simultaneously towed near the surface (0~1 m) at an average speed of 1 m/s for 5 min at each station. Zooplankton samples were preserved in 5%~10% buffered formalin in seawater on board immediately after collection for further identification and counting of zooplankton. At each station, temperature and salinity near the water surface were measured with a portable conductivity-temperature sensor; 1 L of sea surface water was collected in a dark bottle and preserved in an icebox for later measurement of the concentration of chlorophyll *a*. In the laboratory, each sample was repeatedly divided using a Folsom plankton splitter until the subsample contained around 500 specimens. Copepods were then sorted for identification and enumeration. The total number of individuals of each copepod taxon was recorded, and the Shannon diversity index was used to indicate the species diversity at each station.

For chlorophyll *a* analysis, seawater samples were kept below 4°C; 500 ml of seawater was filtered through GF/F filters, and then placed in a centrifuge tube with 10 ml of 90% aqueous acetone. All samples were left for 24 h in a dark refrigerator for full extraction. Tubes were then shaken and centrifuged, and the fluorescence of the supernatant was measured in a fluorescence spectrophotometer (Hitachi F-2000, Japan) before and after acidification with 10% hydrochloric acid. The amount of chlorophyll *a* was calculated using the equations of Strickland and Parsons (1972).

To compare differences in copepod groups among station and month/year samples, the logarithmic abundance (abundance + 1) of the 31 most-common species (those with occurrence rates > 11%) were standardized, then cluster

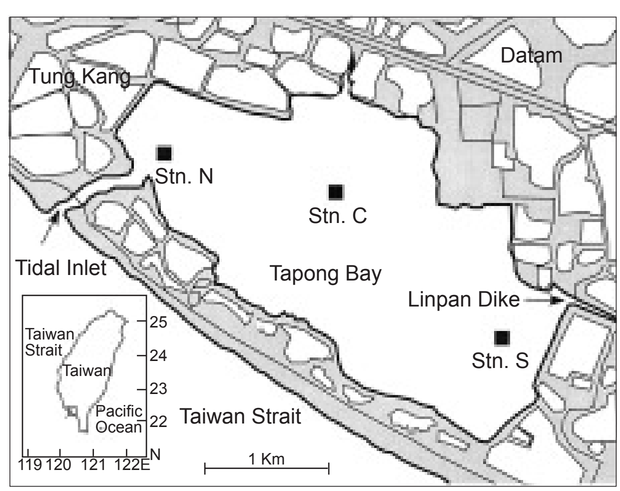

Fig. 1. Location of sampling stations in Tapong Bay, southwestern Taiwan. Fishponds are indicated by the lighter shading.

analysis (CA) was used to place similar species into groups or clusters using the minimum variance (or Ward) linkage. Paired samples whose fusion resulted from the minimum variance (relative to the variances within each cluster taken separately) were first joined and then likewise progressively enlarged by adding the next sample. To identify groups of copepod species that covaried in logarithmic abundance, the data matrix was transposed so that samples became variables, and then cluster analysis was used to determine the co-varying species groups. The numerical abundance of all copepod species in each group was integrated and averaged to display their distribution patterns.

RESULTS

Hydrography

Water temperature and salinity of Tapong Bay showed apparent seasonal changes. Temperatures were usually > 30°C in summer, up to 33.4°C at stn. C in July 2001, and dropped to about 17°C in winter. Differences in water temperature among stations were greater in winter than in summer, and the range seasonal changes in temperature were smaller at stn. N than at the other 2 stations (Fig. 2). The trend of seasonal changes in salinity was reversed, with higher values in winter and the lowest values during summer. Differences in salinity among stations were larger in summer than in winter, and salinities were apparently lower at stns. S and C than at stn. N, particularly in the rainy summer season (Fig. 2). The concentration of chlorophyll *a* showed no clear seasonal changes, but a higher concentration and larger variation were detected in summer.

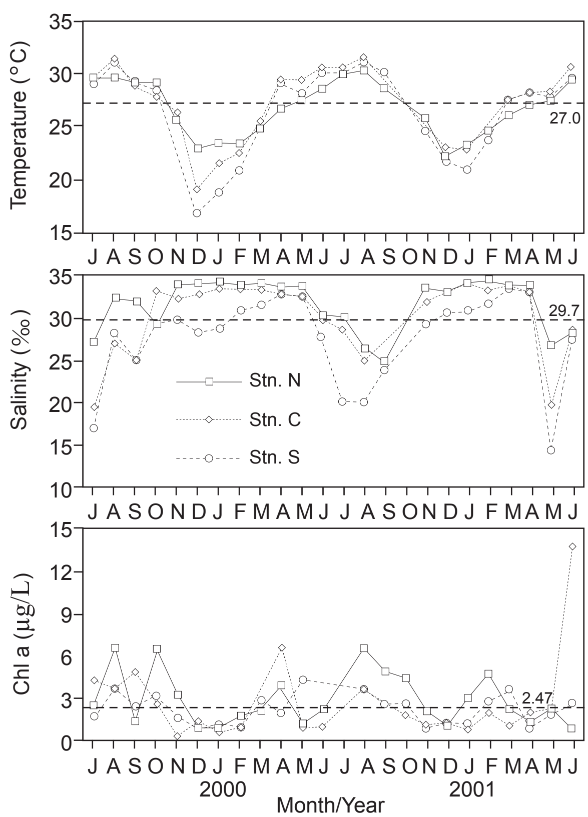

Fig. 2. Seasonal changes in water temperature, salinity, and chlorophyll a in Tapong Bay, southwestern Taiwan during 1999~2001. Dashed lines indicate annual means. In this study, the months of four seasons are: spring, Mar.-May; Summer, June-Aug.; fall, Sept.-Nov.; winter, Dec.-Feb.

The importance of the small-sized fraction

The numerical abundance of the small-sized (100~330 μm) zooplankton was (6.0 ± 14.0) x 10^5 individuals/100 m^3, about 7 times that of the large-sized ones (> 330 μm). Calanoids were the dominant taxon in both groups, comprising 77.6% and 89.1% of the numerical total of zooplankton respectively. However, other dominant taxa differed between the 2 size fractions: cyclopoid copepods, copepod nauplii, and barnacle nauplii were more numerous in the small-sized group, while cladoceran, ephyrae, and crab zoea were common in the large-sized group (Table 1). Since Tapong Bay was dominated by small-sized copepods, copepodites, and nauplii, only copepods were recorded and counted in samples from the 100-μm-mesh net. In total, 35 copepod species were recognized; in addition, 16 taxa were identified to family or genus level (Table 2). Copepodites and nauplii were numerically the most dominant, contributing 54% of the total copepods. The 6 most dominant copepod taxa were nauplii; unidentified copepodites of the Paracalanidae, Oithonidae, and Acartiidae; *Acartia tsuensis*; and *Parvocalanus crassirostris*. Both *A. tsuensis* and *P. crassirostris* belong to small-sized species and were common in fishponds and coastal waters, respectively.

Spatial variations and seasonal succession

The species composition and abundance of copepods varied among stations in Tapong Bay. The annual mean abundance, species number, and diversity of copepods were found to be highest at stn. N, followed by stn. S, and they were the lowest at stn. C (Table 3). Each station was dominated by different taxa. Paracalanidae copepodites and *P. crassirostris* were dominant at stn. N; greater numbers of copepod nauplii and copepodites of the Oithonidae were recorded at stn. C; while *A. tsuensis* and copepodites of the Acartiidae dominated at stn. S. Regarding seasonal changes, the abundance of copepods at stn. N was mostly higher than the annual mean (4.9 x 10^5 individuals/100 m^3) during 1999~2000, but that was not true in 2001, and it was usually higher in autumn than in other seasons (Fig. 3). The abundance at stn. C was always below the annual mean, while at stn. S, the abundance peaked in both summers but was quite low in other seasons. The species number at stn. N showed an apparent seasonal change, with higher numbers in the dry season (Nov.~Apr.) than in the wet season (May~Oct.). Stations C and S exhibited a similar trend, but the difference in seasonal change was not as clear as that of stn. N. The index of species diversity at stn. N was usually higher than the annual mean, and it was higher in the dry season than in the wet season, whereas values at stns. S

Table 1. Mean abundance (individuals/100 m^3) and relative abundance (RA, %) of zooplankton taxa collected by 100 and 330-μm-mesh nets in Tapong Bay during 1999~2001. +: < 0.0005; -: no data

Taxonomic group	100 μm (S)		330 μm (L)		Ratio of L/S
	Mean ± SD	RA	Mean ± SD	RA	
Calanoida	469,148 ± 1,211,112	77.562	73,378 ± 322,210	89.054	0.156
Cyclopoida	44,190 ± 216,540	7.306	154 ± 5260	0.186	0.003
Copepod nauplii	31,348 ± 59,464	5.183	167 ± 529	0.203	0.005
Barnacle nauplii	29,803 ± 81,609	4.927	279 ± 1399	0.339	0.009
Cladocera	10,742 ± 82,727	1.776	4143 ± 30,482	5.028	0.386
Harpacticoida	4735 ± 15,203	0.783	70 ± 247	0.085	0.015
Ostracoda	3421 ± 14,843	0.566	178 ± 633	0.216	0.052
Appendicularia	2787 ± 11,898	0.461	311 ± 1063	0.377	0.112
Fish eggs	2147 ± 15,788	0.355	196 ± 621	0.238	0.091
Other Mollusca	1353 ± 6263	0.224	20 ± 67	0.024	0.015
Polychaeta	959 ± 6447	0.159	50 ± 211	0.06	0.052
Crab zoea	812 ± 2016	0.134	909 ± 2087	1.103	1.119
Amphipoda	777 ± 3149	0.128	104 ± 193	0.126	0.134
Shrimp larvae	592 ± 2893	0.098	251 ± 1084	0.304	0.424
Chaetognatha	454 ± 2403	0.075	69 ± 303	0.084	0.152
Pteropoda	447 ± 1891	0.074	46 ± 161	0.055	0.103
Fish larvae	428 ± 2194	0.071	69 ± 156	0.084	0.161
Siphonophora	181 ± 863	0.03	15 ± 487	0.018	0.083
Echinodermata larvae	126 ± 1101	0.021	1 ± 49	0.001	0.008
Heteropoda	108 ± 709	0.018	12 ± 43	0.015	0.111
Foraminifera	67 ± 314	0.011	20 ± 146	0.024	0.299
Ephyrae	52 ± 333	0.009	1833 ± 11,927	2.225	35.250
Crab megalopa	47 ± 380	0.008	10 ± 53	0.012	0.213
Euphausiacea	40 ± 349	0.007	39 ± 94	0.047	0.975
Others	34 ± 164	0.006	30 ± 88	0.037	0.882
Lucifera	30 ± 205	0.005	19 ± 73	0.023	0.633
Thaliacea	29 ± 180	0.005	1 ± 53	0.001	0.034
Medusa	11 ± 38	0.002	8 ± 36	0.01	0.727
Other Decapoda	4 ± 30	0.001	3 ± 17	0.003	0.750
Mysidacea	0 ± 3	+	12 ± 41	0.015	-
Ctenophora	0 ± 1	+	0 ± 3	+	-
Isopoda	0	0	0 ± 4	0.001	-
Polyps	0	0	1 ± 4	0.001	-
Sergestidae	0	0	1 ± 4	0.001	-
Total zooplankton	604,872 ± 1,404,403	-	82,620 ± 326,757	-	0.136

Table 2. Mean abundance (individuals/100 m^3), relative abundance (RA, %), and occurrence frequency (OR, %) of copepods collected by a 100-μm-mesh net in Tapong Bay during 1999~2001. +: < 0.0005

Copepod species	Mean ± SD	RA	OR
Paracalanidae copepodites	66,781 ± 130,946	13.620	97.1
Copepoda nauplii	62,967 ± 164,024	12.842	100.0
Acartia tsuensis Ito, 1956	60,846 ± 219,950	12.409	56.5
Oithonidae copepodites	59,087 ± 88,603	12.051	100.0
Acartiidae copepodites	53,339 ± 190,854	10.878	97.1
Parvocalanus crassirostris (Dahl, 1893)	52,727 ± 131,655	10.753	84.1
Oithona dissimilis Lindberg, 1940	41,522 ± 91,963	8.468	88.4
Zausodes sp.	15,293 ± 26,432	3.119	97.1
Acrocalanus indicus Tanaka, 1960	13,115 ± 35,770	2.675	63.8
Oithona simplex Farran, 1913	11,752 ± 38,992	2.397	81.2
Pseudodiaptomidae copepodites	9526 ± 51,718	1.943	44.9
Temoridae copepodites	7421 ± 18,962	1.514	58.0
Oithona oculata Farran, 1913	5755 ± 18,202	1.174	63.8
Acartia sinjiensis Mori, 1940	5180 ± 27,220	1.056	43.5
Oithona attenuata Farran, 1913	3553 ± 10,825	0.725	49.3
Oithona brevicornis Giesbrtcht, 1891	3468 ± 8918	0.707	56.5
Temora turbinata (Dana, 1849)	2476 ± 15,208	0.505	17.4
Onceaidae copepodites	2435 ± 12,260	0.497	42.0
Paracalanus gracilis Chen & Zhang, 1965	1608 ± 8365	0.328	11.6
Temora discaudata (Giesbrtcht, 1889)	1454 ± 12,008	0.297	5.8
Oncaea venusta Philippi, 1843	1344 ± 8686	0.274	18.8
Clausocalanidae copepodites	1277 ± 4985	0.260	26.1
Bestiolina amoyensis Li & Huang, 1984	1265 ± 3525	0.258	33.3
Oithona longspina Nishida, 1977	771 ± 2841	0.157	39.1
Corycaeidae copepodites	757 ± 2547	0.154	27.5
Tisbidae copepodites	728 ± 1316	0.148	58.0
Idyella tenuis (Brady, 1910)	491 ± 1254	0.100	49.3
Clausocalanus furcatus (Brady, 1883)	470 ± 3185	0.096	4.3
Pseudodiaptomus trihamatus Wright, 1973	436 ± 2969	0.089	11.6
Acartia erythraea Giesbrtcht, 1889	386 ± 1029	0.079	33.3
Paracalanus parvus (Claus, 1863)	331 ± 1704	0.068	11.6
Microsetella sp.	320 ± 1398	0.065	27.5
Acrocalanus gracilis Giesbrtcht, 1888	219 ± 1712	0.045	4.3
Clausocalanus mastigophorus (Claus,1863)	196 ± 931	0.040	8.7
Corycaeus andrewsi Farran, 1911	134 ± 600	0.027	8.7
Calocalanus pavo (Dana, 1849)	118 ± 716	0.024	5.8
Farranula carinata (Dana, 1847)	118 ± 646	0.024	8.7
Calocalanus pavoninus Farran, 1936	115 ± 952	0.023	1.4
Eucalanidae copepodites	103 ± 856	0.021	1.4
Farranula rostrata Claus, 1863	87 ± 722	0.018	1.4
Euchaetidae copepodites	73 ± 460	0.015	4.3
Calanopia minor A. Scott, 1902	62 ± 335	0.013	11.6
Corycaeus lautus Dana, 1849	59 ± 476	0.012	4.3
Farranula gibulla Giesbrtcht, 1891	59 ± 476	0.012	2.9
Oncaea conifera Giesbrtcht, 1891	53 ± 444	0.011	1.4
Acartia pacifica Steuer, 1915	25 ± 209	0.005	2.9
Pseudodiaptomus pacificus Walter, 1986	8 ± 52	0.002	2.9
Scolecithricidae copepodites	6 ± 45	0.001	2.9
Candaciidae copepodites	5 ± 44	0.001	1.4
Euchaeta rimana Bradford, 1973	5 ± 44	0.001	1.4
Canthocalanus pauper (Giesbrtcht, 1888)	1 ± 8	+	1.4
Total copepods	490,327 ± 747,809		

and C varied monthly and were always below the annual mean. The highest and lowest diversities occurred in Feb. 2000 at stn. N and C, respectively (Fig. 3).

Most of the dominant copepods displayed clear spatial and seasonal distributions. Paracalanidae copepodites, *P*. *crassirostris*, and *Zausodes* sp. primarily appeared at stn. N and had higher abundances in autumn (Fig. 4). *Acartia tsuensis*, copepodites of the Acartiidae, *Acrocalanus indicus*, and *Oithona simplex* were mostly dominant at stn. S. However, *A*. *tsuensis* and copepodites of the Acartiidae had peak abundances in summer, but were scarce or sometimes absent at other stations and in other seasons, while *Acr*. *indicus* and *O*. *simplex* exhibited higher abundances in autumn. The occurrence of copepod nauplii and copepodites of the Oithonidae was 100% (Table 2). Copepodites of the Oithonidae were more numerous in summer at stns. N and S, while the abundance of copepod nauplii peaked only at stn. N in July 2000. *Oithona dissimilis* showed clear seasonal abundances, being higher

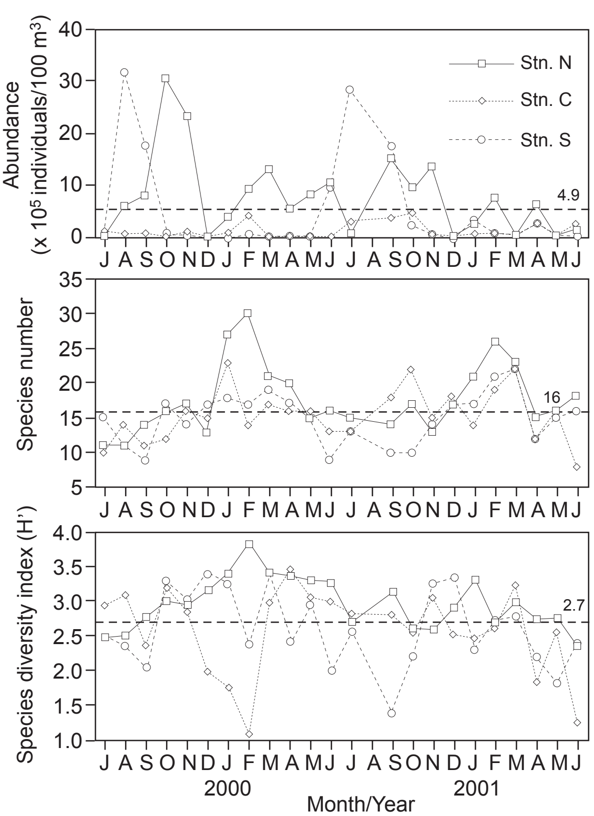

Fig. 3. Seasonal changes in numerical abundance, and species number and diversity of copepods collected by a 100-μm-mesh net in Tapong Bay during 1999~2001. Dashed lines indicate annual means.

in summer at both stns. N and S, but scarce in other seasons. *Zausodes* sp. was found throughout the year at stn. N, but very few occurred at stns. S and C (Fig. 4).

Sampling groups and copepod assemblages

Three sampling groups among the 31 most frequently observed taxa were established from the cluster analysis (CA) using Ward's linkage method (Fig. 5). The 1st group contained 6 samples collected at stn. N in the dry winter season (Jan.~Apr.) in 2000 and 2001. The 2nd group included 2 subgroups, IIa and IIb. Group IIa contained 10 samples which were mainly taken at stn. N in the spring and the autumn of 1999 and 2000; group IIb contained 11 samples mostly collected at stns. S and C in summer of 1999 and 2000. The 3rd group was most distinct from the others by the cluster linkage, and was divided into 2 subgroups, IIIa and IIIb. Group IIIa contained 23 samples mostly collected at stns. S and C; while group IIIb contained 19 samples mainly collected in the dry season (Oct.~May). Four copepod species groups were also distinguished (Fig. 6). Generally, the species groups were separated by spatial and seasonal distributions and had different distribution patterns. The 1st group contained 6 taxa, four of them were copepodites and nauplii; these taxa had higher occurrence frequencies and usually higher abundances at stn. S in summer and at stn. N in autumn, but relatively lower values at stn. C. The 2nd group included 5 taxa that were dominant at stn. N and exhibited higher abundances in the dry season. The 3rd group included 13 taxa, which generally had lower abundances compared with the other groups, and mainly occurred at stn. N with higher abundances in the dry season, but were relatively scarce or absent at stns. S and C. The last group included 7 taxa, with higher abundances at stn. S in summer, but relatively lower values and at times even absent in other seasons and at other stations. The distribution pattern of the 1st species group was similar to that of the 2nd group, but was distinct from those of the 3rd and 4th groups.

Copepods and environmental variables

The abundance of copepods was positively correlated ($p < 0.05$) with temperature, but not significantly with either salinity or chlorophyll *a* (Table 4). The species number was negatively correlated ($p < 0.05$) with temperature and positively correlated ($p < 0.05$) with salinity, but was not significantly correlated with chlorophyll *a*. The index of species diversity of copepods was not significantly correlated with any of these 3 environmental variables. Among the 10 most-dominant copepod taxa, only copepodites of the Oithonidae showed significant positive correlations with temperature ($p < 0.01$) and chlorophyll *a* ($p < 0.05$). Many dominant species exhibited significant correlations with salinity; for instance, *A. tsuensis* had a significant negative correlation with salinity ($p < 0.01$), whereas *P. crassirostris*, *Zausodes* sp., *Acr. indicus*, and *Oithona simplex* exhibited significant positive correlations ($P < 0.05$).

DISCUSSION

Previous studies of marine zooplankton have generally focused on the importance of larger-sized copepods, and neglected or underestimated smaller copepods (Tan 1967, Tseng 1972, Chen et al. 1974, Hirakawa et al. 1990, Christous 1998). However, recent studies have been concerned more with the importance of small-sized copepods, along with nauplii and younger copepodites, as a trophic link between the classical and microbial food webs (Roff et al. 1995, Wickham 1995), particularly in tropical and subtropical coastal waters (Calbet et al. 2000). For instance, Calbet et al. (2001) studied zooplankton in coastal waters of the NW Mediterranean with emphasis on the importance of small-sized zooplankton. They found that the abundance of zooplankton collected with a 53-μm-mesh net was 8 times that obtained with a 200-μm net. Similar results were also found in the present study. We found that small-sized and juvenile stages of copepods usually dominated (>

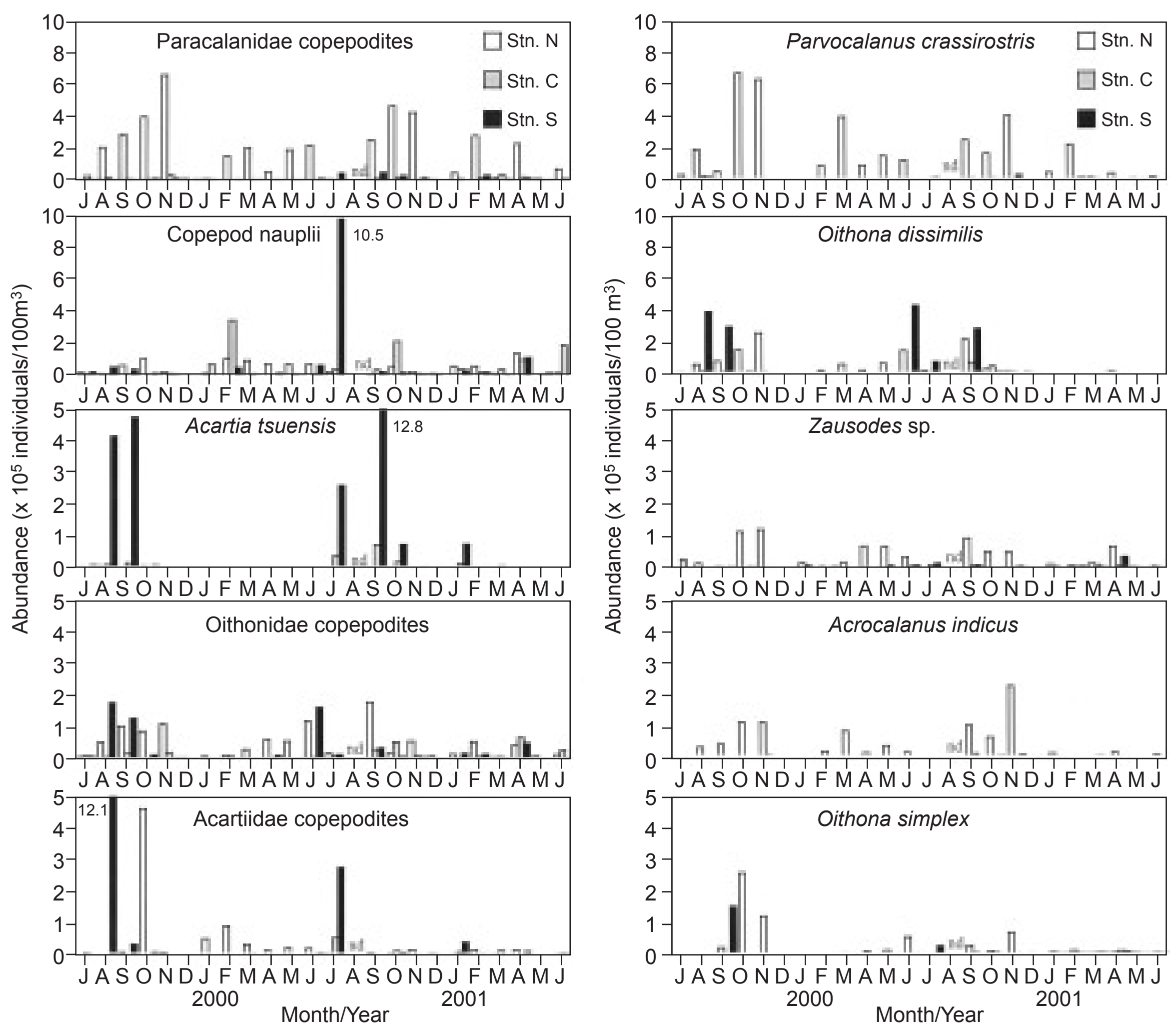

Fig. 4. Seasonal changes in the numerical abundance of the 10 most dominant copepods collected by a 100-μm-mesh Norpac net.

90%) in our samples, except at stns. S and C between late fall and early spring when the ephyrae of *Aurelia aurita* and Cladocera occurred in bulk numbers and therefore reduced the abundance and dominance (< 80%) of copepods.

According to Riós-Jaha (1998), the copepod abundance apparently undergoes seasonal changes in Phosphorescent Bay, Puerto Rico; copepod numbers in the cold, dry season were about 4 times as high as those in the warm, wet season. In Tapong Bay, the species composition

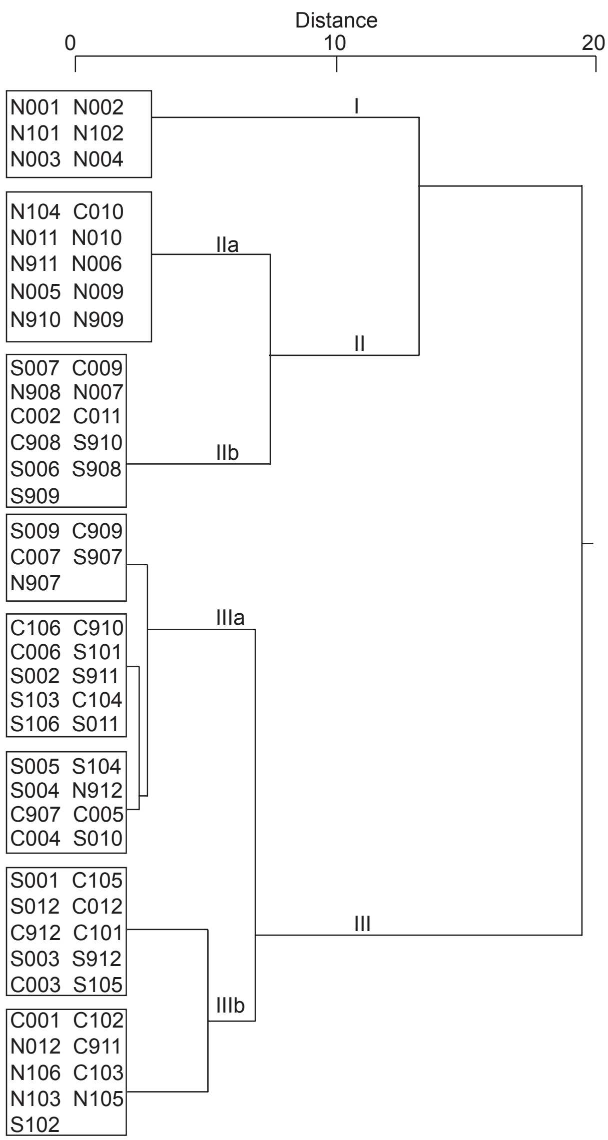

Fig. 5. Tree diagram of sampled groups obtained by Ward linkage cluster analysis based on a Pearson correlation matrix of logarithmic abundances of copepod species collected in Tapong Bay, southwestern Taiwan, during 1999~2001. Compound symbols represent stations (the letters N, S, and C), years (the 1st number: 9, 1999; 0, 2000; and 1, 2001), and months (last 2 numbers) in Tapong Bay during 1999~2001.

and abundance of copepods showed significant variations among seasons and stations (Fig. 3). Copepod abundance was relatively higher in fall at stn. N and in summer at stn. S and became relatively scarce in other seasons at both stations (Fig. 3). These variations were probably due to the fact that each of these stations was characterized by different dominant species with distinct seasonal distribution patterns. Paracalanidae copepodites and *P. crassirostris* were common at stn. N and exhibited higher abundances in autumn, while *A. tsuensis* was the most-abundant species which peaked in summer at stn. S (Table 3, Fig. 4). Based on the description by Yamaji (1984) and Chihara and Murano (1997) on the ecological characteristics and distribution patterns of copepods, *A. tsuensis* is a very common species in aquaculture ponds during summer and can adapt to warmer brackish water. Station S, located near the drainage of Linpan Dike and fishery ponds, was much less saline and was usually flushed with nutrient-rich wastewaters in the rainy summer, favoring the dominance of *A. tsuensis* and copepodites of the Acartiidae. The negative correlation of abundance of *A. tsuensis* with salinity well explains the ecological preference of the species. Station N, near the tidal inlet of the Bay, usually had higher species richness and copepod abundances than those found at the other stations. Copepods at the bay inlet were mostly euryhaline, neritic forms, such as *P. crassirostris* and copepodites of the Paracalanidae. These copepods are very common in coastal waters of southwestern Taiwan (Lo, unpubl. data) and often dominated at stn. N, particularly during the dry season, when they may have been transported into the bay by flooding tidal currents. Copepodites of the Oithonidae had 100% occurrence in the bay (Table 2), with higher abundances in summer and a significant positive correlation with temperature ($p <$ 0.01) (Fig. 4, Table 4). We speculated that copepodites of the Acartiidae, Paracalanidae, and Oithonidae in our samples were mostly, if not all, the copepodite stages of *A. tsuensis*, *P. crassirostris*, and *O. dissimilis*, because their seasonal and spatial distribution patterns were similar (Fig. 4). *Zausodes* sp. is a benthic or semibenthic species, and usually inhabits macroalgae. It was common at stn. N and about 5~6 times as abundant as levels found at stns. S and C (Table 3), probably due to locally higher vertical turbulence caused by the interaction between tidal currents and waves; it was therefore driven up to near the surface in these shallow waters (about 1~2 m deep).

The species composition and distribution of copepods in Tapong Bay were not only affected by physical environmental factors (i.e., temperature, salinity, tides, etc.), but were also influenced by biotic factors. It is suggested that at stns. S and C, the feeding impact of *Aur. aurita* (Scyphomedusa) on zooplankton (mainly copepods) was substantial during winter. On the other hand, the effect of freshwater runoff was greater in summer. At stn. N, the copepod species composition and seasonal distribution pattern were mainly affected by tidal currents and the coastal water mass, and thus significantly differed from those of the communities at stns. S and C. The species found at stn. N were mostly tropical coastal forms that were possibly transported into the bay during the flood tide. Moreover, some species which were found at stns.

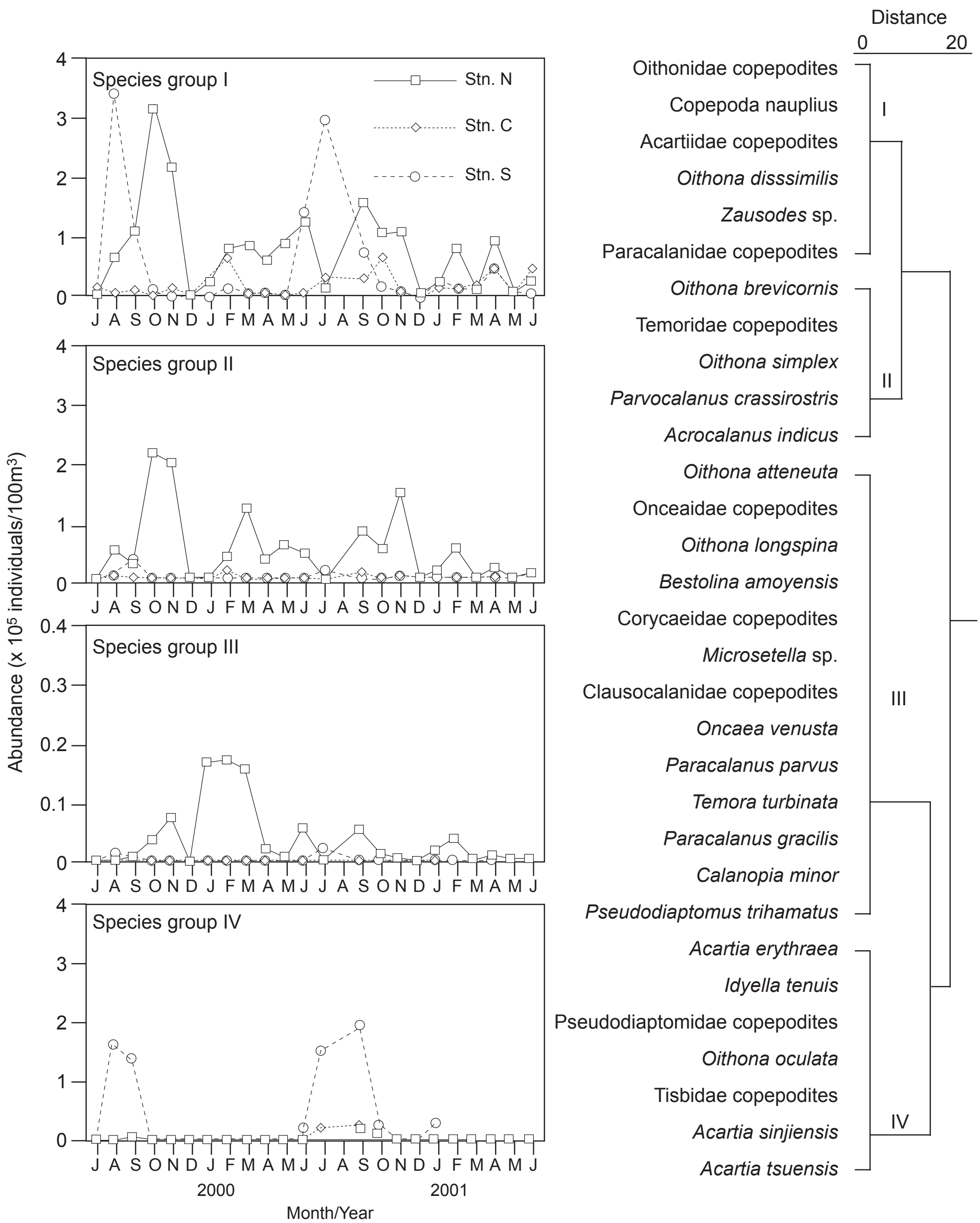

Fig. 6. Copepod assemblages and their distribution patterns in Tapong Bay, southwestern Taiwan, during 1999~2001.

S and C. may also have been brought to stn. N during the ebb tide, thus allowing stn. N to become even more diverse in species composition. *Aurelia aurita* was found year round in the bay and usually formed a patchy distribution at stns. S and C in the dry winter (Lo, unpubl. data). In Jan. 2000, its abundance was up to 14 individuals/m^3. Chen (2002) studied the gut contents of 44 *Aur. aurita* in Tapong Bay, and found that among other taxa, copepods (including copepodites) were the dominant group as a food source for this jellyfish. Furthermore, the feeding rate of *Aur. aurita* was between 200 and 6000 prey items/day and varied with its bell diameter size. It is apparent that *Aur. aurita* feeds primarily on small-sized copepods and exerts a significant feeding impact on their abundances (14%~41%). Omori et al. (1995) measured the feeding rate of *Aur. aurita* in Tokyo Bay and found similar results of 2000~3500 prey items/day, and up to 28,320~54,000 prey items/day for large-sized jellyfish (> 14 cm).

In conclusion, small-sized zooplankton, mostly immature copepods, predominated in Tapong Bay and showed apparent seasonal succession and spatial variation. The multiple biotic and abiotic factors, such as food sources, predation pressure of medusae, and hydrographical heterogeneities, may interactively influence the distribution patterns of copepods; furthermore, different copepod species and different stages of the same species may prefer different areas and perform different seasonal successions that are most advantageous to their survival, particularly in this highly competitive and complex hydrographical subtropical lagoon. In addition, our unpublished data suggest that copepods exerted a low grazing impact (3.5%) on phytoplankton in this lagoon, but their dominance in numbers allows them to be the main food source of other organisms of higher trophic

Table 4. Multiple regression coefficients of the 10 most-common copepod species in monthly samplings of Tapong Bay during 1999~2001. Species as dependent variables are listed in rows, and environmental factors as independent variables are listed in columns. * Significant at the 0.05 level; ** significant at the 0.01 level

Species	Temperature	Salinity	Chl. *a*
Paracalanidae copepodites	1.214	2.617	1.396
Copepoda nauplius	0.771	3.037	0.320
Acartia tsuensis	2.476	-6.353*	0.000
Oithonidae copepodites	12.597**	0.216	4.499*
Acartiidae copepodites	1.336	0.914	0.033
Parvocalanus crassirostris	0.020	5.607*	3.476
Oithona dissimilis	0.591	0.477	-0.064
Zausodes sp.	0.093	4.661*	0.154
Acrocalanus indicus	0.383	6.943*	0.306
Oithona simplex	0.457	5.863*	-0.157
Total copepods	4.726*	0.837	2.436
Species number	-14.119**	11.246**	-3.83
Species diversity index	-0.810	3.948	-1.249

Table 3. Mean abundance (mean ± SD, individuals/100 m^3), relative abundance (RA, %), and occurrence frequency (OR, %) of the 10 most dominant copepods at 3 stations in Tapong Bay during 1999~2001. Numbers within parentheses indicate the number of copepod species identified to family or genus level

	Stn. N			Stn. C			Stn. S		
Copepod species	Abundance	RA	OR	Abundance	RA	OR	Abundance	RA	OR
Paracalanidae copepodites	181,279 ± 179,213	23.31	100	9395 ± 11,876	5.39	23	9670 ± 13,520	1.86	91
Copepoda nauplius	43,736 ± 39,115	5.62	100	78,425 ± 185,428	44.96	100	66,739 ± 215,853	12.81	100
Acartia tsuensis	717 ± 1692	0.09	30	13,334 ± 31,573	7.64	15	168,488 ± 360,942	32.35	74
Oithonidae copepodites	90,780 ± 93,320	11.67	100	30,813 ± 53,064	17.66	100	55,668 ± 104,126	10.69	100
Acartiidae copepodites	64,752 ± 190,414	8.33	96	9907 ± 21,625	5.68	23	85,357 ± 269,595	16.39	96
Parvocalanus crassirostris	151,070 ± 195,800	19.42	96	4102 ± 6063	2.35	20	3008 ± 5761	0.58	70
Oithona dissimilis	50,180 ± 73,426	6.45	96	8356 ± 16,456	4.79	19	66,029 ± 136,463	12.67	87
Zausodes sp.	34,308 ± 38,652	4.41	100	6311 ± 6043	3.62	23	5260 ± 7835	1.01	91
Acrocalanus indicus	37,742 ± 54,737	4.85	91	1025 ± 2315	0.59	11	580 ± 1431	0.11	52
Oithona simplex	26,096 ± 38,320	3.36	100	1072 ± 1759	0.61	18	8089 ± 31,476	1.55	65
Total copepods	777,756 ± 770,656			174,434 ± 25,6415			520,866 ± 939,123		
Species number	33 (16)			24 (13)			26 (13)		
Species diversity index	2.92 ± 0.39			2.55 ± 0.68			2.58 ± 0.57		

levels, and thus they still play a significantly relevant role in trophic fluxes within the bay.

Acknowledgments: This research was supported by a grant from the National Science Council of the R.O.C. (NSC90-2621-Z-110-008) to W.T. Lo and a grant from the National Science Council of the R.O.C. (NSC90-2811-B-056-001) to C.t. Shih. We are grateful to Din-Din Chen, Hung-Yen Hsieh, Yu-Pang Hung, and Hsiang-Hao Huang for collecting the samples and other environmental data related to our study.

REFERENCES

Calbet A, S Garrido, E Saiz, M Alcaraz, CM Duarte. 2001. Annual zooplankton succession in coastal NW Mediterranean waters: the importance of the smaller size fractions. J. Plankton Res. **23:** 319-331.

Calbet A, MR Landry, RD Scheinberg. 2000. Copepod grazing in a subtropical bay. Species-specific responses to a mid-summer increase in nanoplankton standing stock. Mar. Ecol.-Prog. Ser. **193:** 75-84.

Castel J, C Courties. 1982. Composition and differential distribution of zooplankton in Arcachon Bay. J. Plankton Res. **4:** 417-433.

Chen EL. 2002. Population dynamics and feeding of the moon jellyfish (*Aurelia aurita*) in Tapong Bay, southwestern Taiwan. Master's thesis, National Sun Yat-sen Univ., Taiwan, 74 pp.

Chen QC, SZ Zhang, CS Zhu. 1974. On planktonic copepods of the Yellow Sea and the East China Sea, II. Cyclopoida and Harpacticoida. Stud. Mar. Sinica **9:** 27-76. (in Chinese, with English summary)

Cheng CC. 1998. The distributional correlation between planktonic copepods and ichthyoplankton in the western North Pacific. Master's thesis, National Taiwan Univ., Taipei.

Chihara M, M Murano. 1997. An illustrated guide to marine plankton in Japan. Tokyo: Tokai Univ. Press, pp. 649-1004.

Christous E. 1998. Interannual variability of copepods in a Mediterranean coastal area (Saronikos Gulf, Aegean Sea). J. Marine Syst. **15:** 523-532.

Dam HG, X Zhang, M Butler, MR Roman. 1994. Mesozooplankton grazing and metabolism on the equator at 140°W during the JGOFS EQUPAC study. EOS, Trans. Am. Geophys. Union **75:** 50.

Ferrari I, MT Cantarelli, MG Mazzocchi, L Tosi. 1985. Analysis of a 24-hour cycle of zooplankton sampling in a lagoon of the Po River Delta. J. Plankton Res. **7:** 849-865.

Hirakawa K, T Ikeda, N Kajihara. 1990. Vertical distribution of zooplankton in Toyama Bay, southern Japan Sea, with special reference to Copepoda. Bull. Plankton Soc. Jpn. **37:** 111-126.

Hsieh CH, TS Chiu. 1998. Abundance composition of the copepods in Tanshui River estuary and adjacent waters. Acta Zool. Taiwanica **9:** 1-9.

Hsieh CH, TS Chiu. 2002. Summer spatial distribution of copepods and fish larvae in relation to hydrography in the northern Taiwan Strait. Zool. Stud. **41:** 85-98.

Hwang JS, QC Chen, CK Wong. 1998. Taxonomic composition and grazing impact of calanoid copepods in coastal waters of northern Taiwan. Crustaceana **71:** 378-389.

Hwang JS, JT Turner. 1995. Behavior of cyclopoid, harpacticoid and calanoid copepods from coastal waters of Taiwan. Mar. Ecol. **16:** 207-216.

Landry MR, CJ Lorenzen, WK Peterson. 1994. Mesozooplankton grazing in the Southern California Bight. II. Grazing impact and particulate flux. Mar. Ecol. Prog. Ser. **115:** 73-85.

Lo WT, JS Hwang, QC Chen. 2001. Identity and abundance of surface-dwelling, coastal copepods of southwestern Taiwan. Crustaceana **74:** 1139-1157.

Miller CB, BW Frost, B Booth, PA Wheeler, MR Landry, N Welschmeyer. 1991. Ecological processes in the Subarctic Pacific: Iron limitation cannot be the whole story. Oceanography **4:** 71-78.

Omori M, H Ishii, A Fujinaga. 1995. Life history strategy of *Aurelia aurita* (Cnidaria, Scyphomedusae) and its impact on the zooplankton community of Tokyo Bay. ICES J. Mar. Sci. **52:** 597-603.

Riós-Jaha E. 1998. Spatial and temporal variations in the zooplankton community of Phosphorescent Bay, Puerto Rico. Estuar. Coastal Shelf Sci. **46:** 797-809.

Roff JC, JT Turner, MK Webber, RR Hopcroft. 1995. Bacterivory by tropical copepod nauplius, extent and possible significance. Aquat. Microb. Ecol. **9:** 165-175.

Shih CT, TS Chiu. 1998. Copepod diversity in the water masses of the southern East China Sea north of Taiwan. J. Marine Syst. **15:** 533-542.

Strickland JDH, TR Parsons. 1972. A practical handbook of seawater analysis. Bull. Fish. Res. Board Can. **167:** 1-310.

Su HM. 2002. Primary productivity and phytoplankton community in the Tapong Bay and the Kaoping coastal waters. Annual Report of the National Science Council, Taiwan, pp. 893-910. (in Chinese)

Tan, TH 1967. On distribution of copepods in the surrounding waters of Taiwan. Rep. Inst. Fish. Biol. Min. Econ. Affairs. Natl. Taiwan Univ. **2:** 14-20.

Tseng WY. 1972. On Copepoda of the family Candaciidae in the northeast sea-waters of Taiwan. *In* K Sugawara, ed. The Kuroshio II. Proceedings of the Second Symposium on the Results of the Cooperative Study of the Kuroshio and Adjacent Regions. Tokyo. 28 Sept.-1 Oct. 1970. Tokyo: Saikon Publishing, pp. 245-259.

Wickham SA. 1995. Trophic relations between cyclopoid copepods and ciliated protists. Complex interactions link the microbial and classic food webs. Limnol. Oceanogr. **40:** 1173-1181.

Wong CK, JS Hwang, QC Chen. 1998. Taxonomic composition and grazing impact of calanoid copepods in coastal waters near nuclear power plants in northern Taiwan. Zool. Stud. **37:** 330-339.

Yamaji I. 1984. Illustrations of the marine plankton of Japan. Osaka: Hoikusha Publishing, pp. 294-387.