Zoological Studies **47**(2): 172-184 (2008)

Zoological Studies

The Coupling of Copepod Assemblages and Hydrography in a Eutrophic Lagoon in Taiwan: Seasonal and Spatial Variations

Pei-Kai Hsu[1], Wen-Tseng Lo[1,*], and Chang-tai Shih[1,2,3]

[1]*Department of Marine Biotechnology and Resources, National Sun Yat-Sen University, Kaohsiung 804, Taiwan*
[2]*Department of Environmental Biology and Fisheries Science, National Taiwan Ocean University, Keelung 202, Taiwan*
[3]*Canadian Museum of Nature, Ottawa, K1P 6P4, Canada*

(Accepted September 21, 2007)

Pei-Kai Hsu, Wen-Tseng Lo, and Chang-tai Shih (2008) The coupling of copepod assemblages and hydrography in a eutrophic lagoon in Taiwan: seasonal and spatial variations. *Zoological Studies* **47**(2): 172-184. Seasonal and spatial variations in the species composition and abundances of copepods in relation to hydrographic conditions in Tapong Bay, a tropical eutrophic lagoon in southwestern Taiwan, were investigated bimonthly in 2003. The water temperature, salinity, and chlorophyll *a* (Chl *a*) of the bay showed apparent seasonal changes, with cold, saline, low-Chl *a* water in the dry winter (Dec. and Feb.) in contrast to warm, fresh, and high-Chl *a* water in the rainy summer (June and Aug.). In all, 84 copepod species belonging to 15 families and 23 genera were identified. *Parvocalanus crassirostris*, *Bestiolina amoyensis*, *Oithona oculata*, *Acartia sinjiensis*, *Acartia* sp., and *Temora turbinata* were predominant, and together they comprised 86.4% of the total number of copepods. Although copepod parameters showed no significant quantitative differences among seasons or sites, they showed apparent variations and succession in some months and at some stations, implying that different species may dominate different regions with different seasonal distribution patterns. These variations in copepod assemblages can also be seen from results of a principal component analysis of station groups and cluster analysis of species groups. The copepod assemblage showed larger variations in winter and in the inner bay than in other seasons and regions, and each station group displayed a distinctive distribution pattern. Our results suggest that even though removal of oyster culture racks in 2002 resulted in an apparent increase in zooplankton number, multiple environmental variables, such as food sources, wastewater discharges, tidal flushing, and climate, are still interactively influencing the distribution patterns of copepods as they were previously shown to be doing in the bay. http://zoolstud.sinica.edu.tw/Journals/47.2/172.pdf

Key words: Copepods, Distribution, Human impact, Lagoon.

Coastal lagoons, estuaries, and bays are characterized by abrupt changes in environmental parameters both temporally and spatially due to the influences of tides, coastal currents, freshwater runoff, atmospheric processes, and anthropogenic activities. These areas are also recognized as highly dynamic and diverse regions of high productivity of their plankton assemblages (Islam et al. 2005), because regular inputs of allochthonous and anthropogenic nutrients from land (Schlesinger 1991, Malone et al. 1996, Marcus 2004) are beneficial for phytoplankton and zooplankton growth. These areas serve as nursery grounds for larval and juvenile stages of many marine organisms (Wallace et al. 1984, Williamson and Mather 1994, Joyeux and Ward 1998). Copepods usually predominate in marine zooplankton communities and hold a key position in marine food webs as the major secondary producers of the world's oceans (Parsons et al. 1984, Huys and Boxshall 1991, Mauchline 1998). They feed primarily on phytoplankton and also are consumed by marine organisms of higher trophic levels. Thus their distribution patterns may directly affect the dynamics of primary production and fishery resources in the ocean (Castel and Courties

*To whom correspondence and reprint requests should be addressed. E-mail:lowen@mail.nsysu.edu.tw

1982, Ohman and Hirche 2001). The distribution patterns of copepods are often influenced by environmental factors, especially in estuaries, bays, and lagoons. Copepods often exhibit clumped distributions at some times and places, and are obviously influenced by anthropogenic activities and hydrodynamic processes (Carleton and Doherty 1998, Chang et al. 2004, Hsiao et al. 2004, Hsieh et al. 2004, Marcus 2004). Therefore, studying spatiotemporal variations of copepods in relation to environmental variables is important in understanding secondary production and dynamic coastal ecosystems.

The present study site, Tapong Bay, is a semi-enclosed tropical lagoon with a total area of around 4.44 km^2 in southwestern Taiwan (22°27'N, 120°26'E) (Fig. 1). It is a shallow lagoon with an average depth of 2.2 m; the depth varies from 1 m near the tidal inlet in the north to 6 m in the inner bay. The water exchange rate in the bay is low due to there being only a single small inlet (1 km long, 138 m wide, and 1-2 m deep) connecting the bay with the Taiwan Strait. The water flushing time of the inlet region (8% to 25%/d) is generally twice that of the inner region (4% to 12%/d). The resulting differences between the inlet and inner bay in the ecosystem production were described in detail by Su et al. (2004). The bay is characterized by very high primary productivity with significant spatial and temporal variability, generally higher in the inner bay and in summer than in the inlet region and in winter (Su 2002). Before 2002, the impacts of human activities on the bay were obvious due to the extensive aquaculture structures and the surrounding drainages with mass nutrient inputs from urban areas and fishponds that consequently influenced the distribution patterns of organisms in the bay. In 2002, the bay was cleaned up by the complete removal of all culture-racks when the area officially became a National Scenic and Recreational Park. The striking results of the complete culture-rack removal were the disappearance of the jellyfish (*Aurelia aurita*, Lo et al. 2004) and oyster (*Crassostrea gigas*, Lin et al. 2005) from the bay, which were important top-down controllers of copepods and phytoplankton communities, respectively. This thus provided an opportunity to examine seasonal and spatial variations in copepod community structure in relation to environmental variables in the bay after culture-rack removal, and to compare differences in biotic and abiotic variables from those before the removal. The possible causes of environmental variables and anthropogenic perturbations were also evaluated and are discussed.

MATERIALS AND METHODS

Six stations along a transect from the inlet to the inner region of Tapong Bay were selected (Fig. 1). Zooplankton samples were taken during

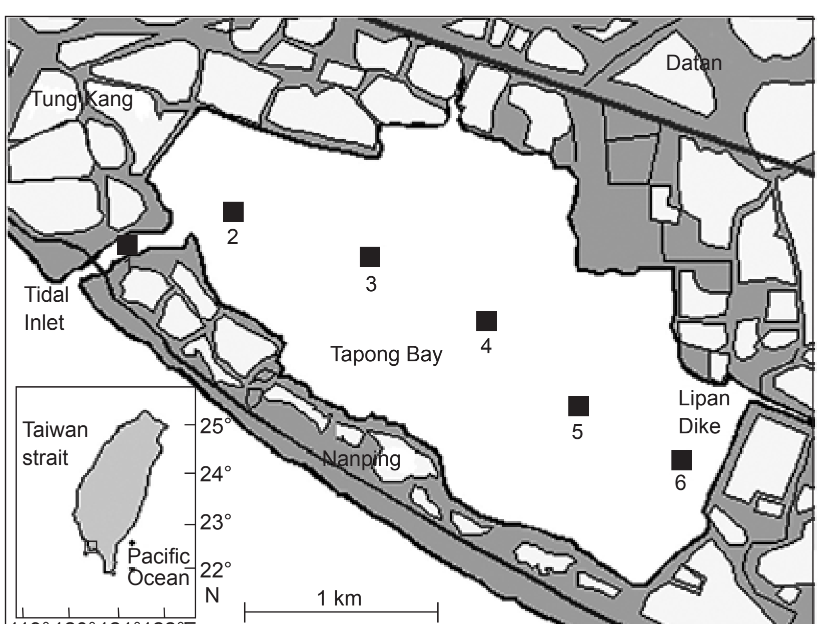

Fig. 1. Location of the sampling stations in Tapong Bay, southwestern Taiwan.

the flood tide in the daytime bimonthly from Feb. to Dec. 2003. Samples were collected using a NorPac net with 45 cm mouth opening and 200 μm mesh, and a flowmeter (HydroBios) mounted in the center of the mouth opening to calculate the filtered water volume. The net was towed near the surface (0-1 m) at a speed of about 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. In the laboratory, each zooplankton sample was repeatedly divided using a Folsom plankton splitter until the subsample contained about 500 specimens. Copepods were then identified and counted. The total number of individuals (ind.) of each copepod taxon was recorded (as ind./m^3), and the Shannon diversity index was calculated for each station.

At each station, temperature and salinity near the water surface were measured with a portable conductivity-temperature sensor, and 1 L of surface seawater was collected in a dark bottle and preserved in an icebox for later measurement of the chlorophyll *a* (Chl *a*) concentration. For Chl *a* analyses, seawater samples were kept below 4°C; 500 ml of seawater was filtered through Whatman 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, Tokyo, Japan) before and after acidification with 10% hydrochloric acid. The amount of Chl *a* was calculated using the equations of Strickland and Parsons (1972).

The Kruskal-Wallis test was used to determine whether environmental factors, Chl *a*, copepod abundance, species number, and the species diversity index significantly differed among study sites (6 levels) or among months (6 levels). If the results of the Kruskal-Wallis test were significant at the $p < 0.05$ probability level, then Fisher's least-squares difference (LSD) test was used to determine which means significantly differed. We also used a forward stepwise regression and partial correlation coefficients to evaluate the relationships of the logarithmic abundance (abundance + 1) of the 6 most-common copepods species with environmental variables.

For the community analysis, the logarithmic

Table 1. Results of the Kruskal-Wallis test of copepod abundance, species number, diversity index (H'), and environmental variables measured at 6 stations in Tapong Bay, Taiwan

Source	*d.f.*	*F* value	*p*	Separation[1]
Abundance				
Station	5	3.523	0.620	
Month	5	11.554	0.041	June^a, Apr.^{a}, Dec.^{ab}, Feb.^{ab}, Oct.^{b}, Aug.^{b}
Species number				
Station	5	11.718	0.039	6^a, 5^{ab}, 1^{ab}, 4^b, 2^b, 3^b
Month	5	9.166	0.102	
H'				
Station	5	4.769	0.445	
Month	5	9.768	0.082	
Temperature				
Station	5	1.432	0.921	
Month	5	31.999	<0.001	Dec.^{a}, Feb.^{b}, Oct.^{c}, Apr.^{d}, June^e, Aug.^{e}
Salinity				
Station	5	3.072	0.689	
Month	5	27.083	<0.001	June^a, Aug.^{a}, Oct.^{b}, Dec.^{bc}, Apr.^{c}, Feb.^{c}
Chl *a*				
Station	5	12.098	0.033	1^a, 2^a, 3^a, 4^{ab}, 5^{ab}, 6^b
Month	5	14.302	0.014	Feb.^{a}, Dec.^{ab}, Apr.^{abc}, Aug.^{bc}, Oct.^{bc}, June^c

[1]If the results of Kruskal-Wallis test indicated significant treatment effects at the $p < 0.05$ probability level, then Fisher's protected least-squares difference test indicated which means significantly differed. Means with the same letter do not significantly differ. *d.f.*, degree of freedom.

abundance (abundance + 1) of the 41 most common species (those with occurrence rates of > 10%) were standardized, and then a principal component analysis (PCA) (Gauch 1982) was used to reveal variations in the copepod assemblages among stations and months. To identify groups of copepod species the logarithmic abundances of which co-varied, the data matrix was transposed so that samples became variables, and then cluster analysis (CA) with the minimum variance (or Ward) linkage (Everitt 1974) was used to determine the co-varying species groups. The numerical abundances of all copepod species in each group were integrated and averaged to display their distribution patterns.

RESULTS

Hydrographic conditions

The hydrography and climate of Tapong Bay showed clear seasonal changes with a distinct dry season (Oct. to May) with lower temperatures, higher salinities, and much less rain than in the wet season (June to Sept.). Results of the Kruskal-Wallis test showed significant differences in water temperature and salinity among months, but not among stations (Table 1), revealing that seasonal changes might be more significant than those among stations. Generally, greater seasonal differences in temperature and salinity were found at inner stations (stns. 5 and 6) than those at inlet stations (stns. 1 and 2), in that temperatures were usually higher in the warm-wet season and lower in the cold-dry season at the inner stations (Fig. 2). Salinity was significantly lower in the wet season than in the dry season due to high precipitation in summer, and again showed larger seasonal differences at the inner stations than at the inlet stations (Table 1, Fig. 2). The Chl *a* concentration exhibited significant differences among stations and months (Table 1), with generally higher values at the inner region (stns. 5 and 6) and in summer and early autumn (June to Oct.) than in the inlet region (particularly at stn. 1) and in winter (Feb.). The highest Chl *a* concentration was found in Oct. in the inner region (stns. 5 and 6) when precipitation apparently decreased and the weather was still warm; the largest difference among stations was also found in that month compared with other seasons (Fig. 2).

Copepod composition and abundances

Copepods were the predominant taxonomic group in the zooplankton community in Tapong Bay during the study period, particularly the calanoid copepods, which comprised 76.3% of the numerical total of all zooplankton (Table 2). We recognized 84 species of copepods belonging to 15 families and 23 genera, with the mean numerical abundance of (1.2 ± 0.3) × 10^4 ind./m^3. The families Corycaeidae and Oithonidae were very diverse in species, containing 15 and 12 species, respectively, while the family Euterpinidae had only 1 species, *Euterpina acutifrons* (Tables 3, 4). Among the copepods, *Parvocalanus crassirostris* was predominant, accounting for

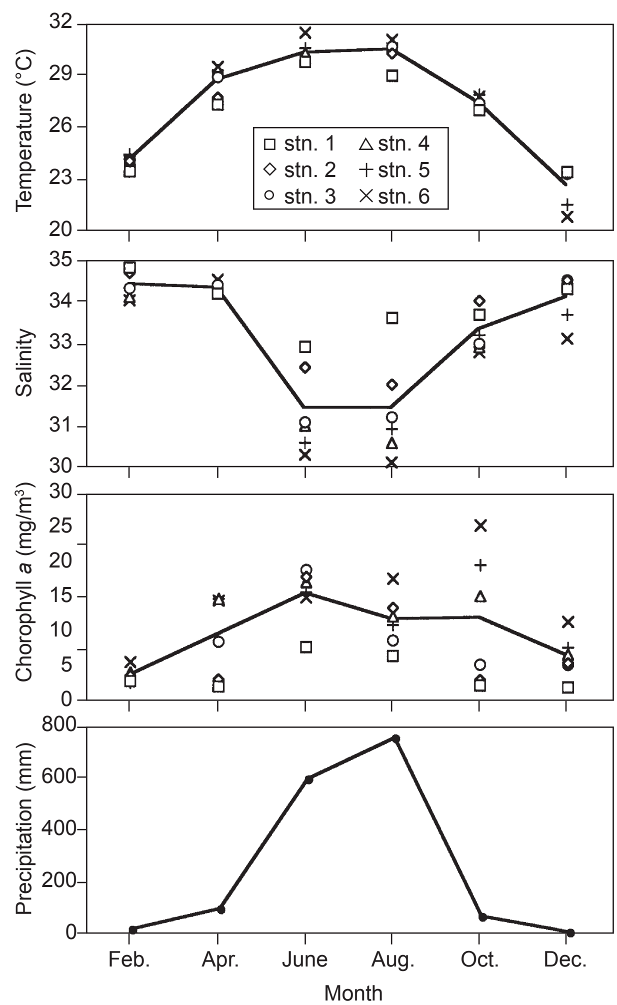

Fig. 2. Seasonal changes in water temperature, salinity, chlorophyll *a*, and precipitation in Tapong Bay, southwestern Taiwan in 2003. The line indicates the mean. Precipitation data are from the Central Weather Bureau of Taiwan (http://www.cwb.gov.tw/).

30% of the total copepod numbers and occurring at almost all stations and in all months. Other common copepods included *Bestiolina amoyensis* (19%), *Oithona oculata* (16%), *Acartia sinjiensis* (11%), *Acartia* sp. (8%), and *Temora turbinata* (4%); their occurrence frequencies were all > 72% (Table 4). The average species number and species diversity index of the copepods were 15 ± 1 and 2.2 ± 0.1, respectively (Table 4).

Spatial and seasonal variations

The copepod abundances showed significant differences among months; species number significantly differed among stations; and the species diversity indices showed no significant differences among stations or months (Table 1). Our preliminary results showed higher mean abundances with larger differences among stations from late summer to winter (Aug. to Feb.) and lower abundances with smaller differences in spring and early summer (Apr. and June), while species numbers and species diversity indices showed small seasonal changes but with generally higher values in the middle region (stns. 3 and 4), lower values in the inner bay at stn. 6, and larger differences among stations during the dry season (Dec. and Feb.) (Fig. 3). Different predominant copepods displayed different spatial and seasonal patterns. *Parvocalanus crassirostris*, a very common species in the coastal waters of southwestern Taiwan, usually dominated in the inlet area (stns. 1 and 2) and from Aug. to Dec.; in Dec., it comprised up to 70% of the total copepod count. *Bestiolina amoyensis* and *Oithona oculata* were very common in the inner bay (stns. 5 and 6) and in the late wet season (Aug. and Oct.); *Acartia sinjiensis* and *Acartia* sp. showed maximum

Table 2. Mean abundances (mean ± SE, individuals (ind./m^3) and relative abundances (RA, %) of zooplankton taxonomic groups in Tapong Bay, Taiwan during 2003

Taxonomic group	Abundance	
	mean ± SE	RA (%)
Calanoida	11,338 ± 2190	76.3
Barnacle nauplius	708 ± 259	4.8
Copepod nauplius	576 ± 320	3.9
Appendicularia	570 ± 139	3.8
Cladocera	493 ± 304	3.3
Cyclopoida	415 ± 112	2.8
Other Mollusca	334 ± 118	2.2
Ostracoda	57 ± 13	0.4
Pteropoda	56 ± 16	0.4
Harpacticoida	55 ± 19	0.4
Echinodermata larva	49 ± 23	0.3
Fish eggs	41 ± 10	0.3
Polychaeta	33 ± 11	0.2
Chaetognatha	32 ± 10	0.2
Crab zoea	30 ± 7	0.2
Shrimp larva	23 ± 5	0.2
Medusa	11 ± 4	0.1
Mysidacea	8 ± 5	0.1
Others	34 ± 17	0.2
Total zooplankton	14,863 ± 2486	100.0

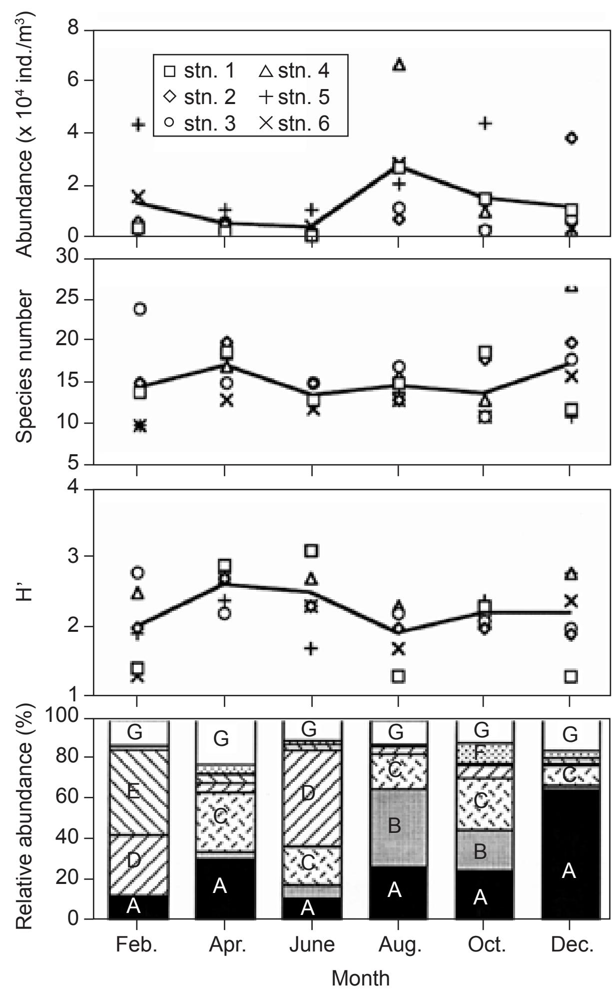

Fig. 3. Seasonal changes in numerical abundance, species number, species diversity index (H'), and the relative abundance of the 6 predominant copepod species in Tapong Bay, southwestern Taiwan in 2003. The line indicates the mean; letters in the lowest graph represent the following: A, *Parvocalanus crassirostris*; B, *Bestiolina amoyensis*; C, *Oithona oculata*; D, *Acartia sinjiensis*; E, *Acartia* sp.; F, *Temora turbinata*; and G, other copepods.

Table 3. List of copepod species identified in Tapong Bay, Taiwan in 2003

Calanoida

Acartiidae

Acartia danae Giesrecht, 1889
A. erythraea Giesrecht, 1889
A. japonica Mori, 1937
A. negligens Dana, 1849
A. omorii Bradford, 1976
A. pacifica Steuer, 1915
A. sinjiensis Mori, 1937
A. tsuensis Ito, 1956
Acartia sp.

Calaniidae

Canthocalanus pauper (Giesbrecht, 1889)
Undinula vulgaris (Dana, 1849)

Centropagidae

Centropages gracilis (Dana, 1849)
C. orsini (Giesbrecht, 1889)
C. tenuiremis Thompson & Scott, 1903

Clausocalanidae

Clausocalanus furtatus (Brady, 1883)
C. parapergens Frost & Fleminger, 1968
Clausocalanus sp.
Pseudocalanus minutus Kroyer, 1845

Euchatidae

Euchaeta concinna (Dana, 1849)

Lucicutiidae

Lucicutia flavicornis (Claus, 1863)

Paracalanidae

Acrocalanus gibber Giesbrecht, 1888
A. gracilis Giesbrecht, 1888
A. longicornis Giesbrecht, 1888
Bestiolina amoyensis Li & Huang, 1984
Calocalanus pavoninus Farran, 1936
Paracalanus aculeatus Giesbrecht, 1888
P. denudatus Sewell, 1929[a]
P. gracilis Chen & Zhang, 1965
P. parvus (Claus, 1863)
Paracalanus sp.
Parvocalanus crassirostris Dahl, 1893

Pontellidae

Labidocera euchaeta Giesbrecht, 1889
L. pavo Giesbrecht, 1889
L. rotunda Mori, 1937
Labidocera sp.
Pontellina sp.
Pontellopsis tenuicauda (Giesbrecht, 1889)

Pseudodiaptomidae

Pseudodiaptomus annandalei Sewell, 1919
P. marinus Sato, 1913
P. pacificus Walter, 1986
P. penicillus Li & Huang, 1984
P. serricaudatus T. Scott, 1894
P. trihamatus Wright, 1973
Pseudodiaptomus sp.

Temoridae

Temora stylifera (Dana, 1849)
T. turbinata (Dana, 1849)
Temora sp.

Cyclopoida

Oithonidae

Oithona aruensis Früchtl, 1923
O. attenuata Farran, 1913
O. brevicornis Giesbrecht, 1891
O. dissimilis Lindberg, 1940
O. fallax Farran, 1913
O. longspina Nishida, 1977
O. oculata Farran, 1913
O. rigida Giesbrecht, 1891
O. robusta Giesbrecht, 1891
O. simplex Farran, 1913
O. setigera Dana, 1849
O. tenuis Rosendorn, 1913
Oithona sp.

Poecilostomatoida

Corycaeidae

Corycaeus (Corycaeus) clause F. Dahl, 1894
C. (C.) crassiusculus Dana, 1849
C. (C.) speciosus Dana, 1849
C. (Ditrichocoryaeus) andrewsi Farran, 1911
C. (D.) dahli Tanaka, 1957
C. (D.) erythraeus Cleve, 1901
C. (Monocorycaeus) robustus Giesbrecht, 1891
C. (Onychocorycaeus) agilis Dana, 1849
C. (O.) catus F. Dahl, 1894
C. (O.) giesbrechti F. Dahl, 1894
Corycaeus sp.
Farranula carinata Giesbrecht, 1891
F. concinna (Dana, 1847)
F. gibulla Giesbrecht, 1891
F. longicaudis Dana, 1849
F. rostratus Claus, 1863

Onceaidae

Oncaea meida Giesbrecht, 1891
O. mediterranea Claus, 1863
O. venusta Philippi, 1843
Oncaea sp.

Harpacticoida

Euterpinidae

Euterpina acutifrons (Dana, 1847)
Euterpina sp.

Ectinosomatidae

Microsetella norvegica (Boeck, 1846)
M. rosea (Dana, 1847)

[a]Andronov (1977) considered this species synonymous with *Paracalanus pygmaeus* (Claus, 1863).

abundances in the inner bay and in Feb.; while *Temora turbinata* had higher abundances in autumn in the inlet region (stns. 1 and 2) (Figs. 3, 4).

Community structure

The result of the PCA run on the logarithmic abundances of the 41 most common copepod species illustrated differences among some sampling months. When plotted subjectively with month, the scattering range among stations in Feb. was separated from that of Aug., as well as other months, implying that copepod assemblages obviously varied among some months (Fig. 5). Also, samples (stations) from the dry winter season (Feb. and Dec.) were more scattered (i.e., had greater variation) than those from other seasons, revealing that variations in copepod assemblages between inner and inlet stations were more apparent in winter than in other seasons.

Table 4. Average abundances (mean ± SE, individuals (ind./m^3), relative abundances (RA, %), and occurrence frequencies (OR, %) of the 20 predominant copepods in Tapong Bay, southwestern Taiwan, in 2003

	Abundance	RA	OR
Parvocalanus crassirostris	3611 ± 972	29.6	97
Bestiolina amoyensis	2306 ± 1125	18.9	72
Oithona oculata	1953 ± 608	16.0	89
Acartia sinjiensis	1265 ± 456	10.4	94
Acartia sp.	1024 ± 664	8.4	89
Temora turbinata	426 ± 132	3.5	92
Copepod nauplius	231 ± 101	1.9	92
Euterpina acutifrons	217 ± 55	1.8	94
Acartia erythraea	197 ± 97	1.6	89
Paracalanus parvus	153 ± 92	1.3	25
Oithona sp.	138 ± 57	1.1	94
Oithona brevicornis	127 ± 30	1.0	92
Acrocalanus gracilis	88 ± 29	0.7	67
Oithona attenuata	69 ± 19	0.6	86
Oithona simplex	67 ± 32	0.5	78
Paracalanus sp.	58 ± 16	0.5	92
Pseudodiaptomus sp.	42 ± 8	0.3	78
Acartia negligens	26 ± 24	0.2	17
Acartia tsuensis	26 ± 15	0.2	22
Temora sp.	22 ± 6	0.2	69
Other copepods (64 species.)	154 ± 91	1.3	-
Total copepods	12,200 ± 2510	100.0	-
Species number	15 ± 1		
Species diversity index H'	2.2 ± 0.1		

Four copepod species groups (I, II, III, and IV) were distinguished by the cluster analysis (Fig. 6). Generally, the species groups were distinctly separated, and each had different spatial and seasonal distribution patterns. The 1st group contained 12 taxa, all of which were predominant with rankings within the top 16 in table 4; these taxa had higher occurrence frequencies and usually had higher abundances in summer and autumn. The 2nd group contained 6 taxa that generally predominated in the inner bay (at stns. 5 and 6) and had peak abundances in Feb. The 3rd group included 21 taxa that generally had lower abundances and occurrence rates in comparison with the other groups, and had higher abundances in winter (i.e., Dec. and Feb.). The last group included only 2 taxa, *Pseudodiaptomus marinus* and *Paracalanus parvus*, which had higher abundances in the inlet and middle (stns. 3 and 4) bay in Aug., but were relatively rare or even absent in other seasons.

Copepods and environmental variables

Results of the multiple regression revealed that only 2 species, *Bestiolina amoyensis* and *Oithona oculata*, showed significant positive correlations with temperature; *Acartia sinjiensis* was positively correlated ($p < 0.05$) with Chl *a*, but the copepod species number was negatively correlated with it ($p < 0.05$) (Table 5). No significant correlations were found between salinity and copepods.

DISCUSSION

Tapong Bay is a highly eutrophic and productive tropical lagoon with obvious seasonal and spatial variations. Higher Chl *a* concentrations were often found in the inner bay and in summer and autumn than in the inlet region and in winter (Table 1, Fig. 2). This probably occurred because the surrounding aquaculture ponds discharge nutrient-rich wastewater through Lipan Dike into the inner bay, particularly in the rainy summer. Furthermore, due to its small area and shallow depth with only 1 small tidal inlet for water exchange, the lagoon water is poorly flushed and thus is easily influenced by human activities, rainfall, and tidal effects. Similar distribution patterns of nutrients, phytoplankton abundance, and gross primary production were also observed by Hung and Hung (2003) and Su et al. (2004) in the same study area, indicating that, compared with the inlet region with higher tidal flushing and turbidity, the inner bay might be more predisposed to developing eutrophication and phytoplankton blooms. Furthermore, the oversupply of nutrients and relatively poor flushing in the inner bay also cause hypoxia and oxygen-deficient conditions near the bottom layer in most seasons except winter when stronger vertical mixing occurs due to an intruding coastal current and the northeast monsoon (Hung and Hung 2003). All of those studies revealed that Tapong Bay is a sensitive ecosystem and obviously influenced by physical and chemical processes and anthropogenic impacts, which consequently may affect the distribution patterns of aquatic organisms in the bay (Lo et al. 2004; Su et al. 2004).

Both the abundance and species numbers of copepods were obviously higher than found during previous studies of Tapong Bay (Table 6). This is probably because the oyster culture racks and fish cages, which had been in place for the past several decades and sometimes occupied up to 80% of the bay's area, were removed in 2002 during development of Tapong Bay as a National Scenic and Recreational Park. Most of the environmental variables, including salinity, light extinction, water motion, and Chl *a* concentration increased after the removal, except the concentration of dissolved inorganic phosphorus (DIP) which significantly decreased (reviewed in table 6), revealing that removal of aquaculture structures caused an apparent chain effect on the aquatic ecosystem of the bay. The water exchange rate between the bay and coastal waters became more rapid than before, implying that more coastal water flowed into and mixed with the bay water per time than before, resulting in increased bay water salinities and copepod species numbers (Table 6). This was more obvious in the middle region of the bay

Table 5. Results of stepwise regression and partial correlation coefficient (*R*) evaluating the relationships of the abundances of the 6 predominant species of copepods with environmental variables in Tapong Bay during the study period in 2003. T, temperature; S, salinity; C, chlorophyll *a*

Species	R for T	R for S	R for C	Predictive equation
Parvocalanus crassirostris	0.046	0.088	-0.193	ns
Bestiolina amoyensis (Ba)	0.564**	-0.108	0.268	Ba = -7.681 + 0.402T
Oithona oculata (Oo)	0.422*	-0.068	0.196	Oo = -1.877 + 0.229T
Acartia sinjiensis (As)	-0.047	-0.145	0.397*	As = 3.281 + 0.083C
Acartia sp.	-0.213	0.071	-0.071	ns
Temora turbinata	-0.042	0.160	-0.112	ns
Total copepods	0.089	-0.110	-0.041	ns
Species number (Sn)	0.015	0.137	-0.344*	Sn = 17.152 - 0.208C
Species diversity index H'	0.123	-0.016	0.179	ns

ns, not significant; * $p < 0.05$; ** $p < 0.01$.

Table 6. Comparisons of environmental variables and copepod abundances (mean ± SE, individuals (ind./m^3) and species number in Tapong Bay between before and after the complete removal of oyster-culture racks in 2002. DIN, dissolved inorganic nitrogen; DIP, dissolved inorganic phosphorus

	Before removal	After removal	References
Water temperature (°C)	26.9 ± 1.2	27.2 ± 0.9	Lo et al. 2004; this study
Salinity	30.7 ± 0.9	33.3 ± 0.3**	Lo et al. 2004; this study
Chl *a* (mg/m^3)	2.8 ± 0.5	9.7 ± 1.7**	Lo et al. 2004; this study
Light extinction (m^{-1})	1.4 ± 0.2	3.0 ± 0.2*	Su et al. 2004; Lin, unpubl. data
Water motion (g/d)	10.2 ± 0.7	16.1 ± 0.4**	Su et al. 2004; Lin unpubl. data
DIN (μM)	21.2 ± 5.5	18.3 ± 4.6	Su et al. 2004; Lin unpubl. data
DIP (μM)	6.4 ± 1.2	3.9 ± 1.2*	Su et al. 2004; Lin unpubl. data
Copepod (ind./m^3)	4969 ± 1334	12200 ± 2510**	Lo et al. 2004; this study
Copepod species number	51	84	Lo et al. 2004; this study

* $p < 0.05$; ** $p < 0.01$.

at stns. 3 and 4, which usually showed higher copepod species richness values and salinities (Figs. 2, 3). We speculated that the middle region of the bay is probably a transition zone where the bay and coastal waters mix, particularly in the dry winter season (Dec. and Feb.) when precipitation is low and the warm and highly saline Kuroshio Branch Current dominates the southwestern coast of Taiwan (Jan et al. 2002) and brings diverse neritic planktonic species into the bay during the flood tide (Huang 2002). Despite the dramatic changes in the bay ecosystem brought about by the removal of the oyster racks (Lin unpubl. data), the spatial distribution of Chl *a* concentrations and copepod abundances generally exhibited similar patterns as before their removal, having higher values in the inner bay and decreasing toward the inlet region. One of the most important factors influencing these plankton distribution patterns might be tidal flushing (Su et al. 2004). The higher velocity of tidal flushing produces higher turbidity in the shallow inlet region (at ca. 1 m deep), which is physically unfavorable for planktonic organisms; in contrast, the poorly flushed, deeper inner bay (1-5 m deep), with lower flow velocities (< 10 cm/s) and nutrient-rich drainage from surrounding fishponds, might be advantageous for phytoplankton blooms. Like other bivalves, oysters are known to be highly efficient filter-feeders that usually have an obvious impact on phytoplankton in lagoons and estuaries

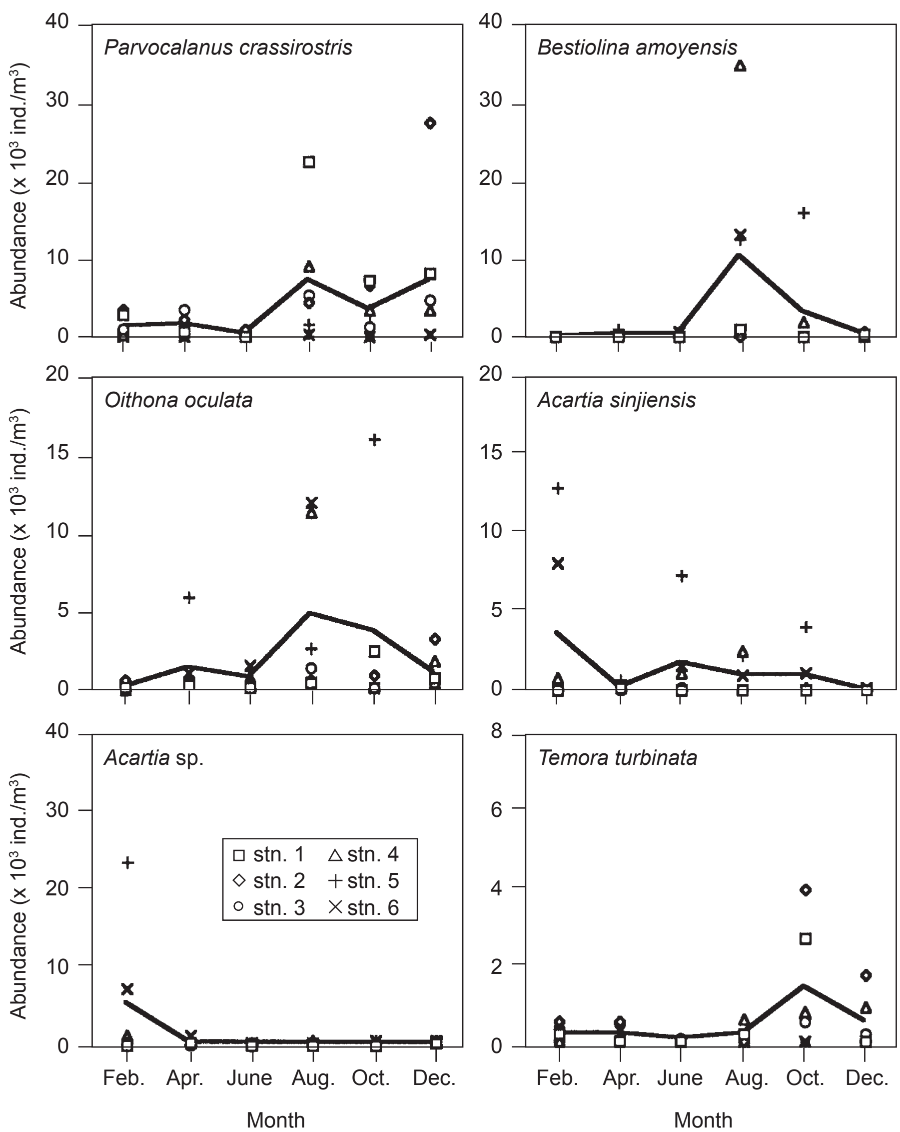

Fig. 4. Seasonal changes in the numerical abundances of the 6 predominant copepod species in Tapong Bay, southwestern Taiwan in 2003. The line indicates the mean.

worldwide (Newell 1998, Souchu et al. 2001). In Tapong Bay, the removal of oyster-culture racks resulted in respective increases in Chl *a* concentrations and phytoplankton abundances of up to 4-10 and 3-20 fold (Su 2003, Lin et al. 2006), suggesting the important role oysters had formerly played in this aquatic food web. In addition, the moon-jellyfish, *Aurelia aurita*, which occurred abundantly in the inner bay before culture rack removal, has disappeared, possibly due to the loss of oyster culture racks as substrata for its polyps. Chen (2002) found that the moon-jellyfish had a significant feeding impact on zooplankton (14%-41%) in the bay, and fed primarily on

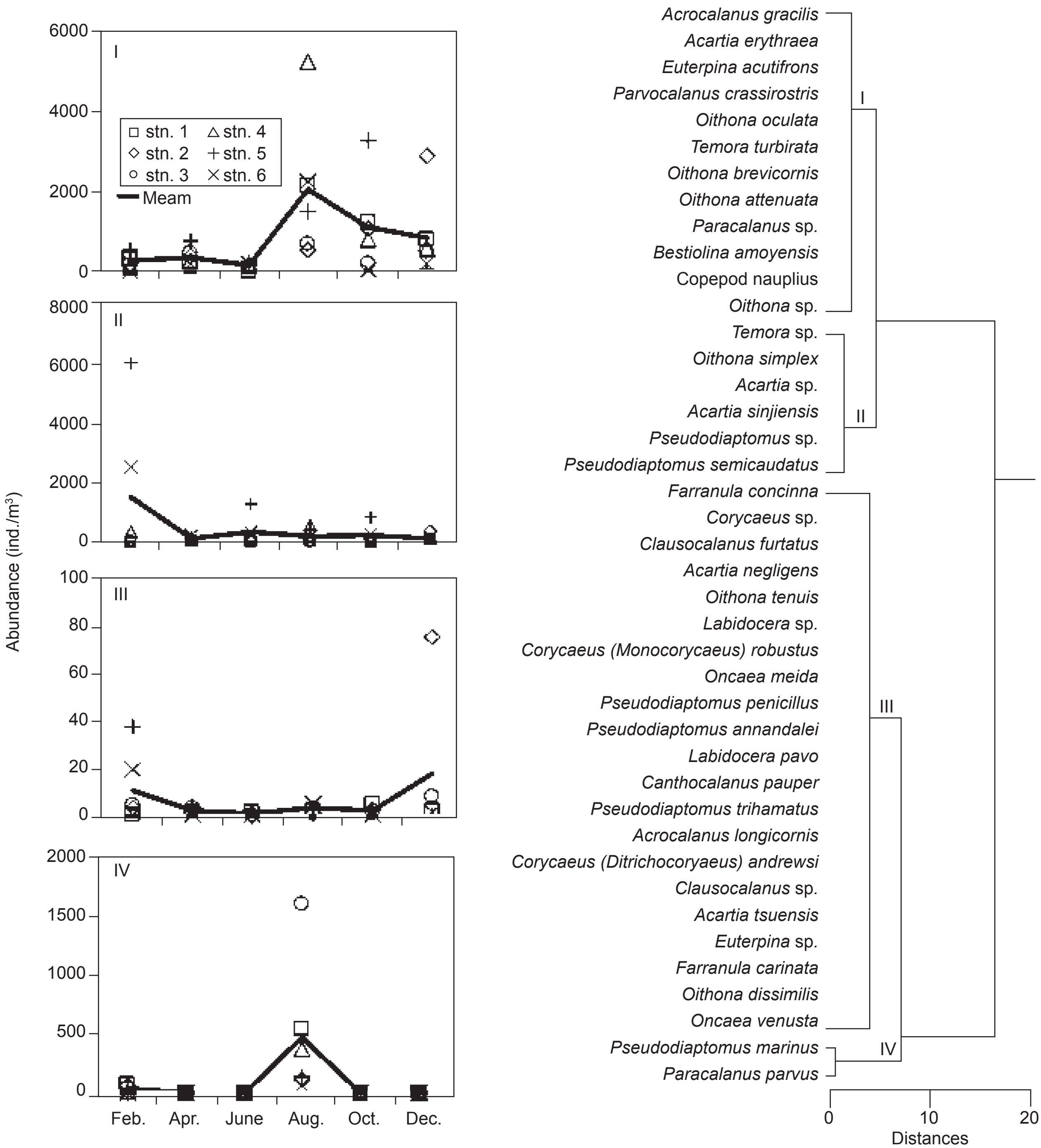

Fig. 5. Copepod assemblages and their distribution patterns in Tapong Bay, southwestern Taiwan in 2003. The line indicates the mean.

copepods (70%). Therefore, we propose that both the release of predation pressure from the jellyfish and oysters and the increase in phytoplankton are 2 important factors causing increased copepod abundances in the inner bay.

Copepods and other planktonic taxa are generally very sensitive to environmental changes and usually exhibit clear spatial and temporal successional patterns, particularly in coastal waters, lagoons, and estuaries where human impacts, climatic influences, and hydrodynamic processes are always strong and species-specific behaviors are also distinct (Carleton and Doherty 1998). Variations in copepod abundances were previously observed in many areas, such as in Phosphorescent Bay, Puerto Rico (Riós-Jaha 1998), St. Lawrence estuary, Canada (Plourde et al. 2002), and Chikugo estuary, Japan (Islam et al. 2005). In Tapong Bay, although the abundance, species number, and diversity index of copepods were not statistically significant (Table 1), they showed obvious differences among stations in some seasons (Fig. 3). For instance, copepod abundances had obvious differences among stations from Aug. to Dec., with relative highs at stations in the middle or inner bay, in contrast to the generally low abundances and smaller differences among stations in spring (Apr.) and early summer (June); copepod species number also showed obvious differences among stations in winter compared to those in summer (Fig. 3). Thus, these variations were probably due to the fact that each of these stations was characterized by different predominant species with distinct seasonal distribution patterns. This can also be clearly seen from the distribution patterns of the copepod assemblages (Fig. 6) and of the 6 predominant copepods (Fig. 4). For example, *Parvocalanus crassirostris*, *Bestiolina amoyensis*, *Oithona oculata*, and *Temora turbinata* predominated during and after the warm-wet season (from Aug. to Dec.), but *P. crassirostris* and *T. turbinata* were more abundant in the inlet region, while *B. amoyensis* and *O. oculata* were abundant in the inner bay. *Acartia sinjiensis* and *Acartia* sp. (probably the copepodite stage of *A. sinjiensis* and having a similar distribution pattern as the latter) were abundant at inner stations in Feb. (Fig. 4). Based on descriptions by Chen and Zhang (1965), Chen et al. (1974), Li and Huang (1984), Yamaji (1984), and Chihara and Murano (1997) of the ecological characteristics and distribution patterns of copepods, *A. sinjiensis*, *Oithona* sp., and *Acartia* sp. are very common species in bays, estuaries, and aquaculture ponds, and can easily adapt to brackish water. The inner region at stns. 5 and 6, near Linpan Dike, which drains the aquaculture ponds, usually had much lower salinities and higher nutrient-rich wastewater inputs during the rainy summer, favoring the abundances of these euryhaline copepods. *Acartia sinjiensis*, first reported by Li and Huang (1984) as a new species record in a subtropical estuary of China, is abundant in Tapong Bay.

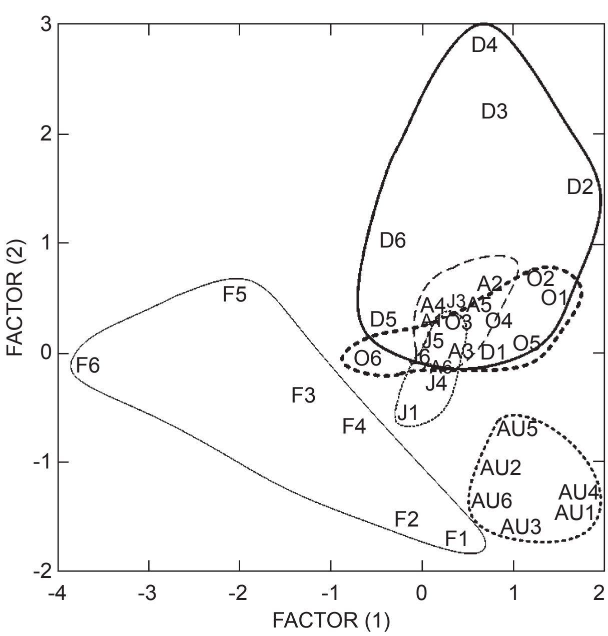

Fig. 6. Station groups delineated from the results of a principal component analysis (PCA) using copepod species with > 10% occurrence frequency. Compound symbols indicate the month (F, Feb.; A, Apr.; J, June; AU, Aug.; O, Oct.; D, Dec.) and station (numbers 1-6).

The middle and inlet regions of the bay usually have high species richness, perhaps because this is an interaction zone where bay and coastal communities mix and form the so-called "edge effect" with higher species diversity. All of our zooplankton collections were taken during the flood tide in daytime; therefore, we speculate that coastal waters would have been flowing into the middle or even inner bay due to the tidal currents (Su et al. 2004). Both *Parvocalanlus crassirostris* and *Temora turbinata* are common, euryhaline, neritic copepods; these 2 copepods are not only predominant in Tapong Bay, but also very common in the adjacent coastal waters (Huang 2002), in Kaohsiung Harbor, about 20 km north of Tapong Bay (Chen 2001), and even in the coastal waters and bays of southern Japan (Chihara and Murano 1997), particularly in late summer and autumn.

In conclusion, copepods predominated in Tapong Bay and showed obvious seasonal succession and spatial variations. Different copepod species may prefer different areas and exhibit different seasonal successional patterns that are most advantageous to their survival, particularly in this highly competitive subtropical lagoon with complex hydrography. The multiple environmental factors, such as food sources, anthropogenic impacts, tidal flushing, and precipitation, may interactively influence the distribution patterns of copepods. The complete removal of the oyster-culture racks caused dramatic changes in the bay ecosystem. Chlorophyll *a* concentrations increased in the inner region, probably due to removal of the filter-feeding cultured oysters, greater tidal flushing, and higher nutrient-rich discharges from surrounding fish ponds. Copepods became more diverse and abundant in the middle and inner bay, probably due to both increases in food sources and the disappearance of the zooplanktivorous medusae. Furthermore, our unpublished results suggest that copepods exert a low grazing impact (3.5%) on phytoplankton in the bay, but their dominance in numbers allows them to be the main food source of other organisms of higher trophic levels, and thus they play important roles in trophic fluxes in this bay ecosystem.

Acknowledgments: This research was supported by a grant from the National Science Council of Taiwan (NSC93-2621-Z-110-002) to W.T. Lo and a grant from the Ministry of Education of Taiwan to W.T. Lo [94-C030220 (Asia-Pacific Marine Research Center-Kuroshio project)]. We are grateful to H.Y. Hsieh, T.I. Yu, and T.H. Liao for collecting the samples and other environmental data related to our study.

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