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Patterns of Zooplankton Distribution along the Marine, Estuarine, and Riverine Portions of the Danshuei Ecosystem in Northern Taiwan

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Jiang-Shiou Hwang, Ram Kumar, Chih-Wei Hsieh, Albert Y. Kuo, Sami Souissi, Ming-Hsi Hsu, Jiunn-Tzong Wu, Wen-Cheng Liu, Chi-Fang Wang, and Qing-Chao Chen (2010) Patterns of zooplankton distribution along the marine, estuarine, and riverine portions of the Danshuei ecosystem in northern Taiwan. *Zoological Studies* **49**(3): 335-352. The Danshuei River embouchure is the largest estuarine ecosystem in northern Taiwan. The interacting effects of wastewater discharge from Taipei City and Taipei County into the river and seawater intrusion are the main determinants of the community composition, distribution, and abundance of zooplankton in this estuarine ecosystem. In the present study, we analyzed the abundance, distribution, and diversity of zooplankton, synoptically collected at 25 (19 marine and 6 estuarine) stations in this ecosystem. In total, 28 zooplankton groups were identified, including the top 3 most abundant groups: Calanoid copepods, larval stages, and Noctilucales. Among copepods, 46 species were identified from the estuarine stretch, whereas during the same period, 86 species of copepods were recorded in waters offshore of the estuary mouth, which is the boundary of the East China Sea and northeastern tip of the Taiwan Strait. Mesozooplankton abundances and distributions were highly variable among stations, indicating a highly fluctuating ecosystem. Zooplankton abundances were not correlated with chlorophyll *a* levels. Copepod diversity but not abundance showed a significant positive correlation with salinity ($r = 0.764$). The recorded salinity levels and zooplankton species compositions suggest that seawater intrusion up to station 3 of our study acts as a major driving force for zooplankton distribution and diversity in the Danshuei Estuary. Hierarchical classification revealed higher interannual variability in the occurrence of copepods species; at the 1st hierarchical level, samples collected in Oct. 2001 at stations 2, 3, and 4 were completely separated from other samples. Among these groups, the upstream station 4 was exclusively represented by the euryhaline estuarine calanoid copepod, *Pseudodiaptomus annandalei*, at a density of 1631 individuals (ind.)/m^3, station 3 was represented by *Pse. annandalei* and *Apocyclops borneoensis* with respective densities of 552.5 and 1.8 ind./m^3, and the seaward station 2 recorded *Pse. annandalei*, *Paracalanus aculeatus*, and *A. borneoensis* at respective densities of 364.9, 6.9, and 1.2 ind./m^3. At the 2nd hierarchical level, samples collected in Apr. 2002 were segregated from the others and exclusively contained coastal marine and euryhaline species. The 3rd hierarchical level included species occurring with no significant variations and classified species into 3 groups: (i) species with relative abundances of 1.4%-2.9% occurring during the post-spring period but without significant temporal variations, (ii) the freshwater species of cyclopoid copepod, *Mesocyclops pehpeiensis*, and (iii) copepod species represented by local coastal, marine, and brackish-water species characteristic of warm tropical and subtropical waters. The Euclidean distance measurement separated the copepod community into 5 groups. The most indicative euryhaline species at upstream stations, *Pse. annandalei* was separated at the 1st level without clustering with any other species. The 2nd most abundant species, *Mesocyclops pehpeiensis*, grouped with other coastal species at the 2nd level of grouping; however it was separated at the 3rd level of grouping without associating with any other coastal or marine species. http://zoolstud.sinica.edu.tw/Journals/49.3/335.pdf

Key words: Zooplankton distribution, Marine copepods, Estuarine copepods, Taiwan.

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The estuarine environment represents an ecotone between freshwater and marine ecosystems and is influenced by both, but is in many ways more complex than either of them (Cearreta et al. 2000, Elliott and De Jonge 2002, Elliott and McLusky 2002). Both river flow and tidal motions drive the riverine and marine communities towards estuaries (Waniek et al. 2005) and hence shape the diversity and abundance of estuarine communities (Mallin and Paerl 1994, Elliott and McLusky 2002, Waniek 2003, Froneman 2004). Despite the well-documented role of zooplankton in the transfer of carbon and energy and in ichthyofaunal abundance, relatively few studies have dealt with the determinants of zooplankton assemblages in estuarine ecosystems (Carlsson et al. 1995, Dalal and Goswami 2001, Tan et al. 2004, Thor et al. 2005).

The Danshuei Estuary is located at the boundary of the East China Sea shelf and the northeastern tip of the Taiwan Strait. The water mass and copepod composition offshore of the Danshuei Estuary are strongly influenced by the Chinese Coastal Current driven by the northeasterly monsoon during winter, and by the northward flow of the South China Sea warm water current along the Taiwan Strait driven by the southwesterly monsoon during summer (Jan et al. 2002, Lee and Chao 2003, Liang et al. 2003, Liu et al. 2003, Tseng et al. 2008). Such seasonal changes in flow patterns may affect the zooplankton community in the estuarine ecosystem. Additionally, the Danshuei River, the largest tidal river in Taiwan, flows through the Taipei basin, and forms the most important riverine ecosystem in northern Taiwan. Large amounts of partially treated or sometimes untreated industrial and domestic effluents from Taipei City and Taipei County are discharged into the river through many points throughout the tidally mixed zone (Liu et al. 2003 2004). The upper and middle estuarine stretches have become degraded, as hypoxic/anoxic conditions were reported to commonly prevail during the summer months (Liu et al. 2003, Wang et al. 2007). The nutrients and pollutants of Taipei City discharged into the estuary control to a great extent the distribution and abundance of less-tolerant species in ecologically sensitive regions. Some pollution-tolerant species with high adaptability may flourish or even immigrate to polluted stretches of the river. If adapted to the altered water conditions, they may flourish in the less-competitive environment. However, considering the extraordinary resilience of estuarine ecosystems (Caprulo et al. 2002, Elliott and McLuskey 2002), analyses of zooplankton community assemblages in 3 contiguous ecosystems - riverine, estuarine and marine - are warranted in order to understand the main determinants of the zooplankton communities in the estuary proper.

Being the largest tidal river in northern Taiwan, the Danshuei Estuary has been the subject of several biological and hydrological investigations. These include studies on the fish fauna (Lee 1992, Tzeng and Wang 1992, Chiu and Chen 1998), crab fauna (Shih et al. 1992), phytoplankton (Wu et al. 1993), microbes (Wu et al. 1993), the distribution of nutrients and temporal variations in physical factors (Chou and Bi 1990), and simulation of hydrological parameters and plankton dynamics (Wang et al. 2007), but limited information is available on the zooplankton community structure and dynamics (Hwang et al. 2006 2008). Recently, some published reports suggested that copepods are the dominant zooplankter in the lower reach of the Danshuei Estuary. Tseng (1975 1976) and Lei (1989) reported copepod species compositions in the area but without recording their abundances or distributions. Zooplankton are the primary consumers of phytoplankton and main prey items of larval and juvenile fishes, comprising a central position of the pelagic food chain (Kiørboe 1997). Zooplanktonic communities are highly influenced by spatiotemporal variations in hydrochemical parameters and physical forces (UNESCO 1981, Cloern et al. 1989, Bianchi et al. 2003, Waniek 2003, Hsiao et al. 2004, Sridhar et al. 2006). Land-based industrial and domestic effluents further impact the abundances and compositions of zooplankton communities in coastal areas (Bianchi et al. 2003, Cornils 2005). Zooplankton abundances, distributions, and diversities have not been investigated along the entire salinity gradient from the open sea to the upstream portion of this estuary.

This prompted us to examine the spatial and temporal distributions of zooplankton abundances along a salinity gradient from fresh water to the estuarine mouth which constitutes the boundary waters between the Taiwan Strait and the East China Sea. Among zooplankton, copepods constitute the major component and are numerically dominant. Copepod abundances and species assemblages are affected by several hydrochemical parameters and physical forces

(Bianchi et al. 2003, Hwang et al. 2006, Tseng et al. 2008). Recently, various copepod species were described as indicator species for different water masses (Bonnet and Frid 2004, Hsieh et al. 2004, Hwang et al. 2008, Tseng et al. 2008). A better understanding of the copepod fauna is, therefore, important for managing and protecting biological resources in estuaries (Jerling and Wooldridge 1995, Dalal and Goswami 2001). Salinity gradients along the riverine, estuarine, and marine stretches are expected to support diverse species of flora and fauna depending on their capacity to tolerate oligohaline, mesohaline, and marine conditions (Mallin and Paerl 1994, Menon et al. 2000). A major objective of biological oceanography is to identify the processes controlling the distributions and abundances of planktonic animals. In the present study in addition to determining the spatiotemporal distributions of mesozooplankton diversity and abundance, we estimated ammonia levels as an indicator of the water quality at 5 selected stations from Taipei City to the estuarine mouth along the riverine, estuarine, and marine sections. In order to elucidate the relative contributions of marine and freshwater copepods to the estuarine copepod community of the Danshuei Estuary, we also synoptically investigated the copepod composition offshore of the estuarine mouth in the boundary waters between the Taiwan Strait and East China Sea. Our findings are essential to understanding the main sources of copepod recruitment in the largest and commercially and esthetically most important estuary in Taiwan.

MATERIALS AND METHODS

Site description

The lower portion of the Danshuei River system (Fig. 1) consisting of 3 major tributaries, the Tahan, Hsintien, and Keelung Rivers, is the largest estuarine system in Taiwan. The main stem of the Danshuei River and the lower reaches of its tributaries are also tidally influenced. Seawater

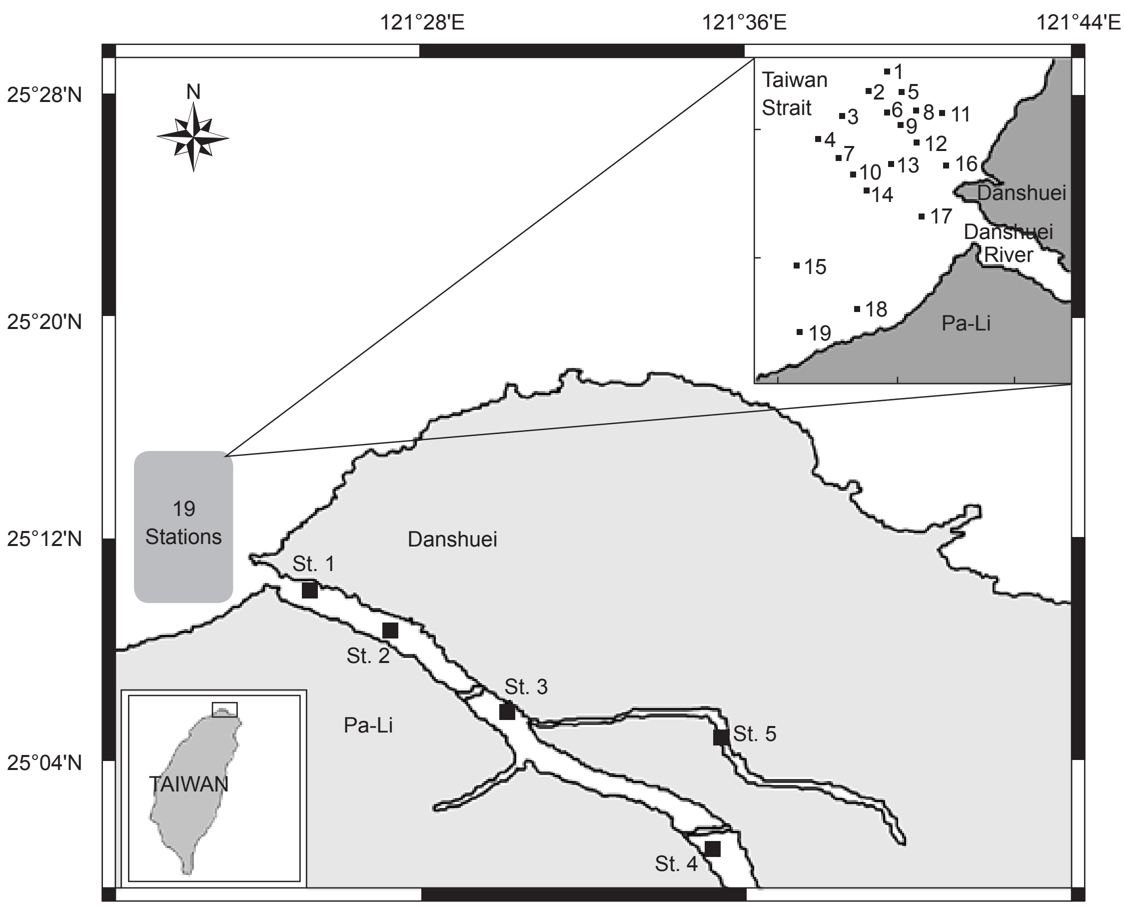

Fig. 1. Map showing locations of sampling stations in the Danshuei Estuary and offshore of the estuarine mouth.

intrusion, river inflow, and the density gradient induced by the mixing of saline and fresh waters mainly regulate the hydrodynamic characteristics of the system (Hsu et al. 1999). The residence time in the main stem estuary was recorded to be ≥ 3 d, which is generally attributed to the relatively large tidal range compared to the depth (Liu et al. 2004).

The purpose of this study was to understand the abundance, distribution, and recruitment sources of zooplankton in the estuarine portion of the Danshuei ecosystem. Based on our preliminary study on salinity and zooplankton abundance along the salinity gradient, 5 different stations were selected for regular sampling, of which 4 stations, 1-4, were located along the main estuary of the Danshuei River from the river mouth to fresh water (Fig. 1), while 1 station (station 5) was selected in the Keelung River between its confluence with the Danshuei River and the Ta-Chih Bridge. For synoptic comparison, 19 stations offshore of the mouth of the estuary in the vicinity of the boundary water between the East China Sea and the Taiwan Strait were also selected for regular sampling (Fig. 1).

Field sampling and data processing

Six cruises in the riverine stretch and 7 cruises outside the estuarine mouth were conducted from Oct. 2001 to Feb. 2003. Zooplankton samples were collected seasonally by fishing boats and the *Ocean Research Vessel II* in the estuarine and marine stretches of the Danshuei ecosystem, respectively. The water temperature and salinity were measured onboard using a Sea Bird conductivity-temperature-depth (CTD) meter (Bellevue, Washtington, USA). The vast majority of oceanic biomass lives in the surface wind-mixed layer, and is trophically dependent on light or primary production based on photosynthesis. Waters from deeper strata naturally contain decay products of sinking organic matter. Such products, in certain concentrations, can inhibit photosynthetic growth or are toxic or debilitating to respirors. Therefore it was decided to collect zooplankton samples from the surface layer (0-2 m). Samples were collected through a modified Norpac zooplankton net (0.45 m in mouth diameter, 200 μm mesh, and 180 cm long, with a Hydrobios flow meter (Kiel-Holtenau, Germany) mounted at the center of the net mouth. Hauls were towed horizontally for 10 min at a speed of about 1 m/s, and plankton samples were immediately preserved in 5% buffered formalin. In the laboratory, samples were split by a Folsom splitter until the subsample contained ≤ 500 specimens. Zooplankton was identified to the lowest possible taxa using standard keys (Chen 1992, Chihara and Murano 1997).

Chlorophyll (Chl)-*a* levels in seawater were measured as described in Parsons et al. (1984). Duplicate seawater samples for the Chl-*a* analysis were extracted overnight in 90% acetone at 4°C in the dark (Parsons et al. 1984). Chl-*a* fluorescence in the acetone extract was measured before and after acidification with a Turner Designs Model 10 spectrofluorometer (Sunnyvale, CA, USA) in the laboratory.

The ammonia content in the water sample collected from estuarine stations was determined using standard procedures for water sampling and examination of water quality (APHA 2005, EPA 1996).

In order to understand tidal effects on zooplankton assemblages, we conducted 4 intensive surveys in which zooplankton samples were collected at about 90 min intervals for a complete tidal cycle at stations 2 and 3 in Oct. 2002 and 2003, and May 2003 and 2004. The 2 sites were selected based on the results of slack-water surveys and past studies.

Data analysis

Spatial and temporal variations in the copepod assemblage were analyzed using a two-factor analysis of variance (ANOVA) without replication, with stations and seasons as major factors. In order to reduce higher heteroscedasticity observed in the original species abundance data for copepods, a transformation power (λ = 0.98) was generated by regression coefficients that were estimated by maximizing the log-likelihood function (Box and Cox 1964). Accordingly, data were log (X+1)-transformed for the statistical analyses. For analyses of spatiotemporal variations, two-way ANOVA was conducted using log-transformed data. For correlations between abiotic factors and zooplankton abundances, Pearson's product moment correlation coefficient was used.

We used cluster analysis, ordination, and indicator species analysis (ISA) to explore patterns in the community structure. "Species density" × "sample date" matrices composed of samples (86) and species (52) (for the estuarine section) were generated for the multivariate analyses, and similarity coefficients among samples were computed using the Bray-Curtis similarity coefficient and clustering strategy of flexible links (Clarke and Gorley 2001). Rare species, defined as those occurring in ≤ 5% of samples, were not included in the analyses. For presentation, the cluster dendrogram was scaled by the percentage of information remaining.

Measurement of species associations

In a univariate example, the Euclidean distance between 2 values is the arithmetic difference, i.e., $value_1 - value_2$. In the bivariate case, the minimum distance is the hypotenuse of a triangle formed from the points. Distances that are not a straight line but which obey certain rules can be measured with the Euclidean distance after standardizing the variables. The species association of the 14 most abundant species (with relative abundance > 0.2%) was evaluated using normalized Euclidean distances. Species with similar distribution patterns formed clusters that showed the extent of co-occurrence of copepod species. The 14 species used for the Euclidean distance measure included 98.18% of the total copepod abundance.

Indicator species analysis (ISA)

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

$$IndVal\ (j,s) = 100SP(j,s)\ FI(j,s); \quad \text{(I)}$$

where (SPj,s) is the specificity and (FIj,s) is the fidelity of a species (s) toward a group of samples (j), given by:

$$SP\ (j,s) = \frac{NI(j,s)}{\Sigma NI(s)} \text{ and } FI\ (j,s) = \frac{NS(j,s)}{\Sigma NS(s)}; \quad \text{(II)}$$

where $NI(j,s)$ is the mean abundance of species s across samples pertaining to j, $\Sigma NI(s)$ is the sum of the mean abundance of species s within the various groups in the partition, $NS(j,s)$ is the number of samples in j where species s is present, and $\Sigma NS(s)$ is the total number of samples in that group. The specificity of a species for a group is greatest if a particular species is found only in a particular group, whereas the fidelity of a species(s) toward a group is greatest if the species is present in all samples of the group considered. Indicator values range from 0 (no indication) to 100 (perfect indication, meaning the species was present in all samples in the group and was absent from all samples in other groups). As in Dufrêne and Legendre (1997) and Souissi et al. (2001), an arbitrary threshold IndVal value of 25% was used to select copepod assemblages.

RESULTS

Hydrography

Time-series values from Oct. 2001 to Feb. 2003 for average surface water temperature and salinity are depicted in figure 2. The highest temperature of 33°C and the lowest of 18.4°C were respectively recorded in Aug. and Jan. 2002. In contrast, the spatial difference in temperature was not significant, while the seasonal variation in surface water temperature was highly significant ($p < 0.05$; Mann-Whitney U-test; Fig. 2). A plume of a progressive increase in salinity was obvious; however, salinity levels recorded at stations 4 and 5 were not statistically significant. Variations in salinity recorded at stations 4 and 5 (Fig. 2) indicate variable influences of fresh water from upstream and the intrusion of seawater from downstream of these points. The spatiotemporal variability in the relative influences of marine and fresh waters at different stations was further tested using the station-wise coefficient of variation (CV) in surface water salinity for the entire sampling duration (Fig. 3). The CV of surface water salinity showed an increasing trend towards the river side, which was minimum (1.8%) in the boundary waters between the Taiwan Strait and the East China Sea and maximum (28.2%) in the surface water at station 5 (Fig. 3).

A significantly higher Chl-*a* level was recorded in late spring in Apr., and spatial variations in Chl-*a* values were not significant (Fig. 4). Chl-*a* ranged 0.18-6.6 ng/ml. The ammonia level ranged 0.22-4.80 ppm during the sampling period (Fig. 5). The upper-estuarine stations 4 and 5 consistently recorded higher levels of ammonia which ranged from 4.80 ppm in the slack period before the flood tide to 1.84 ppm in the slack period before the ebb tide.

Zooplankton composition

In total, 28 mesozooplankton taxa were recorded (Table 1) in the estuary during the study period. Figure 6 illustrates the relative abundances (%) of the top 10 most abundant zooplankton groups. Among the mesozooplankton, barnacle larvae were occasionally dominant among planktonic animals. Among all zooplankton, calanoid copepods were the most dominant group, both in terms of diversity and density throughout the investigation period. In total, 52 copepod species belonging to 30 genera were identified in the river section of the estuary (Table 2), whereas 86 copepod species were recorded from the plume during the investigation period. The one-

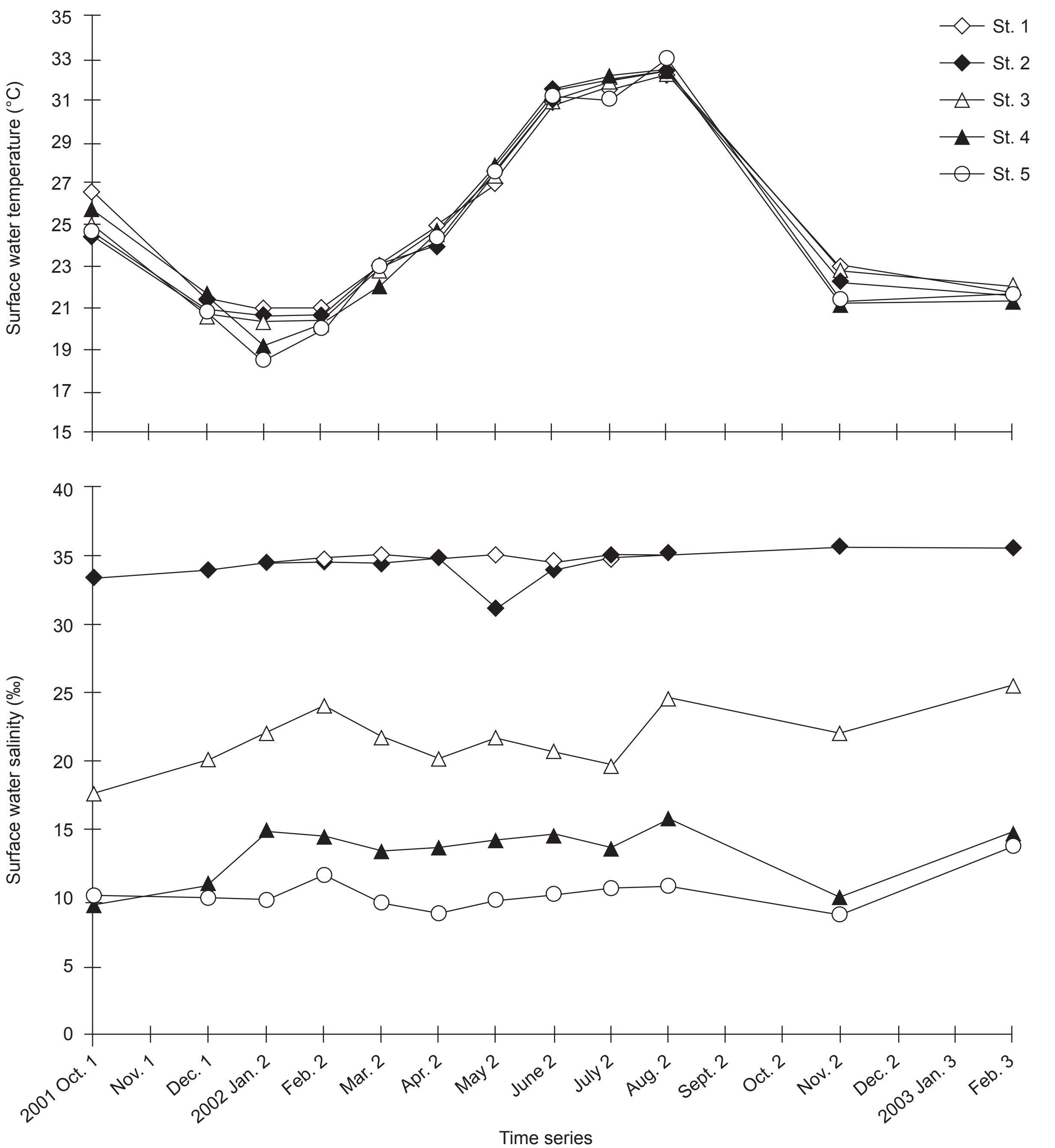

Fig. 2. Time series variations in surface water temperature and salinity at each station of the Danshuei Estuary during Oct. 2001 - Feb. 2003.

way ANOVA (Table 3) conducted for species richness of copepod groups showed the following results: (i) the overall copepod diversity was significantly lower ($p < 0.01$) in the estuary proper than offshore of the Danshuei Estuary (Fig.7), (ii) the richness of calanoid and poecilostomatoid copepods showed similar results to that of total copepod species which was significantly lower in the estuarine proper than outside the Danshuei Estuary ($p < 0.001$, Fig. 7), and (iii) the diversity of cyclopoid copepods did not significantly differ between the marine and estuarine sections of the Danshuei ecosystem (Fig. 7, Table 3). In contrast, the species richness of harpacticoid copepods was significantly higher in the estuarine proper than offshore of the estuarine mouth. The results of post-hoc multiple comparisons among the means of marine (average number of species recorded at 19 stations during each sampling cruise) and estuarine stations using Tukey's honestly significant difference (HSD) test (Table 4) revealed that the marine stations significantly ($p < 0.05$) differed from all other stations except in terms of the richness of the Harpacticoida. The species richness levels of total copepods, Calanoida, and Cyclopoida did not differ between stations 1 and 2; however, richness levels of the Harpacticoida and Poecilostomatoida significantly differed between stations 1 and 2 ($p < 0.05$ Turkey's HSD test, Table 4). Station 2 did not differ from station 3 but differed from all other stations for all parameters. Species richness levels recorded at stations 4 and 5 did not significantly differ; however, these 2 stations differed from all other stations in the richness of total copepod species as well as for each group ($p < 0.05$ Tukey's HSD test, Table 4, Fig. 7). The diversity, but not the abundance, showed a positive correlation with salinity (Fig. 8,

Table 1. Relative abundance (%) and frequency of occurrence (%; in parentheses) of zooplankton taxa recorded in water masses offshore of the estuarine mouth and at 5 stations of the Danshuei River Estuary during Oct. 2001 - Feb. 2003

Zooplankton taxon	Plume	Station 1	Station 2	Station 3	Station 4	Station 5
Noctiluca	3.88 (74.7)	22.67 (66.7)	3.80 (66.7)	0.32 (50)	0.33 (33.3)	0.06 (50)
Radiolaria	0.03 (3.16)	0.00	0.00	0.00	0.00	0.00
Medusa	1.45 (85.8)	0.49 (66.7)	2.03 (66.7)	0.03 (16.7)	0.18 (16.7)	0.01 (16.7)
Ctenophora	0.05 (10.8)	0.00	0.63 (16.7)	0.00	0.00	0.0
Polychaeta	2.03 (48.7)	0.30 (66.7)	0.79 (66.7)	0.19 (16.7)	0.49 (16.7)	0.06 (16.7)
Pteropoda	0.79 (48.9)	0.00	0.63 (16.7)	0.02 (16.7)	0.00	0.00
Heteropoda	0.01 (1.32)	0.00	0.00	0.00	0.00	0.00
Amphipoda	0.31 (41.6)	0.04 (16.7)	0.70 (50)	0.02 (16.7)	0.00	0.00
Lucifera larvae	3.11 (83.4)	0.84 (50)	0.70 (66.7)	0.73 (33.3)	0.02 (16.7)	0.00
Sergestidae	0.16 (12.6)	0.00	0.00	0.00	0.00	0.00
Other Decapoda	0.03 (1.6)	0.00	0.00	0.00	0.00	0.00
Cladocera	0.06 (9.5)	0.00	0.00	0.03 (16.7)	0.00	0.00
Ostracoda	2.29 (9.47)	1.49 (50)	0.13 (33.3)	0.31 (33.3)	0.00	0.00
Copepoda nauplii	0.05 (11.6)	0.02 (16.7)	0.08 (33.3)	0.29 (16.7)	0.00	0.00
Calanoida	69.35 (100)	43.65 (100)	57.51 (100)	36.22 (100)	81.25 (83.3)	99.59 (66.7)
Cyclopoida	0.10 (24.7)	1.98 (66.7)	3.88 (83.3)	5.56 (33.3)	0.81 (33.3)	0.01 (33.3)
Harpacticoida	0.22 (15.5)	0.42 (33.3)	0.17 (50)	0.08 (50)	0.29 (33.3)	0.00
Poecilostomatoida	0.83 (72.1)	11.94 100)	7.59 (50)	0.59 (50)	0.50 (50)	0.05 (33.3)
Mysidacea	0.09 (26.8)	0.37 (33.3)	0.63 (16.7)	0.00	0.00	0.00
Euphausiacea	0.38 (41.6)	0.13 (16.7)	0.00	0.00	0.00	0.00
Echinoderm larva	0.67 (11.8)	0.00	0.00	0.00	0.00	0.00
Chaetognatha	6.97 (95.8)	6.00 (100)	8.03 (83.3)	8.22 (50)	0.35 (50)	0.03 (33.3)
Appendicularia	4.22 (66.6)	7.31 (83.3)	7.57 (66.7)	1.77 (50)	0.31 (16.73)	0.06 (16.7)
Thaliacea	0.19 (21.6)	0.35 (16.7)	0.63 (16.7)	0.00	0.00	0.00
Fish eggs	0.19 (40.3)	0.06 (33.3)	1.43 (50)	0.00	0.00	0.00
Fish larvae	0.25 (44.5)	0.08 (50)	0.70 (66.7)	0.02 (16.7)	0.18 (33.3)	0.0
Other larvae	2.28 (87.4)	1.88 (83.3)	2.39 (83.3)	45.60 (66.7)	15.28 (50)	0.08 (50)

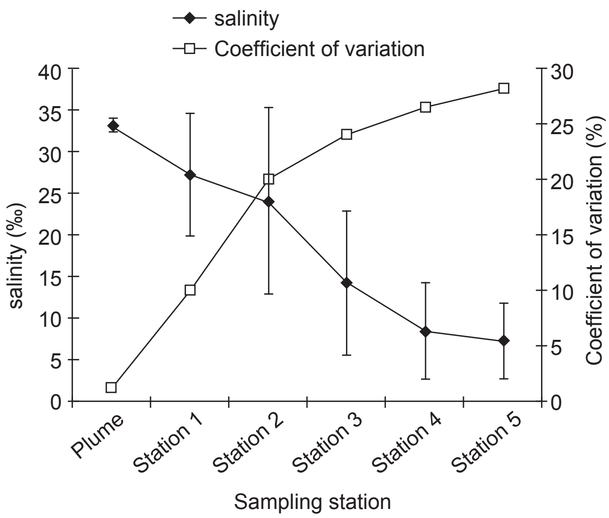

Fig. 3. Annual average salinity of surface water (mean ± S.E.) and percent variation (coefficient of variation) in salinity at each station of the Danshuei Estuary, and offshore of the estuarine mouth (plume) during Oct. 2001 - Feb. 2003.

r = 0.764).

The hierarchical classification revealed higher interannual and seasonal variability levels (Fig. 9, Table 5) in the occurrence of copepod species as for the 1st hierarchical level, i.e., samples collected in Oct. 2001 at stations 2, 3, and 4 were completely separated from the other samples. Among these groups, the upstream station 4 was exclusively represented by *Pseudodiaptomus annandalei* at a density of 1631 individuals (ind.)/m^3, and station 3 was represented by *Pse. annandalei* and *Apocyclops borneoensis* with respective densities of 552.5 and 1.8 ind./m^3. The seaward station 2 recorded *Pse. annandalei*, *Paracalanus aculeatus,* and *A. borneoensis* with respective densities of 364.9, 6.9, and 1.2 ind./m^3. At the 2nd hierarchical level, samples collected during Apr. 2002 were segregated from the others, and coastal, marine, and euryhaline species were exclusively recorded. The 3rd hierarchical level included species occurring with no significant variations

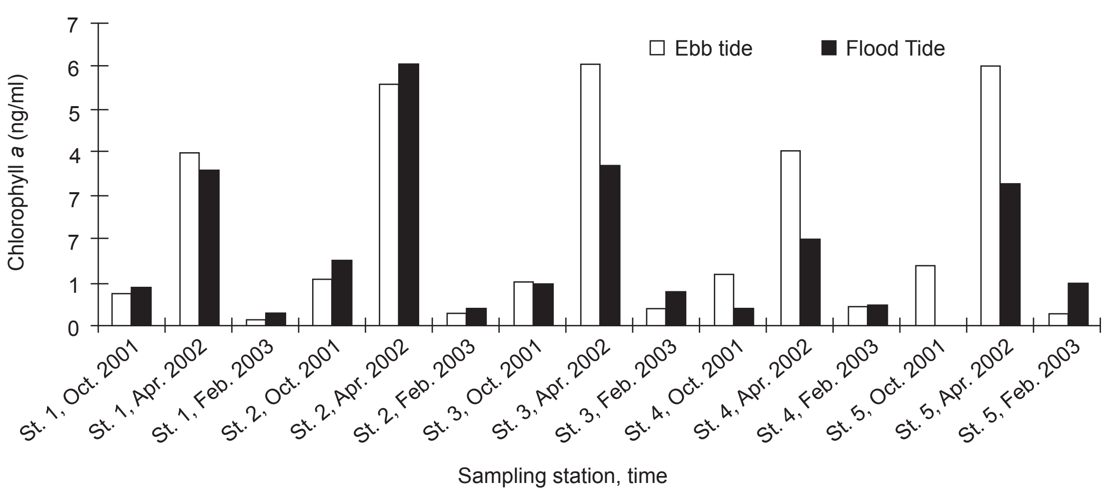

Fig. 4. Chlorophyll *a* values obtained in the slack water before the flood tide (SBF) and in the slack water before the ebb tide (SBE) at 5 estuarine stations during Oct. 2001 - Feb. 2003.

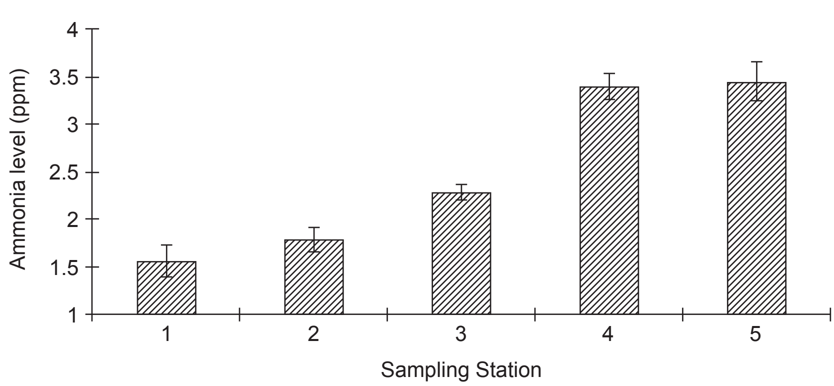

Fig. 5. Ammonia content (ppm) (mean ± S.E.) estimated at 5 stations of the Danshuei Estuary during Oct. 2001 - Feb. 2003.

Table 2. Occurrence frequency (%), relative abundance (%), and average density (individuals/1000 m^3) of copepod species recorded in the Danshuei Estuary, northern Taiwan during Oct. 2001 - Feb. 2003. An asterisk (*) indicates freshwater species, and double asterisks (**) indicate brackish-water species

	Copepod species (mean, individuals/1000 m^3)	Occurrence frequency (%)	Relative abundance (%)	Average abundance (mean ± SD)
1	*Acartia negligens*	13.80	0.23	28.4 ± 118
2	*Acartia southwelli*	39.10	7.69	952 ± 3780
3	*Acartia spinicaudata*	1.15	0.00	0.23 ± 2.14
4	*Acrocalanus gibber*	10.30	0.12	15.2 ± 62.1
5	*Acrocalanus gracilis*	8.05	0.15	18.2 ± 89.6
6	*Calanus sinicus*	3.45	0.07	8.05 ± 70.8
7	*Canthocalanus pauper*	17.20	0.20	25 ± 92.7
8	*Centropages tenuiremis*	4.60	0.03	3.91 ± 25.1
9	*Clausocalanus arcuicornis*	3.45	0.03	3.22 ± 24
10	*C. mastigophora*	3.45	0.04	5.52 ± 47.2
11	*Cosmocalanus darwini*	3.45	0.15	17.9 ± 117
12	*Euchaeta*	3.45	0.04	4.37 ± 30.9
13	*Labidocera acuta*	1.15	0.02	2.53 ± 23.6
14	*Labidocera euchaeta*	14.90	0.13	16.2 ± 70.8
15	*Paracalanus nanus*	6.90	0.55	67.9 ± 418
16	*Paracalanus aculeatus*	31.00	2.89	358 ± 1210
17	*Paracalanus parvus*	4.60	0.04	5.1 ± 31.7
18	*P. crassirostris*	63.20	34.40	4260 ± 15,500
19	*Pseudodiaptomus annandalei***	35.60	15.50	1920 ± 10,400
20	*Scolecithricella longispinosa*	2.30	0.27	33.3 ± 304
21	*Sinocalanus laevidactylus*	1.15	0.00	0.23 ± 2.14
22	*Subeucalanus subcrassus*	4.60	0.13	16.6 ± 99.7
23	*Temora discaudata*	2.30	0.02	2.76 ± 23.7
24	*Temora turbinata*	33.30	0.98	121 ± 447
25	*Undinula vulgaris*	3.45	0.06	7.82 ± 52.5
26	*Cyclopina* sp.*	13.80	18.80	2330 ± 12,600
27	*Mesocyclops* sp.*	10.30	0.04	4.9 ± 26.1
28	*Mesocyclops pehpeiensis**	12.60	12.10	1500 ± 6410
29	*Cyclopina* sp.*	3.45	0.01	0.97 ± 6.83
30	*Oithona brevicornis*	2.30	0.01	1.61 ± 10.7
31	*Oithona rigida*	54.00	2.70	335 ± 998
32	*Oithona setigera*	3.45	0.06	7.82 ± 52.5
33	*Apocyclops borneoensis***	3.45	0.01	1.61 ± 8.74
34	*Clytemnestra scutellata*	3.45	0.04	5.06 ± 42.9
35	*Euterpina acutifrons*	18.40	0.39	48.4 ± 174
36	*Farranula concinnus*	0.00	0.00	0 ± 0
37	unidentified harpacticoid	1.15	0.00	0.46 ± 4.29
38	*Macrosetella gracilis*	1.15	0.02	2.53 ± 23.6
39	*Microsetella norvegica*	1.15	0.04	5.06 ± 47.2
40	*Setella gracilis*	2.30	0.00	0.28 ± 2.37
41	*Corycaeus agilis*	1.15	0.02	2.53 ± 23.6
42	*Corycaeus affinis*	25.30	1.45	179 ± 852
43	*Corycaeus andrewsi*	5.75	0.16	20.2 ± 86.4
44	*Corycaeus catus*	5.75	0.13	16.1 ± 80.9
45	*Corycaeus concinnus*	0.00	0.00	0 ± 0
46	*Corycaeus erythraea*	2.30	0.12	15.2 ± 99.5
47	*Corycaeus longistylis*	3.45	0.03	3.45 ± 24.2
48	*Corycaeus pumilus*	2.30	0.00	0.25 ± 2.15
49	*Corycaeus* spp.	3.45	0.02	2.09 ± 15.3
50	*Euterpina acutifrons*	1.15	0.00	0.23 ± 2.14
51	*Oncaea conifera*	5.75	0.05	6.44 ± 33.9
52	*Oncaea venusta*	1.15	0.00	0.23 ± 2.14

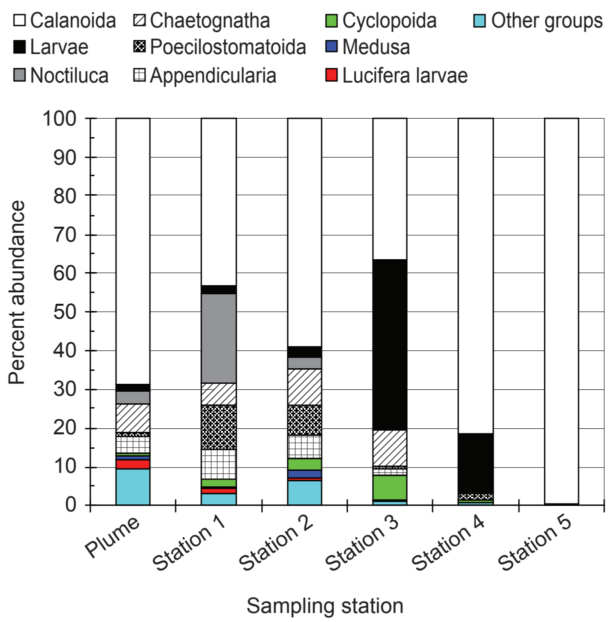

Fig. 6. Relative abundances of the top 10 zooplankton taxa identified in the Danshuei Estuary and offshore of the estuarine mouth during Oct. 2001 - Feb. 2003.

which classified species into 3 groups: (i) species with relative abundances of 1.4%-2.9% occurring during the post-spring period but without significant temporal variations; (ii) the freshwater species of cyclopoid copepod, *Mesocyclops pehpeiensis*; and (iii) copepod species represented by local coastal, marine, and brackish-water species characteristic of warm tropical and subtropical waters.

The more ecologically interesting results of the cluster analysis occurred with the separation of community types into 5 groups by Euclidean distances (Fig. 10). The most indicative euryhaline species at the upstream stations, *Pse. annandalei*, was separated at the 1st level without clustering with any other species. This species showed no significant correlations with physical parameters. The 2nd most abundant species, *M. pehpeiensis,* was grouped with other coastal species at the 2nd level of grouping; however, it was separated at the 3rd level of grouping without associating with any other coastal or marine species. The most abundant species at upper estuarine stations was the calanoid *Pse. annandalei* (1,920 ± 10,400 ind./1000 m^3). The euryhaline estuarine calanoid copepod, *Pse. annadalei* was

Table 3. Results of one-way analysis of variance (ANOVA) for species of total copepods, and each of the 4 orders that occurred among 5 stations in the Danshuei Estuary and 19 stations offshore of the estuarine mouth during Oct. 2001 - Feb. 2003

Parameter		Sum of squares	*d.f.*	Mean square	*F*	Significance
Total copepods	Between groups	12,060.075	1	12,060.075	210.307	< 0.001
	Within groups	6766.717	118	57.345		
	Total	18,826.792	119			
Calanoida	Between groups	13,209.008	1	13209.008	231.910	< 0.001
	Within groups	6720.983	118	56.957		
	Total	19929.992	119			
Cyclopoida	Between groups	4.800	1	4.800	3.641	0.059
	Within groups	155.567	118	1.318		
	Total	160.367	119			
Harpacticoida	Between groups	218.700	1	218.700	125.397	< 0.001
	Within groups	205.800	118	1.744		
	Total	424.500	119			
Poecilostomatoida	Between groups	2125.208	1	2125.208	552.631	< 0.001
	Within groups	453.783	118	3.846		
	Total	2578.992	119			

the only zooplankton species recorded in relatively higher abundances (> 1,112 ind./1000 m^3) from stations 4 and 5. At the upper-estuarine stations 4 and 5, the ammonia concentrations (4.80 ppm in the slack period before the flood tide and 1.84 ppm in the slack period before the ebb tide) were consistently higher than those at other stations (Fig. 4).

Only 2 freshwater (which also occur in hyposaline lakes) copepod species, *Mesocyclops* sp. and *Cyclopina* sp., were recorded from stations 2 and 3. The overall zooplankton density but not the diversity was significantly higher at high tide than at low tide, and regardless of the tidal influence, the highest zooplankton abundance was recorded in Oct. (Fig. 11). From offshore of the Danshuei Estuary, the boundary of the East China Sea and the Taiwan Strait, 86 copepod species were identified during the study period. Among them, *Temora turbinata, Paracalanus aculeatus, Acrocalanus gibber, Parvocalanus crassirostris*, and *Oithona rigida* were the 5 dominant species, comprising 80% of the total copepod abundance. A relatively higher density of copepods with overlapping species compositions between marine stations and stations 1, 2, and 3 of the Danshuei Estuary were recorded throughout the sampling duration.

Neither total zooplankton nor copepod abundances showed any significant correlation with Chl-*a*, and Chl-*a* values were not influenced by the tides (Fig. 3). Neither total mesozooplankton nor total copepod abundances showed a significant correlation with ammonia levels; however, the locally adapted species *Pse. annandalei* showed a significant positive correlation with ammonia levels ($r^2 = 0.024$, $p = 0.02$) (Fig. 12).

DISCUSSION

Our study documents the contribution of marine zooplankton to the estuarine section of the Danshuei ecosystem. The occurrence of only 2 genera (*Mesocyclops* and *Cyclopina*) of freshwater zooplankton (Kumar and Rao 1999, Kumar 2003) with relatively lower abundances than other copepod species recorded and their conspicuous absence from upstream stations (stations 4 and 5) suggest that in the estuarine community, the

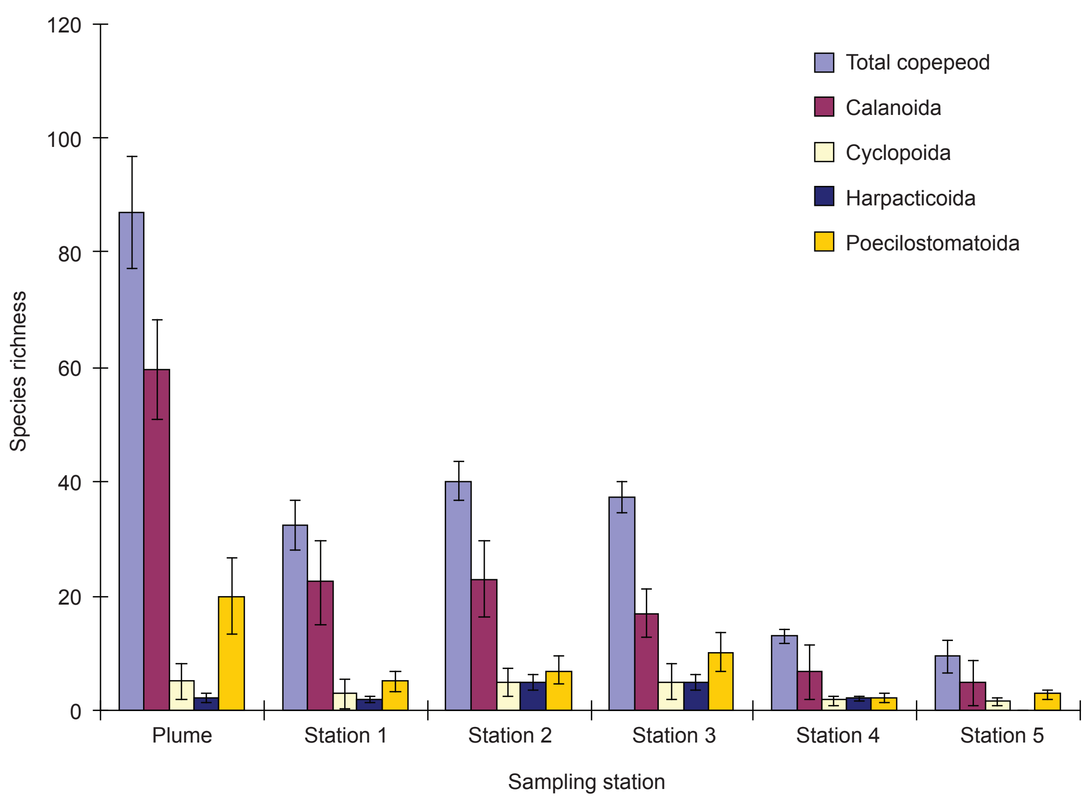

Fig. 7. Copepod species richness (mean ± S.E.) identified at 5 stations in the Danshuei Estuary proper and waters offshore of the estuarine mouth (plume) during Oct. 2001 - Feb. 2003.

freshwater zooplankton, particularly copepods, are not a significant component. However because of their relatively smaller size and omnivorous feeding habits with a relatively wide (unicellular algae to fish larvae) size spectrum of food adapted to eutrophic waters (Kumar and Rao 1998 1999, Rao and Kumar 2002, Kumar 2003), they might play important roles in transferring energy and structuring the community composition in the Danshuei ecosystem. Furthermore, these cyclopoids differ from other freshwater zooplankton species, as they are more adapted to variable salinities, and the females only need to be inseminated once for lifetime reproduction (Kumar and Rao 1999, Kumar 2003). The seasonal abundance patterns of copepod species in a given area may be governed by their locally expressed life-history patterns (temporal patterns of reproductive and developmental stage durations), which may in turn be controlled by several factors including temperature, salinity, and feeding capabilities. However, instances when a zooplankter's seasonal abundance cycle does not match that expected from its expressed life-history pattern are times when predation or advection are particularly important (Lindahl and Hermoth 1988).

The concurrent presence of numerically dominant zooplankton in the downstream reach, in the plume, and further in the neighboring marine community indicates a commonality of species in the boundary waters between the Taiwan Strait and East China Sea (Lo et al. 2001, Hwang et al. 2006 2008), which can be attributed to advective effects. The overlapping copepod concentrations and compositions up to station 3 in the Danshuei Estuary and offshore from the estuarine mouth during Oct. 2001 - Feb. 2003 are likely a reflection of advection that was reported by physical oceanographic studies (Liu 2004, Liu et al. 2004). Several studies also noted the effects

Table 4. Matrix of pair-wise multiple comparisons for species richness among the plume (species richness values of 19 marine stations at each sampling cruise were pooled) and 5 estuarine stations during Oct. 2001 - Feb. 2003 using Tukey's honest significant difference test. Pairs of stations showing significant ($p < 0.05$) differences in the means of a parameter are indicated by a letter representing species richness of (a) total copepods, (b) Calanoida, (c) Cyclopoida, (d) Harpacticoida, and (e) Poecilostomatoida

	Plume	St. 1	St. 2	St. 3	St. 4	St. 5
Plume		e	de	de	e	de
St. 1	abc		de	de		
St. 2	abc				de	de
St. 3	abc	a			de	de
St. 4	abc	ab	abc	abc		
St. 5	abc	ab	abc	abc		

Table 5. Indicator species and indicator values (%) for each cluster identified in figure 9

Hierarchical level (Cluster)	Indicator species	Index value (%)
IIa	*Acartia negligens*	25.00
	Labidocera euchaeta	27.08
	Temora turbinata	53.35
	Corycaeus affinis	37.29
	Paracalanus aculeatus	51.59
IIb	*Acartia southwelli*	81.87
	Parvocalanus crassirostris	75.60
	Pseudodiaptomus annandalei	67.10
	Oithona rigida	36.02
IIIa	*Labidocera euchaeta*	32.50
	Temora turbinata	56.13
	Oithona rigida	26.42
	Corycaeus affinis	44.79
	Paracalanus aculeatus	62.01
IIIb	*Mescyclops pehpeiensis*	99.95
IIIc	*Acartia southwelli*	81.84
	Parvocalanus crassirostris	74.37
	Pseudodiaptomus annandalei	66.00
	Oithona rigida	33.26

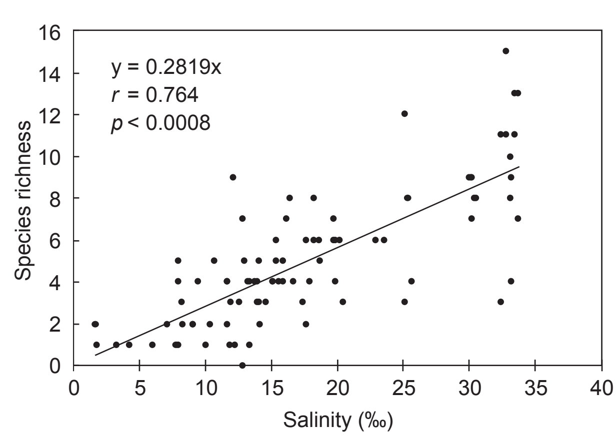

Fig. 8. Species richness (each point represents the number of species that occurred in a single sampling cruise at a particular station) as a function of the surface water salinity. The regression line was drawn using the equation shown.

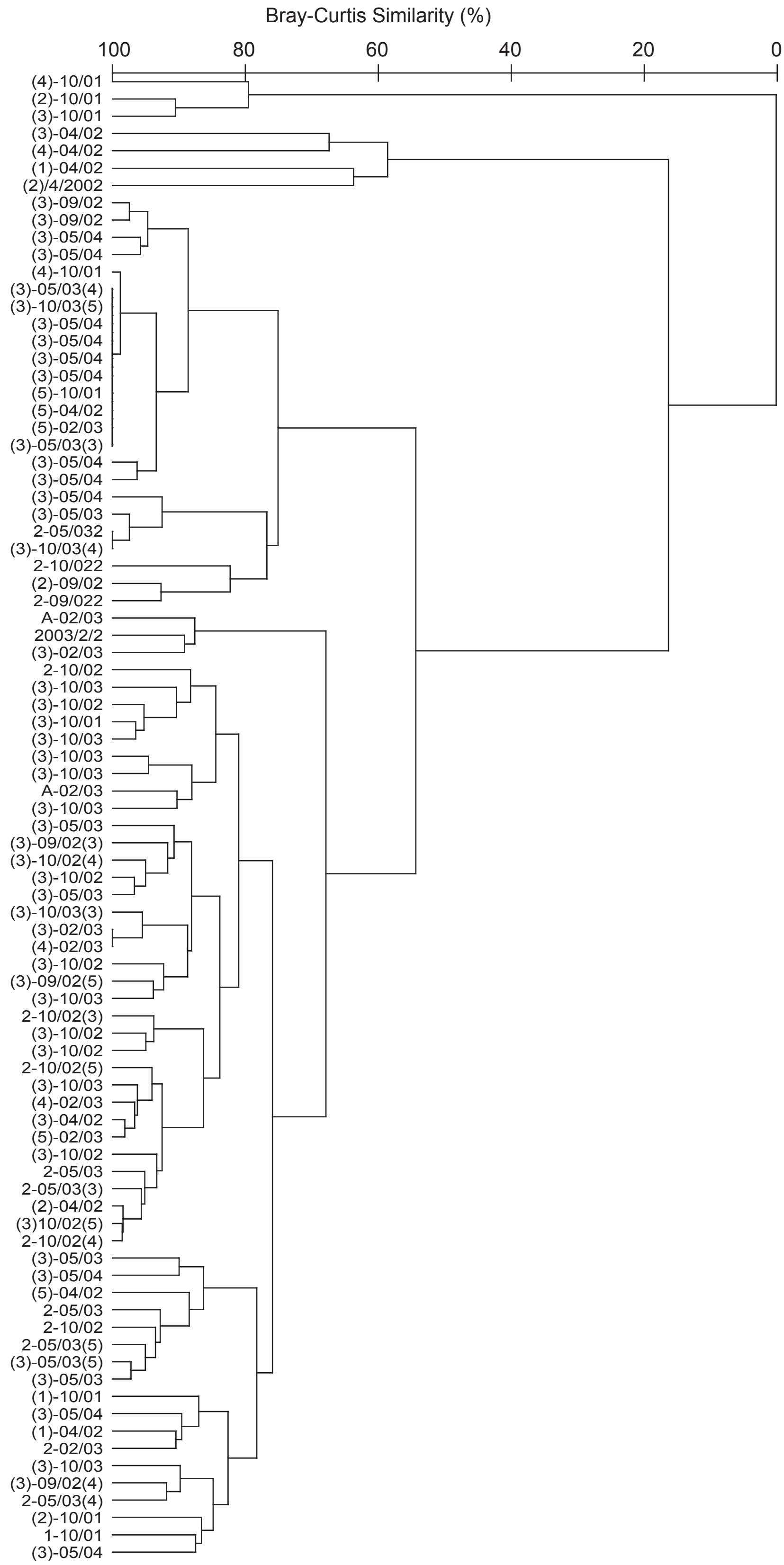

Fig. 9. Classification of samples collected from all stations on each sampling date using the Bray-Curtis similarity and clustering strategy of flexible links. Sampling dates and station numbers are labeled.

that different vertical and horizontal distributions have on the transport of species. Lewis and Thomas (1986) studied tidal transport of copepods across the shallow sill (25 m) of the Indian Arm, a fjord in British Columbia, Canada. They recorded the transport of species located in waters near or above the sill depth but not of species that were below it. The copepod community structures recorded in marine stations and at stations 1, 2, and 3 reflect that the copepod community is carried into the Danshuei River by oceanic tides. Due in part to advective events, the seasonal abundance patterns of copepods could not be predicted based upon their locally expressed life-history patterns. The most striking example of this in the present study is the calanoid, *Pse. annandalei*. Its population decreased during Feb. - Mar. and increased during Sept. - Oct., despite having a major reproductive peak in the spring (according to data from our ongoing field study). Therefore seasonal and interannual variations in copepod composition and the succession of dominant patterns of copepods (Table 6) are influenced by the observed interannual and seasonal variations in the copepod community offshore of the estuary (Hwang et al. 2006 2008).

The role of the marine component in shaping and maintaining the estuarine planktonic

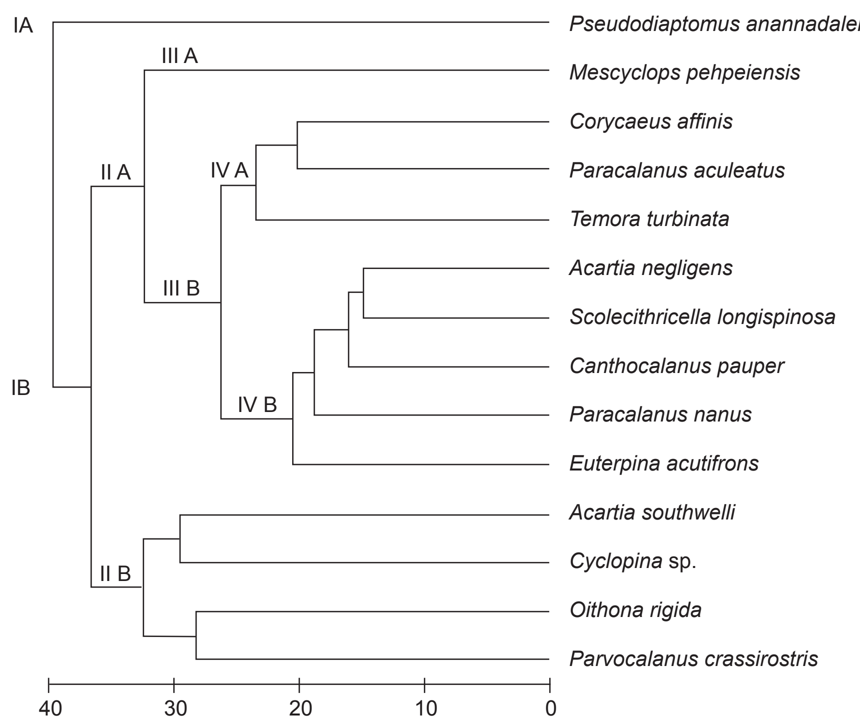

Fig. 10. Dendrogram of the 14 most abundant (with a relative abundance of > 0.2%) copepod species measured by Euclidean distances, showing the degree of relative dissimilarity of the distribution between species in the surface waters of the Danshuei Estuary proper.

Table 6. Top 3 numerically dominant copepod species in the Danshuei Estuary recorded earlier and in the present study

Year of investigation	Rank 1	Rank 2	Rank 3	Reference
1988	*Paracalanus* sp.	*Oithona* sp.	*Corycaeus* sp.	Rei 1989
1996	*Calanus sinicus*	*Temora turbinata*	*Acartia erythrea*	Hsieh and Chiu 1997
1997	*Oithona* sp.	*Paracalanus* sp.	Copepod nauplii	Shao 1999
2000	*Temora turbinata*	*Acrocalanus gibber*	*Canthocalanus pauper*	Lan 2002
2001-2003	*Parvocalanus crassirostris*	*Oithona rigida*	*Acartia southwelli*	Present study*

**Pseudodiaptomus annandalei* and *Temora turbinata* were the 4th and 5th most dominant species, respectively.

community was further supported by the positive correlation between zooplankton diversity and surface water salinity. In our analyses, the coefficient of determination (r^2) between salinity levels and species assemblages at estuarine stations was 0.58, which indicates that 58% of the variation in zooplankton abundance and distribution in the estuary was explained by salinity alone and the remaining 42% by other environmental factors. Among other factors, we considered ammonia levels (1.8-4.6 ppm) to be the major factor adversely affecting the zooplankton distribution in the more-polluted upper stretches of the estuary. Wu et al. (1993) conducted a monitoring study to investigate intra-tidal variations of phytoplankton assemblages and water quality in the lower Danshuei River estuary. Their results showed that green algae were the dominant species during ebb tides, and diatoms were dominant during flood tides. In addition, they also found that water of the ebb tide had lower salinity, less dissolved oxygen, and higher concentrations of various nutrients.

Copepods are generally considered to have low tolerances to poor water quality (Hoff and Snell 1987). Buttino (1994) determined that an ammonia concentration of 0.12 ppm considerably reduced egg production and viability in the calanoid, *Acartia clause*. In the riverine

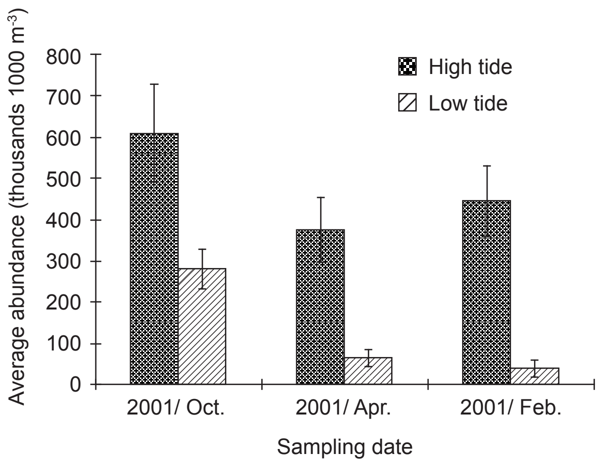

Fig. 11. Average zooplankton abundances recorded from the Danshuei Estuary proper during high and low tides in Oct. 2001, Apr. 2002, and Feb. 2003.

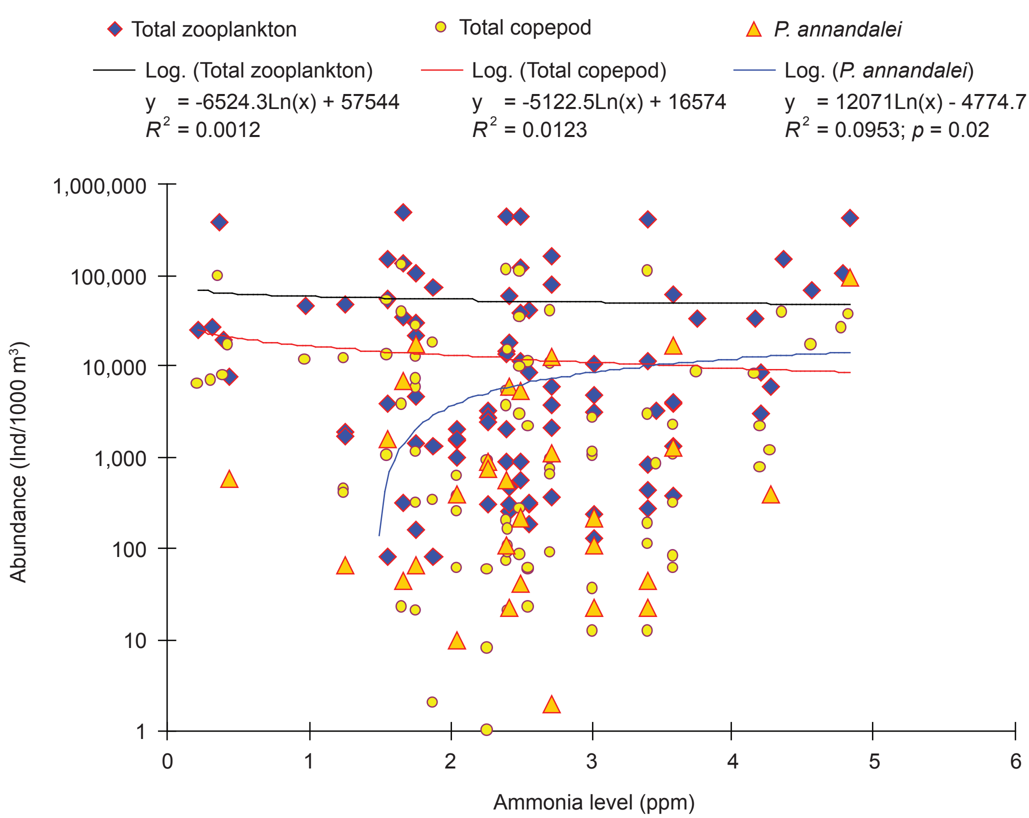

Fig. 12. Densities of total zooplankton, total copepods, and of the most indicative estuarine copepod, *Pseudodiaptomus annandalei*, in relation to the ammonia content of the water at 5 stations of the Danshuei Estuary during Oct. 2001 - Feb. 2003. The regression line was drawn using the equation shown.

portion of the Danshuei Estuary, ammonia concentrations exceeded this level by more than an order of magnitude, and hence, are likely to have affected copepod productivity, particularly survival from nauplii to adulthood, and fecundity. Also, high concentrations of non-nutritional suspended particulate matter (Bonnet and Frid 2004, Wang et al. 2007) may have decreased copepod abundances. In a previous study, it was reported that a higher concentration of suspended particulate matter reduced the fecundity and abundance of the estuarine calanoid, *Eurytemora affinis* (Gasparini et al. 1999). It appears that waste discharges from Taipei City make the lowest reach of the freshwater portion and the upper reach of the brackish-water section of the Danshuei River largely uninhabitable to many species (Hsu et al. 1999, Liu et al. 2001a b). The interacting effects of anthropogenic activities and the continuous release of nutrients and pollutants from the land are determinants of the trophic status and composition of the estuarine community (Elliott and McLusky 2002, Puigserver et al. 2002, Froneman 2004, Ulanowicz 2004). Chl-*a* levels showed a relatively equitable distribution in the estuary. The observed phytoplankton composition and seasonal variations in Chl-*a* levels were similar to patterns observed in other estuaries affected by various anthropogenic activities (Rudek et al. 1991, Waniek 2003, Elliott 2003). In the Danshuei Estuary, a conspicuous absence of freshwater zooplankton in the downstream section of the riverine stretch (stations 4 and 5) and their re-appearance in the middle section of the estuary (stations 2 and 3), albeit in lower abundances, may be due to dilution of the land-based effluent discharge by seawater intrusions, which is in agreement with a previous study (Wu et al. 1993). Dilution by seawater renders the system habitable for planktonic communities. Our results support earlier observations that despite industrialization and land reclamation, estuaries are among the most resilient habitats (Elliott and McLusky 2002) on earth in maintaining their uniqueness in terms of the composition and abundance of their flora and fauna. The presence and dominance of marine copepods support the use of copepods as an indicator of the movement of water masses. Copepods were found to be indicators of water masses (Dur et al. 2007, Hwang et al. 2008, Tseng et al. 2008). This study also provides fresh support for the role of the copepod community as a biological indicator of water quality in this estuary.

Persistent proliferation and swarming of the smaller-sized brackish-water calanoid copepod, *Pse. annandalei*, in the estuarine stretch further demonstrate the adaptive behavior of this species and its ability to utilize resources in degraded waters uninhabitable by other zooplankton. *Pseudodiaptomus annandalei* is a subtropical coastal pelagic species. It is widely distributed from coastal and estuarine waters of the Indian Ocean, Bay of Bengal (Menon et al. 2000) to Taiwan (Chen et al. 2006a b). The euryhaline calanoid, *Pse. annandalie*, commonly occurs in estuaries, backwaters, and marine caves (Menon et al. 2000, Chen et al. 2006a b). In an earlier study from the Cochin backwater system of India, *Pse. annanadalei* was recorded in higher abundances despite a higher degree of salinity fluctuations in that system (Menon et al. 2000). Also in the Danshuei Estuary with relatively higher salinity fluctuations, the dominance of *Pse. Annandale* indicates that this species is adapted to salinity fluctuations, and hence is capable of tolerating a wide range of salinity shocks. The wider range of salinity tolerance by this species was reported in experimental studies by Chen et al. (2006a b). In their study, the tolerance salinity range of females and males were 4.5-40.5 and 12.9-38.7 ppt, respectively, when the salinity was changed from an original salinity of 20 ppt. Therefore the salinity conditions in the upper middle stretch of the estuary are ideal for *Pse. annandalei*. In general, euryhaline copepods easily survive and are widely distributed if euryhaline and stenohaline species are subjected to the same conditions.

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