



Zooplankton Fluctuations in the Surface Waters of the Estuary of a Large Subtropical Urban River

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Specialty section:

This article was submitted to
Biogeography and Macroecology,
a section of the journal
Frontiers in Ecology and Evolution

Received: 24 August 2020

Accepted: 10 February 2021

Published: 03 March 2021

Citation:

Lee P-W, Hsiao S-H, Chou C,
Tseng L-C and Hwang J-S (2021)
Zooplankton Fluctuations in the
Surface Waters of the Estuary of a
Large Subtropical Urban River.
Front. Ecol. Evol. 9:598274.
doi: 10.3389/fevo.2021.598274

The Danshuei River has a third largest catchment area and third longest in Taiwan. It flows through the capital, Taipei, and more than six million people live within its catchment area. Its estuary is characterized by a highly variable chemical and physical environment that is affected by the interaction of inland freshwater runoff with wastewater, and toward the coast is also influenced by the China Coastal Current and the Kuroshio Current. By collecting zooplankton bimonthly in 2014 from the surface layer (0–2 m depth) at five sites in the estuary, we were able to demonstrate that the composition of the zooplankton, and particularly its copepod fraction, varied significantly among sampling stations and months, thereby revealing seasonal succession. Fourteen higher taxa or other categories of zooplankton were identified, with the following being most common taxa: Decapoda, Copepoda (including Calanoida, Cyclopoida, and Harpacticoida), and “other larvae.” The Copepoda comprised 44 taxa (including eight only identified to genus) belonging to 3 orders, 17 families, and 29 genera, the five most abundant of which were *Bestiolina* n. sp. (undescribed), *Corycaeus* spp., *Parvocalanus crassirostris*, *Acartia* sp., and *Paracalanus parvus*. The highest and lowest copepod abundances were recorded in July (2557.88 inds. m⁻³) and January (1.3 inds. m⁻³), respectively. Observed changes in abundance of many kinds of copepod appeared to be significantly related to changes in physico-chemical parameters (e.g., salinity, temperature, pH, and dissolved oxygen concentration). Cluster analysis confirmed the existence of distinct copepod communities, each characterized by a preference for a different set of environmental conditions. Our comprehensive literature review of the copepod biodiversity of Taiwan’s major rivers for comparison with similar data compiled for other estuaries in the world, the first time such a review has been compiled, shows that 32 copepod taxa have been recorded from the brackish and freshwater parts of the Danshuei River. They represent 58.2% of the total number of brackish- and freshwater copepod species in Taiwan, and five of them have so far only been recorded in the Danshuei River: the calanoids *Acartiella sinensis* and *Pseudodiaptomus forbesi*, the cyclopoids *Oithona fragilis* and *Oithona simplex*, and the harpacticoid *Tachidius* (*Tachidius*) *discipes*.

Keywords: brackish water and freshwater copepods, succession, biogeography, urban river, estuary

INTRODUCTION

Estuaries are transitional zones between rivers and the sea (Meire et al., 2005; Wang et al., 2007; Telesh and Khlebovich, 2010; Shan et al., 2013). The physical and chemical aspects of their hydrography are continuously dynamic with regard to both place and time (Elliott and McLusky, 2002; Kibirige and Perissinotto, 2003). For example, the turbidity of the river water increases, and salinity decreases, in the upstream direction (Elliott and McLusky, 2002), the gradient in salinity being caused by the interplay of denser seawater and overlying riverine freshwater (Hwang et al., 2010; Telesh and Khlebovich, 2010). The estuarine biome, too, is distinctive, being characterized by low biodiversity but high abundance of the prevailing taxa, and thus by unique food webs. Estuaries provide nursery grounds for larvae and juveniles of invertebrates and fish and important foraging grounds for migratory birds (Shan et al., 2013). Terrestrial nutrient runoff into estuaries (Godhantaraman and Uye, 2003) nourishes spawning and fishing grounds that are inhabited by many commercially important species of fish and shellfish (Shan et al., 2013).

The Danshuei River is the third longest river has the third largest catchment area in Taiwan, and the largest in the north of the island (LC-FRD, 2005; Hwang et al., 2010, 2006). It has two major branches, the Xindian and Dahan rivers, and flows out into coastal waters at the boundary between the East China Sea and the Taiwan Strait (Wen et al., 2008; Cheng et al., 2011). Its estuary includes a mangrove (*Kandelia candel*) conservation area of about 50 hectares that was established in June, 1986 (Kao and Chang, 1998). The Danshuei River flows through Taipei City, the capital of Taiwan, and also through a portion of New Taipei City, places where more than six million people live (Lai et al., 2010). Extensive water pollution in the river's catchment area, including the discharge of urban sewage and industrial wastewater into the Danshuei River, was formerly prevalent (Wu and Chou, 2003; Wang et al., 2014), but after a sewage treatment system was established in June, 1997, the water quality of the river improved greatly (Putri et al., 2018).

Many species that are commercially exploited by the fishing industry inhabit the Danshuei River. Among them are fishes such as *Oreochromis niloticus* (Cichlidae) (Chen et al., 2014), *Epinephelus coioides* (Serranidae), *Diodon holocanthus* (Diodontidae), and *Pisodonophis cancrivorus* (Ophichthidae); the shrimp *Metapenaeus monoceros*; the crabs *Scylla serrata* and *Portunus sanguinolentus*; and the bivalves *Meretrix petechialis* (Veneridae) (Liu, 2014) and *Perna viridis* (Mytilidae) (Chao, 2006). Several biological studies on, e.g., juvenile fish (Shih, 2007) and hydroids (Tseng et al., 2014) have been conducted in the Danshuei River, and a number of publications have dealt specifically with the copepods that are found there (Yu, 2005; Hwang et al., 2006, 2009, 2010; Hsiao, 2009). Some studies on the seasonal succession of the copepod community have taken place, based on four samplings per year, but such studies have focused on the fundamentally marine species in the plume and estuarine areas (Chen, 2005; Yu, 2005; Hwang et al., 2006, 2010; Hsiao, 2009) while rarely discussing the specifically brackish-water species. The temporal succession of zooplankton in this estuary's

waters thus still remains understudied. Here we make another attempt to study the intra-annual succession and distribution of the zooplankton in the estuary of the Danshuei River, with special reference to the copepods.

To do so, on a bimonthly schedule we recorded hydrographic parameters while collecting zooplankton samples in the Danshuei River's estuary with three aims: (1) documenting the intra-annual succession of the general zooplankton assemblage, with a more specific analysis of the copepod community, (2) providing baseline taxonomic information about these subtropical freshwater and brackish-water copepods, and (3) comparing the historical records of copepods from different rivers and their estuaries in Taiwan.

MATERIALS AND METHODS

Study Area and Field Sampling

Bimonthly collections were made at five selected sampling stations in the estuary of the Danshuei River in northwestern Taiwan (in New Taipei City), within the region bounded by 25°05'–25°11'N latitude and 121°25'–121°31'E longitude (Figure 1 and Table 1). Station 1 was the farthest downstream and station 5, 7.6 km away, was farthest upstream. The investigation and zooplankton collections were carried out from outside the protected area and no specific permission was required. The field studies did not involve endangered or protected species. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The estuary faces, and its waters flow into, the southwestern part of the East China Sea. Samples were collected in daytime during six cruises on January 10, March 19, May 28, July 29, September 29, and November 26, 2014. A standard NORPAC net (mouth opening diameter 0.45 m, length 1.80 m, mesh size 100 μ m) was towed for 10 min at the surface (0–2 m depth), with a Hydrobios (Kiel, Germany) flowmeter mounted in the center of the net opening. The samples were immediately preserved in seawater-diluted formalin (= 5%) on board for later estimation of taxon composition and abundance. Before sampling, a handheld multi-parameter sensor (Model HI 9829, Hanna Instruments, Vöhringen, Germany) was used to measure the salinity, water temperature, dissolved oxygen concentration (DO), and pH at each station.

Identification and Abundance Measurements of Zooplankton

Taxonomic identification and enumeration of zooplankton were done in the laboratory at National Taiwan Ocean University. The samples were divided by a Folsom splitter until each aliquot contained approximately 400–500 specimens. Zooplankters were sorted and identified using the keys of Shen (1979) for freshwater species, and those of Chihara and Murano (1997); Walter et al. (2006), Sakaguchi and Ueda (2010); Ueda et al. (2011), Srinui et al. (2013, 2019), Lian et al. (2018), and Shih et al. (2019) for marine species. The numbers of individuals (ind.) of each zooplankton taxon were recorded (as ind. m^{-3}), with adult copepods being

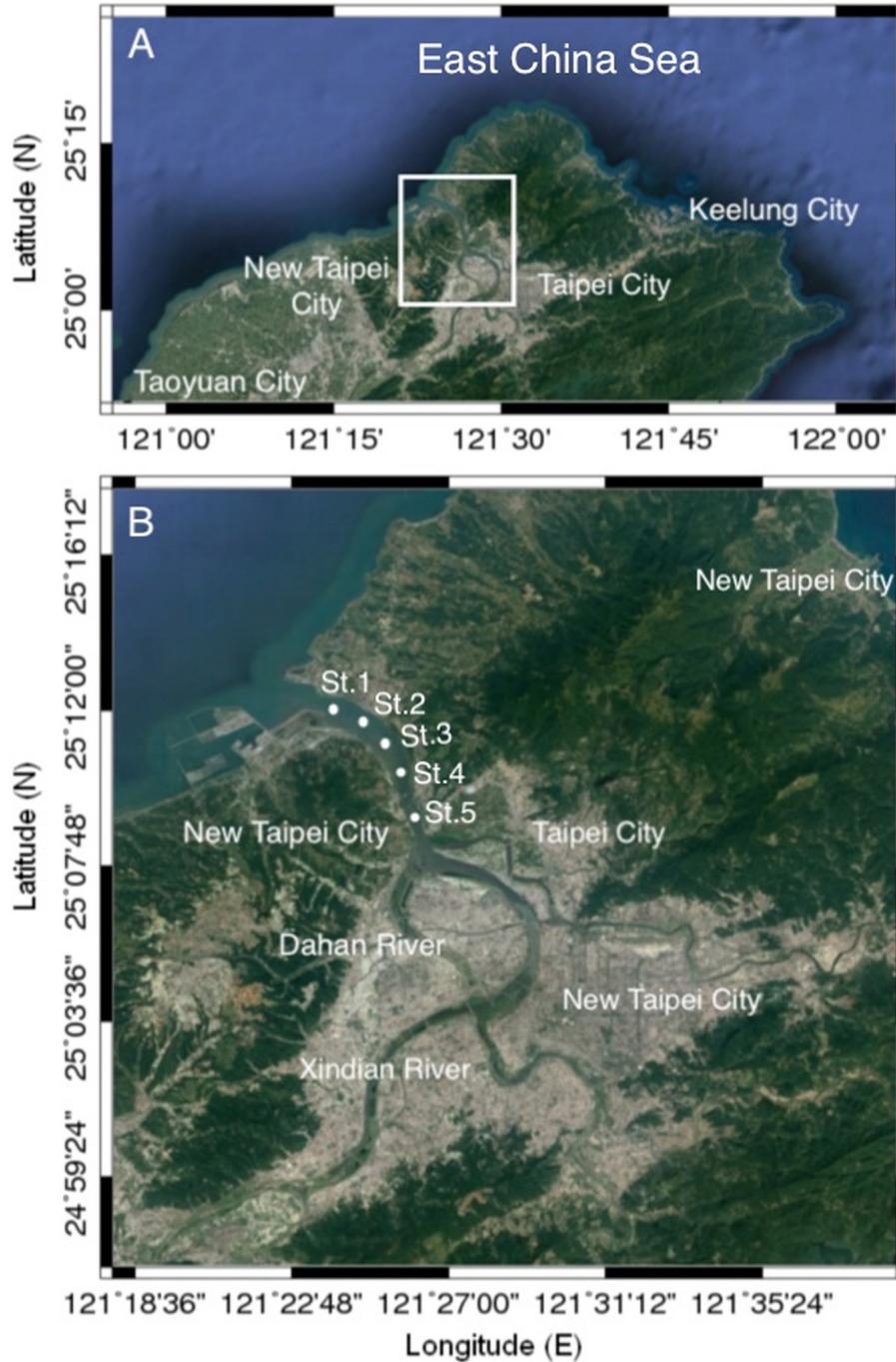


FIGURE 1 | Maps of the study area (A) and the locations of the sampling stations (B) in the estuary of the Danshuei River in northwestern Taiwan.

TABLE 1 | Local name, riverbed depth (m), coordinates, and distance to coast (km) of five sampling stations in the estuarine area of the Danshuei River.

| Station | Local name | Riverbed depth (m) | Latitude (N) | Longitude (E) | Distance to coast (km) |
|---------|------------|--------------------|--------------|---------------|------------------------|
| 1 | Estuary | 9 | 25°10'21" | 121°25'19" | 1.29 |
| 2 | Danshuei | 7 | 25°09'52" | 121°26'18" | 2.88 |
| 3 | Mangrove | 5 | 25°09'05" | 121°26'55" | 4.45 |
| 4 | Zhuwei | 6 | 25°08'09" | 121°27'17 " | 6.33 |
| 5 | Guandu | 7.5 | 25°06'50" | 121°27'39" | 8.89 |

identified to species. Zooplankton was sorted into 14 larger taxa or other categories. Among them, the category “Decapoda” was defined as including small shrimp as well as larvae of *Macrura* and *Brachyura*, whereas the category “Other larva” included cirriped nauplii, ophioplutei, trochophores, and aquatic insect larvae. Sexually mature copepods were also assigned to one of the three taxa Calanoida, Cyclopoida, and Harpacticoida, while all immature copepods were categorized as “Copepoda copepodites.”

Images of the Sea Surface Temperature

Images of sea surface temperature (SST, source: GHRSS-PP/OSTIA, Group for High Resolution Sea Surface Temperature Pilot Project/Operational SST and Sea Ice Analysis) were obtained from the Fisheries Research Institute, Council of Agriculture, Taiwan (Figure 2). These images were used to present and track the movements of water masses and thereby perhaps explain the month-to-month succession of copepod communities.

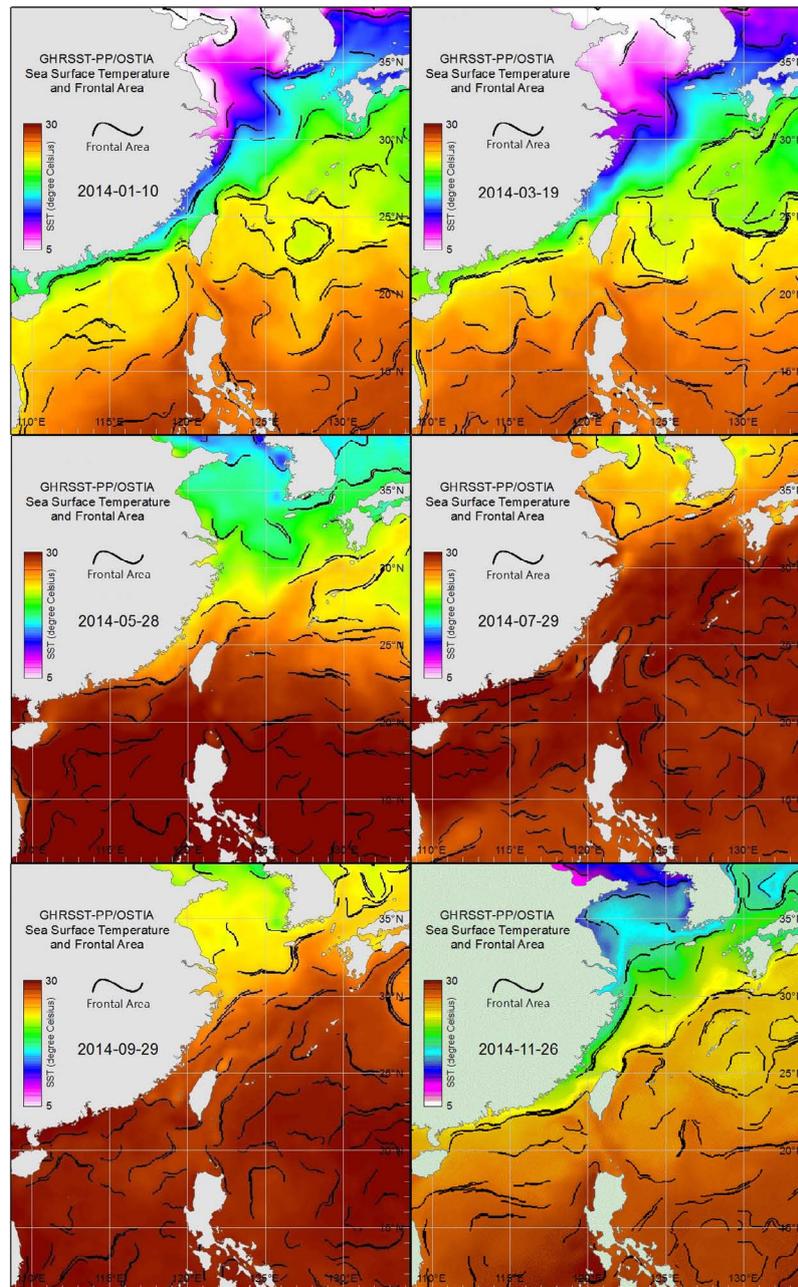


FIGURE 2 | Sea surface water-temperature images for each bimonthly sampling date in 2014 derived from GHRSS-PP/OSTIA, showing water mass distributions in the East China Sea, Taiwan Strait, and South China Sea.

Data Analysis

To elucidate the temporal variation of copepod communities at 2-month intervals over the course of a year, the PAST software package (Paleontological Statistics: Hammer et al., 2001) was used to compare the copepod assemblages in each sample. Among the 30 samples, the top 16 most abundant copepod taxa, those with a relative abundance (RA) exceeding 1.0% (together comprising 93.44% of the total adult copepods), were used to calculate similarities before clustering and nonmetric multidimensional scaling (NMDS) analyses were done. The Bray-Curtis similarity distance was used to evaluate similarities in spatial distribution between taxa. In order to reduce the bias introduced by particularly abundant taxa, a test of the necessity for data transformation (Box and Cox, 1964) was applied prior to conducting the similarity analysis. The value (λ) of the power transformation was 0.92. In consequence, the original abundance data of copepods for all samples were log-transformed, using $\log(x + 1)$, before analysis.

A one-way analysis of variance (ANOVA) with the *post hoc* Tukey's Honestly Significance Difference (HSD) test was applied to reveal differences in copepod community structure among the sampling months. Pearson's correlation analysis was used to estimate the relationship between the abundance of copepods and various hydrographic parameters.

RESULTS

Hydrological Structure

Sea surface temperature images (Figure 2) obtained from GHRSS-PP/OSTIA for each sampling date in January, March, and November showed the cold water mass of the China Coastal Current (CCC) extending southward from the Yellow and Bohai seas, along the coast of mainland China, and into the northern Taiwan Strait, where the zooplankton samples were collected. In contrast, similar GHRSS-PP/OSTI images for each sampling date in May, July, and September showed the northern shores of Taiwan enveloped by warm water masses of the South China Sea and Pacific Ocean (Figure 2).

Tide tables for the Danshuei River issued by Taiwan's Central Weather Bureau (Figures 3A–F) report tidal heights relative to the local annual mean water level. During the present study, the sample collection period was limited to 09:00–16:00 on the cruise dates, and the tidal conditions each time were different. For example, low tide occurred at around 12:00 in January (Figure 3A) whereas high tide occurred then in March and July (Figures 3B,D); high tide occurred around 13:00–14:00 in September and November (Figures 3E,F), while sampling was done on an ebb tide in May (Figure 3C). The lowest (–165 cm) and highest (142 cm) water levels were recorded during the July and November cruises, respectively.

Water temperature in the Danshuei River showed significant variation among sampling cruises (Figure 3G), ranging from a single-reading low of 17.4°C in March during the northeast monsoon period to a high of 30.8°C in July. The lowest average water temperature through the five stations was $18.0 \pm 0.12^\circ\text{C}$

in January whereas the highest was $29.39 \pm 0.89^\circ\text{C}$ in July (Figure 3G).

The salinity at all sampling stations was strongly affected by the tidal cycle (Figures 3A–F) and was highly dynamic on each sampling date (Figure 3H). The salinity records showed that strong intrusions of seawater reached to station 3 in May and July, station 4 in March, and station 5 in September. The cruises of July and November took place on the second and fourth days after the new moon, respectively, because of which the intrusion of seawater into the estuary should have been the strongest during these two cruises. However, because salinity was measured at the surface and because the seawater and river water were not sufficiently and uniformly mixed, the salinities recorded on these two occasions were not the highest we recorded (Figure 3H). The lowest salinity measurements were recorded at upstream station 5, with the lowest value (4.57 PSU) occurring in May, which demonstrates the relatively low influence of seawater there. Throughout the study, salinity records at station 1 were higher than at other stations excepted in September. Low salinity records at all sampling stations in January were the result of rainfall in the upper reaches of the Danshuei River's drainage area (Figure 3H); pH records were also lower then. The lowest pH value of 7.3 was recorded twice at station 5, in January and May (Figure 3I). DO ranged from a low of 2.80 mg/L at station 5 in January to a high of 7.99 mg/L at station 3 in March (Figure 3J). Overall the changing pattern of pH and dissolved oxygen from station to station was similar during each sampling cruise (Figures 3I,J).

Pearson's correlation analysis indicated that pH ($r = 0.902$, $p < 0.001$) and DO ($r = 0.679$, $p < 0.001$) were significantly and positively correlated with salinity. Variations in DO were significant positively correlated with pH ($r = 0.514$, $p = 0.004$), but significant negatively correlated with water temperature ($r = -0.395$, $p = 0.031$).

Zooplankton Abundance and Variation in Community Structure

A total of 14 higher-level taxa and other categories of zooplankton were identified (Supplementary Table 1), the most common of which were Decapoda, Calanoida, Cyclopoida, Harpacticoida, and "other larvae"—all were present on each sampling date. Zooplankton densities (ind. m^{-3}) ranged from 1.53 (station 5, January) to 2902.21 (station 2, July) (Figure 4A). The total abundance of zooplankton clearly varied through the year. The number of zooplankton categories in the community on a given date was lowest at station 4 (1 taxon, January) and highest at station 2 (8 taxa, May). Taxon richness was highest in May, during the northeastern and southwestern monsoon transition period (Figure 4B), and lowest in January and November during the period of the prevailing northeastern monsoon.

The dominance structure within the zooplankton community changed through the year (Figure 4C). Calanoid copepods were always among the most dominant, with a contribution (RA) ranging from 27.65% (January) to 77.49% (September). Cyclopoid copepods were the second most dominant category, contributing from 1.59% (September) to 38.91% (March). Harpacticoid copepods were most highly represented in

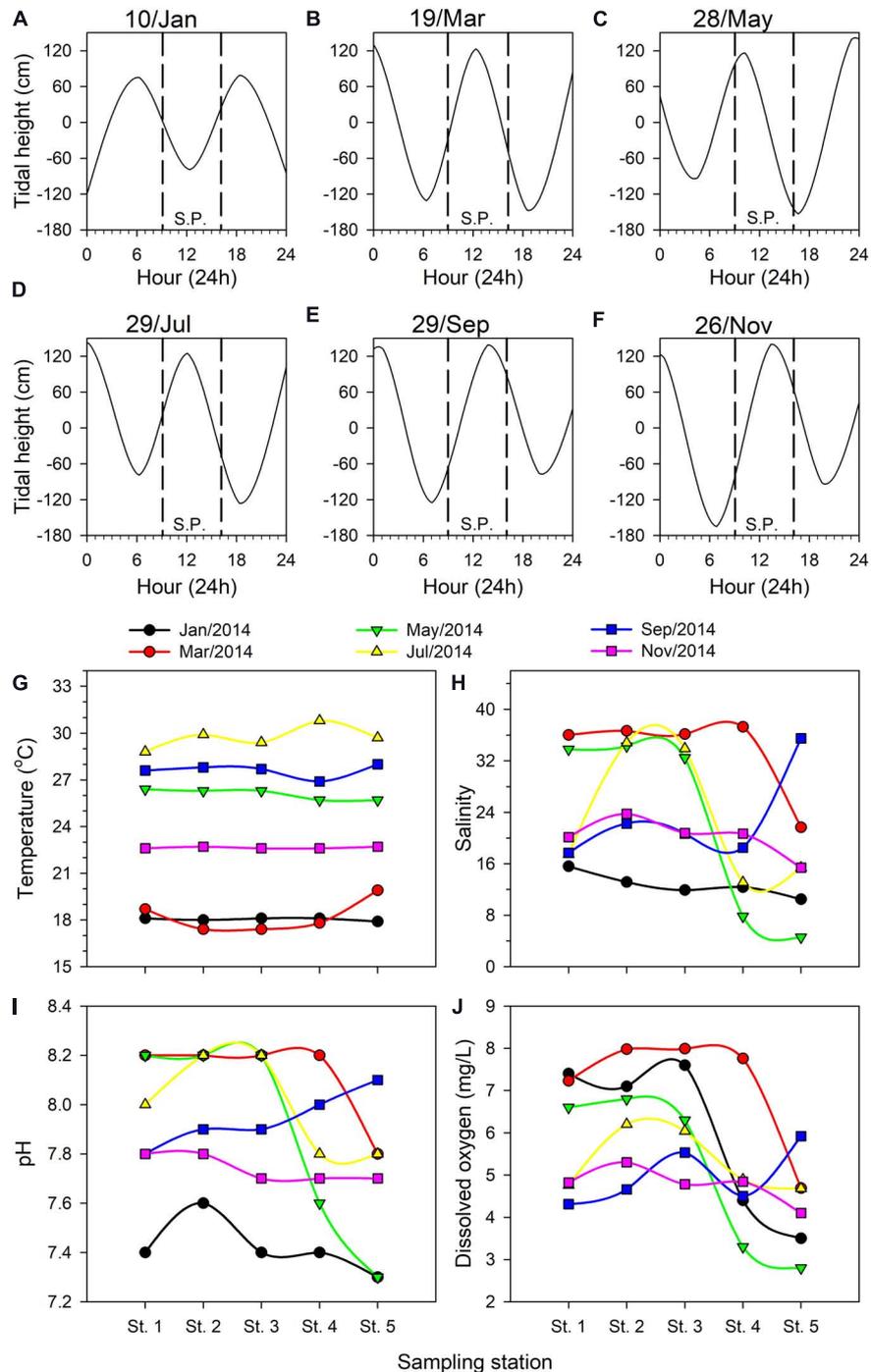


FIGURE 3 | Tidal height (cm) fluctuations on each bimonthly sampling date in 2014 in the Danshuei River estuary: January 10 (A), March 19 (B), May 28 (C), July 29 (D), September 29 (E), and November 26 (F). Upstream-downstream variation in hydrographic parameters among the sampling stations in this estuary on each bimonthly sampling date: water temperature (G), salinity (H), pH (I), dissolved oxygen concentration (J). SP, sampling period.

March, May, and July, with contributions of 4.21%, 4.97%, and 5.42%, respectively. Copepodites were absolutely dominant in January (61.36%), but of only secondary importance in November (16.75%). *Noctiluca scintillans* accounted for 4.64% of the total in May, but in other

months was relatively less abundant. The taxa Appendicularia, Polychaeta, and Decapoda individually accounted for 7.28% in May, 7.08% in March, and 7.69% in July, respectively (Figure 4C), but were not otherwise major components of the community.

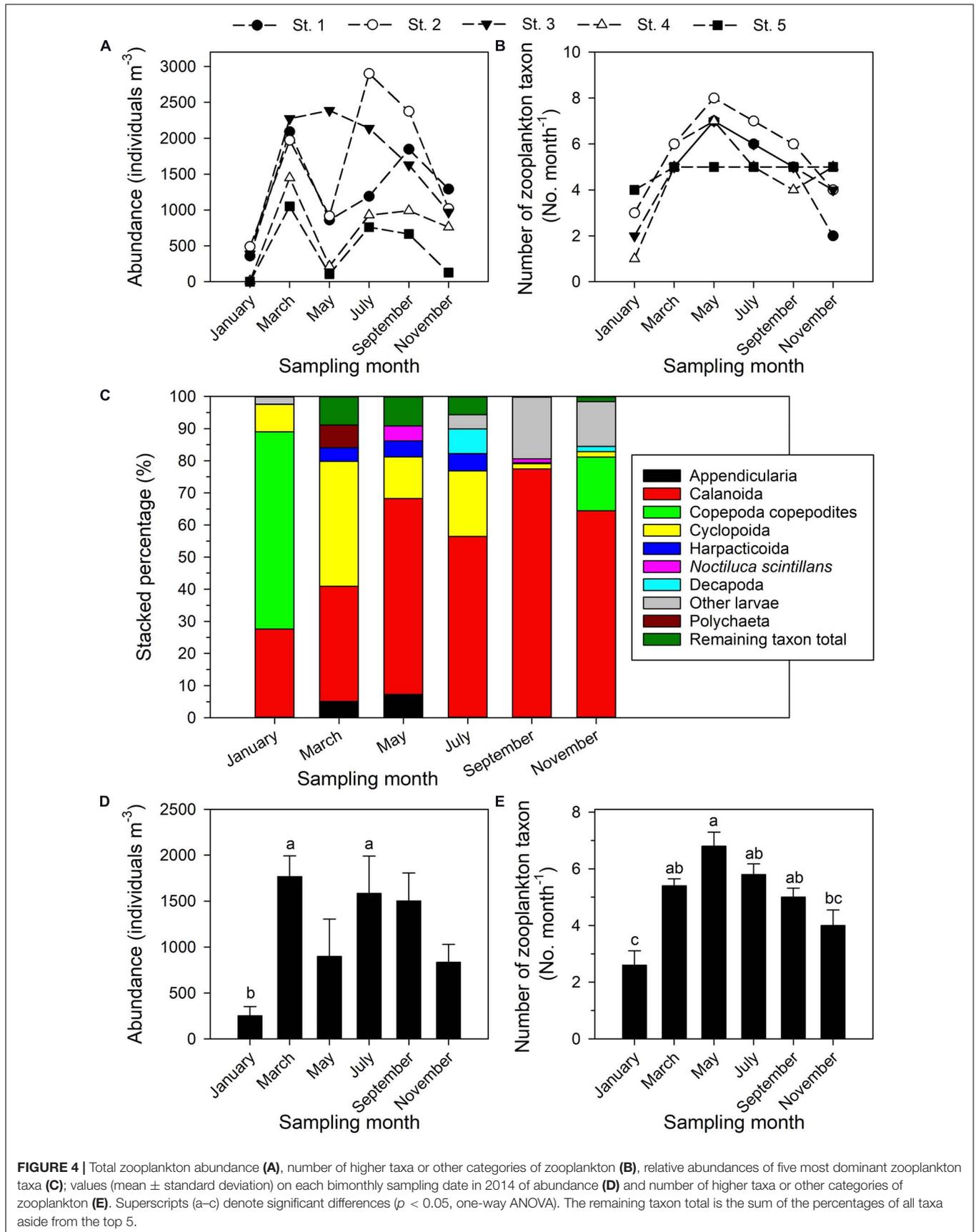


FIGURE 4 | Total zooplankton abundance (A), number of higher taxa or other categories of zooplankton (B), relative abundances of five most dominant zooplankton taxa (C); values (mean \pm standard deviation) on each bimonthly sampling date in 2014 of abundance (D) and number of higher taxa or other categories of zooplankton (E). Superscripts (a–c) denote significant differences ($p < 0.05$, one-way ANOVA). The remaining taxon total is the sum of the percentages of all taxa aside from the top 5.

The ANOVA and Tukey tests conducted to compare zooplankton abundance and taxonomic category diversity among the six bimonthly sampling dates in 2014 confirmed monthly variation in total zooplankton abundance (Figure 4D), this being lowest in January, when it was significantly lower than in March ($p = 0.015$) and July ($p = 0.04$; Figure 4D). The number of higher-level zooplankton taxa and other categories encountered was significantly lower in January than in March ($p = 0.001$), May ($p < 0.001$), July ($p < 0.001$), or September ($p = 0.007$) (Figure 4E). In contrast, neither absolute abundance nor number of taxa was significantly different as annual averages among the five sampling stations ($p > 0.05$, one-way ANOVA).

Community Structure and Variation of Copepods

The 30 samples taken during six bimonthly research cruises in the estuary of the Danshuei River in 2014 included 44

taxa of copepods (among which eight taxa only identified to genus) belonging to 3 orders, 17 families, and 29 genera. The five most abundant taxa were *Bestiolina* n. sp. (an undescribed species; relative abundance (RA) in pooled samples 29.04%), *Corycaeus* spp. (11.17%), *Parvocalanus crassirostris* (10.98%), *Acartia* sp. (8.93%), and *Paracalanus parvus parvus* sensu lato (4.67%) (Supplementary Table 2). Time series values of copepod abundance (Figure 5A), species richness (Figure 5B), and rank abundance (%) (Figure 5C) from January through November revealed a spatiotemporally highly dynamic copepod community structure in this estuary. The highest copepod density was recorded at station 2 in July (2557.88 inds. m^{-3}), followed by station 3 in May 2014 (2155.49 inds. m^{-3}), whereas the lowest copepod density was found at station 5 in January (1.3 inds. m^{-3}) (Figure 5A). The highest number of copepod taxa was recorded at station 5 (16 taxa) in September, whereas the lowest number (1 taxon) was recorded at station 4 in January (Figure 5B). The shapes of the rank abundance curves were considerably

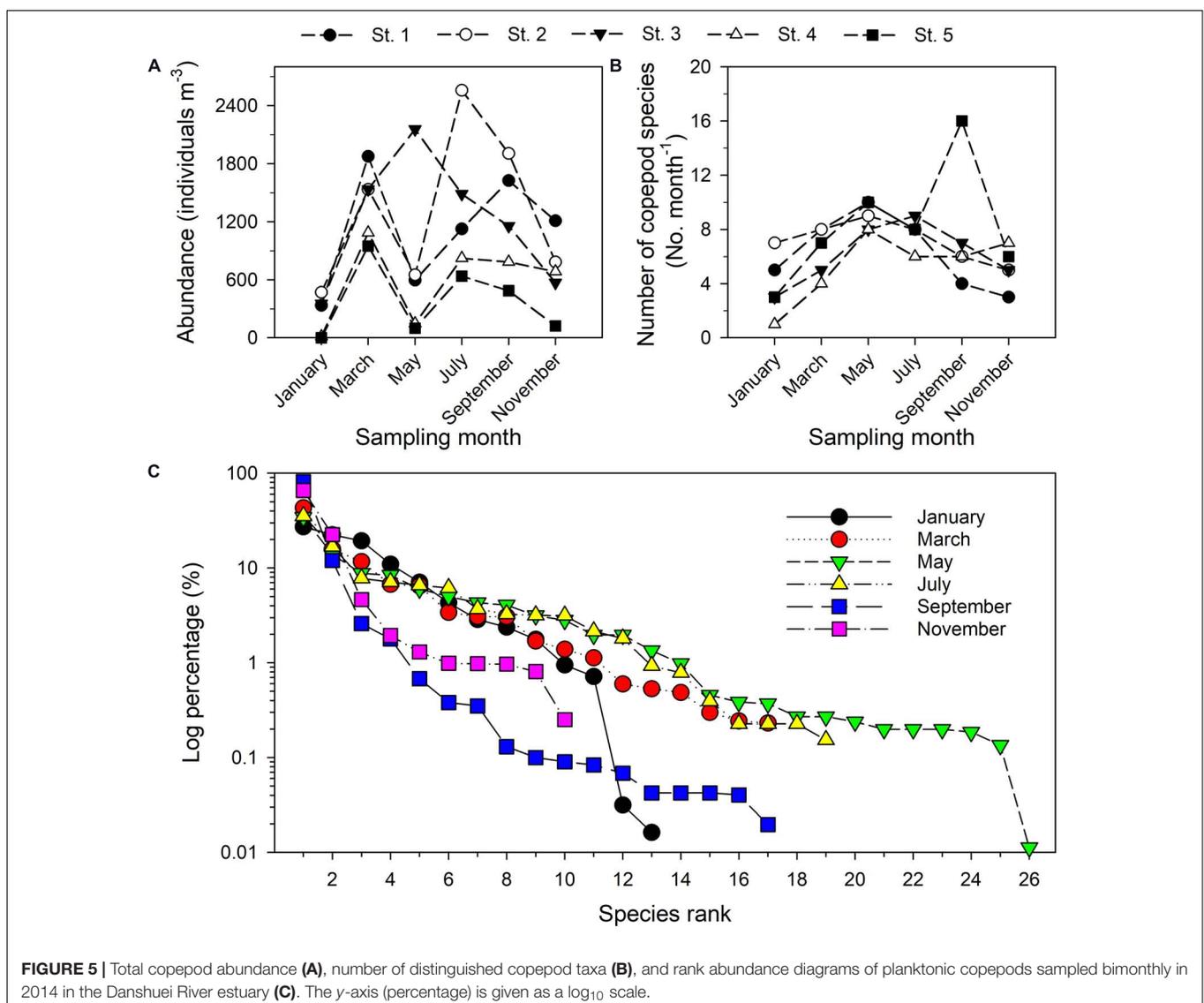


FIGURE 5 | Total copepod abundance (A), number of distinguished copepod taxa (B), and rank abundance diagrams of planktonic copepods sampled bimonthly in 2014 in the Danshuei River estuary (C). The y-axis (percentage) is given as a log₁₀ scale.

different among the six sampling dates, especially so for the curve representing the May cruise in which the highest number of taxa was recorded. During the cruise in January, two copepod taxa with relative abundances smaller than 1.0% (Figure 5C).

The relative rank abundances of the 10 most dominant copepod taxa on successive sampling dates provide evidence of faunal succession within the community (Table 2), with the ranks of the dominant taxa showing changes over time. The harpacticoid *Euterpina acutifrons* was in the dominant group throughout most of the year, but not in January. *Acartia* (*Odontacartia*) *pacifica*, *Paracalanus parvus parvus* sensu lato and *Parvocalanus crassirostris* were among the dominants in three sampling months during July–November, January–May, and May–September, respectively. Two congeneric species, *Acrocalanus gibber* and *A. gracilis*, displayed similar high abundances in March and May, but not in other months. *Oithona dissimilis* and *Temora turbinata* were found among the dominants in May and July. Other adventitiously dominant species, which displayed a short period of dominance and a subsequent rapid decline, included *Ditrichocorycaeus affinis*, *Oithona attenuata*, *Oithona simplex*, *Oncaea venusta*, *Pseudodiaptomus annandalei*, *Tachidius* (*Tachidius*) *discipes*, *Tortanus* (*Eutortanus*) *dextrilobatus*, and *Tortanus* (*Eutortanus*) *derjugini* (Table 2). *Calanus sinicus*, a bioindicator of cold water in the southwestern East China Sea (Figure 3G), was recorded in March (Supplementary Table 2), when the CCC reached into Taiwan's northern waters.

When the Bray-Curtis similarity distance was calculated for associations among the 16 most abundant adult copepod taxa, those with similar distribution patterns formed five clusters or groups that reflected preferences for particular hydrographic

conditions (Figure 6A and Table 3). Group A I, comprising *Oithona simplex* and *Tortanus* spp., occurred in three samples from January, May, and July that were characterized by high salinity (26.82 ± 11.89 PSU), high pH (8.0 ± 0.35), and high DO (6.53 ± 0.49 mg/L). Group A II, comprising the common taxa *Parvocalanus crassirostris*, *Oithona* spp., *Paracalanus parvus parvus* sensu lato, and *Paracalanus* spp., occurred in 15 samples collected throughout the year on all six cruises. The third group (Group B II) comprised four taxa, viz., *Acrocalanus gibber*, *Acrocalanus gracilis*, *Paracalanus aculeatus*, and *Corycaeus* spp., that occurred from January to September, but not in November when water temperatures were low ($23.60 \pm 5.07^\circ\text{C}$). The fourth group (Group C I) included three taxa, *Acartia* (*Odontacartia*) *pacifica*, *Acartia* sp., and *Bestiolina* n. sp., that appeared in 19 samples taken from January to July, when low salinity (20.36 ± 8.77 PSU) and low DO (5.02 ± 1.10 mg/L) were prevalent. The remaining three taxa, viz., *E. acutifrons*, *O. dissimilis*, and *T. turbinata*, comprising Group C II, were characterized by occurring at the highest average water temperature ($26.99 \pm 2.87^\circ\text{C}$). The copepod associations in group C II; among them, 12 samples were collected in May, July, and September when the water temperature was relatively high (Table 3). The present analysis demonstrates a substantial temporal succession within the copepod assemblage in the estuary of the Danshuei River, resulting at least in part from the interaction of river water and seawater (Figure 6A), and also a pattern of preference by certain groups of copepod taxa for particular environmental conditions (Table 3). Nonmetric multidimensional scaling (NMDS) demonstrated a similar distribution pattern as the cluster analysis (Figure 6B). The copepod groups among intra-annual samples were separated by

TABLE 2 | Average density (individuals m^{-3}), and relative abundance (RA, %) of the 10 most abundant copepod species recorded on each bimonthly sampling date in 2014.

| Rank | Sampling month | | | | | |
|------|---|---|--|--|---|--|
| | January | March | May | July | September | November |
| 1 | <i>Tortanus</i> spp. (63.76, 27.19%) | <i>Corycaeus</i> spp. (602.11, 43.15%) | <i>Bestiolina</i> n. sp. (250.21, 34.29%) | <i>P. crassirostris</i> (468.65, 35.33%) | <i>Bestiolina</i> n. sp. (971.01, 81.5%) | <i>Acartia</i> sp. (442.42, 65.64%) |
| 2 | <i>Acartiella</i> sp. (52.57, 22.41%) | <i>P. parvus</i> (220.92, 15.83%) | <i>P. crassirostris</i> (101.4, 13.9%) | <i>Bestiolina</i> n. sp. (222.66, 16.79%) | <i>A. (O.) pacifica</i> (143.54, 12.05%) | <i>Bestiolina</i> n. sp. (151.51, 22.48%) |
| 3 | <i>O. simplex</i> (45.3, 19.32%) | <i>A. gracilis</i> (162.86, 11.67%) | <i>O. dissimilis</i> (64.21, 8.8%) | <i>O. dissimilis</i> (103.34, 7.79%) | <i>P. crassirostris</i> (30.98, 2.6%) | <i>A. (O.) pacifica</i> (31.27, 4.64%) |
| 4 | <i>T. (E.) dextrilobatus</i> (25.72, 10.97%) | <i>P. aculeatus</i> (94.07, 6.74%) | <i>T. turbinata</i> (61.39, 8.41%) | <i>Oithona</i> spp. (94.54, 7.13%) | <i>Oithona</i> spp. (21.32, 1.79%) | <i>Acrocalanus</i> spp. (13.09, 1.94%) |
| 5 | <i>Bestiolina</i> n. sp. (16.62, 7.08%) | <i>Paracalanus</i> spp. (90.09, 6.46%) | <i>E. acutifrons</i> (44.01, 6.03%) | <i>E. acutifrons</i> (87.41, 6.59%) | <i>P. annandalei</i> (8.05, 0.68%) | <i>Apocyclops</i> sp. (8.73, 1.3%) |
| 6 | <i>Oithona</i> spp. (10.08, 4.3%) | <i>E. acutifrons</i> (47.38, 3.4%) | <i>A. gracilis</i> (36.66, 5.02%) | <i>A. (O.) pacifica</i> (81.99, 6.18%) | <i>Paracalanus</i> spp. (4.5, 0.38%) | <i>Oithona</i> spp. (6.7, 0.99%) |
| 7 | <i>P. parvus</i> (6.72, 2.86%) | <i>A. gibber</i> (43.01, 3.08%) | <i>P. parvus</i> (31.44, 4.31%) | <i>O. attenuata</i> (49.09, 3.7%) | <i>E. acutifrons</i> (4.13, 0.35%) | <i>T. (E.) derjugini</i> (6.63, 0.98%) |
| 8 | <i>Paracalanus</i> spp. (5.59, 2.38%) | <i>Oithona</i> spp. (42.91, 3.07%) | <i>A. gibber</i> (29.73, 4.08%) | <i>Acartia</i> sp. (43.33, 3.27%) | <i>P. aculeatus</i> (1.55, 0.13%) | <i>T. (T.) discipes</i> (6.56, 0.97%) |
| 9 | <i>P. aculeatus</i> (4.15, 1.77%) | <i>T. (T.) discipes</i> (23.69, 1.7%) | <i>Parvocalanus</i> spp. (22.98, 3.15%) | <i>T. turbinata</i> (42.05, 3.17%) | <i>O. venusta</i> (1.23, 0.1%) | <i>E. acutifrons</i> (5.44, 0.81%) |
| 10 | <i>T. (E.) derjugini</i> (2.23, 0.95%) | <i>D. affinis</i> (19.37, 1.39%) | <i>Oithona</i> spp. (20.55, 2.82%) | <i>O. simplex</i> (41.76, 3.15%) | <i>Acrocalanus</i> spp. (1.1, 0.09%) | <i>O. attenuata</i> (1.68, 0.25%) |

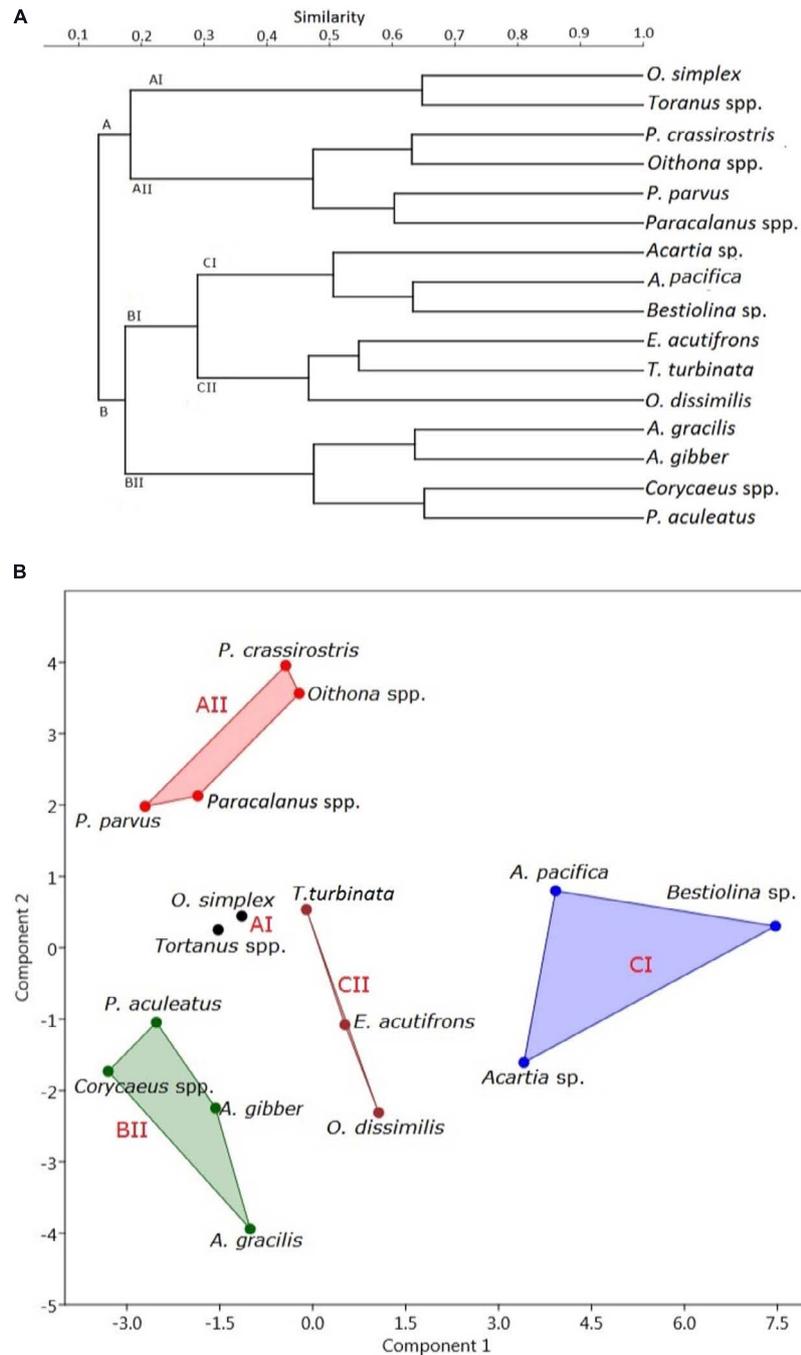


FIGURE 6 | Cluster dendrograms of distribution plotted using the Bray–Curtis similarity distance **(A)** and nonmetric multidimensional scaling **(B)** of the 16 most abundant copepod species (comprising 93.44% of the total copepods; full names given in **Supplementary Table 2**) collected on six bimonthly sampling dates in 2014 in the Danshuei River estuary.

cluster analyses, which further revealed and confirmed a pattern of preference for environmental conditions (**Table 3**).

Statistical Analysis

The copepod community in the study area showed a successional pattern among all six bimonthly cruises (**Table 2** and

Supplementary Table 2). Statistical testing to compare their temporal and spatial variability in more detail confirmed that: (1) copepod abundance showed bimonthly variation (**Figures 7A,A-1**); (2) total copepod abundance was significantly higher in March than in January ($p = 0.038$) (**Figure 7B**); (3) taxon number was significantly higher in May than in

TABLE 3 | Average (mean \pm standard deviation) temperatures, salinity, pH, and dissolved oxygen concentration (DO) of copepod species occurring in the samples included in **Figure 6**.

| Cluster group | Included samples | Temperature ($^{\circ}$ C) | Salinity (PSU) | pH | DO (mg/L) |
|---------------|--|-----------------------------|-------------------|-----------------|-----------------|
| A I | Jan (1), May (1), Jul (1) | 24.73 \pm 6.10 | 26.82 \pm 11.89 | 8.00 \pm 0.35 | 6.53 \pm 0.49 |
| A II | Jan (2), Mar (2), May (3), Jul (3), Sep (4), Nov (1) | 25.44 \pm 4.21 | 24.31 \pm 10.18 | 7.95 \pm 0.26 | 5.62 \pm 1.38 |
| B II | Jan (1), Mar (5), May (5), Jul (2), Sep (1) | 23.60 \pm 5.07 | 25.60 \pm 12.24 | 7.96 \pm 0.32 | 5.99 \pm 1.70 |
| C I | Jan (5), Mar (5), May (5), Jul (4) | 26.08 \pm 3.37 | 20.36 \pm 8.77 | 7.84 \pm 0.25 | 5.02 \pm 1.10 |
| C II | Mar (2), May (5), Jul (5), Sep (2), Nov (1) | 26.99 \pm 2.87 | 23.04 \pm 10.50 | 7.92 \pm 0.27 | 5.12 \pm 1.17 |

Numbers in parentheses indicate the number of samples collected on each bimonthly sampling date.

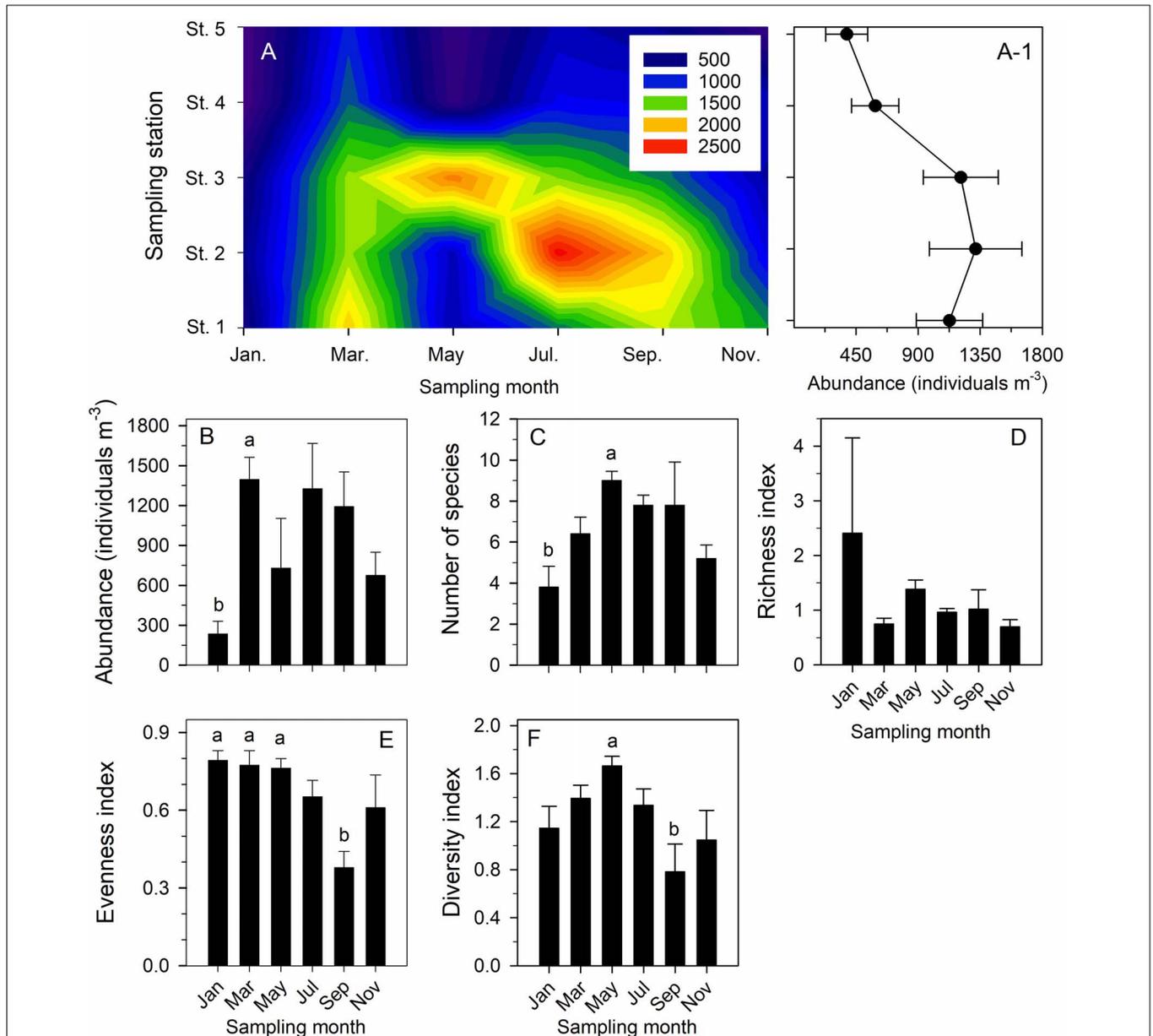


FIGURE 7 | Contour chart showing temporal variation in total copepod abundance (individuals m^{-3}) of six bimonthly sample series taken in Danshuei River estuary in 2014 (A); mean abundance (\pm standard deviation) of total copepod abundance at each sampling station during all six bimonthly sampling cruises (A-1); and comparisons of bimonthly changes in mean (\pm standard deviation) abundance (B), number of species (C), and indices of richness (D), evenness (E), and Shannon-Wiener diversity (F) over the year at all stations. Various superscripts indicate significant differences ($p < 0.05$) confirmed by one-way analyses of variance, followed by Tukey tests.

January ($p = 0.025$) (Figure 7C); (4) the richness index was not significantly different among sampling dates ($p > 0.05$) (Figure 7D); (5) the index of evenness was significantly lower in September than in January ($p = 0.009$), March ($p = 0.008$), and December ($p = 0.01$) (Figure 7E); and (6) the Shannon–Wiener diversity index was significantly higher in May than in September ($p = 0.017$) (Figure 7F). By contrast, the mean values of total copepod abundance and taxon number, the indices of richness and evenness, and the Shannon–Wiener diversity were not significantly different among the five sampling stations based on pooled data ($p > 0.05$).

Pearson's correlation showed that the number of copepod taxa was significant positively correlated with sea surface temperature (SST; $r = 0.49$, $p = 0.006$) but significant negatively correlated with the evenness index ($r = -0.388$, $p = 0.038$). Salinity showed a significant positive correlation with both the number of copepod taxa ($r = 0.371$, $p = 0.043$) and total copepod abundance ($r = 0.636$, $p < 0.001$), and the latter was significant positively correlated with pH ($r = 0.71$, $p < 0.001$) and DO ($r = 0.364$, $p = 0.048$). Among the identified copepods, the abundances of *P. aculeatus* ($r = -0.399$, $p = 0.03$) and *Corycaeus* spp. ($r = -0.497$, $p = 0.01$) were negatively correlated with seawater temperature while five other taxa showed significant positive changes ($p < 0.05$) in abundance with seawater temperature (Table 4): *A. (O.) pacifica*, *Bestiolina* n. sp., *P. crassirostris*, *T. turbinata*, and *O. dissimilis*. The abundance of three taxa (*A. gibber*, *Paracalanus* spp., and *T. turbinata*) were positively correlated with pH ($p < 0.05$) while the abundance of each of the following six species was positively correlated with salinity ($p < 0.05$): *A. gibber*, *A. gracilis*, *P. aculeatus*, *P. parvus*, *T. turbinata*, and *Corycaeus (D.) erythraeus* (Table 4). The abundance of *Sinocalanus sinensis* ($r = -0.358$, $p = 0.05$) was negatively correlated with DO while seven other taxa showing significant positive ($p < 0.05$) changes abundance with increased DO (Table 4).

Remarks on Brackish Water and Freshwater Copepods

Only one truly freshwater copepod species, *Mongolodiptomus birulai*, was present in our samples from the Danshuei River estuary. Most of the other copepods identified in the present study, aside from the marine/brackish-water species and brackish/freshwater species mentioned below, were fully marine species, part of the zooplankton community transported by seawater intrusion into the waters of the estuary. Of the eight species that occur in both marine and brackish-water habitats—*A. (O.) pacifica*, *S. sinensis*, *Pseudodiptomus annandalei*, *Pseudodiptomus inopinus*, *O. attenuata*, *O. simplex*, *T. (T.) discipes*, and *E. acutifrons* (Supplementary Table 2)—the four euryhaline species were *P. annandalei*, *P. inopinus*, *O. attenuata*, and *O. simplex*. Species that occur in both fresh and brackish water accounted for 20.5% of the copepod species recorded in this study, and 11.85% of the individual adult copepods. Overall, the most abundant species was *A. (O.) pacifica* (42.8 ± 87.66 inds. m^{-3} , RA: 4.63%), followed by *E. acutifrons* (31.39 ± 73.21 inds. m^{-3} , RA: 3.39%) and *O. simplex* (16.91 ± 47.77 inds. m^{-3} , RA: 1.83%) while the highest frequency of occurrence was recorded for *A. (O.) pacifica* (present in 36.7%

TABLE 4 | Significant correlations between the density of copepod species and temperature, salinity, pH, and dissolved oxygen concentration (DO), as determined by Pearson's correlation analysis.

| Species | r-Value | p-Value |
|--|---------|----------|
| Temperature | | |
| <i>Acartia (Odontacartia) pacifica</i> | 0.424 | 0.02* |
| <i>Bestiolina</i> n. sp. | 0.459 | 0.01** |
| <i>Paracalanus aculeatus</i> | -0.399 | 0.03* |
| <i>Parvocalanus crassirostris</i> | 0.372 | 0.04* |
| <i>Temora turbinata</i> | 0.389 | 0.03* |
| <i>Corycaeus</i> spp. | -0.497 | 0.01** |
| <i>Oithona dissimilis</i> | 0.368 | 0.05* |
| Salinity | | |
| <i>Acrocalanus gibber</i> | 0.410 | 0.02* |
| <i>Acrocalanus gracilis</i> | 0.385 | 0.04* |
| <i>Paracalanus aculeatus</i> | 0.362 | 0.05* |
| <i>Paracalanus parvus</i> | 0.410 | 0.02* |
| <i>Temora turbinata</i> | 0.498 | 0.01** |
| <i>Corycaeus (D.) erythraeus</i> | 0.372 | 0.04* |
| pH | | |
| <i>Acrocalanus gibber</i> | 0.376 | 0.04* |
| <i>Paracalanus</i> spp. | 0.328 | 0.08 |
| <i>Temora turbinata</i> | 0.502 | <0.001** |
| DO | | |
| <i>Sinocalanus sinensis</i> | -0.358 | 0.05* |
| <i>Acrocalanus gibber</i> | 0.380 | 0.04* |
| <i>Acrocalanus gracilis</i> | 0.364 | 0.05* |
| <i>Paracalanus aculeatus</i> | 0.368 | 0.05* |
| <i>Paracalanus parvus</i> | 0.413 | 0.02* |
| <i>Paracalanus</i> spp. | 0.354 | 0.05* |
| <i>Corycaeus (D.) erythraeus</i> | 0.370 | 0.04* |
| <i>Corycaeus</i> spp. | 0.530 | <0.001** |

*Significant at the $p < 0.05$ level (2-tailed). **Significant at the $p < 0.01$ level (2-tailed).

of the samples), followed by *O. attenuata* and *T. (T.) discipes* (each 20%) (Supplementary Table 2).

DISCUSSION

Seasonal Meteorology and Hydrological Changes

The three main hydrographic factors affecting estuarine hydrosystems are coastal currents, tidal movements, and upstream runoff. Satellite images showed that the present study area was affected by the cold water masses of the CCC, which were replaced by warm water masses from the South China Sea and the Kuroshio Current when the CCC retreated toward the coast of mainland China (Figure 2). Tidal movements occur in cycles, twice a day, and the salinity and temperature records made while sampling show that the estuarine waters were heavily influenced by tidal changes (Figure 3). Most notable was a salinity record of 35 PSU (indicating seawater intrusion) in September at station 5, 8.89 km upstream from the coast (Figure 3H). Marine zooplankton can surely intrude even higher than this in the Danshuei River by means of seawater transport.

The northeast monsoon prevails from November to March in Taiwan (Liang et al., 2003). The air temperature decreases, and rainfall in the mountains causes more freshwater flushing of the

TABLE 5 | List of the dominant copepods recorded from the downstream reaches and estuaries of rivers around the world.

| River | Country | Period | Mesh size | Dominant species | Proportion or abundance (ind m ⁻³ unless otherwise stated) | References |
|------------------------------------|---------|---|-----------|---|---|----------------------|
| ASIA | | | | | | |
| Pearl River estuary | China | Wet season: 14 and 28/Jul. 1999 Dry season: 7–10/Jan. 2000 | 169 μm | Wet season: <i>Acartia spinicauda</i> <i>Parvocalanus crassirostris</i> <i>Oithona rigida</i> <i>Paracalanus aculeatus</i> <i>Euterpina acutifrons</i> <i>Oithona setigera</i> <i>Acartia spinicauda</i> Dry season: <i>Paracalanus serrulus</i> <i>Parvocalanus crassirostris</i> <i>Paracalanus parvus</i> <i>Acartia spinicauda</i> <i>Oithona</i> spp. | Species listed in left column were seasonal dominants | Tan et al. (2004) |
| Changjiang Estuary | China | May 2004–Feb. 2005 | 200 μm | May: <i>Monoculodes limnophilus</i> <i>Schmackeria poplesia</i> (currently <i>Pseudodiaptomus poplesia</i>) <i>Tortanus vermiculus</i> <i>Labidocera euchaeta</i> August: <i>Schmackeria poplesia</i> (currently <i>Pseudodiaptomus poplesia</i>) <i>Acartia pacifica</i> <i>Tortanus vermiculus</i> November: <i>Labidocera euchaeta</i> <i>Paracalanus parvus</i> <i>Paracalanus aculeatus</i> February: <i>Sinocalanus sinensis</i> <i>Acartia hongii</i> | 54.7 30.2 15.8 122.6 158.6 94.9 68.0 89.7 176.1 142.1 1435.4 360.2 | Gao et al. (2008) |
| Tropical estuary | India | Apr., Jul., and Oct. 2003 | 200 μm | Pre-monsoon: <i>Labidocera pectinata</i> <i>Paracalanus crassirostris</i> <i>Paracalanus aculeatus</i> <i>Acartia centrura</i> <i>Acartia bowmani</i> <i>Acartia bilobata</i> <i>Centropages alcocki</i> <i>Pseudodiaptomus serricaudatus</i> <i>Corycaeus</i> sp. <i>Oithona brevicornis</i> <i>Bestiolina similis</i> <i>Pseudodiaptomus annandalei</i> Monsoon: <i>Acartiella gravelyi</i> <i>Pseudodiaptomus binghami malayalus</i> Post-monsoon: <i>Acartia tropica</i> <i>Acartia bilobata</i> | Species listed in left column all >1000 | Madhu et al. (2007) |
| Godavari River (estuary and plume) | India | May 2002 | 120 μm | Large-size: calanoids Small-size: Paracalanidae Acartiidae Oithonidae Corycaeidae Oncaeidae Euterpinae | Total: 8.4% Total: 92% | Rakesh et al. (2013) |
| Ganges River estuary | India | 24–25/Feb. 2019 | 200 μm | <i>Bestiolina similis</i> <i>Paracalanus parvus</i> <i>Acartiella tortaniformis</i> | 121,970 105,530 83,240 | Paul et al. (2019) |

(Continued)

TABLE 5 | Continued

| River | Country | Period | Mesh size | Dominant species | Proportion or abundance (ind m ⁻³ unless otherwise stated) | References |
|--|-----------------|--|----------------------------|---|---|----------------------------------|
| 45 rivers in Japan, 4 rivers in Korea | Japan, Korea | Oct. 2006–Aug. 2009 | 0.1 mm 0.2 mm 0.3 mm | 83 samples from 45 rivers in Japan: <i>Acartia ohtsukai</i> <i>A. sinjiensis</i> <i>A. tsuensis</i> <i>Pseudodiaptomus inopinus</i> <i>P. ishigakiensis</i> <i>Sinocalanus sinensis</i> <i>S. tenellus</i> <i>Tortanus derjugini</i> 7 samples from 4 rivers in Korea: <i>Acartia ohtsukai</i> <i>Acartia</i> sp. <i>Pseudodiaptomus inopinus</i> <i>Pseudodiaptomus</i> sp. <i>Sinocalanus tenellus</i> <i>Tortanus dextrilobatus</i> | | Sakaguchi et al. (2011) |
| Yura River | Japan | Jan. 2007–Dec. 2008 | 200 μm | <i>Oithona</i> spp. <i>Acartia</i> spp. <i>Pseudodiaptomus</i> spp. | Dominant in downstream reaches | Watanabe et al. (2014) |
| Danshuei River (estuary and plume) | Taiwan | Oct. 1998–Jul. 2004 | 333 μm | Summer: <i>Temora turbinata</i> Winter: <i>Calanus sinicus</i> | Species listed in left column were seasonal dominants | Hwang et al. (2009) |
| Danshuei River | Taiwan | Oct. 2001–Feb. 2003 | 200 μm | <i>Parvocalanus crassirostris</i> <i>Cyclopina</i> sp. <i>Pseudodiaptomus annandalei</i> | 4,260 ± 15,500 2,330 ± 12,600 1,920 ± 10,400 | Hwang et al. (2010) |
| Lanyang River | Taiwan | Jun. 2004–Dec. 2005 | 100 μm | <i>Parvocalanus crassirostris</i> <i>Thermocyclops kawamurai</i> <i>Pseudodiaptomus serricaudatus</i> | 473.19 ± 708.37 380.91 ± 514.96 365.22 ± 622.25 | Dahms et al. (2012) |
| AFRICA | | | | | | |
| Annaba Bay | Algeria | Jan. 2009–Mar. 2011 | 200 μm | <i>Paracalanus indicus</i> <i>Oithona similis</i> | 27.4% 14.5% | Ounissi et al. (2016) |
| Mpenjati Estuary | South Africa | 1998–1999 | 90 μm | <i>Pseudodiaptomus hessei</i> <i>Acartia natalensis</i> | | Kibirige and Perissinotto (2003) |
| Kasouga Estuary | South Africa | 2001–2002 | 60 μm | Summer: <i>Pseudodiaptomus hessei</i> <i>Acartia longipatella</i> <i>Halicyclops</i> spp. Winter: <i>Pseudodiaptomus hessei</i> <i>Acartia longipatella</i> <i>Halicyclops</i> spp. | 12,518 1678 760 2,792 864 196 | Froneman (2004) |
| St Lucia Estuary | South Africa | Feb. 2011–Nov. 2013 | 100 μm | <i>Pseudodiaptomus stuhlmanni</i> <i>Acartiella natalensis</i> <i>Oithona brevicornis</i> copepod nauplii | In total >90% of whole zooplankton abundance | Carrasco and Perissinotto (2015) |
| AMERICAS | | | | | | |
| Caeté River estuary (Caeté Bay) | Brazil | Mar. and May 2001 | 300 μm | <i>Pseudodiaptomus marshi</i> <i>Pseudodiaptomus richardi</i> <i>Acartia tonsa</i> <i>Acartia lilljeborgi</i> | 56.9% 22.8% 11.6% 3.3% | Krumme and Liang (2004) |
| Sergipe River | Brazil | Jul. 2001 and Feb. 2002 | 200 μm | July: <i>Acartia lilljeborgi</i> February: <i>Parvocalanus crassirostris</i> <i>Paracalanus quasimodo</i> <i>Temora turbinata</i> | 2.4% 22.9% 6.39% 5.45% | Araujo et al. (2008) |
| Paranagua Estuarine Complex | Brazil | Mar. and Aug. 2012 Feb. and Jun. 2013 | 200 μm | <i>Acartia lilljeborgi</i> <i>Oithona hebes</i> <i>Pseudodiaptomus acutus</i> <i>Temora turbinata</i> | 44% 26% 8% 6% | Salvador and Bersano, 2017 |
| Fraser River | Canada | Jan. 2015–Jul. 2016 | 100 μm | <i>Eurytemora affinis</i> <i>Diacyclops thomasi</i> <i>Pseudobradia</i> spp. | Dominant in estuary stations | Breckenridge et al. (2020) |
| Barnegat Bay | United States | May–Sep. 2012 | 500 μm | <i>Acartia</i> spp. (a) <i>Eurytemora</i> spp. (b) | (a)+(b) = 71.8% | Howson et al. (2017) |

(Continued)

TABLE 5 | Continued

| River | Country | Period | Mesh size | Dominant species | Proportion or abundance (ind m ⁻³ unless otherwise stated) | References |
|----------------------|-----------|----------------------------|---------------------------------|---|---|----------------------|
| EUROPE | | | | | | |
| Mondego River | Portugal | Jul. 1999–Jun. 2000 | 63 μm 125 μm | 63 μm: | | Vieira et al. (2003) |
| | | | | <i>Acartia</i> spp. copepodites | 3,976 | |
| | | | | <i>Oithona nana</i> | 3,540 | |
| | | | | <i>Acartia tonsa</i> | 2,412 | |
| | | | | 125 μm: | | |
| | | | | <i>Temora longicornis</i> | 1,615 | |
| | | | <i>Acartia tonsa</i> | 1,121 | | |
| | | | <i>Acartia</i> spp. copepodites | 1,029 | | |
| OCEANIA | | | | | | |
| Swan-Canning Estuary | Australia | Austral winter, 1986–1987) | 200 μm | <i>Gladioferens imparipes</i> Harpacticoid sp.1 (c) <i>Acartia cf. clausi</i> (d) | 54% (c)+(d) = 22% | Rose et al. (2020) |

Danshuei River during that period. The monsoon thus potentially affects the hydrographic conditions of the estuary (Wyrki, 1961; Liang et al., 2003), and may induce changes in the river's plankton diversity (Khanna et al., 2012; Bhutiani and Khanna, 2014). The monsoon also influences the mass transport of water along the northwest coast of Taiwan, thereby also changing the structure of the marine coastal planktonic copepod communities (Hwang and Wong, 2005; Yu, 2005; Tseng et al., 2008; Hwang et al., 2014). During the present study, the present survey area along with the rest of northern Taiwan experienced two meteorological events, the moderate Typhoon Matmo (July 21–23, 2014) and the mild Typhoon Fung-Wong (September 19–22, 2014). Typhoons can affect the marine plankton's community structure, as has been documented for phytoplankton (Chung et al., 2012; Yasuki et al., 2013; Grossmann et al., 2014), jellyfish (López-López et al., 2012; Tseng et al., 2015), and copepods (Chou et al., 2012; Beyrend-Dur et al., 2013; Grossmann et al., 2014). However, the July and September samplings in the present study both took place about a week after these typhoons had passed, long enough for any runoff-caused changes in the estuary's zooplankton assemblages to have dissipated.

The present study's hydrological data show clear differences in water temperature from one bimonthly sampling date to the next. Other hydrological parameters (salinity, pH, and DO), however, were subject to mixing by tidal movements and the interplay of seawater and river water, and showed no such definite long-term temporal pattern. In other words, hydrographic changes reflecting the seasonal alternation of coastal water masses were clearer than fluctuations engendered by the tidal cycle.

Dynamic Assemblages of Zooplankton and Copepods

In the present study, significant structural changes were evident in the composition of the zooplankton (Figure 4) and its copepod fraction (Table 2 and Figure 5) in different sampling months. Even so, copepods (including Calanoida, Cyclopoida, and Harpacticoida) always dominated the zooplankton, as has been reported many times previously from waters in the East China Sea (e.g., Lan et al., 2008), South China Sea (e.g., Lo et al., 2014), and coastal areas of Taiwan (e.g., Lee et al., 2018).

The composition of zooplankton in Taiwan's northern waters is known to be affected by the CCC and the Kuroshio Current (Lan et al., 2008; Chou et al., 2012; López-López et al., 2013; Hsieh et al., 2004). The CCC, originating from the Yellow and Bohai seas, is characterized by low-temperature and low-salinity waters. It occupies the southwestern part of the East China Sea while the northeast monsoon prevails (Tseng et al., 2008). The dominant bioindicator of planktonic copepods in the CCC is the calanoid *Calanus sinicus* (Hwang and Wong, 2005; Lan et al., 2008). Its population size in the southern East China Sea changes in response to climate change and the monsoon (Molinero et al., 2018), and there are biogeographic indications that the CCC transports it along the coast of mainland China as far as Hainan Island in the northwestern South China Sea (Yin et al., 2011) and Kueishan Island off northeastern Taiwan (Tseng et al., 2013). During the present study, our record of *C. sinicus* in March (Supplementary Table 2), which corresponded to the lowest water temperature observed all year (Figure 3A), also confirmed past reports of *C. sinicus* in the estuary and plume areas of the Danshuei River (Hwang et al., 2006, 2009, 2010), although at a lower density than before, 3.23 ± 7.22 inds. m⁻³ versus 6852 ± 39039 inds. 10⁻³ m⁻³ (Hwang et al., 2006). The relatively low density was probably due to dilution of the seawater by river water in the estuary.

The waters of the Kuroshio Current, which affect the northern waters of Taiwan while the southwest monsoon prevails, are characterized by both high temperature and high salinity (Lan et al., 2008; Tseng et al., 2011b). After the seawater temperature rises, the calanoid *Temora turbinata* becomes the most dominant species of copepod off northern coastal Taiwan, occurring widely in both the northwestern (Chang and Fang, 2004; Tseng et al., 2008) and northeastern coastal waters (Hwang et al., 2004, 2006, 2009, 2010; Chou et al., 2012). In the present study it appeared in May, July, and September, and its abundance was ranked 4th (RA: 8.41%), 9th (RA: 3.17%) and 11th (RA: 0.08%), respectively, among all identified communities in samples collected in May, July, and September (Supplementary Table 2). Its appearance was significant positively correlated with increasing water temperature and salinity (Table 4). All the present results concerning *T. turbinata* are consistent the

TABLE 6 | List of previously recorded brackish-water and freshwater copepod species from the Danshuei (DR), Lanyang (LR), and Gaoping (GR) rivers in Taiwan, along with those recorded from the Danshuei River in the present study.

| Rivers in Taiwan | DR | | | LR | | | GR |
|--|----|---|---|----|---|---|----|
| | 1 | 2 | P | 3 | 4 | 5 | 1 |
| Order Calanoida | | | | | | | |
| <i>Acartia (Euacartia) southwelli</i> Sewell, 1914 ^B | | + | | | | + | + |
| <i>Acartia (Odontacartia) pacifica</i> Steuer, 1915 ^B | | | + | | | | + |
| <i>Acartia sinjiensis</i> Mori, 1940 ^{B, *1} | + | | | | | | + |
| <i>Acartiella sinensis</i> Shen & Lee, 1963 ^B | + | | | | | | |
| <i>Eurytemora pacifica</i> Sato, 1913 ^B | + | | | | | | + |
| <i>Mongolodiptomus birulai</i> (Rylov, 1922) ^F | | | + | + | + | | + |
| <i>Mongolodiptomus uenoi</i> (Kikuchi K., 1936) ^F | | | | | | | + |
| <i>Neodiaptomus schmackeri</i> (Poppe & Richard, 1892) ^F | | | | | | | + |
| <i>Neurodiaptomus tumidus</i> Kiefer, 1937 ^F | | | | | | | + |
| <i>Pseudodiaptomus annandalei</i> Sewell, 1919 ^{B, F} | + | + | + | + | + | + | + |
| <i>Pseudodiaptomus forbesi</i> (Poppe & Richard, 1890) ^{B, F} | | | | | | | + |
| <i>Pseudodiaptomus inopinus</i> Burckhardt, 1913 ^{B, F} | + | | + | | | | |
| <i>Pseudodiaptomus marinus</i> Sato, 1913 ^B | + | | | | | | + |
| <i>Sinodiaptomus sarsi</i> (Rylov, 1923) ^F | | | | | | + | |
| <i>Sinocalanus sinensis</i> (Poppe, 1889) ^B | + | | + | | | + | + |
| <i>Sinocalanus tenellus</i> (Kikuchi K., 1928) ^B | | | | + | + | + | |
| Order Cyclopoida | | | | | | | |
| <i>Apocyclops borneoensis</i> Lindberg, 1954 ^{B, F} | | + | | + | + | | |
| <i>Cyclopina</i> sp. | | + | | | | | |
| <i>Corycaeus andrewsi</i> Farran, 1911 ^{B, *2} | + | | | | | | |
| <i>Corycaeus clausi</i> Dahl F., 1894 ^B | + | | | | | | + |
| <i>Corycaeus crassiusculus</i> Dana, 1849 ^B | + | | | | | | + |
| <i>Corycaeus lubbocki</i> Giesbrecht, 1891 ^{B, *3} | + | | | | | | + |
| <i>Corycaeus speciosus</i> Dana, 1849 ^B | + | | | | | | + |
| <i>Corycaeus subtilis</i> Dahl M., 1912 ^{B, *4} | | | | + | + | | |
| <i>Cyclops vicinus</i> Uljanin, 1875 ^{F, *5} | | | | | | + | |
| <i>Ditrichocorycaeus andrewsi</i> (Farran, 1911) ^B | | | | | | | + |
| <i>Ditrichocorycaeus asiaticus</i> (Dahl F., 1894) ^B | + | | | | | | + |
| <i>Limnoithona sinensis</i> (Burckhardt, 1913) ^B | | | | | | + | + |
| <i>Limnoithona tetraspina</i> Zhang & Li, 1976 ^{B, F} | | | | | | | + |
| <i>Macrocyclus oligolasius</i> Kiefer, 1938 ^F | | | | | | | + |
| <i>Mesocyclops</i> sp. | | + | | | | | |
| <i>Mesocyclops pehpeiensis</i> Hu, 1943 ^F | | + | | + | + | | |
| <i>Microcyclops tricolor</i> (Lindberg, 1937) ^F | | | | | | + | + |
| <i>Microcyclops uenoi</i> Kiefer, 1937 ^F | | | | | | | + |
| <i>Oithona attenuata</i> Farran, 1913 ^{B, F} | + | | + | | | | + |
| <i>Oithona decipiens</i> Farran, 1913 ^B | | | | | | + | |
| <i>Oithona fallax</i> Farran, 1913 ^F | + | | | | | | + |
| <i>Oithona fragilis</i> Nishida, 1979 ^{B, F} | + | | | | | | + |
| <i>Oithona similis</i> Claus, 1866 ^{B, F} | | | | + | + | | |
| <i>Oithona simplex</i> Farran, 1913 ^{B, F} | + | | + | | | | |
| <i>Oithona tenuis</i> Rosendorn, 1917 ^{B, F} | + | | | | | | + |
| <i>Oithona longispina</i> Nishida, Tanaka & Omori, 1977 ^{B, F} | + | | | | | | + |
| <i>Oithona nana</i> Giesbrecht, 1893 ^{B, F} | + | | | | | | + |
| <i>Oithona robusta</i> Giesbrecht, 1891 ^{B, F} | + | | | | | | + |
| <i>Paracyclops affinis</i> (Sars G.O., 1863) ^F | | | | | | + | |
| <i>Paracyclops fimbriatus fimbriatus</i> (Fischer, 1853) ^F | + | | | | | + | |
| <i>Thermocyclops hyalinus</i> (Rehberg, 1880) ^F | | | | | | | + |
| <i>Thermocyclops kawamurai</i> Kikuchi K., 1940 ^F | | | | + | + | | |
| Order Harpacticoida | | | | | | | |
| <i>Canthocamptus staphylinus staphylinus</i> (Jurine, 1820) ^F | | | | | | + | |

(Continued)

TABLE 6 | Continued

| Rivers in Taiwan | DR | | | LR | | | GR |
|---|----|---|---|----|---|---|----|
| | 1 | 2 | P | 3 | 4 | 5 | 1 |
| <i>Euterpina acutifrons</i> (Dana, 1847) ^B | + | | | + | + | + | + |
| <i>Mesochra quadrispinosa</i> Shen & Tai, 1965 ^B | | | | | | + | |
| <i>Microsetella norvegica</i> (Boeck, 1865) ^B | + | | | | | + | |
| <i>Tachidius (Tachidius) discipes</i> Giesbrecht, 1881 ^B | | | + | | | | |

References: 1 = Yu (2005); 2 = Hwang et al. (2010); 3 = Dahms et al. (2012); 4 = Dahms et al. (2013); 5 = Tseng et al. (2016).

Other symbols and superscripts: P = present study. + = present; ^B = brackish water, ^F = freshwater, *¹⁻⁵ = current names given in footnote.

Current names:

*¹ *Acartia sinjiensis* Mori, 1940 = *Acartia (Acanthacartia) sinjiensis* Mori, 1940.

*² *Corycaeus andrewsi* Farran, 1911 = *Ditrichocorycaeus andrewsi* (Farran, 1911).

*³ *Corycaeus lubbocki* Giesbrecht, 1891 = *Ditrichocorycaeus lubbocki* (Giesbrecht, 1891).

*⁴ *Corycaeus subtilis* Dahl M., 1912 = *Ditrichocorycaeus subtilis* (Dahl M., 1912).

*⁵ *Cyclops vicinus* Uljanin, 1875 = *Cyclops vicinus vicinus* Uljanin, 1875.

above-cited previous observations from the coastal waters of northern Taiwan (Hwang et al., 2004, 2006, 2009, 2014; Chou et al., 2012).

In the present study, several of the dominant copepod taxa appeared in the estuary of the Danshuei River only during specific periods (Table 2). For example, *Parvocalanus crassirostris* (RA: 10.98%) appeared in March–September, when its abundance was significantly positive correlated with water temperature and *Paracalanus aculeatus* was recorded in January–May and September, when its density was significant negatively correlated with seawater temperature but significantly positively correlated with salinity and dissolved oxygen. Several studies have investigated the planktonic copepod composition in various parts of the southern East China Sea for periods longer than 1 year (Hwang et al., 2004, 2006, 2009; Chou et al., 2012), but the temporal scale was seasonal (four sampling intervals per year) and the information of the change in dominant species were less accurate than here. The sampling interval in the present study was every 2 months, which has improved our understanding of the temporal occurrence of the species. Shortening the sampling interval in the Danshuei River estuary to monthly would allow an even more precise understanding of copepod community succession there.

In the copepod assemblages revealed by the present study, most of the taxa were of marine origin (Supplementary Table 2) and the densities of many copepod taxa were significantly correlated with one or more hydrographic parameters (Table 4). Although salinity and temperature (Stepien et al., 1981; Milione and Zeng, 2008), intruding seawater, rainfall, and freshwater runoff (Yu, 2005; Dahms et al., 2012, 2013; Tseng et al., 2013), tidal movements (Shih, 2007), turbidity (Islam et al., 2005), and assorted physico-chemical parameters of river water (Khanna et al., 2005; Kumar et al., 2015) are known to affect the community composition of both phytoplankton and the zooplankton, the present results show that intruding seawater is the most important transportation vector in the Danshuei River estuary. Namely, the number of taxa and the total abundance/density of copepods were both significant positively correlated with changes in salinity, most copepods in the estuary belonged to marine species, and intrusive seawater was shown to deliver marine species to at 8.89 km upstream from the coast.

These results are furthermore consistent with earlier studies of zooplankton and copepods in Taiwan's Lanyang River (Dahms et al., 2012, 2013; Tseng et al., 2016).

Copepods in Estuaries

A comparison of the present study's results with similar data from estuaries around the world indicates a clear pattern of geographic regionalism in most cases (Table 5). The composition of the dominant taxa of copepods in estuaries around the world varies greatly. A comparison with the neighboring countries of China (Tan et al., 2004; Gao et al., 2008), Japan (Sakaguchi et al., 2011; Watanabe et al., 2014), and South Korea (Sakaguchi et al., 2011) reveals, however, a common pattern was in the changes of seasonally dominant species. Especially interesting is a study from Japan involving eight dominant copepods collected from 45 estuaries. Among them, *Acartia ohtsukai*, *Pseudodiaptomus inopinatus* and *Sinocalanus tenellus* also occur in four estuaries in South Korea (Sakaguchi et al., 2011), but only *P. inopinatus* appeared in the present study in Taiwan. This may be an indication that predominantly estuarine species cannot easily undergo long-distance dispersal across oceans. In different parts of the world such as India (Madhu et al., 2007; Rakesh et al., 2013; Paul et al., 2019), Europe (Vieira et al., 2003), Africa (Kibirige and Perissinotto, 2003; Froneman, 2004; Carrasco and Perissinotto, 2015; Ounissi et al., 2016), America (Krumme and Liang, 2004; Araujo et al., 2008; Howson et al., 2017; Salvador and Bersano, 2017; Breckenridge et al., 2020), and Oceania (Rose et al., 2020), it has been shown repeatedly that differences in the composition of the dominant copepod fauna in estuaries increase with distance. The abundance and diversity of zooplankton communities showed spatial, seasonal, and interannual trends in Barnegat Bay (Howson et al., 2017), and also in the Paranagua estuary (Salvador and Bersano, 2017). Worth mentioning is that Paul et al. (2019) recorded extremely high value of zooplankton gatherings, with a density of 1,090,550 (Inds/m³) in the estuary of the Ganges River. The different mesh sizes of nets used to collect estuarine zooplankton, ranging from 60 μm (Froneman, 2004) to 500 μm (Howson et al., 2017), might also affect the composition of the dominant species (Tseng et al., 2011a). The mesh size of zooplankton nets used to collect samples in the estuary ranged from 60 μm (Froneman, 2004) to 500 μm (Howson et al., 2017).

Studies using small-mesh nets have found copepodites to be the most dominant fraction in the samples (Vieira et al., 2003), but most of the literature, including the present study, has been focused on adult copepods (Table 5), mainly because of the difficulty in identifying copepodites.

Previous research on brackish-water and freshwater copepods in Taiwan has been limited (Dahms et al., 2012, 2013; Tseng et al., 2016). Nonetheless, the existing literature on the taxonomy of copepods in different rivers in Taiwan, including the Danshuei River in the island's northwest (Chen, 2005; Yu, 2005; Hwang et al., 2006, 2009, 2010), is due for a review. The three other previously surveyed rivers in Taiwan are the Choshuei River in the west-central part of the island (Sun et al., 2014), the Gaoping River in the southwest (Yu, 2005; Mai, 2016), and the Lanyang River in the northeast (Dahms et al., 2012, 2013; Tseng et al., 2016). Most of the reports surveyed zooplankton and/or copepods in the both rivers' estuaries and plume areas (Chen, 2005; Yu, 2005; Hwang et al., 2006, 2009, 2010; Mai, 2016), but only a few surveys were conducted in estuaries (Dahms et al., 2012, 2013; Tseng et al., 2016). The copepods studied by Chen (2005) and Sun et al. (2014) were identified only to the generic level, and Hwang et al. (2006, 2009) did not record the purely brackish-water and freshwater species.

Before the present study, 55 species of copepod from brackish water and freshwater had been recorded in Taiwan (Table 6). It is noteworthy that 32 of them were found in the Danshuei River, accounting for 58.2% of the total number of known brackish-water and freshwater species in Taiwan. Among them, five species occurred only in the Danshuei River: the calanoids *A. sinensis* and *P. forbesi*, the cyclopoids *O. fragilis* and *O. simplex*, and the harpacticoid *T. (T.) discipes* (Yu, 2005; Hwang et al., 2010; present study). It is worth noting that five species of brackish-water copepods were commonly recorded in all three of the other rivers: the calanoids *A. (E.) southwelli*, *S. sinensis*, and *P. annandalei*, the cyclopoid *O. attenuata*, and the harpacticoid *E. acutifrons*; as well as *M. birulai*, a freshwater calanoid copepod (Yu, 2005; Dahms et al., 2012, 2013; Sun et al., 2014; Mai, 2016) (Table 5).

CONCLUSION

The present study has shown that the spatial and temporal patterns of zooplankton distribution in the estuary of the Danshuei River were more affected by tidal movements than by other hydrographic changes, and that the assemblages of zooplankton, and in particular copepods, underwent a clear succession pattern during the course of the year. In addition, this study provided evidence that the CCC and Kuroshio Current affect the composition and abundance of zooplankton and copepods in the Danshuei River. Tidal movements transported many coastal zooplankters far up into the estuary. Up until now there have been only scant reports on the zooplankton and copepods of the Danshuei River, based on samples taken at long intervals. The present results suggest that an increase in sampling frequency and number of sampling stations will provide better data for understanding the intra-annual changes of zooplankton composition in river estuaries.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding authors.

AUTHOR CONTRIBUTIONS

P-WL contributed to the manuscript preparation, data analysis and interpretation, field sampling, and manuscript review and editing. S-HH contributed to the copepod identification, and manuscript review and editing. CC contributed to the data interpretation, and manuscript review and editing. L-CT contributed to the manuscript preparation, statistical analysis, data analysis and interpretation, field sampling, and manuscript review and editing. J-SH contributed to the funding acquisition, participation in discussions, and overseeing of manuscript production as a project leader. All authors contributed to the article and approved the submitted version.

FUNDING

The financial support from the Ministry of Science and Technology of Taiwan to J-SH (Grant Nos. MOST 107-2621-M-019-001, MOST 108-2621-M-019-003, and MOST 109-2621-M-019-002) and Center of Excellence for Ocean Engineering (Grant No. 109J13801-51), as well as to L-CT (MOST 107-2811-M-019-004, MOST 108-2811-M-019-504, and MOST 109-2811-M-019-504). The funders had no role in the study design, data collection and analysis, or decision to publish, nor in the manuscript preparation.

ACKNOWLEDGMENTS

We would like to thank the reviewers for their invaluable, detailed suggestions and criticisms, which greatly enhanced this paper, and Dr. Mark J. Grygier for post-review English revision. We are grateful to Dr. Kandasamy Kalimuthu and Captain Wan-Yi Weng of the fishing boat *Wanjing X* for their assistance during the fieldwork in the Danshuei River. We are equally thankful to Mr. Chih-Ming Lin and Mrs. Hsin-Yi Lo for their assistance in the laboratory. We finally thank the Fisheries Research Institute for providing the Sea Surface Temperature images (<https://en.tfrin.gov.tw/>), and the National Land Surveying and Mapping Center Taiwan MAP Service (<https://maps.nlsc.gov.tw/>) for providing other maps.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2021.598274/full#supplementary-material>

Supplementary File 1 | The supporting information file provides information about all figures.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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