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ORIGINAL ARTICLE

Delphine Beyrend-Dur · Sami Souissi
Jiang-Shiou Hwang

Population dynamics of calanoid copepods in the subtropical mesohaline Danshuei Estuary (Taiwan) and typhoon effects

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Abstract We studied the populations of the dominant calanoid copepods *Pseudodiaptomus annandalei* and *Acartia* spp. in the mesohaline Danshuei Estuary for two successive springs and summers. We analyzed environmental factors (i.e., temperature, salinity, chlorophyll *a*, light attenuation coefficient, and suspended particulate matter) and the population densities and structures at the surface and near the estuarine bed. The population of *P. annandalei* dominated the zooplankton community from surface to bottom, except during a medusa bloom in 2009 and during the post-typhoon period, when *Acartia spinicauda* dominated. The relationships between environmental factors and densities differed between and within populations of *P. annandalei* and *Acartia* spp. We concluded that the primary determinants of the *P. annandalei* population are predation and the typhoon-related freshwater runoff, which can strongly influence the copepod succession in this part of the estuary.

Keywords Zooplankton · Typhoon · Phenology · *Pseudodiaptomus* · *Acartia* spp.

Introduction

Environmental factors strongly influence the distribution of estuarine zooplankton. Temperature, salinity, and food supply are the most important environmental factors influencing the calanoid copepod phenology in estuaries. Temperature mainly arbitrates the composition and relative dominance of copepod populations (Mouny and Dauvin 2002; Hwang and Wong 2005; Hwang et al. 2006), whereas both temperature and food supply regulate growth and production rates (Hirst and Lampitt 1998; Uye 1988; Vidal 1980). Salinity influences the distribution of the species in the estuary, because the optimal osmotic regulation of each species occurs at a specific range of salinity (Cervetto et al. 1999; Hwang et al. 2010; Marques et al. 2006; Mouny and Dauvin 2002).

Heavy rainfall events during monsoon seasons and occasional typhoons (i.e., tropical storms or hurricanes) affect the near-shore ecosystems in East Asia (Zhao et al. 2009; Zheng and Tang 2007). In estuaries, the extreme wind, rainfall, and surge associated with typhoons cause intense mixing, circulation alteration, and occasionally, geomorphological changes. Storm-induced floodwaters in estuaries often have decreased salinity and increased nutrients, organic matter, and inorganic matter (Herbeck et al. 2011; Peierls et al. 2003; Zhang et al. 2009). The frequency and the strength of typhoons are expected to increase during this century because of global climate change; therefore, more information is needed on the effects of tropical storms on estuarine ecosystems. Although these storm-related changes affect the estuarine phytoplankton community (Chang et al. 1996; Zhao et al. 2009), relatively few studies have investigated the effects that storms have on them (Gierach et al. 2009). The unpredictability of typhoon formation and tracking, combined with their harsh weather conditions, complicates the organization of appropriate pre-and post-typhoon sampling for zooplankton studies. However, the effects of an important storm can be still observed several months to years after its passage (Paerl et al. 2001; Zhang et al. 2009).

The subtropical Danshuei Estuary in Northern Taiwan has its drainage basin in Taipei City. The Danshuei Estuary is one of the most polluted estuaries in Taiwan, with extremely high nutrient levels (Wen et al. 2008) and

D. Beyrend-Dur · S. Souissi
CNRS-UMR 8187 LOG, Station Marine, Université
Lille 1-Sciences et Technologies, Wimereux, France

D. Beyrend-Dur · J.-S. Hwang (✉)
Institute of Marine Biology, National Taiwan Ocean
University, Keelung 202, Taiwan, ROC
E-mail: jshwang@mail.ntou.edu.tw

Present address:
D. Beyrend-Dur
Department of Ecosystem Study, School of Environmental
Science, University of Shiga Prefecture, 2500
Hassaka-cho, Hikone, Shiga 522-8533, Japan

heavy-metal concentrations (Chiu and Chou 1991) caused by large quantities of untreated wastewater from urbanized areas and local industry. The upper part of the estuary is particularly affected by pollution, and commonly becomes hypoxic during summer months (Wang et al. 2007). Physicochemical research (Hsu et al. 2006; Liu et al. 2005; Wang et al. 2004; Wen et al. 2008) and biological studies (Hsieh and Chiu 1997; Hwang et al. 2009, 2010; Lin and Shao 1999; Shih et al. 1992; Wu et al. 1992) have contributed to recent attempts to model the ecosystem functioning of this estuary (Lin et al. 2007; Wang et al. 2007). Most of the zooplankton studies conducted in the Danshuei Estuary have focused on the off-estuary mouth or the lower estuary, neglecting the upper and middle estuary where the true estuarine zooplankton (euryhaline species) occurs.

Calanoid species of the genera *Pseudodiaptomus* and *Acartia* dominate the zooplankton community, and are the prime food source of many planktivorous fish species in many subtropical and tropical estuaries (e.g., Blaber 1997; Hwang et al. 2010; Pagano et al. 2003). In the upper region of the Danshuei Estuary, *P. annandalei* dominates the zooplankton community throughout the year, and coexists with three species of the genus *Acartia*, *A. spinicauda, A. bilobata*, and *A. negligens* (Hwang et al. 2010). Previous studies have shown that *P. annandalei* commonly appears in coastal and estuarine waters, and the brackish waterbodies of the subtropical and tropical Indo-Pacific (Chen et al. 2006; Golez et al. 2004; Madhupratap 1987; Walter et al. 2006). Although *P. annandalei* is an apparent key copepod species in certain food webs (e.g., the Danshuei Estuary), comprehensive studies on its population dynamics in situ have not been conducted.

This study presents the population dynamics (i.e., densities, population structure, and fecundity) of dominant copepods for two successive spring-summers in the mesohaline zone of the Danshuei Estuary, and identifies their relationships to environmental parameters. This study also presents a discussion of the effects of three typhoons observed on the estuarine ecosystem during the sampling period.

Methods

Sampling area

The Danshuei Estuary is located in northern Taiwan and is formed by the confluence of three tributaries: the Tahan Stream, the Hsintien Stream, and Keelung River (Fig. 1). Together, these tributaries form the largest estuarine system in Taiwan and have a total length of approximately 327 km. Semidiurnal tides and river discharges are the main flow-forcing mechanisms. The mean tidal range in the estuary is 2.22 m, and can reach as high as 3.1 m during spring tides. The mean river discharges of the Tahan Stream, the Hsintien Stream, and Keelung River are 62.1, 72.7, and 26.1 $m^3 s^{-1}$, respectively (Liu et al. 2005). The influence of saline

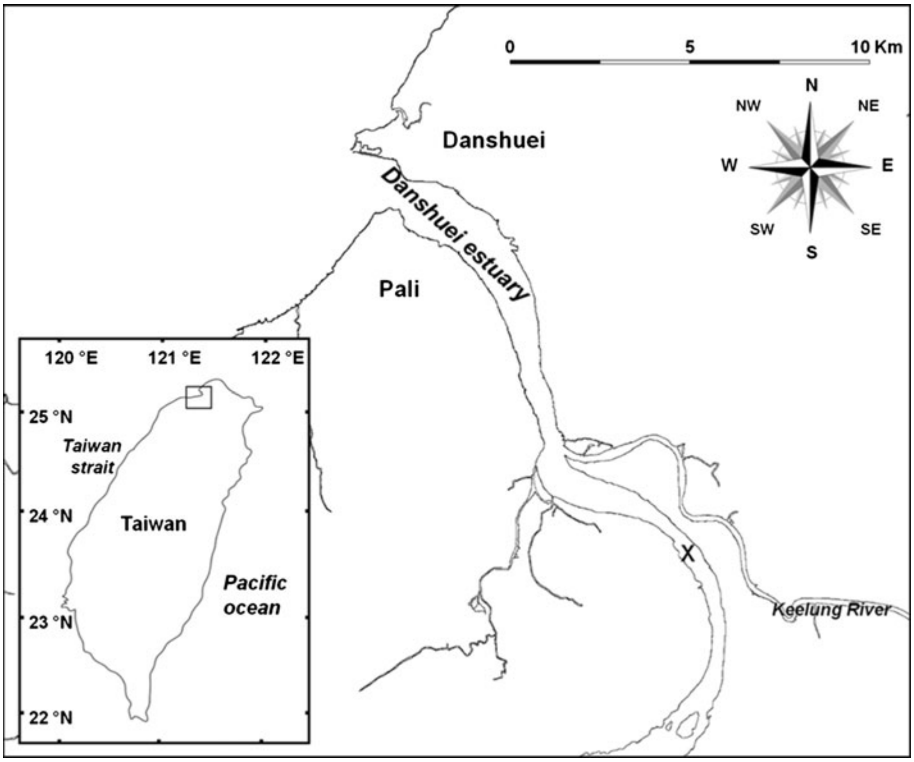

Fig. 1 Map of the Danshuei Estuary, Taiwan. The "X" represents the sampling point of this study

ocean water can reach up to 25 km from the estuarine mouth during low flows. The sampling in this study was conducted in the middle part of the Danshuei Estuary at approximately 15 km from the estuarine mouth, from early spring to midsummer in 2008 (March 6, April 23, June 5, July 7, and August 6) and to late summer in 2009 (March 30, May 11, June 24, August 24, and September 23). The winter season was omitted because it is unfavorable for the reproduction and development of *P. annandalei* and *Acartia* spp. The sampling strategy adopted in this study was diurnal and Eulerian, and used a fishing boat anchored near Chong Yang Bridge (25°05′02″N; 121°30′10″E) in the area of maximum abundance of *P. annandalei* (Hwang JS, pers. comm.). At high tide, the depth at this location is approximately 6.5–6.6 m. Because the Danshuei Estuary is a partially mixed estuary (Liu et al. 2001), waters were sampled near the surface (hereafter referred to as the surface) and near the estuarine bed (hereafter referred to as the bottom). Sampling started at high tide, when the concentration of zooplankton is at its maximum (Hwang et al. 2010), between 10:00 a.m. and 2:00 p.m. Typhoons passed over the sampling area on July 17–18 and July 27–28 of 2008 and August 7–8, 2009.

Measurement of abiotic and biotic environmental factors

Temperature was recorded at 1 Hz (one recording per second) with a TD probe (Temperature-Depth; model 70S) attached 40 cm below a Niskin bottle. Salinity was measured directly on board with a handheld refractometer (JAF Optics) that was calibrated before each sampling.

A Secchi disc was used to estimate the light attenuation coefficient K_d, which is a well-validated index of visual water clarity. The Secchi depth was measured by the same observer in the optimal time range between 10:00 a.m. and 2:00 p.m. (Cole 1994) based on the relationship previously determined by Liu et al. (2005) in the Danshuei Estuary:

$$K_d = 1.305 \times (1/\bar{X}) \quad (1)$$

where $\bar{X}$ is the mean Secchi depth (m) of three replicate readings.

The concentration of chlorophyll *a* (Chl *a*) was also determined. Water was sampled using a 5-L Niskin bottle at the surface and bottom, collected in 500-ml containers, and then kept on ice until laboratory analysis a few hours later. In the laboratory, 50 ml of sampled water was filtered through a 0.45-μm cellulose nitrate membrane, and Chl *a* was extracted with absolute acetone for 24 h at 4 °C. The extracted chlorophyll was measured using a Turner 10-AU-fluorometer. The suspended particulate matter (SPM) concentrations were estimated as dry weight (70 °C, 24 h) after the filtration of 250 ml of estuarine water through Whatman GF/C glass fiber filters. Samples from the surface and the bottom were analyzed in triplicate.

Zooplankton sampling

The zooplankton populations were sampled using a Niskin bottle at high tide between 10:00 a.m. and 2:00 p.m. because copepods can migrate vertically and because the estuarine waters were partially mixed. The Niskin bottle sampled a defined water volume at a determined depth (1 m below the water surface and 1 m above the estuarine bed), and collected all the microorganisms (e.g., microalgae, larval stages, and young copepodids) contained in this water volume. The Niskin bottle has been successfully used to study the population structure of the estuarine copepod *Eurytemora affinis* over a tidal cycle in the Seine Estuary (Devreker et al. 2010). In this study, the samples (three replicates) were immediately filtered through a 33-μm sieve, concentrated in 500-ml containers, and fixed with a 5 % buffered formaldehyde solution. All microorganisms in the samples were counted under a dissecting microscope in the laboratory. All developmental stages were counted, including nauplii, which play a key role in food webs (Kimmerer et al. 1998; Makino and Ban 2000). We differentiated males from females (C5 and adult stages) and ovigerous from non-ovigerous females as performed for the temperate estuarine copepod *E. affinis* (Devreker et al. 2010). The nauplii and early copepodids of the genus *Acartia* were pooled in the complex *Acartia* spp. because it is difficult to discriminate the species at these developmental stages. Therefore, only the late copepodid stages (C5 and adult) were identified at the species level.

A vertically towed WP2 plankton net was used to collect enough individuals to determine the body weight and clutch size of *P. annandalei* females, the sex ratio of the copepod populations, and the proportion of species within the *Acartia* spp. complex.

Body weight and clutch size

The prosome size (length L and width W) of 24–70 ovigerous females was measured at each sampling date using a video camera "CoolSNAP-PROcf COLOR" (Media Cybernetics Inc.) connected to a Nikon Eclipse E600 microscope. Image-Pro Plus software was used to measure the prosome size on the digital images. We used the equations by Svetlichny (1983) and Postel et al. (2000) to estimate the female dry weight (DW, μg):

$$DW = (0.6LW^2) \times 0.135 \quad (2)$$

The clutch size of the females was determined under a dissecting microscope.

Data analysis

Following the approach by Souissi and Ban (2001), the developmental stages of copepods were divided into four groups: the N1–N3 group represented the early naupliar stages, the N4–N6 group represented the late naupliar stages, the C1–C3 group consisted of individuals in the early copepodid stages, and the C4–C5 group consisted of individuals in the late copepodid stages.

Temporal (sampling dates) and spatial (depth) variations in copepod densities, female clutch size, and body weight were examined using one-way ANOVA (Anova-1) (Sokal and Rohlf 1995). Two-way ANOVA (Anova-2) was used to examine the differences in environmental factors and total copepod densities among dates (temporal patterns), depth (spatial patterns), and interactive effects. The densities analyzed with ANOVA were log-transformed [log 10 ($x + 1$)], and significant differences were further analyzed using the Tukey–Kramer multiple comparison of the means. After averaging the near-surface and near-bottom data for each sample, the Spearman rank correlation was analyzed for environmental data to identify any relationships between environmental factors and mean copepod densities. Similar correlation analyses were performed between environmental data (surface-bottom averaged) and the means of body weight and clutch size of *P. annandalei*. All statistical tests were performed using MATLAB 6.5 software (The MathWorks Inc. 2002).

Results

Environmental factors

The recorded temperature, salinity, Chl *a*, and SPM concentrations at the surface differed significantly from those at the bottom (Anova-2, $p < 0.01$; except temperature and salinity in September 2009). At this sampling site, temperatures gradually increased from a mean of 16 °C ± 0.2 in early spring to a mean of 30 °C ± 0.6 in the summer, and salinities ranged from 2.7 to 16 at the surface and from 8.7 to 17.3 at the bottom (Fig. 2). In 2008, salinity gradually decreased in the spring and slightly varied in the summer, with high stratification. In 2009, salinity gradually increased in the spring and then decreased in the summer, with a loss of stratification. The Chl *a* concentrations ranged from 0.18 to 1.75 μg l^{-1} in 2008 and from 4.14 to 16.77 μg l^{-1} in 2009. The Chl *a* concentrations differed significantly between seasons (Anova-2, $p < 0.001$) and between the surface and the bottom (Anova-2, $p < 0.01$). The Chl *a* and K_d concentrations differed significantly between 2008 and 2009 (Chl *a*, Anova-2, $p < 0.0001$; K_d, Anova-1, $p < 0.05$). The SPM concentrations estimated in 2009 varied seasonally (Anova-2, $p < 0.0001$). The concentrations at the surface differed significantly from those at the bottom (Anova-2, $p < 0.001$). Typhoons significantly reduced the temperatures, salinities, and Chl *a* (Anova-1, $p < 0.001$), but significantly increased the Kd coefficient (Anova-1, $p < 0.001$).

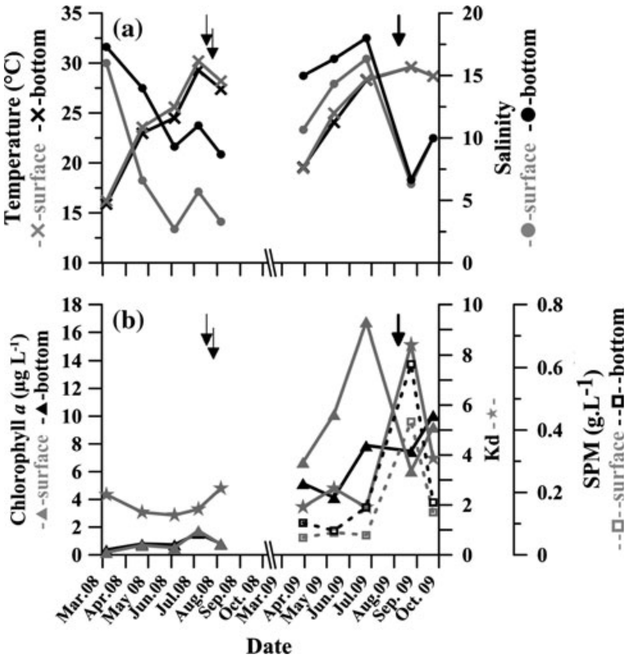

Fig. 2 Environmental parameters of the Danshuei Estuary, Taiwan, for two consecutive years. **a** Water temperature and salinity; **b** chlorophyll *a* concentration, coefficient of light attenuation K_d, and suspended particulate matter (SPM). *Arrows* indicate the peak intensity of typhoons, and the *arrow thickness* represents the duration of the typhoons

Density and structure of copepod populations

The peak density of *P. annandalei* occurred in early summer (Fig. 3a). Despite low densities in the spring of 2008, important changes in the population structure occurred (Figs. 3b, c, 5a, b). In early spring in 2008, the population of *P. annandalei* consisted primarily of naupliar stages (N1–N6) at the surface, and copepodid stages, including adults, at the bottom. Less than 30 % of the females were ovigerous (Fig. 4b). The proportion of early naupliar stages (N1–N3) rose to 90 % of the population throughout the water column in mid-spring (Fig. 3b, c), with the highest ovigerous to non-ovigerous female ratio (i.e., ovF : novF ≈76 %), and the lowest male-to-female ratio of adults (i.e., adult M:F ≈0.6). In the summer before the typhoon, the mean total density reached a maximum of 138,400 ind m^{-3} with a population consisting of 81 % copepodid stages (C1-Adult) at the bottom and an M:F ratio of approximately 2 (Fig. 3). After the typhoon, the mean total density of *P. annandalei* dropped to 22,930 ind m^{-3}, with a significantly lower density at the surface, where naupliar stages dominated, than at the bottom, where copepodids dominated (Anova 1, $p < 0.05$) (Fig. 3b, c).

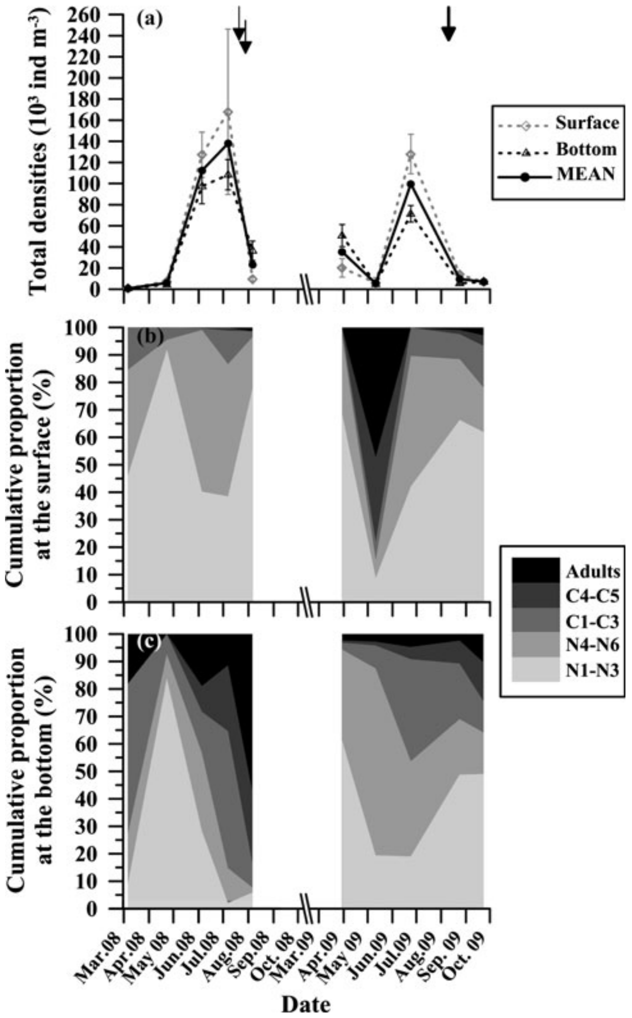

Fig. 3 Mean total densities (**a**) and population structure (**b**, **c**) of *P. annandalei* at the surface (**a**) and bottom (**b**) for two consecutive years in the Danshuei Estuary, Taiwan. The *vertical bars* represent the standard error of three replicates. *Arrows* indicate the peak intensity of typhoons, and the *arrow thickness* represents the duration of the typhoons

In the spring of 2009, the mean total density of *P. annandalei* was approximately 35,470 ind m^{-3}, with a higher density at the bottom than at the surface (Fig. 3a). In that season, ≥94 % of the population was in naupliar stages (Fig. 3b, c). The density of *P. annandalei* dropped to a mean of 5,430 ind m^{-3} in late spring, and the proportion of naupliar stages drastically decreased to below 20 % (Fig. 3b, c). At that time, the zooplankton community was dominated by another calanoid *Labidocera* sp., which density was 1,796 ± 270 ind m^{-3} (plankton net samples) whereas at other sampling dates it never exceeded 20 ind m^{-3}. In early summer before the typhoon, the peak density was 99,670 ind m^{-3}, with an M:F ratio of 2.8 (Fig. 4a). The density of *P. annandalei* abruptly decreased to 7,000–9,000 ind m^{-3} after the typhoon, and remained low until late summer.

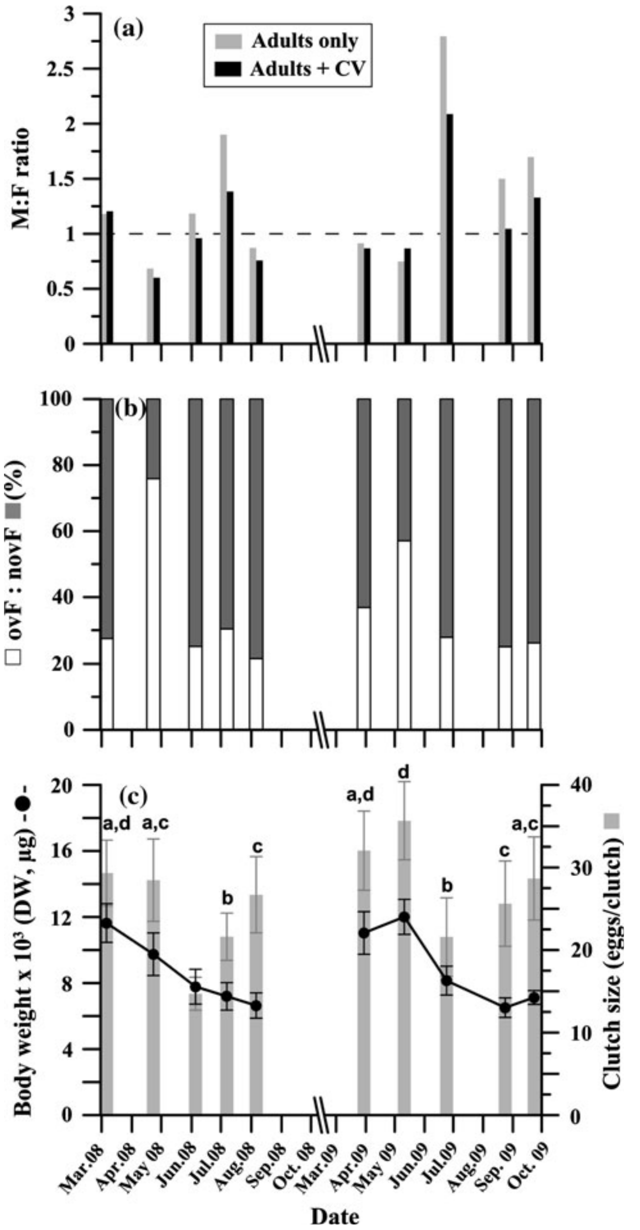

Fig. 4 Sex ratio (**a**), proportion of ovigerous and non-ovigerous females (**b**), and female body weight and clutch size (**c**) of *P. annandalei* for two consecutive years in the Danshuei Estuary, Taiwan. The *discontinuous line* indicates M:F = 1. *Vertical bars* represent standard deviations. *Bar charts with the same letter* are not significantly different at $p < 0.05$

The mean clutch size of *P. annandalei* ranged from 14.71 to 35.7 eggs clutch^{-1} and was significantly lower in early and midsummer compared to other seasons both years (Fig. 4c). The clutch sizes recorded in 2009 were significantly higher than those in 2008 (Anova-1, $p < 0.0001$). The female body weight ranged from 6.5 to 12 µg ind^{-1}. This value gradually decreased from early spring to late summer 2008 as the temperature rose, but it was correlated with the clutch size in 2009 (Spearman, $R = 0.54$, $p < 0.001$, $n = 120$). The second most numerous copepod population, *Acartia* spp., was absent before early summer 2008 (Fig. 5) and reached 9,000 ind m^{-3} at the bottom in midsummer. In 2009, the population appeared earlier in the spring, and it became the most dominant population after the typhoon that

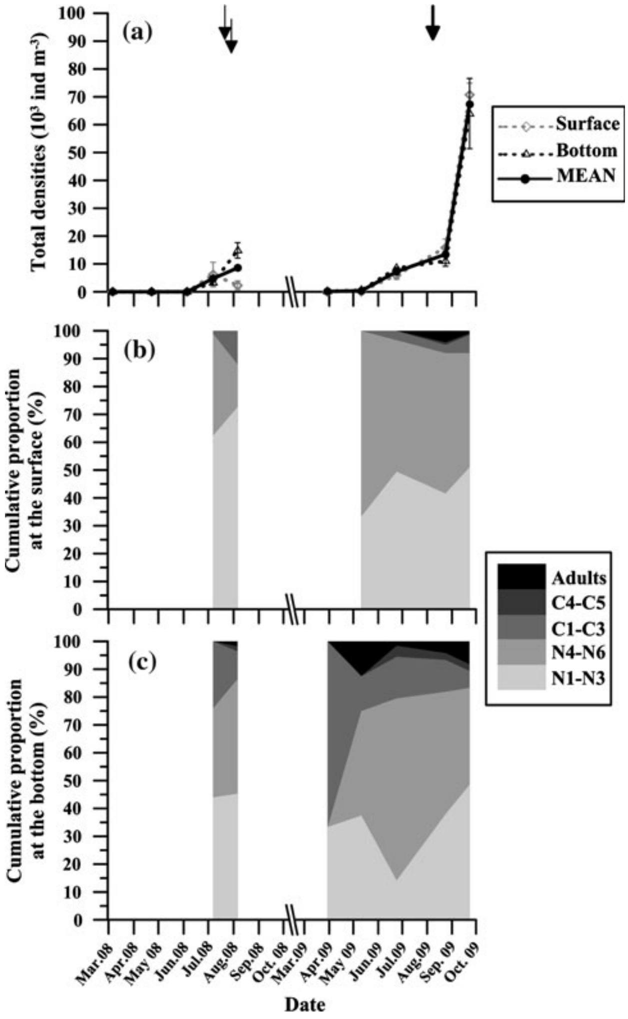

Fig. 5 Mean total densities (**a**) and population structure (**b**, **c**) of *Acartia* spp. at the surface and bottom for two consecutive years in the Danshuei Estuary, Taiwan. The *vertical bars* represent the standard error of three replicates. *Arrows* indicate the peak intensity of typhoons, and the *arrow thickness* represents the duration of the typhoons

year (1.4-fold higher than that of *P. annandalei*), reaching a maximum density of 67,400 ind m^{-3} in late summer. In both years, the population of *Acartia* spp. consisted primarily of naupliar stages (>76 %) throughout the water column, except in March 2009 (33 %) when the density was extremely low (100 ind m^{-3}). The genus complex mainly comprised *A. spinicauda* (>60 %) and *A. bilobata* (Fig. 6b), and another species, *A. negligens*, appeared only in 2009 (<6 %).

Population dynamics and environmental factors

The densities of all developmental stages in both populations were positively correlated with the temperature, with the exception of adults of *P. annandalei* (Table 1). Late copepodid stages (C4-adult) of *P. annandalei* were negatively correlated with salinity, whereas naupliar stages and ovigerous females were negatively correlated with K_d and SPM, respectively. The female body weight and clutch size of *P. annandalei* were positively correlated with the salinity and negatively correlated with SPM. The female body weight was negatively correlated with the temperature. The densities of all developmental stages of *Acartia* spp. were strongly correlated with Kd, Chl *a*, and SPM concentrations, but not with salinity.

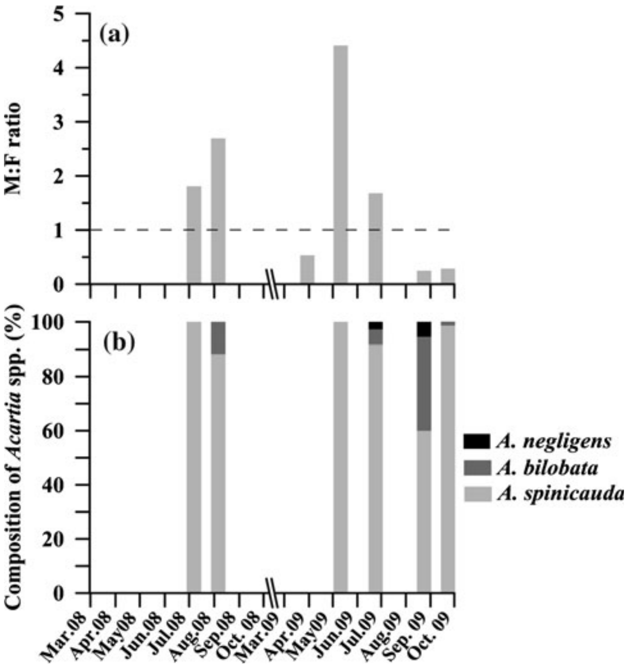

Fig. 6 Sex ratio (**a**) and species composition (**b**) of *Acartia* spp. for two consecutive years in the Danshuei Estuary, Taiwan. *Discontinuous lines* indicate M:F = 1

Discussion

Environmental factors strongly influence the dynamics of estuarine zooplankton. Temperature, salinity, and food supply are the most important factors influencing the calanoid copepod phenology. We observed that episodic factors can also influence the copepod population dynamics and copepod succession in the subtropical Danshuei Estuary. Estuarine studies have shown drastic changes in abiotic and biotic factors following storm precipitation (Herbeck et al. 2011; Peierls et al. 2003). Freshwater runoff caused by heavy rainfall lowers salinity, disrupts water stratification, and causes a massive input of suspended materials, making estuarine waters more turbid after a typhoon (Fig. 2). The sudden environmental changes induced by a typhoon have a serious effect on estuarine organisms, especially on the planktonic community. The resulting decrease in water transparency also limits phytoplankton activity (Herberck et al. 2011; present study). The strong freshwater pulse, which reduces the residence time, is responsible for the loss of phytoplankton and zooplankton stocks

Table 1 Spearman correlations (r) between environmental factors and densities of stages of dominant copepods ($n = 30$, $n = 15$ for SPM), body weight (BW) and clutch size (CS) (BW and CS; $n = 402$, $n = 120$ for SPM)

	Temperature	Salinity	Chl *a*	K_d	SPM $_{2009}$
Species					
P. annandalei					
Nauplii	0.44*	−0.31	0.12	−0.50**	0.18
C1–C3	0.63***	−0.36	0.16	−0.26	0.27
C4–C5	0.62***	−0.50**	0.07	−0.17	0.17
Adults	0.36	−0.40*	0.01	−0.24	−0.39
ovF	0.33	−0.48**	−0.04	−0.26	−0.42
Total	0.44*	−0.35	0.11	−0.48**	−0.03
BW	−0.83**	0.74*	−0.07	−0.07	−0.68
CS	−0.40	0.46	0.19	−0.10	−0.39
Acartia spp.					
Nauplii	0.79***	−0.24	0.61***	0.67***	0.74**
C1–C3	0.75***	−0.28	0.47**	0.53**	0.78***
C4–C5	0.56**	−0.11	0.55**	0.59***	0.76**
Adults	0.53**	−0.20	0.51**	0.74***	0.74**
Total	0.79***	−0.23	0.63***	0.68***	0.76**

Values in *bold* indicate moderate correlations ($0.40 \leq r \leq 0.70$) and values in *bold and shaded* indicate strong correlations ($r > 0.70$)
K_d coefficient of light attenuation, SPM_{2009} suspended particulate matter recorded in 2009
Significance levels * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

washed out of the estuary (present study; Yuka and Hiroshi 1999; Herberck et al. 2011).

In this study, we observed a post-typhoon collapse of the population density of the dominant copepod *P. annandalei* in the middle estuary reflecting the flush-out induced by typhoon. However, some individuals remained. This is likely because of the vertical migratory behavior and substratum affinity exhibited by several *Pseudodiaptomus* species, including *P. annandalei* (Hart 1978; Jacoby and Greenwood 1988; Kouassi et al. 2001; Shang et al. 2008; present study). During typhoons, the remaining individuals are submitted to a quick drop of salinity, which is known to regulate the composition, density, and distribution of *Pseudodiaptomus* species in coastal waters (Collins and Williams 1981; Magalhães et al. 2006; Mitra and Patra 1990; Sarkar and Choudhury 1998). Although *P. annandalei* tolerates a wide range of salinity (i.e., 4.5–38.7; Chen et al. 2006; Beyrend-Dur et al. 2011), a salinity shock below 5 causes the death of more than 73 % of adults (Chen et al. 2006). The middle part of the Danshuei Estuary likely reaches salinities <5 during and following a typhoon event. Despite a return to suitable salinities for the reproduction and development of *P. annandalei* (Beyrend-Dur et al. 2011; Chen et al. 2006; Golez et al. 2004) and an estimated development (egg to adult) period of <10 days at temperatures recorded after the typhoon strike, i.e., 25–30 °C (Beyrend-Dur 2010; Golez et al. 2004), the population of *P. annandalei* did not exhibit the same density as that observed before. When the *P. annandalei* densities dropped below 20,000 ind m^{-3}, the *Acartia* spp. population replaced *P. annandalei* as the dominant population within the zooplankton community. A rapid reduction in salinity (such as that observed after a typhoon) accompanied by nutrient enrichment can alter the phytoplankton composition of estuaries (Paerl et al. 2007; Peierls et al. 2003). The changes in food composition and availability are known to affect the copepod assemblages by enhancing one copepod population over another one as observed in different subtropical estuaries (Murell and Lores 2004; Wooldridge and Melville-Smith 1979). In the tropical Cochin Estuary, diatoms are the most dominant group but after monsoon rainfalls dinoflagellates become more dominant (Madhu et al. 2007). In this estuary, *P. annandalei* is commonly found during the pre-monsoon season, but after the monsoon rainfalls, it disappears and *Acartia* spp. becomes the most abundant calanoid species (Madhu et al. 2007). This copepod succession is similar to that observed in the Danshuei Estuary. Although no study is available on the change of phytoplankton composition after typhoon in the Danshuei Estuary, if a shift from diatoms to dinoflagellates occurs, it could partly explain the domination of *Acartia* spp. over *P. annandalei* as *A. spinicauda* commonly feed on dinoflagellates (Tianjiu and Sang 1994; Sang 1993). Moreover, the suspended particulate matter, which drastically increases after a typhoon, negatively affects both the reproduction and densities of ovigerous females of *P. annandalei*. Conversely, this seems to enhance the densities of *Acartia* spp.

Another advantage of *Acartia* spp. over *P. annandalei* is the production of resting eggs that can be resuspended from the seabed during a storm (Landry 1978b), as observed in *A. spinicauda* (referred to as *A. spinacauda* in Marcus 1996). This egg stock represents a non-negligible number of individuals ready to quickly repopulate the estuarine waters after a typhoon. It seems that *Acartia* spp. can take advantage of a typhoon strike and the subsequent changes in environmental factors to outnumber its former competitor *P. annandalei* in this part of the Danshuei Estuary. The effect of typhoons on plankton also depends on their strength (wind stress), duration, and location near the shore (Zhao et al. 2008).

At the studied site, Typhoon Morakot in 2009 was observed to have serious effect on environmental factors and copepod populations. Although this typhoon was not more powerful than the typhoons observed in 2008 (i.e., Typhoons Kalmaegi and Fung-Wong), Typhoon Morakot passed closer to the study site for a longer period (JMA 2008–2009), and its maximum cumulative rainfall approached a world record (Shieh et al. 2010).

Other factors can also influence the copepod population dynamics of the Danshuei Estuary. In the spring of 2009, we observed a decline in the *P. annandalei* population, when the zooplankton community was briefly dominated by medusae (Beyrend-Dur, unpublished data) and another copepod species from the genus *Labidocera*. According to the monthly water-monitoring records of the Environmental Protection Administration (2008–2009), the same sampling station as that in the present study exhibited a record dissolved oxygen (DO) value of 10.4 mg l^{-1} on May 6, although the average for the 2008–2009 period is 2.9 mg l^{-1}. The increase of water DO may also facilitate the intrusion of medusae in less hypoxic waters as most of the medusae occur in waters where DO are >2 mg l^{-1} (Purcell et al. 2001). Chung et al. (2009) showed that medusa populations in the Danshuei Estuary have a strong negative effect on the copepod community because they are efficient predators of calanoid copepods in estuaries (Purcell 1992; Wintzer et al. 2011). However, not all copepod species are affected by medusa blooms and some copepods are more vulnerable than others to predation (Behrends and Schneider 1995) mostly because medusa exhibit prey selection based on prey vulnerability (Costello and Colin 1994; Sullivan et al. 1994). For example, neustonic copepods, such as *Labidocera* species, exhibits peculiar escape abilities (Gemmel et al. 2012) that lead to less predation pressure from medusae. Species of the genus *Labidocera* (and the entire family Pontellidae) has also been known as predator of nauplii and early copepodids of smaller copepod species (Landry 1978a; Ohtsuka and Onbé 1991). Thus, these two predators likely contribute to the decline and the change in population structure observed in the population of *P. annandalei* although no gut content analysis has been conducted to prove their direct impact. After the bloom of those two pelagic predators in mid-spring, *P. annandalei* showed a marked recovery in early summer, with a mean density slightly lower than that recorded in 2008 (i.e., 112,000 and 99,700 ind m^{-3}, respectively, in 2008 and 2009). In mid-spring (i.e., April–May), when the temperature–salinity combinations are the most appropriate for its reproduction (i.e., 20–25 °C and salinity range 10–15; Beyrend-Dur et al. 2011), *P. annandalei* exhibited a clear breeding period responsible for the density peak in early summer. This breeding period is highlighted by a female-biased sex ratio (≤ 1 male per female), a high proportion of ovigerous females (57–76 % of females), a large clutch size (28–36 eggs clutch^{-1}), and an important recruitment of nauplii (90 % of N1–N3). Thus, the high productivity during the breeding period seems to promote the repopulation of *P. annandalei* after the decline of pelagic predators.

Interestingly, *P. annandalei* is able to dominate in this part of the estuary when the phytoplankton was quite limited as observed in 2008. In general, small phytoplankton and microzooplankton are the most important parts of the estuarine calanoid copepod dietary intake (Mauchline 1998; Tackx et al. 1995) and accordingly, *P. annandalei* exhibits an omnivorous behavior (Dhanker et al. 2012). When phytoplankton populations are low, such as in oligotrophic waters, the protozoa (e.g., ciliates) that colonize detritus appear to be as suitable a food source as phytoplankton for copepods, considering their nutritional value (Heinle and Flemer 1975; Roman 1984). Roff et al. (1995) also suggested that tropical nauplii cannot be food-limited because they predominantly feed on small particles (e.g., bacterioplankton and picoplankton). Detritus is so abundant in the Danshuei Estuary that Lin et al. (2007) considered that detritivory is more important than herbivory in the Danshuei Estuary's food web. This study shows that several parameters of the population dynamics (i.e., density, clutch size, and body weight) of *P. annandalei* are positively or negatively related to food proxies other than Chl *a* (i.e., K_d and SPM). These results suggest that the population can be influenced by food sources other than phytoplankton. Complementary studies on the feeding behavior of this copepod species are necessary to identify its ecological niche in the Danshuei Estuary. However, considering the primary position of *P. annandalei* as the dominant zooplankton species, this species is likely essential to the food web in the middle part of the Danshuei Estuary.

We found that a typhoon strike, typhoon-related environmental changes, and predation all affect the copepod populations, particularly that of *P. annandalei*, and play an important role in copepod succession. Future research should evaluate the association between the dynamics of copepod populations and other biological and physical factors, such as food resources (e.g., phytoplankton and microzooplankton) and water currents.

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