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Occurrence characteristics of two sibling species, Pseudodiaptomus inopinus and Pseudodiaptomus poplesia (Copepoda, Calanoida, Pseudodiaptomidae), in the Mankyung River estuary, South Korea

Eun-Ok Park[1,2*], Jeffery R Cordell[3] and Ho Young Soh[4]

Abstract

Background: Abundances of two closely related *Pseudodiaptomus* species, *Pseudodiaptomus inopinus* and *Pseudodiaptomus poplesia*, and salinity, temperature, and chlorophyll (Chl) *a* levels were measured monthly at a station in the Mankyung River estuary, South Korea, through a spring tide flood-ebb series.

Results: Both species occurred mostly under mesohaline to polyhaline conditions throughout the year. *P. poplesia* was abundant under winter polyhaline conditions and reached its peak abundance under mesohaline conditions in spring, when the Chl *a* concentration was highest. *P. inopinus* had lower densities than *P. poplesia* at all salinities in spring and had peak densities under mesohaline and polyhaline conditions in November, when a second Chl *a* peak concentration occurred. Egg-bearing females of both *P. poplesia* and *P. inopinus* were present in spring and fall, but the ratio of gravid females of the former was higher under mesohaline and polyhaline conditions in April and May, while that of the latter was higher under polyhaline conditions in March.

Conclusion: These facts indicate that abundances of *P. poplesia* and *P. inopinus* may be controlled by Chl *a* concentrations and salinity conditions.

Keywords: River estuary; Copepods; Salinity gradient; Chlorophyll *a* concentration; Co-occurrence

Background

Estuaries are dynamic and variable environments, and the spatiotemporal distribution of estuarine species is affected by environmental factors such as temperature and salinity. These fluctuations in environmental factors may also result in a low level of species diversity and promote the coexistence of congeneric species (Jeffries 1962; Wooldridge and Melville-Smith 1979; Sullivan and McManus 1986). Most studies on the coexistence of zooplankton species in estuarine and coastal environments addressed the mechanisms responsible for interspecific competition, spatial segregation, and reproductive isolation (Greenwood 1981;

Ueda 1987; Laprise and Dodson 1993). Strategies by which congeneric species may avoid or reduce direct competition include maintaining different temporal and spatial distributions and partitioning available food resources by selective feeding (Greenwood 1981; Ueda 1987; Laprise and Dodson 1993).

The mesozooplankton of many estuaries are dominated by calanoid copepods, particularly the demersal calanoid family Pseudodiaptomidae, which accounts for 70% of the abundance of calanoid copepods in the Mankung River estuary, South Korea. In Korean estuaries, five species of the genus *Pseudodiaptomus* have been recorded, and two species, *Pseudodiaptomus inopinus* and *Pseudodiaptomus poplesia*, are predominant (Suh et al. 1991; Soh et al. 2001). Of these two species, *P. inopinus* is more common and widespread in brackish

* Correspondence: ej0731@daum.net
[1]Department of Oceanography, Chonnam National University, Gwangju 500-757, South Korea
[2]Department of Life Science, Hanyang University, Seoul 133-791, South Korea
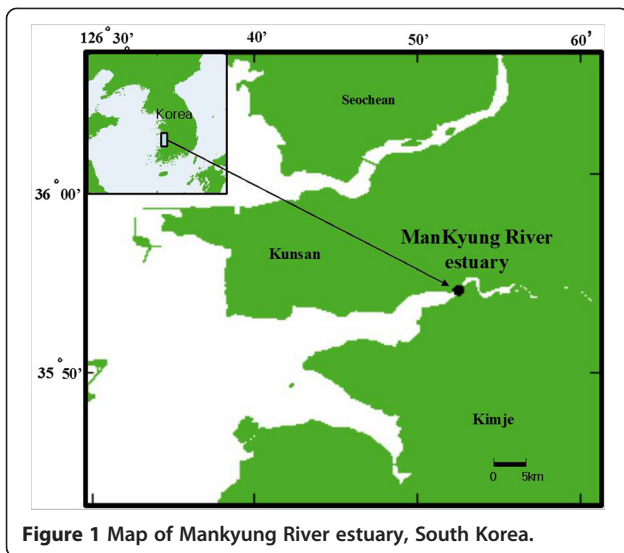Full list of author information is available at the end of the article

Figure 1 Map of Mankyung River estuary, South Korea.

and/or freshwaters of northeast Asia in general and Korea in particular (Chen and Zhang 1965; Shen and Song 1979; Chang and Kim 1986; Oka et al. 1991; Uye et al. 2000; Lee et al. 2007; Chang 2009; Sakaguchi et al. 2011). In contrast, *P. poplesia* has only been documented on the Yellow Sea side of the Korean Peninsula and in estuaries of the South China Sea (Shen and Song 1979; Soh et al. 2001; Tan et al. 2004; Lee et al. 2007; Shang et al. 2007; Chang 2009). In addition to its wide occurrence in Asia, *P. inopinus* was introduced into the Columbia River estuary on the Pacific coast of North America between 1980 and 1990, presumably by way of ballast water of ships, and has rapidly expanded its range since then (Cordell et al. 1992, 2008; Cordell and Morrison 1996; Bollens et al. 2002). In estuaries where it was introduced, *P. inopinus* tends to seasonally dominate the mesozooplankton and may have resulted in changes in the food webs of those estuaries (Cordell
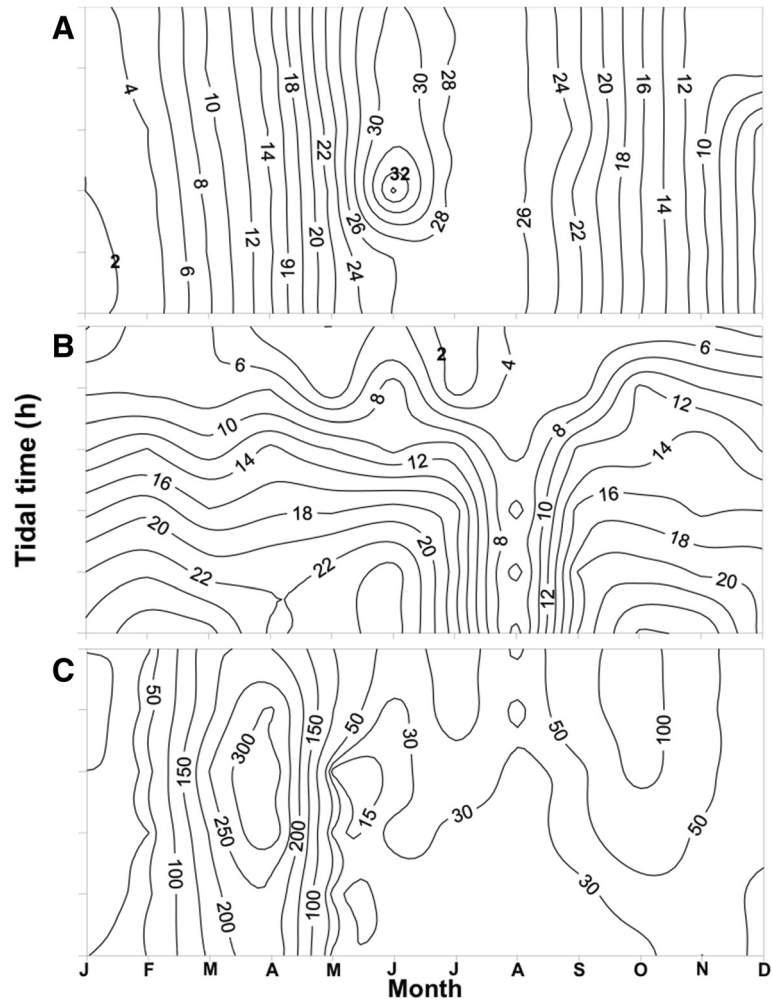

Figure 2 Monthly spatial and temporal variations in water temperature, salinity, and chlorophyll *a* concentration in the estuary. (A) Temperature (°C), **(B)** salinity, and **(C)** chlorophyll a (μg/L).

and Morrison 1996; Cordell et al. 2007). Several studies focused on the biology of both native and introduced populations of *P. inopinus* (Ueda et al. 2004; Cordell et al. 2007), while little or no information of this type exists for *P. poplesia*.

In this study, we examined the seasonal occurrence patterns of *P. inopinus* and *P. poplesia*, the dominant copepods in the Mankyung River estuary, in order to document patterns of occurrence in relation to temperature, salinity, food, and specifically chlorophyll (Chl) *a* concentrations. The goal of this study was to better understand how these two closely related species coexist in the estuary and provide more information regarding their biology.

Methods

The Mankyung River estuary is located on the central portion of the west coast of Korea (Figure 1). The estuary is shallow and wellmixed, with semidiurnal tides that occur over a range of about 6 m. Annual rainfall in the area is *ca.* 1,371 mm, mainly occurring during the summer rainy season.

Zooplankton were collected monthly between January and December 2000 at one station in the Mankyung River estuary (Figure 1). Sampling was done during one spring tide flood-ebb cycle at approximately 1-h intervals. Zooplankton samples were obliquely towed from near the bottom to the surface using a weighted conical net (with a mouth diameter of 45 cm and a mesh size of 200 μm). Samples were immediately preserved in a 5% neutralized formalin/seawater solution. In the laboratory, *Pseudodiaptomus* species were sorted and counted under a dissecting microscope. Counts were converted to individuals per cubic meter of seawater (ind./m^3).

Water temperature and salinity were measured using a T-S meter (Model 30, YSI, Yellow Springs, OH, USA) from the surface to the bottom at 1-m intervals. To measure the Chl *a* concentration, 1,000 ml of seawater was collected from the surface layer once during each sampling. Chl *a* was extracted by grinding the filter paper in a dark room and placing it in 90% acetone, as recommended by SCOR-UNESCO (1980). The extracted sample was centrifuged, and the absorbance of the
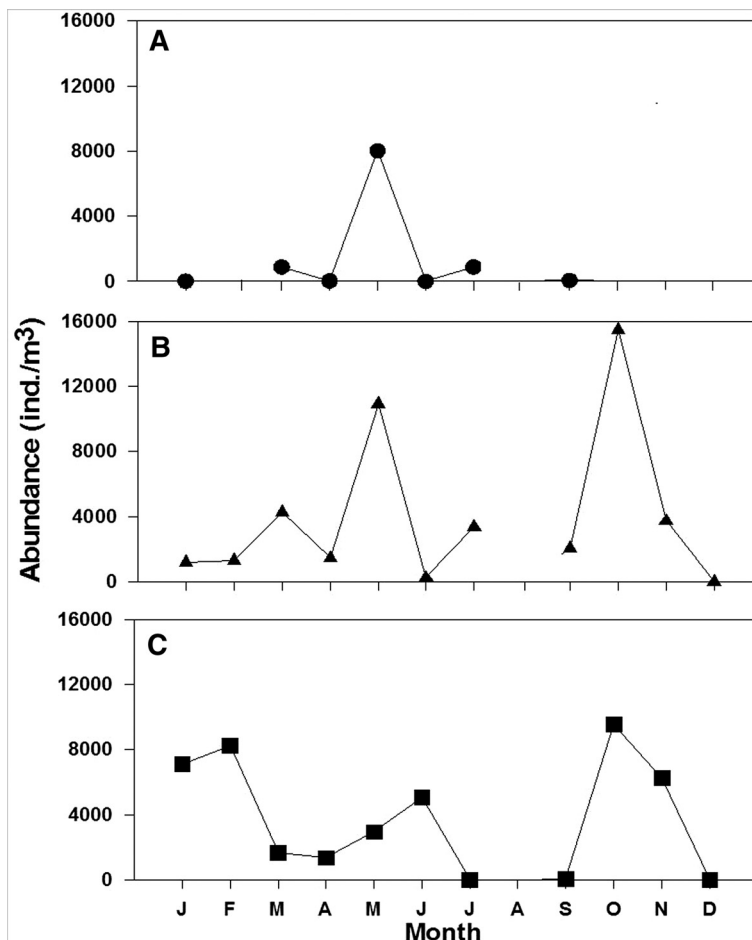
Figure 3 Seasonal variations in abundances (ind./m^3) of *P. poplesia*. (A) Oligohaline, **(B)** mesohaline, and **(C)** polyhaline.

supernatant was measured at 750, 664, 647, and 630 nm using a spectrophotometer (UNICAM Helios Alpha, Gloucester, UK). Water column conditions for each sample were designated as oligohaline (0 to 5 practical salinity unit (psu)), mesohaline (5 to 18 psu), and polyhaline (>18 psu) on the basis of Ekman's classification system (Day et al. 1989).

To evaluate correlations between abiotic factors and the abundances of the two *Pseudodiaptomus* species, data were log (*x*+1)-transformed, and a multivariate regression model analysis (Afifi et al. 2004) was conducted using SAS version 9.2 (Cary, NC, USA). For correlations between the abundances of *P. poplesia* and *P. inopinus*, Pearson's correlation coefficient was used.

Results

Water temperature and salinity

The mean temperature ranged from a high of 29.6°C ± 1.6°C (standard deviation) in August 2000 to a low of 2.3°C ± 3.1°C in February 2000 (Figure 2A). Water temperature varied seasonally: winter (December, January, and February) temperatures ranged from 2.3°C to 3.8°C; spring (March, April, and May) temperatures ranged from

9.1°C to 22.9°C; summer (June, July, and August) temperatures remained above 26°C; and fall (September, October, and November) temperatures ranged from 10.7°C to 22.4°C. Differences between the surface and bottom temperatures were <2°C, except in June, when they were <4°C.

Salinity ranged from 0.8 to 27.7 psu, but there were seasonal differences in this parameter. In particular, salinities were lower during the rainy season. In July, conditions were oligohaline to mesohaline, with salinities remaining below 18 psu, while in August, only oligohaline conditions occurred (<5 psu). During the dry season in October to December, salinities increased again and, for the most part, remained in the mesohaline to polyhaline ranges regardless of the tide or sampling interval. Differences between the surface and bottom layers were also <1 psu (Figure 2B).

Chl *a* concentrations

Chl *a* concentrations ranged from 6.8 to 342.7 μg/L during the study period and were more than three times greater during the spring phytoplankton bloom than during the other seasons (Figure 2C). In oligohaline
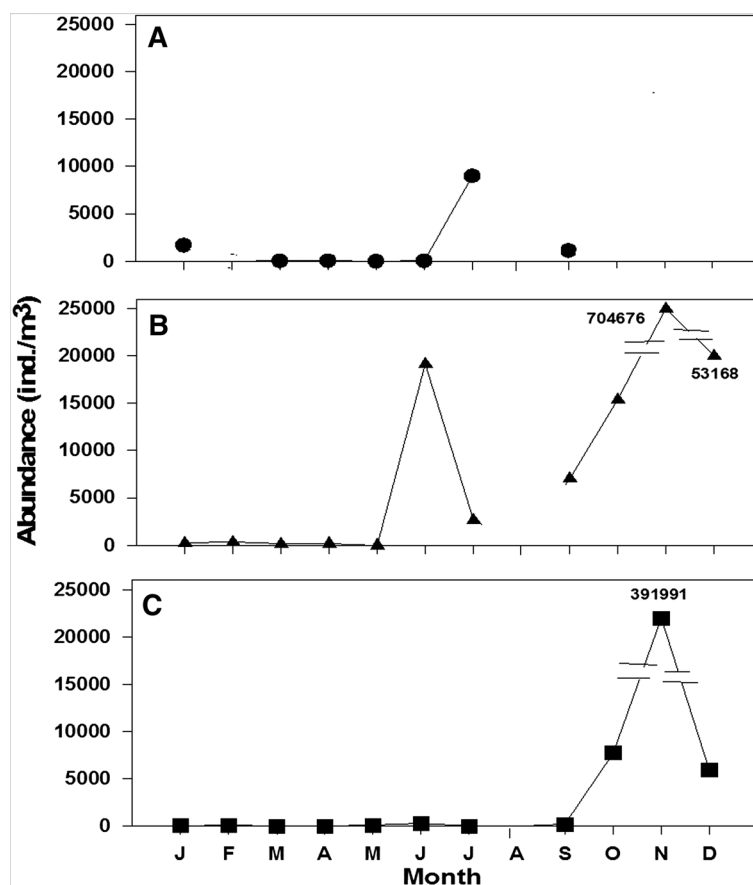

Figure 4 Seasonal variations in abundances (ind./m³) of *P. inopinus*. (A) Oligohaline, **(B)** mesohaline, and **(C)** polyhaline.

conditions, concentrations ranged from 16.0 to 200.1 μg/L, with the highest concentration in April and the lowest in January. In mesohaline conditions, concentrations ranged from 21.5 to 272.9 μg/L and, as in oligohaline conditions, were highest in April and lowest in January. Under polyhaline conditions, concentrations of Chl *a* were highest in May (94.0 μg/L) and lowest in November (7.1 μg/L). Overall mean Chl *a* concentrations were found under mesohaline conditions.

Seasonal occurrence patterns of *P. inopinus* and *P. poplesia*

P. inopinus and *P. poplesia* occurred throughout the salinity range and during the entire study period, with the exception of the summer rainy season. The density of *P. poplesia* ranged from 30 to 8,022 ind./m^3 under oligohaline conditions in spring, when the Chl *a* concentration was >162 μg/L, but decreased to 7 to 895 ind./m^3 in June and July with a decline in Chl *a* concentrations (<42.3 μg/L) and was lowest (<1 ind./m^3) in August (Figure 3A). After that, the density increased (<62 ind./m^3)

in October, when the Chl *a* concentration was >86.8 μg/L, but then declined to <17 ind./m^3 during the winter months. Densities of *P. inopinus* were somewhat higher than those of *P. poplesia* under oligohaline conditions, except in spring (Figures 4A and 5A) and October through December, when neither species occurred. Under mesohaline conditions, the density of *P. inopinus* increased after spring, with a peak density of 704,676 ind./m^3 in November (Figure 4B). Under mesohaline and polyhaline conditions, *P. inopinus* densities remained high during the fall months, when Chl *a* concentrations were lower than in spring (Figures 4B,C and 5B,C). In contrast, *P. poplesia* did not occur under mesohaline conditions in November and December or in polyhaline conditions in December (Figures 3B,C and 5B,C). Results of the multivariate regression analysis of correlations of environmental factors, such as temperature, salinity, and Chl *a*, with densities of the two*Pseudodiaptomus* species showed that densities of *P. poplesia* and *P. inopinus* were significantly affected by both salinity ($p < 0.05$) and Chl *a* concentrations ($p < 0.001$), but were not significantly affected
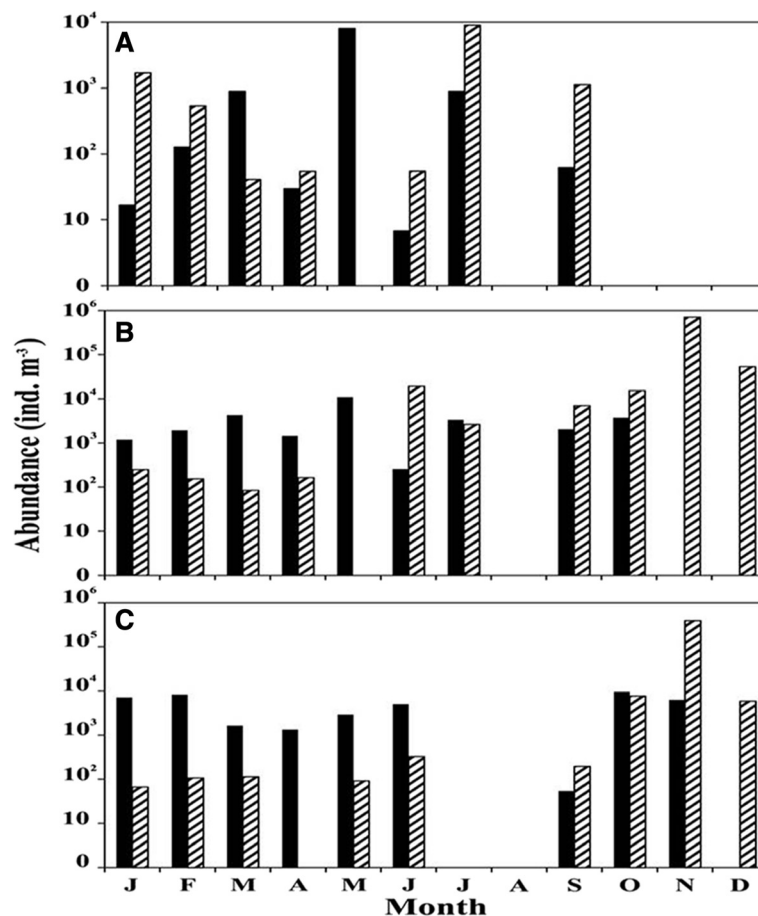

Figure 5 Diagram of seasonal variations in abundances of *P. poplesia* (solid bar) and *P. inopinus* (streaked bar). (A) Oligohaline, **(B)** mesohaline, and **(C)** polyhaline.

Table 1 Results of the multivariate regression model analysis of *P. poplesia* and *P. inopinus*

	P. poplesia		*P. inopinus*		Wilks' lambda	
	Coefficient	Standard error	Coefficient	Standard error	Value	*p* value
Intercept	−0.05488	1.21296	4.22593	1.41962		
Temperature	0.02418	0.04065	−0.05326	0.04758	0.96879	0.1435
Salinity	0.27194	0.05029	0.12803	0.05886	0.93223	0.0295
Chlorophyll *a*	0.01006	0.00460	−0.01297	0.00539	0.81822	0.0002

by temperature ($p > 0.05$) (Table 1). In particular, densities of *P. poplesia* were higher than those of *P. inopinus* at high Chl *a* concentrations, while the latter species was more abundant under relatively low Chl *a* concentrations.

Sex ratio and gravid females of *P. poplesia* and *P. inopinus*
Males of *P. poplesia* were more abundant than females across the entire salinity range throughout the study period, except under oligohaline conditions in April, and the ratio of males to females reached 50% under mesohaline and polyhaline conditions in spring (Figure 6).

Males of *P. inopinus* were more abundant than females throughout the study period and across the entire range of salinity, but the ratio of males to females exceeded 50% under oligohaline conditions in January, mesohaline conditions in late fall and winter, and polyhaline conditions in early winter (Figure 7).

Gravid females of *P. inopinus* appeared in oligohaline conditions only in March, July, and September and accounted for >50% of all females present in September (Figure 8). Under mesohaline conditions, they occurred in June to October, and under polyhaline conditions,
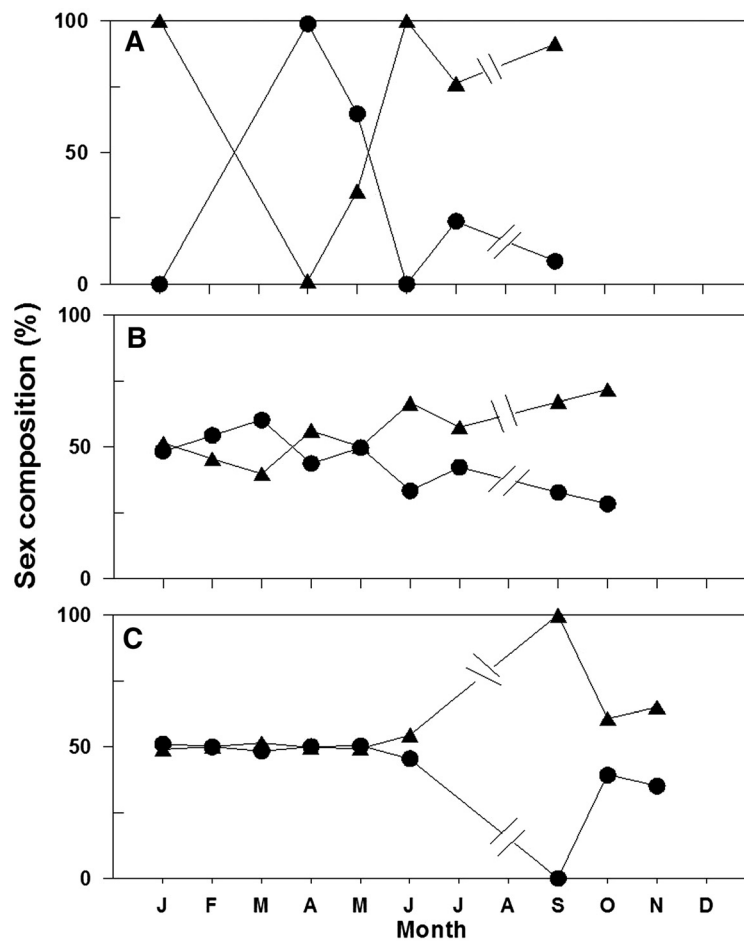

Figure 6 Seasonal variations in the adult sex composition of *P. poplesia*. (A) Oligohaline, **(B)** mesohaline, and **(C)** polyhaline. Circle, female; triangle, male.
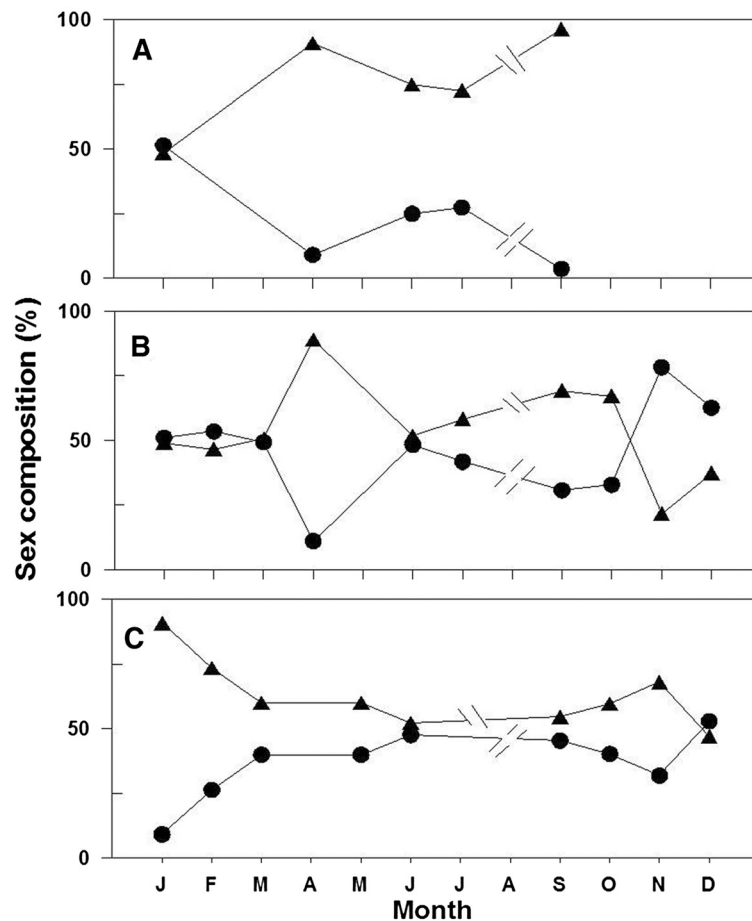
Figure 7 Seasonal variations in the adult sex composition of *P. inopinus*. (A) Oligohaline, **(B)** mesohaline, and **(C)** polyhaline. Circle, female; triangle, male.

they occurred only in June and October, and >50% of all females were gravid in October. Gravid females of *P. poplesia* were present in March to October, comprising 3% to 72% of the female population (Figure 9). Under oligohaline conditions, >50% of the female population was gravid in July and also under mesohaline and polyhaline conditions in April and May. Percentages of gravid females of *P. poplesia* were very low during fall months, and they did not occur under oligohaline conditions.

Discussion

In the Mankyung River estuary of South Korea, two sibling species, *P. inopinus* and *P. poplesia*, co-occurred throughout the year under all salinity categories except in August, when most estuarine zooplankton are swept downstream because of increased freshwater flows during the rainy season (see Suh et al. 1991). In addition, water temperatures in the Mankyung River estuary were similar during spring and fall, being within the range of

9.0°C to 23.6°C in both seasons, while Chl *a* concentrations were higher in spring than fall (Figure 2). However, this study showed that the abundance of *P. inopinus* was affected by the presence or absence of *P. poplesia* and/or low water temperatures, with no relation to salinity. However, abundances of the two species significantly differed with salinity and Chl *a* concentrations. Our finding that the abundances of the two species significantly differed on the basis of Chl *a* concentrations could be due to their distinct feeding strategies. In the case of *Pseudocalanus minutus*, non-living particles, mainly dead organisms or simply detritus, are supplementary food sources and serve as a basic food source (Poulet 1976). Likewise, the consumption of particles by the two *Pseudodiaptomus* species may be associated with changes in both the total concentration and the composition of suspended particulate materials, and non-overlapping food niches are possible if two copepod species differ in size (Hutchinson 1967; Maly and Maly 1974). Sandercock (1967) suggested that the coexistence of species depends upon the additive effects of two factors or
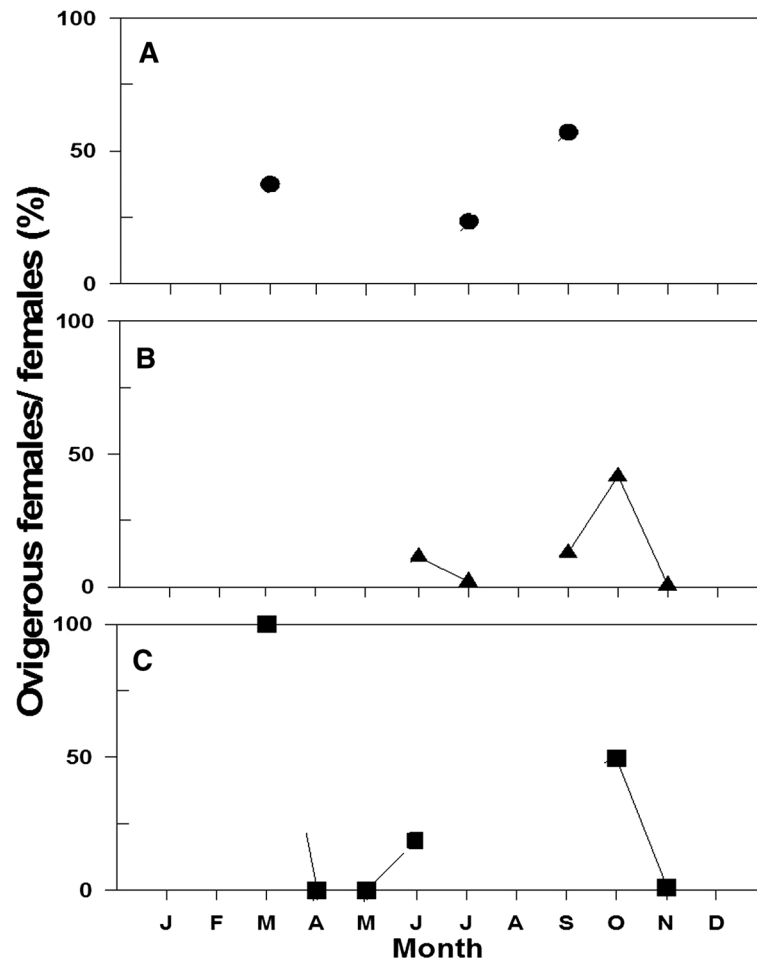
Figure 8 Seasonal variations in the composition of ovigerous adult females of *P. inopinus*. (A) Oligohaline, **(B)** mesohaline, and **(C)** polyhaline.

mechanisms. Therefore, the coexistence of *P. poplesia* and *P. inopinus* could be controlled by dietary differences and the salinity gradient.

P. inopinus was introduced (probably via ballast water) to a number of estuaries along the Pacific coast of the USA, where it has become the dominant brackish-oligohaline mesozooplankton species and has probably altered estuarine food webs (Cordell and Morrison 1996; Cordell et al. 2007). In northeastern Pacific estuaries, it reaches peak abundances in late summer/early autumn (17.4°C to 20.8°C) over a salinity range of 0 to10 psu (Cordell et al. 2007, 2010). *Pseudodiaptomus koreanus* from the Seomjin River estuary in south-central Korea is also restricted to oligohaline and mesohaline waters and differs from *P. inopinus* in that it mainly occurs in oligohaline conditions (Park et al. 2005; Soh et al. 2012). Around the Japanese mainland, *P. inopinus* and *Pseudodiaptomus nansei* coexist, but the latter species is restricted to Nansei Islands (Sakaguchi and Ueda

2010; Sakaguchi et al. 2011). Recently, Sakaguchi and Ueda (2010) distinguished a separate species, *P. nansei*, from *P. inopinus* on Kyushu Island, Japan, and also identified the presence of *P. inopinus* in the eastern Sea of Japan; the population on the Pacific side of Japan consists of a complex of species that are morphologically similar but genetically distinct. Populations of *P. inopinus* also differ genetically among the western and southern/eastern parts of Korea and from Japanese populations (Soh et al. 2012). Accordingly, it would be interesting to genetically characterize populations of the putative species, *P. inopinus*, introduced into the USA in order to provide clues as to the origins of the introductions and to establish whether or not it was introduced more than once. Unlike *P. inopinus*, *P. poplesia* has not been reported as an introduced species in any location. This is interesting since the two species nearly always co-occur in the Mankyung River estuary, and *P. poplesia* co-occurs in Chinese estuaries
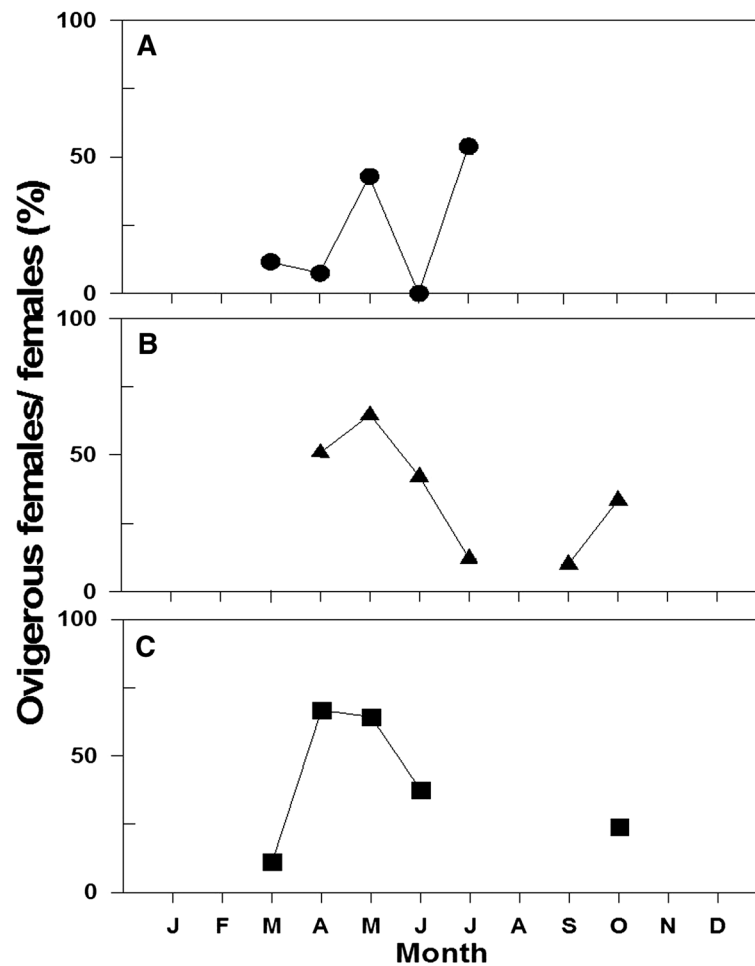
Figure 9 Seasonal variations in the composition of ovigerous adult females of *P. poplesia*. (A) Oligohaline, **(B)** mesohaline, and **(C)** polyhaline.

with *Pseudodiaptomus forbesi* and/or *P. inopinus* (Shen and Song 1979; Tan et al. 2004).

Conclusions

In this study, the annual maximal peak abundance of *P. poplesia* occurred during spring, when Chl *a* concentrations were highest (>150 μg/L). Food conditions at that time may be sufficient to allow the coexistence of *P. poplesia* and *P. inopinus*. However, there may be more competition for food between the two species when Chl *a* concentrations decrease in fall (<30 μg/L). Under these conditions, differences in their body sizes and shapes would likely be a significant factor in partitioning their food niches. In addition, *P. poplesia* has an enlarged 'naupliar eye', which could be more effective in food selectivity, while *P. inopinus* has two small, ordinary naupliar eyes.

P. poplesia occurs under stenohaline conditions and is adapted to a narrower salinity range than species adapted for euryhaline conditions, such as *P. inopinus*. This provides a plausible reason why *P. poplesia* has not been introduced to estuaries of the Pacific coast of the USA, unlike other Asian estuarine species (Cordell and Morrison 1996; Orsi and Ohtsuka 1999).

Author details
[1]Department of Oceanography, Chonnam National University, Gwangju 500-757, South Korea. [2]Department of Life Science, Hanyang University, Seoul 133-791, South Korea. [3]School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98195-5020, USA. [4]Faculty of Marine Technology, Chonnam National University, Yeosu 550-749, South Korea.

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