Spatio-temporal distribution of *Acartia* (Copepoda: Calanoida) species along a salinity gradient in the Seomjin River estuary, South Korea

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(Received 6 October 2014; accepted 11 February 2015; first published online 29 June 2015)

The spatio-temporal distribution of four coexisting *Acartia* (Copepoda: Calanoida: Acartiidae) species, *A. hudsonica*, *A. omorii*, *A. ohtsukai* and *A. forticrusa* was examined along a salinity gradient in the Seomjin River estuary, during the spring tide of each month for one year from January to December 2000. Most of the *Acartia* species were found in mesohaline (5–18 psu) and polyhaline regions (>18 psu), but their densities varied seasonally both along the salinity gradient and with chlorophyll *a* concentration. *Acartia hudsonica* showed a high density in mesohaline and polyhaline regions in March and April when chlorophyll *a* concentration was >20 µg l⁻¹, but *A. omorii* showed high density only in the polyhaline region in April. *Acartia ohtsukai* occurred both in mesohaline and polyhaline regions after June, but its peak density occurred in the polyhaline region in October when there was an autumn diatom bloom in the mesohaline. *Acartia forticrusa* showed peak density in the mesohaline in June when the water temperature was >20°C. These results indicate that food can be an important factor in controlling spatio-temporal distributions in the Seomjin River estuary, in addition to other environmental factors.

Keywords: acartiid species; co-existence; spatio-temporal distribution; salinity gradient; temperature; chlorophyll *a* concentration

Introduction

Acartia species (Copepoda: Calanoida) are seasonally dominant and attain high densities within the mesozooplankton community in estuarine areas (Jeffries 1962; Lee and McAlice 1979; Kimmel and Roman 2004; Lawrence et al. 2004). They also exhibit different spatio-temporal distributions along the salinity gradient within estuaries, where environmental factors such as temperature, salinity, food and tidal exchange, may play a key role in determining the spatial and temporal distributions of copepods (Jeffries 1962; Lee and McAlice 1979; Wooldridge and Melville-Smith 1979; Greenwood 1981; Ueda 1987; Durbin and Durbin 1992; Cervetto et al. 1999). The spatio-temporal segregation and continued coexistence of *Acartia* species are inferred to result from slight differences between species in terms of their ability to adapt to, and their preference for, particular environmental conditions (Alcaraz 1983; Uye 1985; Rodriguez and Jiménez 1990; Lakkis 1994).

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In Korean waters, 11 species of *Acartia* had been reported up until 2000 (Yoo et al. 1991; Soh and Suh 2000) and two more species (*A. ohtsukai* and *A. forticrusa*) were recently added, in the Seomjin River estuary (Ueda and Bucklin 2006; Moon et al. 2008; Soh et al. 2013). Recent molecular studies, however, suggest that there might be many new species in the *Acartia* complex in this region (Ueda and Bucklin 2006; Chen and Hare 2008; Costa et al. 2011; Soh et al. 2013). For example, three species of *Acartia* (*A. hudsonica*, *A. omorii* and *A. pacifica*) were reported in the Seomjin River estuary (Yoo et al. 1991), but one species (subsequently described as *A. ohtsukai*) was misidentified as *A. pacifica* (Moon et al. 2008), and an additional unidentified *Acartia* sp. was identified recently as *A. forticrusa* using molecular techniques (Park 2005; Soh et al. 2013).

This study re-evaluates the coexistence and separation between four *Acartia* species in the Seomjin River estuary, southern Korea, and discusses the various environmental factors controlling their spatio-temporal distributions.

Materials and methods

Study area

The Seomjin River, Korea is 226 km long and the area of its basin 4897 km². The annual average rainfall is 1253 mm, with over 70% concentrated in summer. In the estuary the seawater reaches 25 km upstream from the mouth and is well mixed vertically with freshwater because of the large tide range (up to a maximum of 4.5 m). Water depth in the estuary averages 7–8 m with a maximum of 15 m at station 5 (Figure 1). The Seomjin River estuary was divided into oligohaline (0–5 psu), mesohaline (5–18 psu), and polyhaline (>18 psu) regions, according to Ekman's classification system (Day et al. 1989).

Sampling methods

Zooplankton samples were collected monthly from January to December 2000 at six stations between Seomjin Village (35°05'N), where salinity is nearly 0 psu, and Gwangyang Bridge (34°40'N), where salinity is >25.0 psu. The stations were established along a salinity gradient, approximately 5.0 psu apart. Zooplankton samples were taken by oblique tows from the bottom layer to the surface layer using a conical net (mouth diameter: 45 cm, mesh size: 200 µm) equipped with a flow meter (Rigosha Co., Japan), for 5 min at a speed of 2.5 knots. Sampling began at station 1 at high tide and was completed in 3 h. Water temperature and salinity were measured using a T-S meter (YSI, Model 30, USA) from the surface to the bottom layer at intervals of 1 m. To measure chlorophyll *a* concentration, 1000 ml of water was collected from the surface layer of each station and filtered through glass-fibre filter paper (Whatman GF/F, England), using a vacuum pump. Pigment was extracted by grinding the filter paper in a dark room, and placing it in 90% acetone, as recommended by SCOR-UNESCO (1984). Each extract was centrifuged, and the absorbance (at 750, 664, 647 and 630 nm) of the supernatant was measured with a spectrophotometer (UNICAM Helios *a*, UK). The abundance of the *Acartia* species was expressed as individuals per cubic meter (ind. m⁻³). Spearman rank correlations

Figure 1. Sampling stations in the Seomjin River estuary, Southern Korea.

were used to investigate the relationships between environmental parameters and the densities of the four *Acartia* species, using SPSS program, version 18.

Results

Water temperature

Water temperature ranged from 0.6 to 27.5°C during the research period (Figure 2A). Water column thermal stratification was not observed along the sampling transect, although there were small differences between surface and bottom layers at all stations. Seasonal variation of water temperature ranged from 2 to >26°C with minimum surface temperature in January/February and maximum in June/August. The water column throughout the estuary was thermally homogeneous between the

Figure 2. Monthly spatial and temporal variation in water temperature and chlorophyll *a* concentration in the Seomjin River Estuary: (A) temperature (°C); (B) chlorophyll *a* (µg l⁻¹).

surface and the bottom layers except for June and July, and it became thermally stratified among sampling station from September to December.

Chlorophyll a concentration

The chlorophyll *a* (chl. *a*) concentration during the period was 2.5–108.9 $\mu\text{g l}^{-1}$ and differed with season and station (Figure 2B). At station 1 the chlorophyll *a* concentration was 2.5–18.2 $\mu\text{g l}^{-1}$ throughout the year, with the peak value in July and the minimum in November. At station 2 the chlorophyll *a* concentration was 3.7–108.9 $\mu\text{g l}^{-1}$, with the highest values in October (108.9 $\mu\text{g l}^{-1}$) and May (43.1 $\mu\text{g l}^{-1}$). In addition, stations 3 and 4 showed high chlorophyll *a* concentrations of 3.0–44.4 $\mu\text{g l}^{-1}$ and 3.8–45.2 $\mu\text{g l}^{-1}$, respectively, although the concentrations were highest in May (45.2 $\mu\text{g l}^{-1}$). At stations 5 and 6, the chlorophyll *a* concentrations were 2.5–48.5 $\mu\text{g l}^{-1}$ and 2.8–23.7 $\mu\text{g l}^{-1}$, respectively, with the peak value recorded in April and the minimum in December.

Salinity

Salinity measured during the research period ranged from 0.0 to 32.2 psu, but there were spatio-temporal differences according to season and station (Figure 3). Station 1 showed salinity below 5.0 psu throughout the year, and the difference between the surface and bottom layers was around 0.2 psu. Stations 2 and 3 showed salinities of 7.0–10.2 and 11.1–16.3 psu, respectively, throughout the year; at these two stations, the difference between surface and bottom layers was <1. Station 4 varied in salinity between 14.7 and 20.5 psu, and the differences in salinity between the surface and the bottom layers was <1.0 psu in spring and winter, but >5.0 psu in summer and autumn. Stations 5 and 6 were in the polyhaline region and >25.0 psu throughout most of the year, although they fell below 18.0 psu from July to September, due to the seasonal rainfall. In addition, the difference between the surface and the bottom layers at stations 5 and 6 was on average 5.0 psu, although this difference was as large as 10.0 psu in summer.

Spatio-temporal distribution

The four acartiid species *A. hudsonica*, *A. omorii*, *A. ohtsukai* and *A. forticrura* were predominant in the mesohaline and polyhaline regions throughout the year (Figure 4). However, the peak density of each differed spatio-temporally in relation to environmental parameters such as temperature, salinity, and chl. *a*. *Acartia hudsonica* appeared in a range of 4.0–25.0°C, 8.0–25.0 psu and 5.2–45.2 $\mu\text{g l}^{-1}$ throughout the year (Figures 4A, 5A), but its highest density (>20,000 ind. m^{-3}) was at station 4 (18.5–22.2 psu) in March and April and a high density (10,420 ind. m^{-3}) was also found in April (4.2 psu and 10.6 $\mu\text{g l}^{-1}$). *Acartia omorii* showed a similar spatio-temporal distribution pattern to that of *A. hudsonica* (Figure 4B), and its peak density was in the mesohaline region in April (7233 ind. m^{-3}) when the salinity was >19.5 (Figure 5B) and chl. *a* was 39.5 $\mu\text{g l}^{-1}$ (Figure 2B). *Acartia ohtsukai* was dominant in conditions above 10°C and 10 psu (Figure 6A), and its peak density occurred in October (2426 ind. m^{-3}) in polyhaline waters (Figure 4C). *Acartia forticrura* was dominant at higher temperatures and in less saline waters than *A. ohtsukai*

Figure 3. Monthly spatial and temporal variation in salinity between surface and bottom layers at all sampling stations. Bold line indicating salinity overlaps between sampling stations.

(Figure 6B). The highest density of *A. forticrusa* was in mesohaline waters in June (6739 ind. m⁻³) and this species maintained high density (2588 ind. m⁻³) in mesohaline waters through until September (Figure 4D). Correlations of environmental factors (temperature, salinity and chl. *a*) with density of the four acartiid species were as

Figure 4. Temporal variation in the four *Acartia* species abundance at all sampling stations. (A). *A. hudsonica*; (B) *A. omorii*; (C) *A. ohitsukai*; (D) *A. forticrusa*.

follows: density of *A. hudsonica* was positively significant with chl. *a* concentration ($r = 0.554$, $p < 0.001$) and negatively significant with temperature ($r = -0.370$, $p < 0.001$), *A. omorii* was positively significant with salinity ($r = 0.650$, $p < 0.001$),

Figure 5. Seasonal changes in the abundance-temperature-salinity diagram of (A) *Acartia hudsonica*; (B) *A. omorii*. Showing peak abundance in relation to temperature and salinity conditions.

Figure 6. Seasonal changes in the abundance-temperature-salinity diagram of (A) *Acartia ohtsukai*; (B) *A. forticrusa*. Showing peak abundance in relation to temperature and salinity conditions.

and *A. forticrusa* was positively significant with temperature ($r = 0.454$, $p < 0.001$). Significant positive correlations were also found between the densities of *A. hudsonica* and *A. omorii* ($r = 0.641$, $p < 0.001$), and *A. forticrusa* and *A. ohtsukai* ($r = 0.439$, $p < 0.001$).

Sex-ratios of four acartiid species

The sex-ratio of *Acartia hudsonica* was consistently <1.0 during the winter and spring in mesohaline and polyhaline waters. The ratio was highest in polyhaline waters in June, and only males were found in mesohaline waters in June and December (Table 1). The sex-ratio of *A. omorii* was similar to that of *A. hudsonica*, except that there was a shift in the ratio in polyhaline waters in spring (Table 1). The sex-ratio of *A. ohtsukai* changed from 0.47 to 1.28 in mesohaline and polyhaline waters from summer to autumn and males were more numerous than females (Table 1). The sex-ratio of *A. forticrusa* was similar to that of *A. ohtsukai*, but males were more numerous than females in polyhaline waters in August and October and females were twice as abundant as males in mesohaline waters in summer, except in June (Table 1).

Discussion

Many *Acartia* species display different spatio-temporal distribution patterns determined by their adaptation abilities and preferences for particular environmental conditions (Alcaraz 1983; Ueda 1987; Gaudy et al. 2000; Chinnery and Williams 2004). Salinity and temperature are reliable indicators for discriminating species in estuaries, but there are difficulties in identifying the factors allowing continued species coexistence. According to some of previous studies on *Acartia*, temperature and salinity are important factors underlying temporal succession and spatial segregation patterns, and can explain the hatching of resting eggs and grazing rates, which are evolutionary strategies for inhabiting variable environments (Lee and McAlice 1979; Collins and Williams 1981; Uye 1985; Milione and Zeng 2008). The succession of *A. tonsa* and *A. clausi* was affected by temperature, and their ability to adjust to salinity changes (Jeffries 1962). Likewise, the seasonal succession of *A. hudsonica* and *A. tonsa* was controlled by temperature, although they indicated that the number of species may vary with the quantity and quality of food (Sullivan and McManus 1986).

In the Seomjin River estuary, the four acartiid species (*A. hudsonica*, *A. omorii*, *A. ohtsukai* and *A. forticrusa*) displayed distinct seasonal and spatial distribution patterns. *Acartia hudsonica* and *A. omorii* were dominant in winter and spring, while *A. forticrusa* and *A. ohtsukai* dominated in early summer and autumn, respectively. However, the timing of peak density differed according to salinity. In March *A. hudsonica* showed peak density in the polyhaline when chl. *a* was increased by $c.10 \mu\text{g l}^{-1}$ and also maintained high density in the oligohaline and mesohaline. In April *A. omorii* attained peak density in polyhaline conditions when chl. *a* concentration was $>20 \mu\text{g l}^{-1}$, although *A. hudsonica* continuously maintained higher density in the mesohaline and polyhaline. Ueda (1987) suggested that the habitat segregation of *A. omorii* and *A. hudsonica* co-occurring in Maizuru Bay, Japan appeared to be moderated by preference for salinity and by interspecific competition. Paffenhöfer and Stearns (1988) indicated that the restriction of *A. tonsa* to near-shore and

Table 1. Seasonal changes in male: female sex ratios of four *Acartia* species.

Species	Station	Winter		Spring			Summer			Fall			Winter	
		Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Dec.
<i>A. hudsonica</i>	A	-	-	-	1	-	-	-	-	-	-	-	-	-
	B	0.61	0.81	0.31	0.81	0.5	M	-	0.22	-	-	-	M	M
	C	0.39	1.48	0.53	0.83	1.11	2.15	-	-	-	F	-	-	-
<i>A. omorii</i>	A	-	-	-	-	-	-	-	-	-	-	-	-	-
	B	-	0.90	-	-	-	-	-	-	-	-	M	-	-
	C	2.4	0.43	0.35	0.88	1.32	1.05	-	-	-	-	0.31	1.14	1.14
<i>A. ohsumukai</i>	A	-	-	-	-	-	-	-	-	0.86	-	-	-	-
	B	-	-	-	-	-	-	1	0.84	-	-	-	-	-
	C	-	-	-	-	-	1.28	1	0.47	M	1.84	0.70	0.21	0.21
<i>A. forticrusa</i>	A	-	-	-	-	-	-	-	-	M	-	-	-	-
	B	-	-	-	-	-	0.89	F	2.58	0.72	0.17	0.30	-	-
	C	-	-	-	-	-	1.34	F	M	0.5	3	0.56	-	-

Note: M = males only, F = females only, A = oligohaline, B = mesohaline, C = polyhaline.

brackish habits was affected by differences in food concentrations. In the Seomjin River estuary, *A. hudsonica* thrives across a wider salinity gradient and in relatively low chl. *a* concentration than *A. omorii*, which is restricted to polyhaline conditions and high chl. *a* ($39.5 \mu\text{g l}^{-1}$). The correlation between these two species and environmental factors showed that the density of *A. hudsonica* was positively significant for chl. *a* concentration ($r = 0.554$, $p < 0.001$) while *A. omorii* was positively significant for salinity ($r = 0.650$, $p < 0.001$). There is a strong positive correlation between the densities of these two species ($r = 0.641$, $p < 0.001$). This suggests that in the Seomjin River estuary a preference for salinity and food between two species can control their populations, although the range between the maximum and minimum salinities is almost the same in the two species.

At temperatures $>20.0^{\circ}\text{C}$, *A. hudsonica* and *A. omorii* were replaced by *A. forticrusa* and *A. ohtsukai*. However, *A. forticrusa* was restricted to mesohaline conditions and showed peak density in June when chl. *a* decreased to $<10 \mu\text{g l}^{-1}$, while *A. ohtsukai* was at low density. Peak density of *A. ohtsukai* occurred in polyhaline conditions when there was a diatom bloom in the mesohaline in October. The density of *A. forticrusa* showed strong positive correlation with temperature ($p < 0.001$, $r = 0.454$), but *A. ohtsukai* showed a relatively weak positive correlation with temperature and salinity ($p < 0.01$), and chl. *a* ($r = 0.360$, $p < 0.05$). Although there was a strong positive correlation between *A. forticrusa* and *A. ohtsukai* ($r = 0.439$, $p < 0.001$), there may not be competition for food between these two species due to differences in their preferences for salinity and food. Kwon et al. (2001) showed that in the same study area, very small cryptophyte *Chroomonas* spp. increased in abundance in mesohaline waters in spring, while there was a diatom bloom of *Skeletonema costatum* in autumn in the mesohaline to polyhaline region. In addition, egg production and hatching success between *Acartia* species have been found to vary under different temperature and salinity regimes (Castro-Longoria 2003), as well as with food quality (Shin et al. 2003). In the Seomjin River estuary, males of *A. hudsonica* were more numerous than females in the mesohaline, but male of *A. omorii* was more abundant in polyhaline in winter and spring. In the case of *A. forticrusa* males were dominant in the mesohaline, but male of *A. ohtsukai* was more abundant in polyhaline in summer and fall seasons. Our results indicate that the density of the four *Acartia* species could be controlled not only by tolerance to temperature and salinity, but also by their differences in feeding strategy. The present study also revealed that the adaptation to different salinity changes differs between the sexes. It would be interesting to test whether the reproductive strategies of both sexes of *Acartia* species vary according to the salinity gradient.

Acknowledgements

We sincerely thank two anonymous reviewers for their constructive comments and also express our sincere thanks to Dr BAV Maran (Korea Institute of Ocean Science & Technology, South Korea). Our thanks are extended to Mr Jeong-In Park for statistical analysis.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the grants from the Basic Science Research Programme of the National Research Foundation of Korea (NRF) funded by the Ministry of Education, Science and Technology of the Republic of Korea [2012R1A1A2005312] and Fisheries Science Institute, Chonnam National University.

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