

Diel Pattern of Littoral Swarming in *Moina macrocopa* and Impact of Juvenile Fish Density

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The diel swarming of *Moina macrocopa* and the relationship between environmental factors were evaluated in a shallow reservoir. The littoral density of *Moina macrocopa* maintained low from night to noon, reached maximum density at the afternoon with compact swarms at the waters' edge, and dispersed after sunset. The recruitment of *Moina macrocopa* and changes of water temperature ($r=0.709$, $p<0.001$) and juvenile fish density ($r=0.511$, $p=0.002$) in the littoral zone showed a significant positive relationships. After the induction of diel horizontal migration toward littoral zone, therefore, direct juvenile fish predation pressure should be induced *Moina macrocopa* swarming.

Key words : *Moina macrocopa*, swarm, predation, Diel horizontal migration

INTRODUCTION

Predation regulates community structure of prey, and affects their distribution at both spatial and temporal scales (Kerfoot and Sih, 1987). Among the behavioral responses of large zooplankton to predation, diel vertical migration (DVM) in *Daphnia* as a spatial separation strategy became the most extensively studied topic (Lampert, 1993). In a deep and stratified lake environment, predation pressure induces the migration of *Daphnia*. The cold and dark hypolimnion provides a daytime refuge from fish predators (Gliwicz, 1986).

In subtropical latitudes, however, shallow lakes which do not provide a deep refuge are very scattered (Steinman *et al.*, 1997). The biomass of fish in shallow lakes is relatively high, and predation

pressure from planktivorous fish can be maintained at high levels (Jeppesen *et al.*, 1997). In those environments, DVM is not applicable due to low water depth; therefore, as an alternative of DVM, cladocerans show diel horizontal migration (DHM) (Timms and Moss, 1984). During DHM, they migrate between the pelagic and littoral zone to avoid pelagic predators. In this scenario, macrophytes in the littoral zone provide a refuge for cladocerans from fish predators (Burks *et al.*, 2001).

The dense distribution in the littoral zone during DHM often related to the swarming, and in case of small cladoceran *Bosmina longispina*, the daytime density reached up to several thousand individuals per liter in the littoral zone of lake (Jakobsen and Johnsen, 1988). Swarming is wide spread behavior among zooplankton, especially cladocerans formed swarms (Ratzlaff, 1974). Swarming is

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known to provide a direct increase of survivorship through the confusion effect (Allen, 1920). In addition, swarms sometimes contain males and sexual females, and increase of mating chances for the production of resting eggs and it overcomes the predation pressure indirectly (Colebrook, 1960; Young, 1978).

The experiments on DVM well described in 24 h scale (Loose, 1993). However, information on *in situ* diel pattern of littoral movement of cladocerans and potential driving factors is insufficient. In this study, we evaluated the littoral movement and swarming patterns of cladoceran, *M. macrocopa*, commonly distributed in shallow and eutrophicated reservoirs. Then we analyzed the relationship between *M. macrocopa* density and environmental factors such as juvenile fish density and various environmental factors. In addition, sex ratio was analyzed to determine the occurrence of mating during swarming.

MATERIALS AND METHODS

Field samplings were carried out in the littoral zone of Dongpan reservoir (E: 128° 41' 22.73", N: 35° 18' 12.75", mean depth *ca.* 1.5 m) in Changwon, S. Korea. Dongpan reservoir is connected with two adjacent reservoirs by the channels and contains various fish species (Cho *et al.*, 2003). We selected fifteen sampling sites at two-meter intervals arranged within littoral zone (A, B and C-zone; five sites for each zone, respectively) (Fig. 1). Zooplankton samplings were conducted every

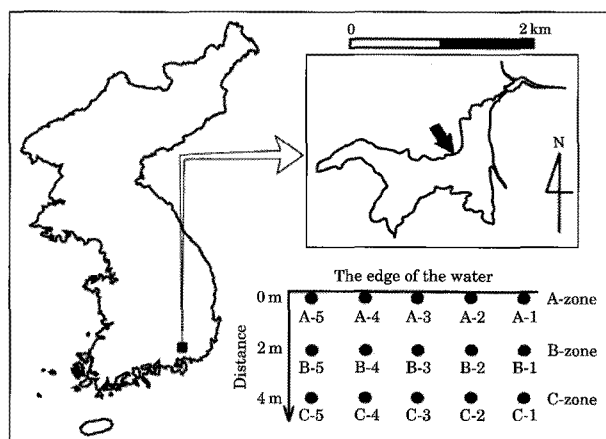


Fig. 1. The location and description of study sites in the Dongpan Reservoir.

2 hr on 27 May 2007 (500 mL, $n=12$ from 01:00 to 23:00), then filtered with a 32 μm mesh net, and fixed with sucrose-formalin for enumeration (Haney and Hall, 1972). Physico-chemical factors such as water temperature, pH, dissolved oxygen and turbidity of the A-zone were determined using a multi-parameter water quality monitoring system (YSI-6600, USA). To estimate diel juvenile fish density in the A-zone, one meter distance of surface water toward the waters' edge was filtered ten times with a 500 μm mesh dip net (20 cm \times 15 cm), at a 4 hr intervals for minimal disturbance. Sex composition of *M. macrocopa* population in A-zone was classified into males and females based on the possession of long first antennules. After sex classification, females were divided into ephippial (sexual), asexual females with embryos and small immatures with empty brood chambers.

To describe any relationship between these variables and environmental factors, correlation analyses (Pearson Correlation analysis) between *M. macrocopa* density and environmental factors were conducted using SPSS version 12.0 (SPSS Inc., USA).

RESULTS

The mean density ($n=60$) of *M. macrocopa* at the waters' edge was higher (A-zone; 5,476 ind. L^{-1}) than in the pelagic direction (B-zone; 391 ind. L^{-1} and C-zone; 374 ind. L^{-1}). B-zone and C-zone did not show any diel changes in distributional pattern, however, the recruitment of *M. macrocopa* toward A-zone was remarkable; they began to gather in the afternoon (13:00, local time), then the density drastically increased until 15:00, and reached its maximum at 17:00 (22,993 ind. L^{-1}). From 15:00 to 17:00, *M. macrocopa* formed distinguishable greenish swarms in a band approximately 10 cm wide along the A-zone, which continuously changed its shape. In most cases, the primary swarms remained dense, with smaller separated flocks rejoining immediately. After swarming, a steep decrease in density occurred before sunset (19:00), and then continued to disperse to the nighttime density at 21:00 (Fig. 2).

Among the environmental factors, the water temperature and juvenile fish density showed relationships with *M. macrocopa* density. The water temperature ranged from 20.2°C to 28.1°C.

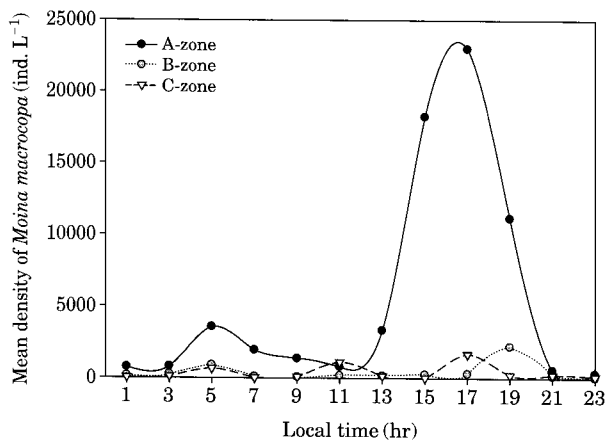


Fig. 2. Diel changes in the mean density of *Moina macrocopa* in the different zones.

Table 1. Correlation between *Moina macrocopa* density and environmental factors.

Environmental factors		Correlation	
		A-zone	
Abiotic factor	Water temperature (°C)	r	0.709
		p	<0.001
	pH	r	0.203
		p	0.105
	DO (mg L ⁻¹)	r	0.245
		p	0.049
Turbidity (NTU)	r	-0.214	
	p	0.087	
Biotic factor	Juvenile fish density (ind. m ⁻³)	r	0.511
		p	0.002

As a result, water temperature and density of *M. macrocopa* were positively correlated ($r=0.709$, $p<0.001$) (Table 1).

Five fish species were collected at the A-zone. The most dominant species during a day was *Pseudorasbora parva* (mean 8.8 ind. m⁻³). The mean size of the juvenile fish ranged from 0.88 to 1.94 cm. Although species composition fluctuated over time, the total density showed distinctively high in the afternoon, and reached maximum density at 17:00. At that time, *Micropterus salmoides* was dominant species (22.7 ind. m⁻³). The total density of juvenile fish showed a significantly positive correlation with *M. macrocopa* density ($r=0.511$, $p=0.002$) (Fig. 3 and Table 1). The swarming *M. macrocopa* population consisted of both sexes. The males were found occasionally

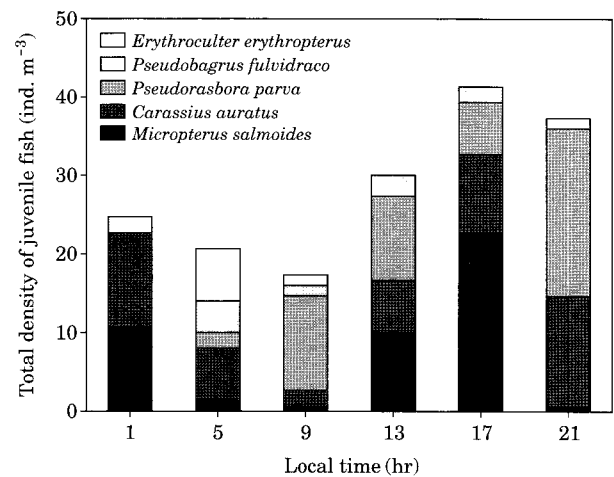


Fig. 3. Diel changes in juvenile fish density in the littoral zone.

Table 2. The sex composition (%) of *Moina macrocopa* population at each sampling time.

Time (hr)	Females			Males
	Asexual	Sexual	Immatures	
1	59.5	0.0	40.5	0.0
3	47.7	0.0	52.3	0.0
5	21.3	0.0	78.7	0.0
7	40.2	0.0	59.6	0.2
9	42.2	0.0	57.6	0.2
11	35.9	0.0	64.1	0.0
13	32.6	0.0	67.1	0.3
15	45.1	0.0	54.9	0.0
17	38.1	0.0	61.6	0.3
19	37.2	0.0	62.4	0.4
21	53.5	0.0	46.5	0.0
23	55.8	0.0	44.2	0.0

through the day in very low proportions (0.2~0.4 %). Among females, the proportion of immatures (mean 57.4%) was higher than adult females (mean 42.5%), while sexual females with an ephippium were not found (Table 2).

DISCUSSION

In this study, *M. macrocopa* showed DHM pattern. The scarcity of *M. macrocopa* in the B and C-zones during daytime did not fully support the extreme density found in the A-zone. *M. macrocopa* did not migrate toward A-zone before sunrise (05:15) but dispersed after sunset (19:31). Interestingly, water depth of sampling sites was

very shallow (< 1 m depth), and there were no observations on the movement toward the A-zone beneath water surface during a day. Thus the response to avoid light may be presented in horizontally migrating *M. macrocopa*, and the migration occurred through the lower depth. Although both DVM and DHM are behavioral response to the predators, there are some differences. Large *Daphnia* females migrate deeper water than small individuals during DVM (De Meester, 1994). *Moina* population representing DHM relatively more consisted of immature females without eggs. The change of light intensity induces a corresponding time of DVM, the ascent and descent of *Daphnia* follows local time of sunrise and sunset (Ringelberg *et al.*, 1991).

DHM is advantageous in that it makes feeding difficulty for predators by using macrophyte beds for refuge (Engels, 1988), and its effectiveness as a refuge is often related to its density and species (Jacobsen *et al.*, 1997; Burks *et al.*, 2001). However, aquatic plants in the study sites nearly absent until mid summer. Although the littoral zone did not provide actual refuge against juvenile fish in May, migration toward littoral zone still occurred.

They feed and swarm during the day in the littoral zone and rest on the bottom at night (Emery, 1973). In fact, increased juvenile fish density implies that high predation risk for *M. macrocopa* still maintained in the littoral zone, which is used as a refuge. In this circumstance, the possible response of *M. macrocopa* can be the swarming to reduce predation risks by using a very large number of individuals to confuse the predators. The occurrence of DHM followed by swarming was fully exhibited by *M. macrocopa*. The concentration of fish kairomones positively affects the amplitude of DVM (Loose, 1993), and induces an immediate behavioural response (De Meester and Cousyn, 1997). Our results showed the coincidence of juvenile fish density increase and *M. macrocopa* swarming in the littoral zone. Based on the confusion effect, predators suffer difficulty in prey selection among large numbers of swarming participants, and group vigilance which is directly related to the rate of survivorship increased (Allen, 1920; Neill and Cullen, 1974; Jennings and Evans, 1980). In general, fish predation pressure increases in warm water, and increases sexual reproduction in *M. macrocopa* (D'Abramo, 1980; Mehner *et al.*, 1998). Thus, littoral swarming observed in the reservoir can provide additional

benefit by the increase of mating chance as the coexistence of both sexes.

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