

Influences of diel and tidal cycles on fish assemblage in eelgrass (*Zostera marina*) bed of southern Korea during autumn

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Abstract

Short-term tidal and diel variations of autumn fish assemblage in a *Zostera marina* bed were investigated using 3 h interval samplings for 24 h in both spring and neap tide using a small beam trawl. A total of 1 346 fishes belonging to 19 species were collected at spring tide, whereas 1 115 fishes belonging to 17 species were at neap tide. The common fish species were *Nuclequula nuchalis*, *Acanthogobius flavimanus*, *Takifugu niphobles*, *Acentrogobius pflaumii*, and *Pholis nebulosa* with the former three species dominating at spring tide, while the latter two species being abundant at neap tide. Diel variation in abundance was significant with higher abundance at night than day, but there were no significant differences between spring and neap tides, and between ebb and flood tides (three-way ANOVAs). Diel variation in the abundance of fishes may be influenced by tidal range and cycle, and day-night differences of food availability and behaviors of fishes indirectly. Non-metric multidimensional scaling (nMDS) ordination and analysis of similarity (ANOSIM) results revealed significant differences in species compositions both between day and night, and between spring and neap tide. Eelgrass beds are highly productive marine ecosystem, and thus, our results will contribute to conservation of seagrass ecosystem in the study area.

Key words: tidal and diel variations, fish assemblage, eelgrass, *Zostera marina*, southern Korea

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1 Introduction

Seagrass beds have long been recognized as important habitats for various benthic invertebrates due to high primary productivity and organic materials they support (Thayer et al., 1975). These habitats also provide feeding grounds, shelter or nursery ground for early stage of fishes (Klumpp et al., 1989; Huh and Kwak, 1997c; Jenkins and Wheatley, 1998; Guidetti, 2000; Hemminga and Duarte, 2000). In many shallow seagrass habitats, tidal and diel effects are important factors that control fish assemblages (Sogard et al., 1989), and these effects may have one of the greatest influences on the pattern of biological inter-habitat connectivity (Sheaves, 2005). Several studies have reported diel and tidal variations in seagrass fish assemblage in the Wadden Sea (Polte and Asmus, 2006) and Wakatobi Marine National Park of Indonesia (Unsworth et al., 2007). The number of individuals and biomass of fishes have shown significant variation with tidal and diel cycles in the intertidal seagrass beds worldwide which can be facilitated by small-scale movement of fishes (Guidetti and Bussotti, 2000; Nagelkerken et al., 2002; Kopp et al., 2007). Morrison et al. (2002) reported that small-scale movement patterns over short temporal and spatial scales in shallow intertidal zone may be directly related to feeding dynamics, habitat usage and avoidance of potential predators. Kopp et al. (2007) also showed that diel assemblage shift in the seagrass beds was due to

nocturnal trophic incursions of fishes into seagrass habitats from nearby coral reef. Such movements may be strongly structured by tidal and day/night cycles. Thus, such studies are essential for their future management because they elucidate the ecological mechanisms pertinent to their effective management (Parrish, 1989; Sheaves, 2005; Larkum et al., 2006).

Zostera marina (eelgrass) is the most common seagrass species in temperate waters and forms seagrass beds in shallow coastal areas that increases habitat complexity and provides living space for various marine animals (Klumpp et al., 1989; Hemminga and Duarte, 2000; Nagelkerken et al., 2002). Several studies have been made on seagrass fish assemblage in southern Korean waters (e.g., Lee et al., 2000; Baeck et al., 2005). In the study area, there have been some studies on seasonal variation in abundance of fish assemblage (Im, 2004), comparison of fish assemblages between eelgrass bed and unvegetated habitat (Kwak et al., 2006), and feeding habits and partitioning food resource of abundant fish species (Kwak and Huh, 2004; Kwak et al., 2003, 2004, 2005). However, little is known about short term variations in fish assemblage and factors influencing such variations in intertidal seagrass habitats of Korea.

The present study focused on changes in species composition and abundance of fish assemblage with respect to day/night, spring/neap and ebb/flood tidal cycles to determine how tidal

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phase and diel rhythm affect fish assemblage structure. Results from this study will contribute to understanding short-term dynamics of the fish assemblage in seagrass habitats locally and globally.

2 Materials and methods

2.1 Study area and sampling

The study area of the Jinhae Bay is a semi-closed inland sea, and has long been known as important fishing ground, because the area forms a productive nursery with abundant food resources for early stage fishes, and provides overwintering and feeding grounds for a variety of commercially important fish (Kang et al., 1996; Kim et al., 2001). Eelgrass beds (*Zostera marina*) are prevalent along the shallow waters of the northern Jinhae Bay. This study was performed at an eelgrass bed of the northern Jinhae Bay, Korea (Fig. 1). The mean tidal ranges between high and low tides are 1.8 m and 0.7 m at the spring and the neap tide, respectively. Three-hour interval trawl nettings were conducted over 24 h during both spring and neap tides in November 2002. The fish samples were collected using a small beam trawl with 5-m length, 3-m width, 19 mm mesh wing and 10 mm mesh liner at depths of 5–6 m. A 180-m² area per towing and four repeated samplings were conducted on each sample occasion. Immediately after capture, specimens were preserved in 5% formalin with seawater for 24 h and later transferred to 70% ethanol for storage. All scientific names of fishes identified were verified following FishBase (Froese and Pauly, 2017). The size and weight of each fish specimen was recorded to the nearest millimeter in standard length and the nearest gram in preserved weight, respectively. The collected fishes were categorized as juveniles or adults, according to the general description of Korean

fishes (Kim et al., 2005) and FishBase (Froese and Pauly, 2017).

2.2 Data analysis

The diversity index (H') was calculated using Shannon and Wiener's formula to compare temporal population diversity (Spellerberg and Fedor, 2003). Univariate analysis was performed to test for any significant differences in fish abundances and assemblage structures among factors. Three factors were considered, i.e., spring/neap tides, day/night and ebb/flood tides. Three-way analysis of variances (ANOVAs) with an orthogonal design was used to analyze effects of the three factors, and interaction of these factors on number of species, fish abundance (number of individuals) and diversity. Abundance data of fish assemblage were analyzed using a combination of multivariate analyses including non-metric multidimensional scaling (nMDS), analysis of similarity (ANOSIM) and similarity percentages (SIMPER) to make tidal and diel comparisons of fish assemblages (Clarke and Warwick, 1994). To examine differences in species compositions, fish assemblages were categorized into four groups: spring tide-day, spring tide-night, neap tide-day and neap tide-night. Abundance data were square-root transformed to avoid any tendency for the main species to be excessively dominant and Bray-Curtis similarity matrices were constructed for each of the resultant groups. The Bray-Curtis similarity matrix was also visualized via nMDS ordination. Two way crossed ANOSIMs were used to test for any significant differences in the structure of fish assemblages between groups. SIMPER was used to determine which species contributed to any dissimilarities among assemblage groups. The cut off in SIMPER for fish species to be reported was chosen to be a contribution to dissimilarity of more than 10%. The differences in fish sizes between day and night was analyzed using Wilcoxon signed ranks test. For four common species which constituted more than 8% in total abundance and occurred during both spring and neap tides, spatial and seasonal variations in mean abundance were analyzed. All analyses were performed using routines in the PRIMER v5 multivariate statistics package (www.primers-e.com), and the SPSS v18 for Windows (SPSS Inc. Chicago, Illinois). For all the tests, the significance level was set at $\alpha=0.05$.

3 Results

3.1 Species composition

A total of 2 461 fishes belonging to 22 species and 18 families were collected (Table 1). Most of the fishes collected were juveniles, while only nine species occurred as adults. The five numerically abundant species were *Nuchequula nuchalis* (22.9%), *Acanthogobius flavimanus* (21.6%), *Acentrogobius pflaumii* (14.8%), *Takifugu niphobles* (8.7%) and *Pholis nebulosa* (8.2%), which together accounted 76.1% of the catch and 69.6% of the biomass (Table 1).

3.2 Variations in fish abundance and diversity in relation to diel and tidal cycles

Number of species, number of individuals and species diversity varied with diurnal cycles of day/night and tidal levels (Fig. 2). Three-way ANOVA results demonstrated that the number of species differed significantly between spring and neap tide, and between day and night ($P<0.05$), but there were no significant effect of ebb/flood tide and no two-way or three-way interactions among these three factors (Table 2). Abundance and diversity varied significantly between day and night, while there were no significant differences observed between spring and

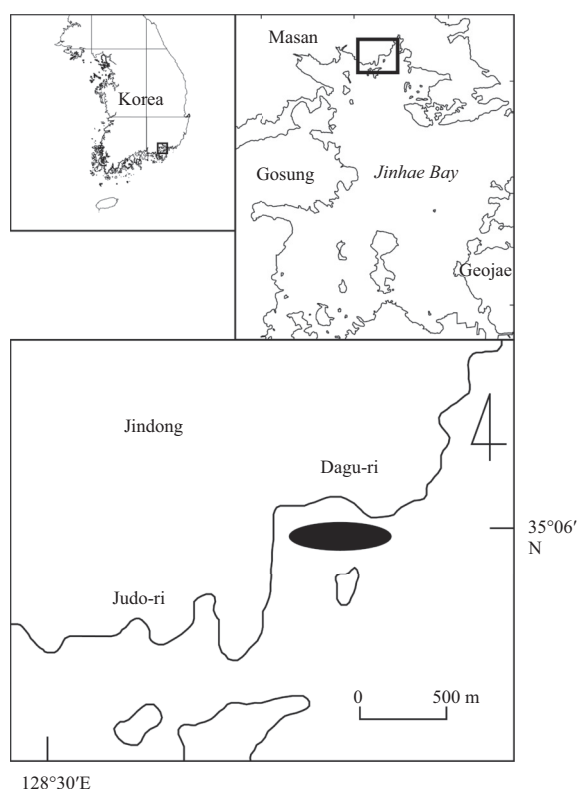


Fig. 1. Map of study site in Jindong, Korea (black area).

Table 1. Fishes occurring in an eelgrass bed of the northern Jinhae Bay during spring and neap tides in order of decreasing number of individuals

Family	Species	Habitat type	N	W	%N	%W	Size range /cm SL	Developmental stage
Leiognathidae	<i>Nuchequula nuchalis</i>	pelagic	563	1 404.6	22.9	7.3	2.7–6.3	J
Gobiidae	<i>Acanthogobius flavimanus</i>	demersal	532	7 413.8	21.6	38.8	7.3–13.4	J, A
Gobiidae	<i>Acentrogobius pflaumii</i>	demersal	363	480.5	14.8	2.5	2.7–6.2	J, A
Tetraodontidae	<i>Takifugu niphobles</i>	pelagic	215	2 823.5	8.7	14.8	3.5–7.2	J, A
Pholidae	<i>Pholis nebulosa</i>	demersal	201	1 187.7	8.2	6.2	10.2–14.1	J, A
Congridae	<i>Conger myriaster</i>	demersal	145	2 080.7	5.9	10.9	15.6–22.2	J
Monacanthidae	<i>Rudarius ercodes</i>	demersal	131	510.6	5.3	2.7	2.5–5.8	J, A
Callionymidae	<i>Callionymus valenciennei</i>	demersal	118	329.0	4.8	1.7	3.1–6.4	J, A
Hexagrammidae	<i>Hexagrammos otakii</i>	demersal	56	1 486.7	2.3	7.8	4.9–8.5	J
Pleuronectidae	<i>Pseudopleuronectes yokohamae</i>	demersal	35	348.8	1.4	1.8	6.6–12.1	J
Syngnathidae	<i>Hippocampus mohnikae</i>	demersal	31	51.7	1.3	0.3	4.4–7.9	J, A
Platycephalidae	<i>Platycephalus indicus</i>	demersal	15	249.6	0.6	1.3	7.7–12.2	J
Sillaginidae	<i>Sillago japonica</i>	pelagic	15	101.1	0.6	0.5	4.6–9.8	J
Pholidae	<i>Pholis fangi</i>	demersal	14	84.8	0.6	0.4	7.2–11.2	J, A
Syngnathidae	<i>Syngnathus schlegeli</i>	demersal	10	32.5	0.4	0.2	6.9–13.3	J, A
Sparidae	<i>Acanthopagrus schlegeli</i>	demersal	6	162.9	0.2	0.9	3.3–11.1	J
Ostraciidae	<i>Lactoria cornutus</i>	demersal	4	128.4	0.2	0.7	4.4–4.7	J
Sebastidae	<i>Sebastes inermis</i>	demersal	3	48.9	0.1	0.3	4.2–5.2	J
Lateolabracidae	<i>Lateolabrax japonicus</i>	pelagic	1	41.6	<0.1	0.2	6.2	J
Mugilidae	<i>Mugil cephalus</i>	pelagic	1	130.4	<0.1	0.7	13.3	J
Clupeidae	<i>Konosirus punctatus</i>	pelagic	1	10.7	<0.1	<0.1	9.8	J
Sebastidae	<i>Sebastes longispinis</i>	demersal	1	3.1	<0.1	<0.1	6.6	J
Total			2 461	19 111.6				

Note: N represents total number of individuals, W total wet weight (g), J juvenile, and A adult.

neap tide, and between ebb and flood tide or the interaction between these two factors (Table 2), indicating higher fish abundance and diversity at night than day regardless of tidal phases. In the interaction terms, abundance and diversity was significantly related to the interaction between two factors of day/night and ebb/flood tide, and between spring/neap tide and day/night, respectively, and other two-way or three-way interactions were not significant (Table 2). During spring tide, the number of fish species and abundance were the highest at flood tide of night, whereas these were the lowest in ebb tide of day. During neap tide, the highest values of the number of species and abundance were recorded at high tide of night (at 23:00), while the values were the lowest at low tide of day (at 11:00 and 14:00, respectively). Species diversity was varied from 1.52 to 1.94 during spring tide, and from 1.75 to 2.29 during neap tide, but did not showed any tendency in relation to tidal level and day-night change.

Total abundance and abundances of dominant species were different between spring and neap tide, and between day and night (Fig. 3). During spring tide, a total of 581 fishes were caught at daytime, and 765 fishes were caught at night. While 414 and 701 fishes were collected at day and night of neap tide, respectively. Total abundance was higher in night than day during both spring and neap tide. In terms of dominant species, during spring tide, *A. pflaumii*, *T. niphobles* and *Rudarius ercodes* were numerically abundant at night, whereas *N. nuchalis*, *T. niphobles* and *A. pflaumii* were abundant at daytime (Fig. 3). During neap tide, however, *A. flavimanus*, *N. nuchalis*, *P. nebulosa* predominated at night, and *N. nuchalis*, *A. flavimanus*, *A. pflaumii* at daytime.

3.3 Fish assemblage structure

The nMDS ordination plot displayed discrete groups of samples according to both day/night and spring/neap tide, and

the day-night difference was higher during spring tide than neap tide (Fig. 4). Two-way crossed ANOSIM showed that the fish assemblage structures differed significantly with both diel and tidal factors ($P=0.001$ for day/night, $P=0.004$ for spring/neap tide). SIMPER analysis indicated that the dissimilarity between structures of fish assemblages ranged from 26.04% to 43.30%, with the highest value between spring tide-day and neap tide-night, and the lowest between day and night of neap tide (Table 3). The most-observed fish species that contributed to the dissimilarity between spring and neap tide were *T. niphobles* and *A. pflaumii*, while those between day and night were *N. nuchalis* and *C. myriaster* in spring tide, and *C. myriaster* and *A. pflaumii* in neap tide (Table 3).

3.4 Variations in size distribution of common species

With the exception of *N. nuchalis*, size frequency distributions of the three most common species were significantly different between day and night in both spring and neap tide (Wilcoxon sign *t*-test, $P<0.05$; Fig. 5). For *N. nuchalis*, although no difference in size distribution was evident between day and night in spring tide, moderate sizes of *N. nuchalis* (4.0–5.0 cm SL (standard length)) were present more during the daytime, while larger size classes (>5.5 cm SL) were abundant at night of neap tide. For *A. flavimanus*, *A. pflaumii* and *P. nebulosa*, larger sizes of fishes were caught more at night in both spring and neap tide.

4 Discussion

In the present study, species composition and abundance of fish assemblage varied with tidal (spring and neap tide) and diel (day and night) cycles, but there was no effect of ebb/flood tidal cycle. The interplay of these two factors influenced fish assemblage compositions. The tide determines the habitat accessibility for tidal migrating fish species, while the diel cycle con-

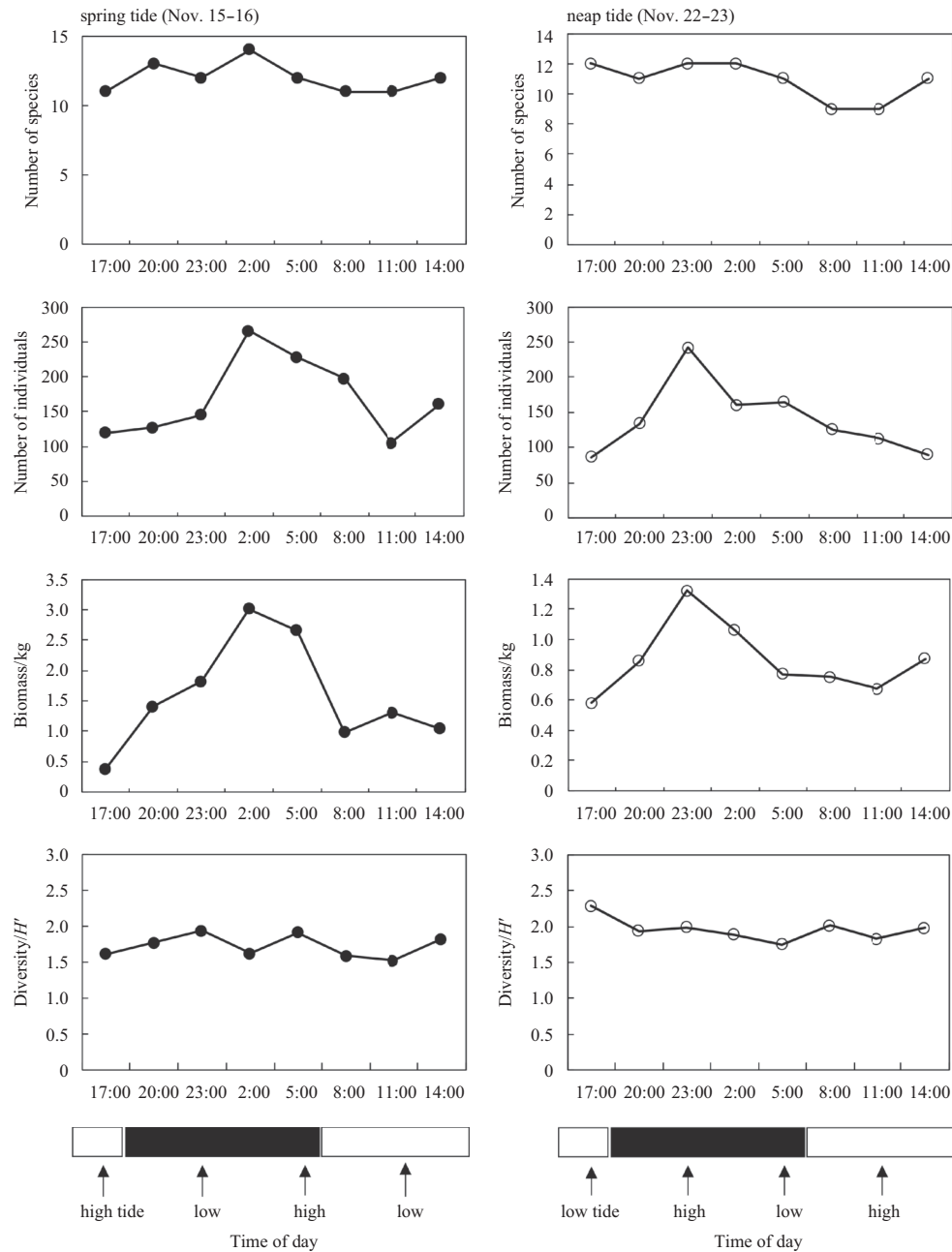


Fig. 2. Diurnal variations in number of species, number of individuals and diversity index of fish species in an eelgrass bed during the spring tide and neap tides in November 2002 (□ day; ■ night).

trols the visual conditions and diel changes in the prey organisms (Krumme et al., 2004). The influence of the tidal and diel cycle on the movements of tidal migrating fish is well established (Gibson, 1998), and Krumme et al. (2004) reported that evidence for distinct assemblages resulted from such movements. An nMDS ordination plot and two-way ANOSIM result showed that the fish assemblage structure differed significantly with tidal and diel cycles. The differences between day and night, however, were higher during spring tide than neap tide. This was probably due to strong currents during spring tide leading to a more heterogeneous assemblage structure.

Although there were no significant differences in abundance and diversity between spring and neap tide (three-way ANOVAs, $P > 0.05$), the number of species was significantly higher during

spring than neap tide ($P < 0.05$). Fish assemblage structures were also significantly different between spring and neap tide. These spring/neap tide changes in species composition may be due to the differences in the amount of the intertidal zone that can be accessed at spring tide compared to neap tide (Wilson and Sheaves, 2001). During spring tide, the tidal level shifted from 0.2 m to 2 m, and the upper parts of the intertidal zone can be accessed by various fish species at high tide. During neap tide, however, the tide does not rise as high as spring tide, and consequently, fish are forced completely into the lower zone for longer periods of time. In addition, a high tidal range may be great enough to allow large predators to readily access shallow water habitats such as seagrass at high tide, altering fish assemblage structure and changing behavioral interactions

Table 2. Results of a threeway ANOVA testing the effects of spring/neap tide, day/night and ebb/flood cycles on number of species, fish abundance and diversity

Source	Df	MS	F	P
Number of species				
Spring/Neap tide (S/N)	1	6.250	10.000	0.013
Day/Night (D/N)	1	9.000	14.400	0.005
Ebb/Flood tide (E/F)	1	2.250	3.600	0.094
S/N×D/N	1	0.250	0.400	0.545
S/N×E/F	1	2.000	3.200	0.070
D/N×E/F	1	0.250	0.400	0.545
S/N×D/N×E/F	1	1.000	1.600	0.242
Error	8	0.625		
Abundance				
Spring/Neap tide (S/N)	1	5.443	4.232	0.074
Day/Night (D/N)	1	22.337	17.367	0.003
Ebb/Flood tide (E/F)	1	0.289	0.225	0.648
S/N×D/N	1	1.694	1.317	0.284
S/N×E/F	1	3.264	2.538	0.150
D/N×E/F	1	14.079	10.947	0.011
S/N×D/N×E/F	1	9.279	7.214	0.028
Error	8	1.286		
Diversity				
Spring/Neap tide (S/N)	1	0.007	0.277	0.613
Day/Night (D/N)	1	0.264	9.872	0.014
Ebb/Flood tide (E/F)	1	0.033	1.220	0.302
S/N×D/N	1	0.246	9.225	0.016
S/N×E/F	1	0.020	0.766	0.407
D/N×E/F	1	0.135	5.047	0.055
S/N×D/N×E/F	1	0.007	0.254	0.628
Error	8	0.027		

(Blaber, 1986; Sheaves, 2005). Thus, more fish species are likely able to use shallow eelgrass beds during spring tide.

The structure of species composition varied with changes in day-night and tide heights. Abundance and biomass of fishes showed a tendency to increase as tide level increased with a peak at high tide during night. Increasing fish abundance with increasing tidal level is probably the result of fish migrating from deeper water into shallower habitats as a function of small changes in

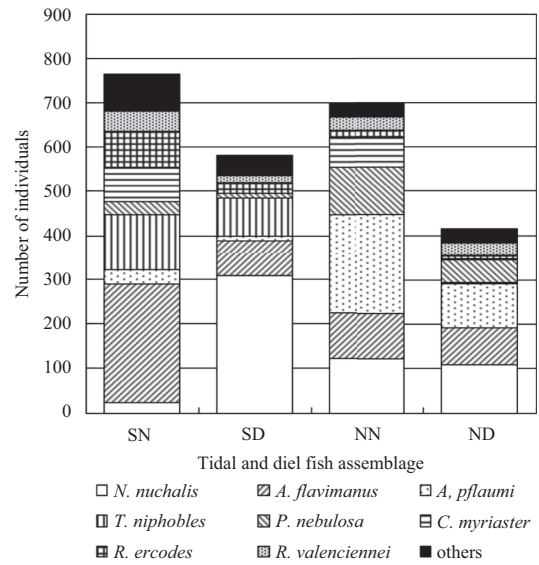


Fig. 3. Total number of individuals of each fish species captured in intertidal eelgrass bed by small beam trawl water at spring tide-night (SN), spring tide-day (SD), neap tide-night (NN) and neap tide-day (ND). Stacked columns consider species contributing on number of individuals.

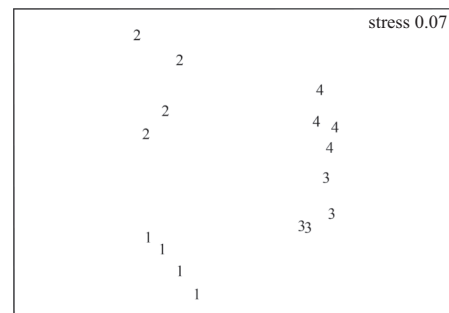


Fig. 4. nMDS plots representing similarity of fish assemblage. The numbers 1, 2, 3 and 4 indicate the fish assemblage in spring tide-day, spring tide-night, neap tide-day and neap tide-night, respectively.

Table 3. Summary of results from the similarity of percentages (SIMPER) pairwise tests for differences between the fish assemblages of day/night in spring and neap tide

Code	SN	SD	NN	ND
SN		37.86	38.25	42.17
SD	<i>N. nuchalis</i> (23.62) <i>C. myriaster</i> (15.62) <i>A. flavimanus</i> (12.38)		43.30	34.24
NN	<i>T. niphobles</i> (18.32) <i>A. pflaumi</i> (15.36) <i>N. nuchalis</i> (10.13)	<i>A. pflaumi</i> (21.07) <i>T. niphobles</i> (15.90) <i>C. myriaster</i> (14.12) <i>N. nuchalis</i> (12.67) <i>P. nebulosa</i> (12.12)		26.04
ND	<i>T. niphobles</i> (16.61) <i>C. myriaster</i> (13.70) <i>A. flavimanus</i> (11.39) <i>N. nuchalis</i> (10.39) <i>R. ercodes</i> (10.38)	<i>T. niphobles</i> (20.04) <i>A. pflaumi</i> (18.60) <i>N. nuchalis</i> (17.03)	<i>C. myriaster</i> (22.94) <i>A. pflaumi</i> (14.39)	

Note: Above the diagonal are the dissimilarities between the fish assemblages, and beneath are the main fish species (percentage of contribution) that contributed to the assemblage dissimilarities between the species. Fish assemblage codes are given in the caption of Fig. 3.

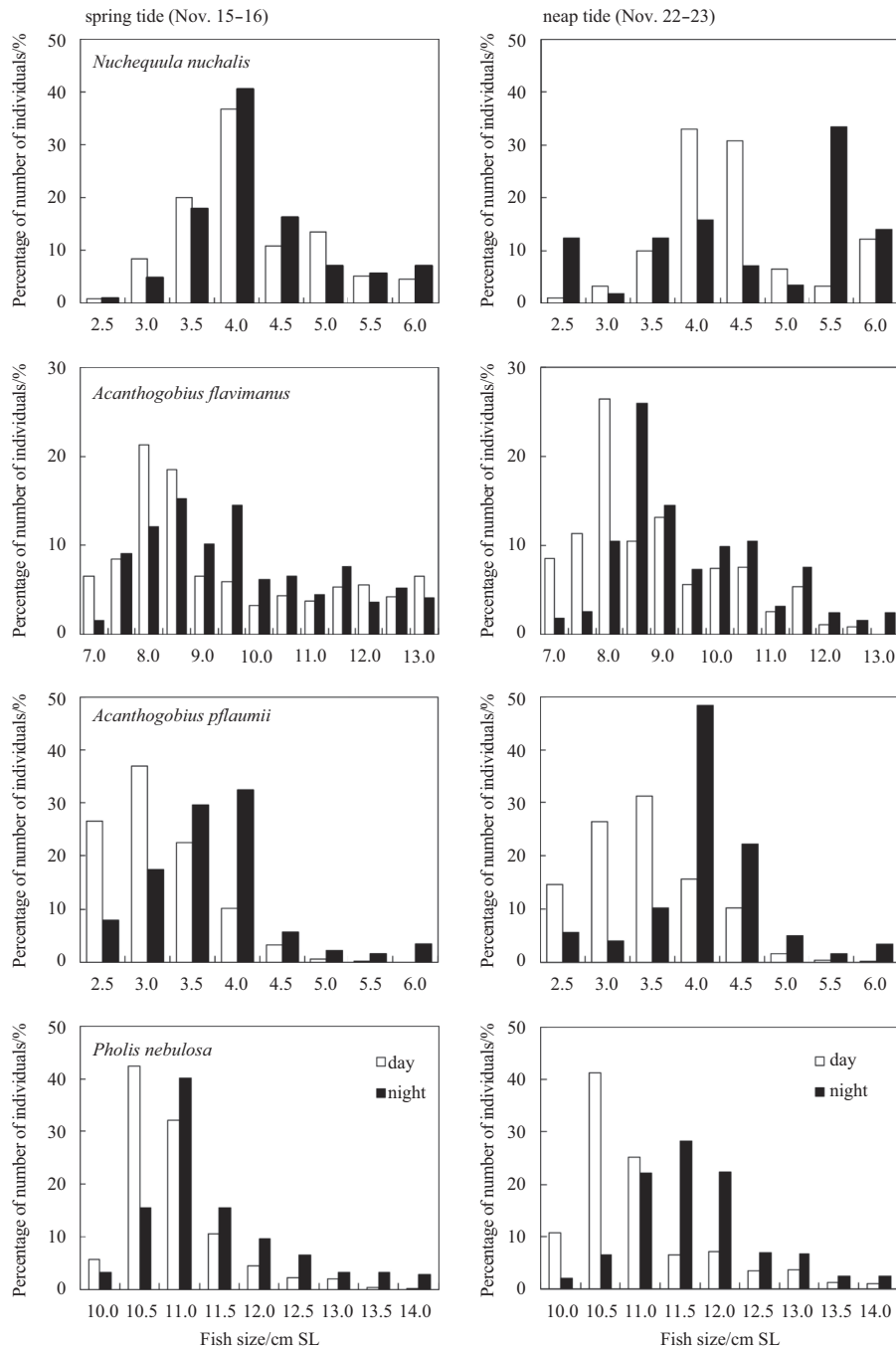


Fig. 5. Size distribution of common fish species collected in an eelgrass bed during the spring tide and neap tides in November 2002.

tidal height (Unsworth et al., 2007). Furthermore, overall abundance of fishes was higher at night than day. Nagelkerken et al. (2002) reported that fish abundance in coastal habitat including seagrass beds was higher at night. Results for seagrass bed fish assemblages in Philippine and Indonesia also supported this (Hemminga and Duarte, 2000; Unsworth et al., 2007). These diel differences in species composition and abundance might relate to diurnal changes in fish behaviors associated with diel variation in light intensity. This can be explained by some form of visual gear avoidance or escapement during trawl survey (Walsh, 1991), because fish can easily escape from the path of the survey vessel before the sampling gear arrived during the day. The day/night differences of prey availability are another possible

factor explaining diel variation of fish abundance in a seagrass bed. In the study area, most of common species mainly preyed on seagrass-associated crustaceans and polychaetes which are abundant in seagrass beds of southern Korean waters (Huh and Kwak, 1997a, b, 1998a, b, 1999). Probably the feeding shift of these fish species toward the small-sized crustaceans at night can be attributed to these prey items becoming more available for predation, as a result of their nocturnal movement from substrate into the water column (Robertson and Howard, 1978; Robertson and Klumpp, 1983). In addition, epiphytic crustaceans have been found to increase in abundance during the nocturnal hours in shallow seagrass habitats (Guest et al., 2003; Unsworth et al., 2007). Other studies have shown similar patterns of

variable food availability in diel variation of fish communities of seagrass beds. For example, movements of the planktivorous *Atherina presbyter* as well as piscivorous *Belone belone* to the intertidal seagrass beds with rising tide at night can be satisfactorily explained by increased food supply (Polte and Asmus, 2006), and higher abundances of common fish species found in mixed meadows of *Cymodocea nodosa* and *Zostera noltii* are explained by seagrass beds at night acting as feeding and spawning grounds (Guidetti and Bussotti, 2000). Hence, we suggest that the day-night differences of food availability are responsible for the diel variation of fish abundance through predator-prey interactions in this eelgrass bed.

Most of the common fish species excluding *N. nuchalis* were recorded at higher numbers at night, and these fish species have also occurred in unvegetated habitat near the eelgrass bed in the study area (Kwak et al., 2006). In contrast, *N. nuchalis* was higher in abundance during daytime of spring tide. Modde and Ross (1981) reported higher abundance of clupeoid fishes during day, because the shoaling behavior of these fishes may allow them to occur in daylight since in this formation they are protected from visual predators, such as adult fish or shore birds. Similarly to clupeoid fishes, *N. nuchalis* aggregates in schools and can occur in high numbers at the daytime of spring tide. There was also a tendency for larger fishes to dominate the catch at night, whereas smaller conspecifics were more abundant at daytime. In the study area, sizes of common fish species were also larger in adjacent unvegetated habitat than eelgrass bed (Kwak et al., 2006). Thus, we concluded that larger individuals of common species migrate from nearby coastal habitat to eelgrass bed at night on a diel basis.

5 Conclusions

This study gives important insights into the short-term changes in species composition and abundance of fish assemblage in relation to diel and tidal cycle in an eelgrass bed of southern Korean waters. Results indicated that fish assemblage structure varied with diel and tidal cycles, and thus these changes are probably due to the movements of common fish species. Such results are essential for understanding fish diversity in seagrass habitats, and are an important baseline for studies on management and conservation efforts of marine coastal habitats in southern Korean waters.

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