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Seasonal variability of community structure and breeding activity in marine phytal harpacticoid copepods on *Ulva pertusa* from Pohang, east coast of Korea

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ABSTRACT

Seasonal changes in community structure and reproductive status of phytal harpacticoid copepods in the shallow sublittoral bottom at two sites (Masan-ri and Guryongpo) in Pohang (Korea) are described monthly over a period of 1 year (October 1996 to September 1997). A total of 36 harpacticoid species was identified and the numerically dominant copepods were made up of the families Porcellidiidae and Tisbidae. Although the number of species did not show a seasonal trend, total harpacticoid density revealed a favorable distribution for the warmer season (spring and summer) at both sites. Multiple linear regression analyses showed that univariate indices such as density, evenness and diversity are closely associated with certain environmental parameters. For example, the dominant species fluctuated seasonally in abundance and their maximum densities were found to be temperature- (+ with *Porcellidium ofunatense*) and nutrient-dependent (+ with *Scutellidium longicauda acheloides*, + with *Zaus unisetosus*, and − with *P. wandoensis*). In addition, the dominant species appeared to breed year round and their reproductive indices are significantly correlated with some environmental parameters such as temperature (−), pH (+), and phosphate (+). Three species (*S. l. acheloides*, *P. wandoensis*, and *P. ofunatense*) showed maximum density two or three months after their reproductive activity reached a maximum. Overall, the seasonal changes in a phytal harpacticoid community could be explained by combinations of environmental parameters supporting the complexity and biodiversity for this specific group of species in coastal ecosystems.

1. Introduction

Research on phytal meiobenthos began in the 1930s with several pioneering taxonomic studies in the Bay of Kiel (Germany) (Fraser, 1936; Otto, 1936; Remane, 1933). The seasonal dynamics of phytal animals have been widely investigated on the macrofaunal population and/or community level (Edgar, 1983; Hagerman, 1966; Kito, 1975; Lewis, 1987). However, relatively little attention has been paid to seasonal variation of the phytal meiobenthos (Gunnill, 1983; Hicks, 1977b; Mukai, 1971). The research on population and reproduction of phytal harpacticoid copepods is mainly limited to a few studies in New Zealand, performed by Hicks (1977a,b,c) in the 1970s, while such a comprehensive study has never been carried out elsewhere until now.

In Korea, the first study on marine harpacticoid copepods ecology was performed by Lee (1972) in Jinhae Bay and then many harpacticoids have been described from a variety of habitats including intertidal flats (Lee, 2007; Song et al., 2003), algae and seagrass (Song et al., 2007a,b), and certain invertebrates (Kim and Kim, 1997, 1998) since the 1990s. However, those earlier studies on harpacticoids in Korea have mainly focused on taxonomic description and/or spatial distribution. So far, a total of 61 harpacticoid species, including 23 new species in Korean waters, has been reported. *Ulva pertusa*, a green alga occurring year round, is distributed in the mid-littoral to shallow sublittoral zone along the coasts of Korea (Kim et al., 1992; Park et al., 1994). Harmful effects of phytal harpacticoids, such as producing gall or boring, have been reported for cultured species of *Undaria* spp. in Korea (Ho and Hong, 1988). However, *U. pertusa* is not being cultured and its associated phytal fauna has never been studied before in Korea. The mass production of macroalgae likely contributes to carbon sequestration and helps to combat against global warming. They are also a promising feedstock for biofuel/biodiesel production (Chisti, 2007; Groom et al., 2008). Thus, ecological studies on phytal animals would be of great significance to Korean marine industry, even globally, in terms of the mass production of macroalgae.

Total density of a community usually depends on the abundance of the dominant species, thus understanding species-specific reproduction

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would be important to interpret the seasonal dynamics of abundance at the community and population levels. Seasonal variations of abundance and reproduction of harpacticoid copepods have been well studied, but are limited to interstitial species (Barnett, 1970; Bodin, 1972; Coull and Vernberg, 1975; Harris, 1972a,b; Huys et al., 1986; Mielke, 1976). Only a few studies have focused on the reproduction of phytal copepods (Gunnill, 1983; Hicks, 1977c). Although harpacticoid copepods are known to be one of the most numerically dominant groups in meiobenthic assemblages, their functional inter-relationships with the biotic and abiotic environments (e.g., competition and environmental parameters) have not been described well (Hicks and Coull, 1983).

Here, we present the first study on phytal harpacticoid copepods on *U. pertusa* in Korea, focusing on the seasonal dynamics of community and population over the course of one year. The objective of this study is to examine the seasonal changes of the marine phytal harpacticoid copepod community in terms of 1) species composition, 2) population density, 3) reproductive activity of dominant species, and 4) the relationships with environmental parameters.

2. Materials and methods

2.1. Site description

The study was conducted at two field sites of shallow sublittoral rocky shore at Pohang (on the east coast of Korea) from October 1996 to September 1997. Unfortunately, sampling in January could not be performed due to a seasonal disappearance of *U. pertusa* in the corresponding month. Masan-ri (MS) is located in the inner bay of Pohang (Yeongil Bay), while Guryongpo (GR) is situated offshore facing the East Sea, and receives a higher wave energy than MS (Fig. 1). The tidal range is low (~0.3 m) in these areas. Sampling locations are situated ~50 m offshore and remain inundated over the complete year (<0.5 m depth). The bottom plate constituted of volcanic rock on which pebbles and sands were sparsely distributed.

2.2. Field sampling

U. pertusa is a dominant and abundant macroalga species which inhabits both sites year round (except for January). Other macroalgae such as *Sargassum thunbergii*, *Codium fragile*, *Chondrus ocellatus*, *Colpomenia sinuosa* and *Chondria crassicaulis* are also present around the study area. Thalli of *U. pertusa* were collected by hand after cutting the frond off the rocky substrata. Four different spots in each site/month were randomly selected with the distance of tens to hundred meters. Macroalgae were harvested into separate bags, but monthly data of species composition were represented by a pooled value of these four replicates. The *Ulva* samples were fixed in a 5% buffered formalin solution and were transported to the laboratory. At both sites, environmental parameters (temperature, salinity and pH) were measured *in situ* during the day of sample collection. Finally, water samples (500 mL) were collected in polyethylene bottles and immediately transported to the laboratory for nutrient analyses.

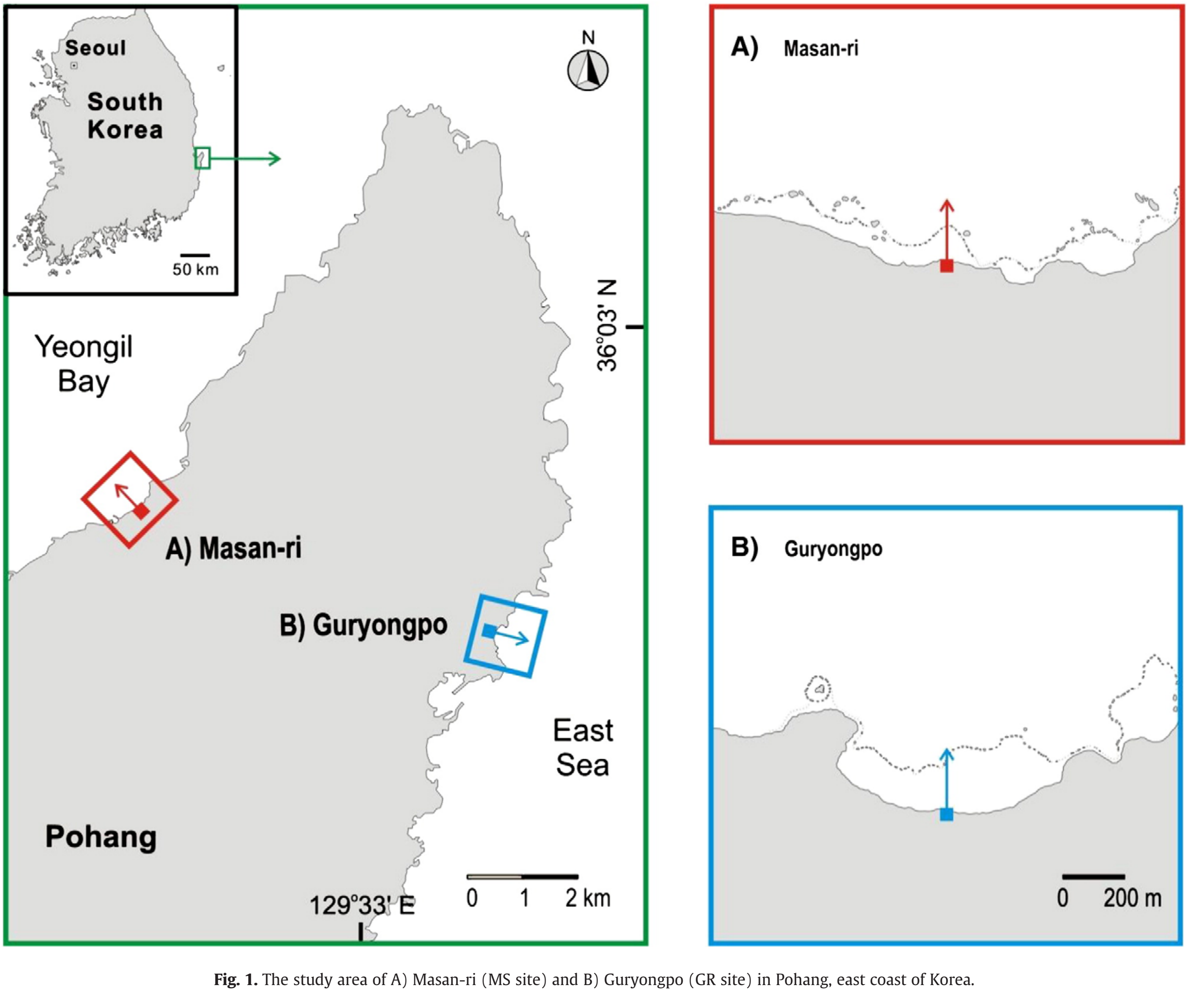

Fig. 1. The study area of A) Masan-ri (MS site) and B) Guryongpo (GR site) in Pohang, east coast of Korea.

2.3. Laboratory analysis

In the laboratory, nutrient analysis and taxonomic identification were performed as follows. Firstly, water samples were filtered through a 0.45 μm pore size membrane and nutrients (ammonia, nitrate, nitrite, phosphate, and silicate) were measured spectrophotometrically according to the method of Parsons et al. (1984). Secondly, *Ulva* samples were rinsed and sorted by sieving (60 μm mesh size). Samples were preserved in a 5–8% buffered formalin solution for further species identification. Phytal harpacticoid copepods were identified at the species level under a dissecting microscope (Olympus BX 50). And there were very few copepods larvae that remained unidentified. These unidentified larvae were included in data analyses (represented as Mis-unids.). Abundance was measured as individuals per unit surface area of *Ulva* (ind. m^{-2}), including adults and larvae. The leaf surface area of *Ulva* was determined from the relationship between leaf area and dry weight based on preliminary measurements of 46 randomly sampled *Ulva* (Area $(cm^2) = 420.7 \times (\text{dry weight (g)}) + 9.5$, $r = 0.91$). The correlation coefficient ($r = 0.91$) showed that area and dry weight of *Ulva* leaf were significantly correlated. An average of 1.3 m^2 of *Ulva* thallus was monthly sampled per site and used for collecting the phytal fauna.

The five most dominant species at the MS site were selected to study seasonal breeding activity. Gender was determined (female-%) and female individuals with eggs were denoted as ovigerous female (Ovigerous female-%). The numbers of eggs and volumes of the egg sacs were counted from randomly selected ovigerous females. Finally, body lengths of males and females were measured. All measurements were performed under a dissecting microscope with a differential interference contrast (×1000).

2.4. Data analysis

Univariate measures and non-metric multidimensional scaling (MDS) were utilized to study the monthly variations of phytal harpacticoid community. Univariate measures included number of species, abundance, Margalef's species richness (d) (Margalef, 1958), Pielou's evenness (J') (Pielou, 1966), Shannon–Wiener diversity (H', natural log) (Shannon and Weaver, 1963), and Simpson's diversity ($1 - \lambda$) (Simpson, 1949). The similarity matrix (data set of 22 samples × 36 species) was calculated using Bray–Curtis coefficient based on the fourth root transformed abundance data, and then two dimensional MDS plotting was performed to show monthly variation of community data. Multiple linear regression analyses were employed to investigate the relationships between univariate measures and abiotic factors. All the abiotic factors and univariate measures used in the regression analysis were natural log transformed. Finally, a BIOENV procedure was adopted to extract the best combination of abiotic factors that account for the monthly variations in community data. Multiple linear regression was also used to study relationships of environmental factors versus density and reproductive indices of dominant species. MDS and BIOENV were analyzed using PRIMER software (Clarke and Gorley, 2006), and regression analysis was performed using the statistical software package SPSS 14.

3. Results

3.1. Environmental analysis

3.1.1. Temperature, salinity, and pH

Both sites, MS and GR, showed a similar temporal pattern of temperature, salinity, and pH in surface seawater over the period of one year. Temperature during winter and spring ranged between 11 and 15 °C at both sites, and almost doubled during summer (mean = 23 °C at MS and 24 °C at GR) (Fig. 2A). The MS site showed a relatively lower and higher temperature (by 1–3 °C each) in winter and summer, respectively. The relatively little variation on year-round temperature found at the GR site would most likely be due to the fact that it opens directly to a large and deep seawater body facing the East Sea.

The salinity at both sites did not change significantly on either monthly or seasonal timeline, and remained relatively constant throughout the year (mean ± SD = 33.8 ± 1.1 ppt at MS and 34.1 ± 1.1 ppt at GR), except for June (31.1 ppt at MS and 31.3 ppt at GR). The lower salinity in June is possibly due to dilution effect as a result of heavy rainfall during the summer season (Fig. 2B). The pH was relatively constant during spring to fall, ranging from 8.0 and 8.9 at both sites, but slightly increased during winter time (8.9–10) (Fig. 2C).

3.1.2. Nutrients

Five nutrients (including ammonia, nitrate, nitrite, phosphate and silicate) from overlying seawater were measured monthly in addition to *in situ* measurements of environmental parameters. All measured nutrients fluctuated on a monthly and/or seasonal basis at both sites, and some showed similar seasonal fluctuation between the two sites. For example, ammonia concentrations at both sites were relatively higher during April–June (1–2 mg L^{-1}) with a sharp peak in May (>10 mg L^{-1}) and lower during the rest of the year (≤0.5 mg L^{-1}) (Fig. 2D). Annual mean concentrations of ammonia at both sites were similar (mean = 1.8 mg L^{-1} at MS and 2.3 mg L^{-1} at GR).

Certain nutrients such as nitrate, nitrite and phosphate showed similar monthly fluctuation except for a distinct period with highly elevated concentrations. For example, nitrate peaked during winter at the MS site and nitrite peaked during spring at the GR site (Fig. 2E–F). It should be noted that nitrite (mean = 0.4 mg L^{-1}) was approximately one order of magnitude lower than other N-related nutrients such as ammonia (mean = 1.8 mg L^{-1}) and nitrate (mean = 3.2 mg L^{-1}) during the complete year (Fig. 2D–F).

Similar to nitrite, phosphate concentrations at both sites were consistently lower over the year except for a peak during spring (>2 mg L^{-1}) at the MS site (Fig. 2G). Among the nutrients measured, silicate showed the greatest month to month variation over the year at both sites. However, there was a clear seasonal trend in which concentrations decreased in approach of the summer season (Fig. 2H). Annual mean concentrations of silicate at both sites were similar (mean = 4.6 mg L^{-1} at MS and 5.3 mg L^{-1} at GR).

3.2. Community analysis

A total of 36 harpacticoid species with 92 964 individuals was collected from the study sites MS and GR during the year-round monthly sampling. The taxonomic description of the harpacticoid species found in this study has been presented in an earlier publication (Song and Yun, 1999) which reported one new species (*Peltidium quinquesetosum*) and sixteen species newly recorded in Korea. Out of the 36 species found during the entire period of this study, 28 species (ca. 80%) were present at both sites, indicating similar species composition between the two sites. The numerically dominant taxa were the families of Porcellidiidae and Tisbidae for both sites. The family Thalestridae was regarded as the most prevalent taxon in terms of number of species, both at the MS (7 species) and GR sites (6 species).

3.2.1. Univariate indices

The number of species found at the MS and GR sites varied between 11 and 20 during the year. No monthly or seasonal trends were observed and number of species appeared to fluctuate in an irregular manner (Fig. 3A). Monthly species numbers between the two sites did not differ greatly from each other, on an annual basis, with a mean of 16.3 species at MS and 14.4 species at GR. However, when looking at the abundance data (Fig. 3B), the GR site had

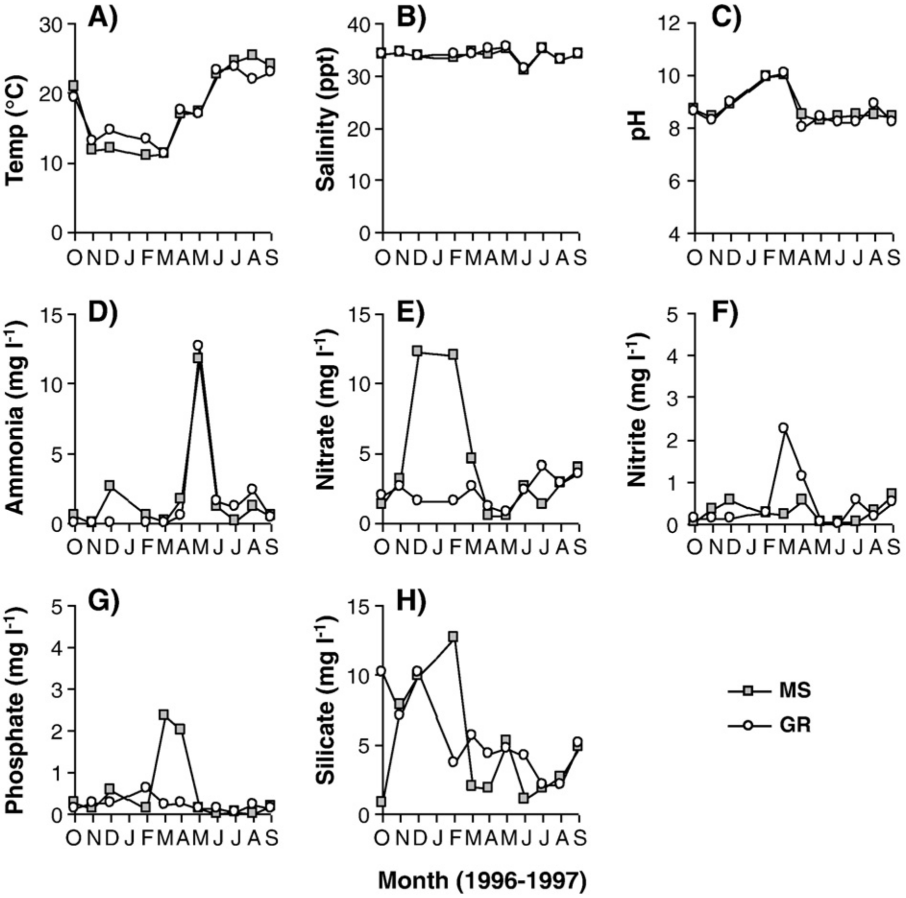

Fig. 2. Seasonal variations of environmental parameters of A) temperature, B) salinity, and C) pH and nutrients of D) ammonia, E) nitrate, F) nitrite, G) phosphate, and H) silicate at MS and GR sites in 1996–97.

significantly higher abundance (4370 ind. m^{-2}) than the MS site (1168 ind. m^{-2}). This was mainly due to the rapid population increase of the most dominant species (*Porcellidium ofunatense*) during summer time (from June to September) at the GR site. Elevated population densities for the species of *Scutellidium longicauda acheloides*, *Porcellidium wandoensis* and *Tisbe celata* were observed at the MS site during early spring to summer. Densities were reduced in approach of the cold season.

Biological indices such as species richness (d), evenness (J'), and diversity (H' and $1-\lambda$) for phytal assemblages were calculated at

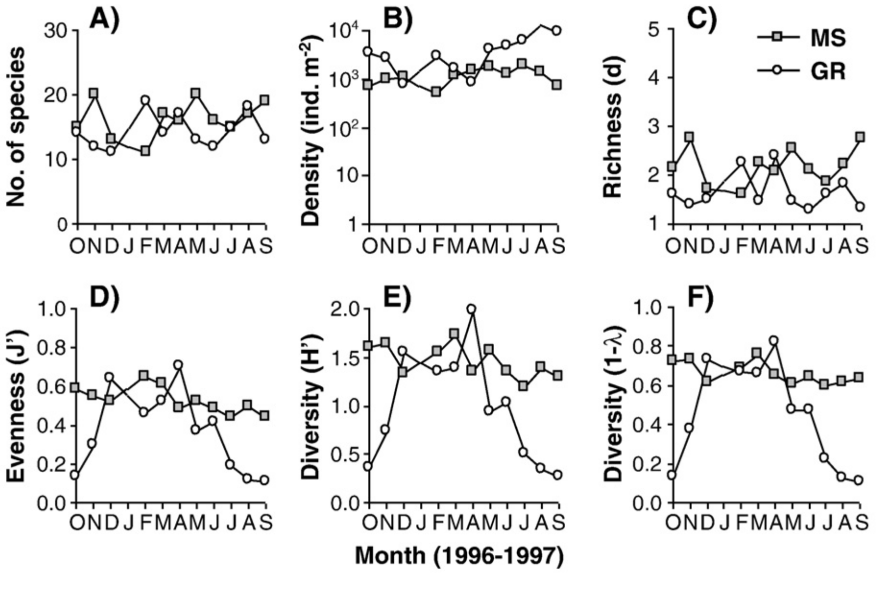

Fig. 3. Seasonal variations of univariate indices of A) number of species, B) abundance, C) Margalef's richness (d), D) Pielou's evenness (J'), E) Shannon–Wiener diversity (H'), and F) Simpson's diversity ($1-\lambda$) indices for the phytal harpacticoid assemblage at MS and GR sites in 1996–97.

both sites and presented herein (Fig. 3C–F). The MS site showed relatively high richness except during the winter season and generally exhibited higher richness values than GR over the entire sampling period. This increased richness is most likely due to a favorable habitat for phytal harpacticoids in the more sheltered area of MS. Furthermore, the MS site did not show great monthly variations on evenness (J'), Shannon–Wiener index (H'), and Simpson's index ($1-\lambda$), indicating more stable or less sensitive harpacticoid assemblages throughout the different seasons (viz. temperature) (Fig. 3D–F). Contrary herewith, those indices showed very clear seasonal variations at the GR site with significantly lower values in summer and fall compared to winter and spring, reflecting a less diverse harpacticoid community at GR during warmer seasons despite the similar number of species. This was due to a rapid increase of certain dominant species during the summer time, particularly *Porcellidium* spp. (e.g., from abundance of <1000 (during December–February) to >10 000 (in August) ind. m^{-2} for *P. ofunatense*).

3.2.2. Species composition and MDS

Monthly species compositions at both sites are presented in Table 1, with the dominant species accounting for >1% to total abundance in each site (see Supplementary material for full monthly records of 36 species). The top five dominant species accounted for 98% and 84% of the total harpacticoid community at the GR site and at the MS site, respectively. This result indicates that those five species could be both dominant and widespread in the Pohang area. However, it should be noted that the most dominant species at the MS and GR sites were different, i.e., *S. l. acheloides* at the MS (41%) and *P. ofunatense* at the GR site (80%), reflecting site-specific differences for the habitat preference of these two species. Other dominant species showed distinct monthly variations in abundance over the period of a year (i.e., some dominated during warm periods and others during the cold season). The peak abundance of the same species at the MS and GR sites was found to be temporally different. However, the seasonal changes in abundance were more likely due to environmental conditions rather than species-specific responses to seasons. Eleven species were found during more than 9 sampling months at the MS site, while only 6 species were identified as frequently occurring species at the GR, supporting the high richness characteristics for the phytal community at the MS site.

The MDS plot revealed that both sites had their own community cyclic pathway over time at least on a seasonal scale (Fig. 4). Both the MS and GR sites did not show clear month to month variation patterns but apparently were grouped together by season, implying similar species composition between the two sites in terms of climate. A total of three distinct seasonal community groups at the GR site could be identified based on the proximity of samples in MDS plot, where those groups (Group-I: GR3–5 and GR12, Group-II: GR6–9, and Group-III: GR10–11) reflected the winter–spring, summer, and autumn season, respectively (ANOSIM global $R = 0.659$, $p = 0.001$). Not clearly grouped for MS data though (ANOSIM global $R = 0.456$, $p = 0.01$), it was reasonable to divide two groups at least by the summer–autumn (Group-I: MS5–9 and 11) and winter–spring season (Group-II: MS12 and 2–4). Interestingly, three MS samples are closely plotted with GR samples of the following two months later (e.g., MS10–GR12, MS12–GR2 and MS2–GR4), implying that MS harpacticoid communities occurred at the GR site after two months during winter to early spring.

3.2.3. Community response to environment

A multiple linear regression was performed to find the environmental factors associated with univariate indices obtained from the harpacticoid community data (Table 2). The number of species and total density from the GR site were significantly correlated with certain nutrients (+/−) and temperature (+), respectively, but those relationships could not be found at MS. Among the environmental parameters measured, temperature (−) was found to be the most significant factor associated with univariate indices, particularly for evenness ($p < 0.01$ at MS and $p < 0.05$ at GR). This resulted from the fact that dramatic decreases of some dominant species were found as the cold season approached at both sites. A positive correlation ($r = 0.67$, $p < 0.05$) between temperature and abundance also supported the above correlations. Furthermore, Bio-Env analysis revealed that the combination of temperature and phosphate ($\rho = 0.50$) was the best match of environmental factors explaining seasonal variation of species composition at GR site, while pH ($\rho = 0.31$) was found to be the most significant parameter at MS (Table 3).

3.3. Population analysis

3.3.1. Abundance of dominant species

The top five co-occurring dominant species explaining more than 80% of relative abundance at both sites (84% at MS and 98% at GR) were examined in greater detail to find population characteristics for each site. Nearly all of these dominant species occurred at both the MS and GR sites over the entire year (Table 1 and Fig. 5). Overall, seasonal variations in abundance for selected species did not differ greatly between sites, but monthly change and the peak in abundance showed relatively great variations. For example, the peak abundance for the top dominant species, *P. ofunatense*, was found in August at GR (11 594 ind. m^{-2}), while MS showed the maximum density in

Table 1

Monthly abundance (ind. m^{-2}), averaging four samples per site, of phytal harparticoids accounting for >1% of total abundance at MS and GR sites.

Species name	1996			1997								Annual	
	Oct	Nov	Dec	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Mean	(%)
Masan-ri (MS)													
Scutellidium longicauda acheloides	201	349	641	252	322	640	1077	667	20	780	351	482	(41)
Porcellidium wandoensis	91	154	59	59	165	132	123	352	677	246	96	196	(17)
Zaus unisetosus	21	8	185	52	422	561	56	13	2	50	3	125	(11)
Porcellidium ofunatense	287	347	114	44	30	15	23	84	77	119	201	122	(10)
Tisbe celata	10	15	10	–	2	1	5	–	959	50	1	96	(8.2)
Porcellidium gamoi	15	60	61	44	119	51	39	107	72	6	3	52	(4.5)
Paradactylopodia koreana	6	26	1	14	21	23	103	5	2	4	1	19	(1.6)
Dactylopodamphiascopsis latifolius	–	15	–	1	1	2	112	7	8	2	3	14	(1.2)
Paralaophonte lacerdai	–	11	2	6	1	5	85	11	20	2	3	13	(1.1)
Alteutha depressa	7	6	9	2	27	15	1	4	4	43	8	11	(1.0)
Guryongpo (GR)													
Porcellidium ofunatense	3117	2039	292	762	702	233	2674	3385	5181	11,594	8544	3502	(80)
Scutellidium longicauda acheloides	95	425	255	1356	600	168	922	250	65	194	399	430	(9.8)
Porcellidium wandoensis	12	–	90	58	91	131	107	591	496	275	39	172	(3.9)
Zaus unisetosus	30	3	2	542	76	107	82	79	17	235	47	111	(2.5)
Porcellidium gamoi	11	149	89	61	61	50	82	327	78	42	5	87	(2.0)

November (347 ind. m^{-2}) (Table 1). The peak in abundance at the two sites was also temperature-independent for the second dominant species of *S. l. acheloides* (Fig. 5B), indicating temperature was not necessarily the factor associated with population dynamics. Some species had more than two distinct peaks in abundance at two different seasons (mostly summer versus winter) over the year. Other environmental parameters could be important for determining temporal distribution of mean abundance in population. Meanwhile, some dominant species such as *P. wandoensis* (Fig. 5C) and *Z. unisetosus* (Fig. 5D) showed the greatest abundances of the two sites within the close time period of months.

Most of these dominant species showed comparable abundances between the sites, on an annual basis, except for *P. ofunatense* that was over 30 times more abundant at GR compared to MS (Table 1), indicating extremely favorable habitat condition for this species at GR (at autumn season even explaining >90% of relative abundance). Except for this species, the order of dominant species (including all 36 species; see Supplementary material) at both sites was found to be quite similar, and their abundances at both sites were also fairly comparable with slope of 1.1 between two sites ($r^2 = 0.96$, $p < 0.01$).

3.3.2. Reproductive activity

To explain the seasonal breeding activity of phytal harpacticoids, the top five dominant species from the MS site were selected. Monthly variations of several reproductive parameters (sex ratio of female, relative abundance of ovigerous females, number of eggs, volume of egg sac, and body length of female) for these species are presented (Fig. 6). There was no direct relation between reproductive activity and an increase or decrease in population abundance. For certain species, however, reproductive indices could explain annual population growth or seasonal variations over the year-round period. For example, the annual mean of four reproductive indices (sex ratio, egg number, egg sac volume, and female body length) for *S. l. acheloides* at MS (Fig. 6B) was found to be the greatest, which would support the highest abundance of this species throughout the year (Table 4 and Figs. 5 and 6).

Some indices such as egg number and egg sac volume explained population growth, either for corresponding (±1 month) and/or forthcoming month(s) or season(s). For example, for the *Z. unisetosus* population, the peak in abundance was found when the ovigerous female, egg number, and egg sac volume reached their greatest values (March–April) (Fig. 6D). Similarly, the population growth of *P. wandoensis* during spring (May to July) could be explained by the rapid recruitment of this species during winter (December to April) (Fig. 6C). Overall, the strong positive relationships between certain reproductive parameter and population abundance highlighted the significant impact of reproduction on harpacticoid population growth.

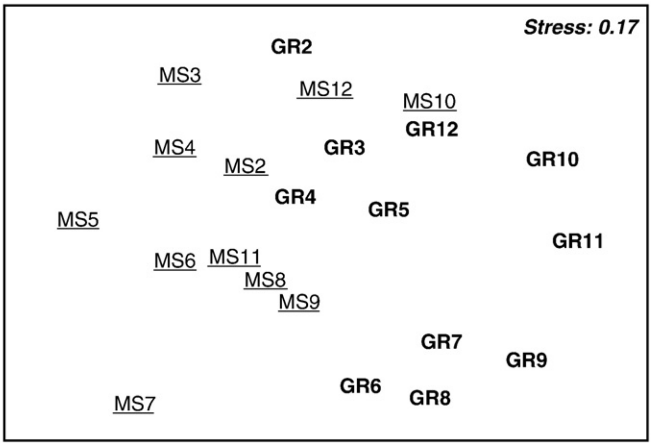

Fig. 4. Ordination of monthly phytal harpacticoid assemblage data by MDS (multidimensional scaling) at MS and GR sites in 1996–97 (numbers denote sampling month).

Table 2
Multiple linear regression analysis showing the relationships between environmental factors and community indices at MS and GR sites (only significant correlations represented).

Community index	Environmental factor	Pearson correlation coefficient (r)	Significant level (p)[a]
Masan-ri (MS)			
Evenness (J')	pH	0.78	**
	Temperature	−0.75	**
Diversity (H')	Temperature	−0.64	*
Guryongpo (GR)			
Species number	SiO_2 (−) + PO_4 (+)	0.81	*
	SiO_2	−0.61	*
Total density	Temperature	0.67	*
Evenness (J)	Temperature	−0.65	*
Diversity (H')	NO_3	−0.61	*

[a] $*p < 0.05$, $**p < 0.01$.

3.3.3. Population response to environment

Population responses to the environment were examined using a multiple linear regression for the top five dominant species found at both sites. Significant relationships between population indices (density and breeding activity) and environmental parameters were found for the most of the dominant species selected for this analysis, except for *P. gamoi* that showed no significant relationships (Table 5). Population abundance was closely related with temperature and certain nutrients, but these significant correlations were not always observed for both sites of MS and GR. In general, the GR population showed a stronger relationship between density and environmental parameters compared to the MS population. Among the five nutrients measured, phosphate was the most commonly observed factor (for 3 species of 5) that was associated with population abundance ($r \geq 0.63$, $p < 0.05$).

Reproductive parameters (MS data only) also showed a close relationship to a single or combined environmental parameters (Table 5). For example, temperature was the most dominant factor associated with breeding activity and this correlation was always negative (−), indicating active reproduction of these dominant species at the MS site during colder season(s). No single reproductive parameter showed a consistent relationship to certain environmental parameter. Overall, the population responses of these dominant taxa to environmental conditions could collectively account for the overall community structure, where a combination of temperature and phosphate were identified as the most prevalent factor for this study area over the course of a year (Tables 2 and 5).

4. Discussion

Seasonal responses of phytal harpacticoid copepods from two study sites have been observed at the community level. The number of species and four ecological indices did not show similar seasonal trends at both sites, but rather reflected site-specific variations. Total

Table 3
Best matches of similarity matrices of harpacticoid assemblage and environmental parameters at MS and GR sites from Bio-Env analysis.

	Weighted Spearman rank correlation coefficient (rho-w)	
	Masan-ri (MS)	Guryongpo (GR)
Best matches	pH (0.306)	Temperature + PO_4 (0.504)

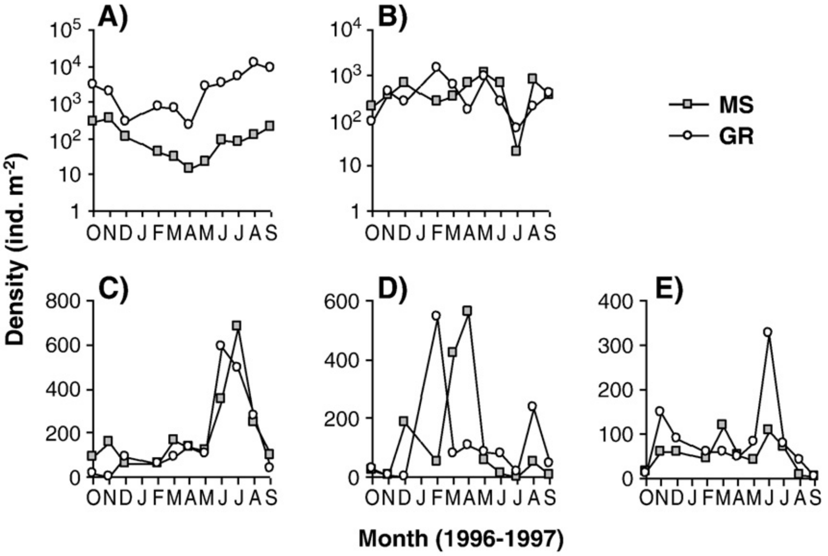

Fig. 5. Abundance of five dominant phytal harpacticoid species of A) *P. ofunatense*, B) *S. I. acheloides*, C) *P. wandoensis*, D) *Z. unisetosus,* and E) *P. gamoi* at MS and GR sites in 1996–97.

density was relatively high during spring and summer periods at both sites, which was mainly due to the rapid increase of certain dominant species. For example, *P. ofunatense*, the most dominant species at the GR site, accounted for >70–90% of the total density peak during the period of July to October. At the MS site, the dominant species such as *S. l. acheloides*, *P. wandoensis*, and *T. celata* collectively accounted for over 60–90% of relative abundance in summer. However, it should be noted that the seasonal variation in abundance of certain dominant species at the two sites were independent of each other. The MS site showed a moderate range and less variation in three ecological indices (J', H' and $1-\lambda$), while the GR assemblage revealed noticeable decreases of certain indices during certain periods (particularly, the warmer season). There was no clear link between ecological indices and environmental parameters except for temperature during this time. The rapid increase of certain dominant species, such as *P. ofunatense*, following a decrease in the abundance of other species at the GR site resulted in fairly low and consistent evenness and diversity indices during the warmer periods of the year. Altogether, the community indices measured in the present study reflected the site-specific seasonal responses of the harpacticoid community (Gunnill, 1983).

The species compositions at the two sites were found to be very similar as shown by the high proportion of co-occurring species (28 of a total of 36 species) present during the year. While two communities showed seasonally different responses, it is apparent that certain dominant species similarly occur at the two sites in a seasonal basis. For example, although the annual mean of total harpacticoid density at the GR site (4370 ind. m^{-2}) was significantly higher than at MS (1168 ind. m^{-2}), the monthly population densities of the top 5 dominant species showed similar temporal variations at two sites (Fig. 5). In particular, for the *P. ofunatense* population, there were great differences between two sites in terms of relative abundance (80% at GR and 10% at MS site), but temporal variations were quite similar. Peak abundances of two species (*P. wandoensis* and *Z. unisetosus*) at the two sites occurred in similar timing. Thus, temperature-dependent population distribution could still be an important characteristic at some point. Overall, the population level responses observed at both sites are not to be site-specific, but to be species-dependent.

Several studies on phytal meiofauna have been published since the 1930s, where copepods were found to be one of the dominant groups of phytal meiofauna (Coull et al., 1983; Hicks, 1986). Only a few studies focused on the phytal copepods of *Ulva* spp. Hicks (1977b) reported densities of three phytal copepods (*Tisbe holothuriae*, *Robertsonia propinqua*, and *Mesochra flava*) on *Enteromorpha intestinalis* from supralittoral pools in Cook Strait (New Zealand), with annual mean densities of 8000, 25 900, and 39 800 ind. m^{-2}, respectively. Later, Coull et al. (1983) found the density of 13 harpacticoid copepods on *Ulva lactuca* ranging from 80 to 101 ind. g^{-1} dw, equivalent to 1701–2148 ind. m^{-2} (using a weight-to-size conversion factor of *U. pertusa* estimated in the present study). Our study found an annual mean density of 4370 ind. m^{-2} at the GR and 1168 ind. m^{-2} at the MS site, and both were comparable to the data reported by Coull et al. (1983). The sublittoral zone is known to have lower population densities of copepods compared to intertidal habitats (Hicks, 1977a; McIntyre, 1969), thus the relatively low density of phytal copepods in subtidal algae sampled in the present study was consistent with previous findings.

Other phytal invertebrates found included gastropods, polychaetes, amphipods, isopods, ostracods and nematodes. Total annual mean density of invertebrates (including copepods) was 3436 ind. m^{-2} and copepods were the most abundant taxon accounting for 81% of relative abundance, followed by amphipods (10%), gastropods (5%), polychaetes (2%), ostracods (1%) and isopods (1%). The high proportion of phytal copepods found in the present study was not surprising and was comparable to previous studies. For example, Mukai (1971) reported that benthic copepods contributed >50% of relative abundance in annual mean and upto >80% at seasonal maximum to the total density of phytal fauna on the brown algae, *Sargassum serratifolium*. A few other studies reported a relatively lower contribution of harpacticoids to total density of phytal meiofauna, but copepods remained one of the dominant taxa (Hagerman, 1966; Hicks, 1977a). Coull et al. (1983) also mentioned that harpacticoids in three species of macroalgae (including *U. lactuca*) comprised only 15% numerically, and that temporary meiofauna (*sensu* McIntyre, 1969), such as gammarids, caprellids and mussels, were found to dominate the phytal meiofauna. Nematodes are known to be one of the dominant taxa in phytal meiofauna (Coull et al., 1983), but occurred with very low densities in our study. Previous studies show that nematods appear to dominate in semi-estuarine sea-grasses with high levels of deposited muddy sediments and/or detritus (Coull et al., 1983). Meanwhile, relatively clean macrophytes in open saline regions are likely dominated by mobile taxa such as copepods, ostracods, and mites (Hicks, 1977a; Kikuchi, 1967). This is likely to be the case in our study and there is also the possibility that the thallus of *U. pertusa* would be too flat and smooth to trap sediments (viz. organic particles) suitable for nematodes.

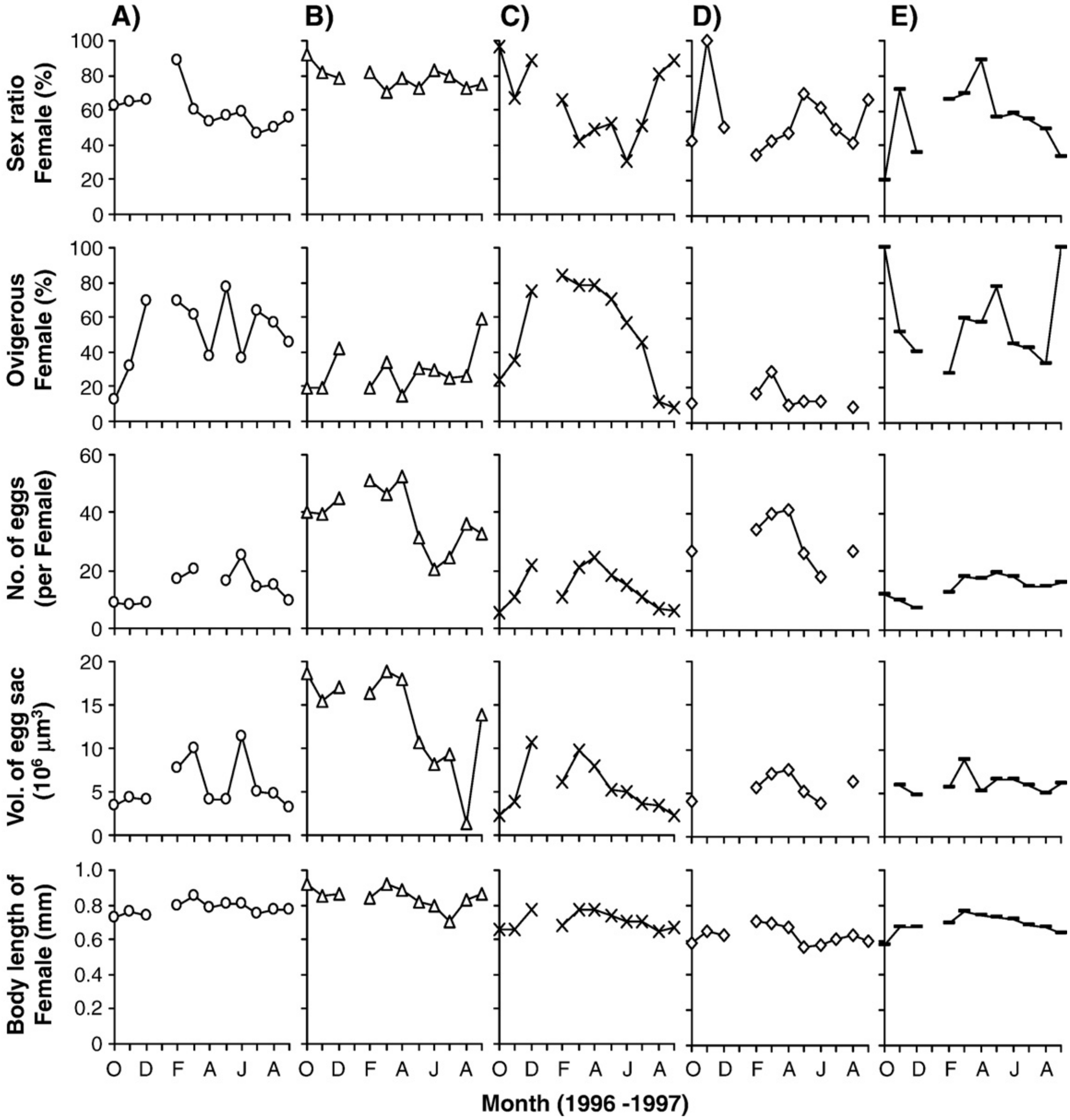

Fig. 6. Reproductive parameters (sex ratio of female, relative abundance of ovigerous female, number of eggs per female, volume of egg sac, and body length of female) of five dominant harpacticoid species: A) *P. ofunatense*, B) *S. I. acheloides*, C) *P. wandoensis*, D) *Z. unisetosus*, and E) *P. gamoi* at MS site in 1996–97.

Altogether, the relatively high dominance of copepods and lack of nematode species on *U. pertusa* seemed to be comparable to previous findings.

Certain morphological characteristics enable phytal harpacticoids to live on algae in considerable densities, often in very turbulent environments. For example, Warwick and Gee (1984) designated copepods to one of eight body forms. Following this classification, the top three dominant taxa (*Porcellidium*, *Scutellidium*, *Zaus*) of the present study belong to the 'scutelliform' body shape (i.e., with dorso-ventral flattened body shape) and also possess 1st endopod which is well-shaped for adhesion to flat algal surfaces. In addition, the genera *Porcellidium* and *Scutellidium* are known to carry a suction apparatus enhancing adhesion to algae (Hicks, 1986). Those morphological characteristics allow the above copepods to withstand the strong water flow over the flat, thalloid surfaces of *U. pertusa*. However, it should be noted that *T. celata* dominated in the MS site in July, and this could not be explained by its general morphological characteristics as this species is 'pyriform' which is less suitable to inhabit on the flattened surface of *Ulva* than 'scutelliform'. This peak in abundance (959 ind. m^{-2}) was likely due to other biological and environmental parameters not analyzed in this study. Considering that *Tisbe* is a scavenger (Hagerman, 1966), there could have been a sudden change in food condition which caused rapid population growth of this species. Overall, the dominance and species composition of phytal harpacticoids found in the present study was fairly well explained by their morphological characteristics.

There was no comparable temporal (monthly and seasonal) pattern in reproductive activity among the five most dominant species at the MS site. However, 5 species showed year-round breeding activity. Several previous studies have reported year-round breeding activity in a phytal environment of temperate seas. Hicks (1977c) reported that phytal harpacticoids found in New Zealand showed either a continuous (year round) or protracted (>6 months) breeding activity, and breeding was not directly correlated with temperature and/or food supply. However, he indicated that the relatively small variation in temperature and the unlimited availability of food are likely related to the continuous breeding activity, which could also support the prevalence of year-round breeding activity at the MS site. A couple of earlier studies also found that the interstitial and epibenthic species dwelling in soft bottoms mainly breed

Table 4
Annual mean of reproductive indices of sex ratio, ovigerous female, number of eggs, volume of egg sac, and body length of female for five dominant phytal harpacticoids at MS site.

Species name	Sex ratio (female %)	Ovigerous female (%)	Number of eggs (per female)	Volume of egg sac (μm^3)	Body length of female (μm)
S. l. acheloides	79 ± 6.3 (5300)[a]	29 ± 13 (4093)	38 ± 10 (66)	13,410 ± 5482 (59)	850 ± 62 (128)
P. wandoensis	65 ± 21 (2184)	52 ± 28 (1257)	14 ± 6.8 (97)	5486 ± 2903 (80)	710 ± 42 (191)
P. ofunatense	60 ± 11 (1341)	51 ± 20 (817)	14 ± 4 (106)	5645 ± 2230 (86)	780 ± 28 (219)
Z. unisetosus	55 ± 18 (1373)	9.3 ± 9.1 (645)	31 ± 6.8 (26)	5672 ± 1488 (24)	630 ± 42 (81)
P. gamoi	55 ± 20 (577)	58 ± 25 (353)	15 ± 3.0 (72)	6002 ± 1156 (52)	690 ± 38 (119)

[a] Number of individuals measured for each reproductive index measure.

intermittently, while phytal species mainly breed continuously (Gunnill, 1983; Hicks, 1979; Hicks and Coull, 1983; Huys et al., 1986). Overall, the present result was consistent with these previous findings but further information on feeding conditions will give a better understanding of reproductive strategies in marine copepods (Niehoff, 2007).

Although temperature was found to be the most prevalent factor influencing breeding activities, the timing of maximum breeding activity of the most dominant species differed from each other. However, relatively great breeding activities (e.g., maximum number of eggs) were always found during early spring (March and April; Fig. 6) and corresponding population densities reached a maximum in and/or after the following month or season. Many meiofauna species are known to have a generation time of ca. one month and at least 2–4 generations occur per year (McIntyre, 1969). Thus, the maximum population density observed after the peak of breeding activity for certain species, e.g., *S. l. acheloides*, *P. wandoensis*, *P. ofunatense*, and *Z. unisetosus*, indicated that reproduction itself contributed to the population growth of these species. However, one to three months of time lag between the peak of breeding activity and abundance does not necessarily represent the period required to develop from egg to adult. Nevertheless, the strong positive relationships between reproductive parameters (egg indices and body length etc.) and population indices (viz. abundance and/or year-round growth) highlighted the significant impact of reproduction on harpacticoid population dynamics.

Table 5
Multiple linear regression analysis showing the relationships of environmental factors versus density (GR and MS) and reproductive indices (MS only) of dominant species.

Biological index	Environmental factor	Pearson correlation coefficient (*r*)	Significance level (*p*)[a]
P. ofunatense			
Density (GR)	Temperature	0.69	*
Female ratio	Temperature	−0.71	*
Body length of male	PO_4 (+) + NO_2 (−) + SiO_2 (+)	0.96	***
	PO_4	0.77	**
	Temperature	−0.62	*
S. l. acheloides			
Density (GR)	PO_4	0.64	*
Number of eggs	Temperature	−0.68	*
P. wandoensis			
Density (GR)	SiO_2	−0.62	*
Ovigerous female	Temperature	−0.64	*
Number of eggs	PO_4	0.63	*
Volume of eggs	Temperature	−0.68	*
Body length of female	PO_4 (+) + NH_4 (+)	0.85	**
	PO_4	0.73	*
Body length of male	Temperature	−0.65	*
Z. unisetosus			
Density (MS)	PO_4	0.79	**
Female ratio	pH (−) + Temp. (−)	0.82	*
	pH	−0.62	*
Body length of female	pH	0.75	**

[a] $^*p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$.

As indicated earlier, the peak in population density for the phytal harpacticoid species observed in this study was temporally different and site-specific. Considering the lack of difference on several environmental parameters at both sites, the dissimilarity for population dynamics at the GR and MS sites might be explained by biological factors. For example, while the density of *S. l. acheloides* decreased dramatically in July at both sites, abundance of *P. wandoensis* reached a maximum at the same time indicating a direct species competition. Alternation of reproductive cycles in these species would aid to reduce competition and allow maximum utilization of resources (Coull and Vernberg, 1975). It is well known that certain co-existing harpacticoids would forage at different spatial levels (Fleeger and Gee, 1986; Hicks, 1977b) or partition to preferable food resources (Arroyo et al., 2007; Pace and Carman, 1996; Vanden Berghe and Bergmans, 1981) in order to minimize competition. Similar community changes within two-month intervals at the GR and MS sites during the winter period would also reflect biological responses among these phytal harpacticoid species.

Throughout Korea and Japan, *U. pertusa* is harvested for food products. Aquaculture of *Ulva* has not been reported yet, although some brown (*Undaria* spp. and *Laminaria* spp.) and red algae (*Porphyra* spp.) have been cultivated for mass production in coastal areas of both countries. In recent years, increasing oil prices have drawn attention to the use of plankton or macroalgae as feedstocks for biofuel (e.g., alcohol) and biodiesel (Chisti, 2007; Groom et al., 2008). Terrestrial crops such as corn and sugarcane would be a good candidate for biofuel, but they are valuable for food products as well. Furthermore, the use of biofuel feedstocks increases prices for grain and other food products (e.g., early 2008). Certain techniques for extracting biodiesel from plankton with high lipid contents have been developed and recently a Korean institute succeeded to refine bioethanol from *U. pertusa* (not published). The remaining issue would be the economic efficiency and technical applicability in using these alternative energy sources (US Department of Energy, 1998). Hence, macroalgae could be a promising energy resource and thus improving the ecological understanding of macroalgae and/or associated phytal invertebrate fauna (e.g., parasites) would be of great value and importance. The present study is the first to report phytal harparticoid copepods on *U. pertusa* in Korea and describes the year-round population and community level responses to environmental parameters in the highly productive environment of a coastal area.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.seares.2009.08.004.

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