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Research Article

Distribution and growth of non-native bryozoan *Pectinatella magnifica* (Leidy, 1851) in four large rivers in South Korea

Eui-Jeong Ko[1], Jeong-Soo Gim[1], Sungwon Hong[1], Hyunbin Jo[2,3], Ji Yoon Kim[4], Masato Hirose[5], Doo Hee Won[6], Hyun-Woo Kim[7] and Gea-Jae Joo[1,*]

[1]*Department of Biological Sciences, Pusan National University, Busan 46241, Republic of Korea*
[2]*Department of Bioscience, Aarhus University, Vejlsøvej 25, 8600 Silkeborg, Denmark*
[3]*Institute of Environmental Technology and Industry, Pusan National University, Busan 46241, Republic of Korea*
[4]*Department of Environmental Science, Toho University, Tokyo 143-8540, Japan*
[5]*Department of Natural History Sciences, Faculty of Science, Hokkaido University, N10 W8, Sapporo 060-0810, Japan*
[6]*Doohee Institute of Ecological Research, Korea Ecosystem Service, Inc., Gwacheon 13814, Republic of Korea*
[7]*Department of Environmental Education, Sunchon National University, Suncheon 57922, Republic of Korea*

Author e-mails: *koui@pusan.ac.kr (EJK), revenant1@naver.com (JSG), nanhsw@pusan.ac.kr (SU), prozeva@hanmail.net (HJ), tapegrass.kim@gmail.com (JYK), m-hirose@sci.hokudai.ac.jp (MH), kes@kes.re.kr (DHW), hwkim@sunchon.ac.kr (HWK), gjjoo@pusan.ac.kr (GJJ)*

**Corresponding author*

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Abstract

Pectinatella magnifica Leidy, 1851 is a non-native freshwater bryozoan species that has successfully established in temperate climate regions in the northern hemisphere. There is an ongoing rapid spread of this species in East Asia, but distribution studies to date have failed to examine the growth characteristics of *P. magnifica*. We surveyed the distribution of *P. magnifica* and its temporal growth at 52 sites in the four major rivers of South Korea. We used artificial substrates in the four rivers to observe their growth. The frequency of occurrence of colonies across all sites was 28.2%. *Pectinatella magnifica* was broadly distributed from meso- to eutrophic conditions. The dominant substrates for colony attachment were submerged dead trees and stones; however, *P. magnifica* showed no specific preference. Colonies were identified from May to June, but these became detached owing to heavy flooding during the monsoon season. Our study identified habitat conditions of *P. magnifica* and provides a guidance for the effective management of introduced freshwater bryozoan species.

Key words: introduced species, freshwater bryozoan, substrate preferences, floods, monsoons

Introduction

Pectinatella magnifica (Leidy, 1851) is a freshwater bryozoan, which is a colonial sessile invertebrate, native to North America. The natural habitat of *P. magnifica* is the shallow riparian zone, where they establish colonies on fixed, shaded, and submerged substrates and occasionally are found in deep-water bodies. Their zooid (=individual) size is about 1 mm (Wood 2009) but colonies can grow up to 2 m (Wang et al. 2017). *Pectinatella magnifica* is spreading rapidly throughout the world. The invasion of *P. magnifica* began in North America, spreading throughout USA, and has since established in Canada (Ricciardi and Reiswig 1994). In Europe, this species was first found in 1883 in Germany (Zimmer 1906). Recent studies show that *P. magnifica* has spread to Austria (Bauer et al. 2010) and Finland (Vuorio et al. 2018). In Asia, proliferation of *P. magnifica* has been reported in Japan (Oda 1974, 1997; Mukai 1998), South Korea (Seo et al. 1998; Jo et al. 2014; Jeong et al. 2015) and China (Wang et al. 2017). Although their introduced range is continually expanding, *P. magnifica* has not yet been found in the southern hemisphere (Balounová et al. 2013).

Introduction and spread of aquatic invertebrates generally occurs with assisted movement by different mediators (i.e., wind, animals, ships; Bilton et al. 2001). Typically, zebra mussels (*Dreissena polymorpha*) spread through ballast-water of ships (Olson 2018). Freshwater bryozoans, including *P. magnifica*, disperse in a similar manner. Further, as their asexual dormant buds (="statoblasts") can withstand harsh conditions (i.e., desiccation, freezing water temperatures, and disturbance), and can easily attach to substrates due to their spined morphology, statoblasts are their general dispersal mechanism. Statoblasts are also buoyant, allowing this sessile invertebrate to spread with water circulation (Rodriguez and Vergon 2002). Waterfowl migration (Bushnell 1973; Hirose and Mawatari 2011) and accidental attachment to fishing equipment (Oda 1997, 1984) and fishing boats (Balounová et al. 2013; Lacourt 1968) can contribute to the dispersal of statoblasts. The order of introduction in East Asia (i.e., Japan–Korea–China) reflects the direction of trade routes from America. Chinese colonies were first discovered in the eastern region in 2005, and this species is currently spreading to the western region through waterways (Wang et al. 2017). Since the spread of *P. magnifica* originating in East Asia is still continuing, focus is needed on the spread of this species in Asia.

In South Korea, *P. magnifica* was first found in lakes and reservoirs where fishes have been imported and released for aquaculture (Seo 1998; NIER 2014). To date, colonies have occasionally been reported in large rivers, but a massive national proliferation of *P. magnifica* was observed in 2014 (Jo et al. 2014). The unfamiliar shape of *P. magnifica* colonies resulted in concerns in the public media, and the occurrence of massive colonies was considered an ecological disaster in aquatic ecosystems (Kang and An 2015). To ease these concerns, basic distribution surveys of *P. magnifica* were carried out in major rivers (Jo et al. 2014; Jeong et al. 2015), but information of their temporal growth and relationships with environmental conditions in rivers (i.e., flooding) has been limited. Further, previous studies have mostly focused on records of distribution and origin of the introduced bryozoan species. The identification of *P. magnifica* colonies is relatively easy. However, as colonies can disappear from, and subsequently recolonize, sites following disturbance, survey results may not always sufficiently reflect the temporal and spatial distributions of *P. magnifica*. It is

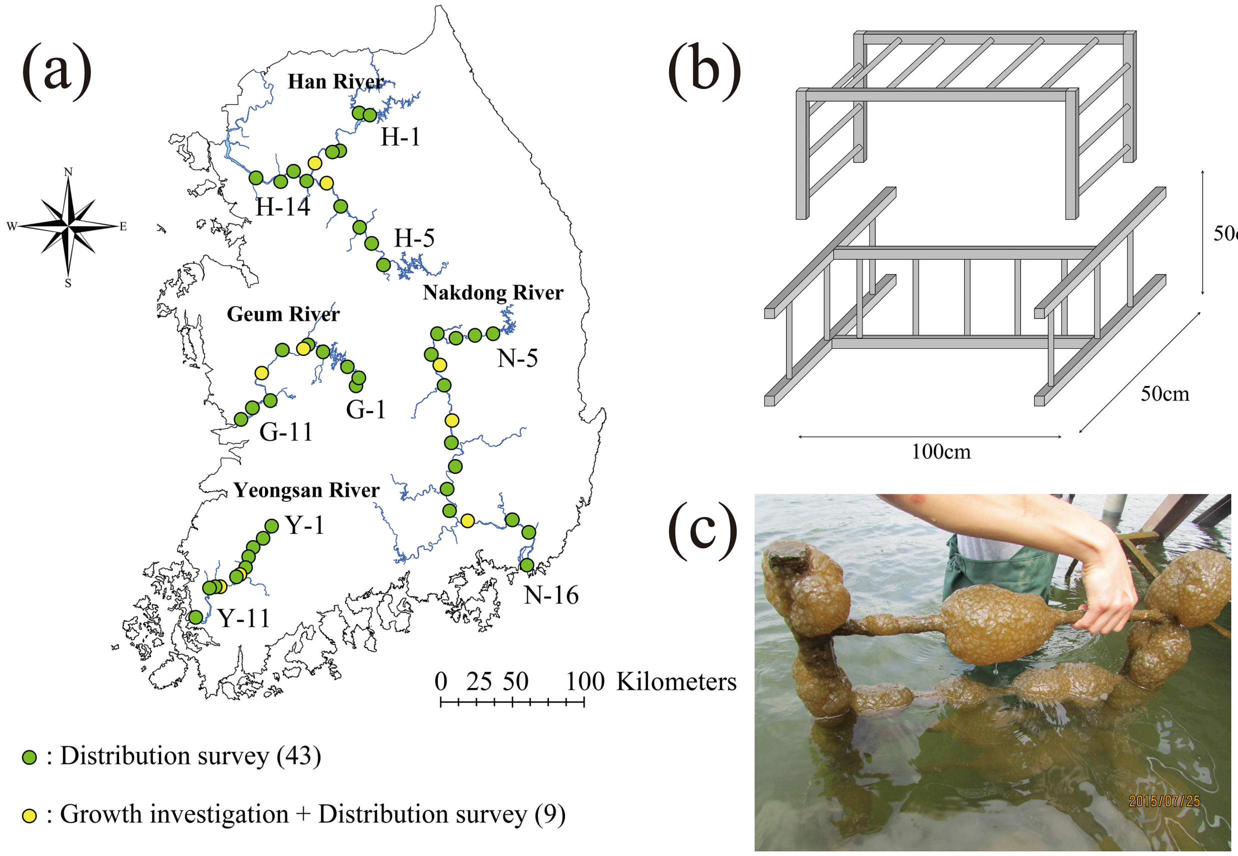

Figure 1. Study sites in four large rivers in South Korea (a). Green points represent sites of the distribution survey, and yellow points are sites with artificial substrate structures (b) to trace the attachment of statoblasts and *Pectinatella magnifica* colony development (c).

also necessary to identify suitable conditions for *P. magnifica* proliferation, as introduced populations may have severe impacts, including fish farm biofouling and clogging of pipe lines (Wang et al. 2017).

The objectives of our study were to; 1) investigate the distribution of *P. magnifica* in four large rivers in South Korea, 2) compare the habitat preference of *P. magnifica* with water quality and substrate composition, and 3) identity the temporal trend of statoblasts and colonies in the field.

Materials and methods

Study sties

South Korea has four major rivers, including the Han (ca. 481 km), Nakdong (521 km), Geum (395 km), and Yeongsan (138 km) rivers (Figure 1a), and belongs to a temperate climate region. The average annual precipitation from the past 30 years is 1,150 mm, of which about 60% is concentrated in June to September (Jeong et al. 2007). This summer monsoon has a strong influence on the condition of aquatic ecosystems in East Asia. To survey *P. magnifica* distribution, a total of 52 sites from the four river channels were investigated (Han River, n = 14; Nakdong River, n = 16; Geum River, n = 11; Yeongsan River, n = 11). We selected sites where water flow was relatively slow and where potential substrate for *P. magnifica* existed (Cooper and Burris 1984). The average distance between survey sites was about 10 km. The geographical coordinates of monitoring sites were recorded using GPS units, and the same points were visited at different sampling times.

Distribution survey

We conducted distribution surveys of *P. magnifica* from 2015 to 2016 (first survey: June 2015; second: October 2015; third: June 2016). From June to August, more than half of the annual precipitation is concentrated in the rainy season of the Korean Peninsula (Jeong et al. 2001). At each site, we walked 100 m along the littoral area and surveyed the occurrence of *P. magnifica*. Previous studies revealed that *P. magnifica* preferred shallow environments of about 0.5 m (Schopt 1969); thus, we searched areas up to 1 m water depths. We recorded the occurrence, colony density, and biomass of *P. magnifica*. Colony density was represented as the number of colonies per 100 m transect (unit: colonies·100 m^{-1}). Determining the biomass of *P. magnifica* in the field was difficult as they are fragile when taken out of water (Joo et al. 1992); therefore, we estimated the biomass of *P. magnifica* using the volume equation for cones. Because colonies of this species accumulate self-secreted gelatinous materials to supplement the scarce substrates, the shape of colony appears as a cone or a combination of two cones. Bryozoan colonies mostly consist of 99% water; therefore, we converted the volume into the biomass by multiplying with the density of water (i.e., 1 g·cm^{-3}). The length and height of colonies were measured in the water. To identify seasonal or regional differences in the number of colonies, and total biomass at the four large rivers, we employed a generalized linear model (GLM) with negative binomial and gamma distribution. We used R version 3.4.3 (R Development Core Team 2018) with an add-on package "lme4" (ver. 1.1.17).

Habitat condition

During the occurrence survey of the bryozoan colony, we recorded the type of substrate that the bryozoan colony was attached to. We categorized the substrate groups into stones, macrophytes, dead trees, artificial substrates (tires, PVC pipes, etc.), and bryozoan colonies detached from substrates (Wood 2009; Choi et al. 2015). The substrate preference of *P. magnifica* was compared with GLM with binomial distribution. We calculated a relative ratio of each substrate (i.e. ranging from 0 to 1) and used this as a response variable of the model. Four water quality variables, including water temperature (°C), dissolved oxygen (DO, mg·L^{-1}, YSI Incorporated, 550A), pH (Thermo Scientific, Orion Star A221), and conductivity (μS·cm^{-1}, YSI Incorporated, 30) were measured in the field using handheld water quality sensors. The difference in water quality between sites where *P. magnifica* was present or absent was compared with the GLM with a gamma distribution. Presence and absence records of *P. magnifica* were used as factor variables in the GLM. Meteorological and hydrological data were collected from an automatic weather monitoring system located close to each survey site (www.nier.go.kr).

Growth experiment using artificial substrate

We performed a growth experiment using artificial substrates to monitor early growth patterns and to trace the growth of individual colonies in the field (Figure 1b). Two forms of artificial substrate were installed at nine monitoring sites where colonies of *P. magnifica* were previously reported (Han River: H-5, H-10; Nakdong River: N-6, N-8, N-13; Geum River: G-6, G-8; Yeongsan River: Y-6, Y-8). The two different artificial substrates, allowing for horizontal and vertical growth, were used to ensure that the direction of the substrate did not affect the species. Artificial substrates were produced with eleven pine timber sticks and connected into a ladder-shaped structure (Figure 1b, c). The artificial structure was place under the water on 4 April 2015, and the colonization of *P. magnifica* was monitored weekly from 10 April to 14 August 2015. Statoblasts were counted weekly from April to the end of May. After growth of the *P. magnifica* colony, it became difficult to distinguish and count individual statoblasts. Several representative colonies were thus tagged based on their relative position on the frame, and their size was continually measured. The total number of statoblasts on the artificial substrate was also counted weekly. During 18 June–3 July and 3 July–25 July, the survey could not be carried out owing to heavy rainfall and flooding.

Results

Distribution of P. magnifica

During the entire survey period, *P. magnifica* colonies were observed at 44 of the 156 sites in the four large rivers (Table 1). The occurrence frequency was highest at Geum River (14 sites (42.4%), 202 colonies), followed by Nakdong (17 sites (35.4%), 117 colonies), and Yeongsan (11 sites (33.3%), 531 colonies) rivers. Han River had the lowest frequency of occurrence frequency (2 sites (4.8%), 53 colonies). The occurrence of *P. magnifica* colonies was higher in spring (June 2015: 40.4%) than in fall (October 2015, 17.3%). However, the occurrence was varied greatly among the years (June 2016: 26.9%). From three surveys in four rivers, a total of 516 colonies were identified and measured (Table 1). Colony density was the highest in June 2015 (χ^2: 55.75, df = 2, p < 0.001), and the density tended to decrease after the monsoon season. The colony density was different among the four rivers (χ^2: 3, df = 113.88, p < 0.001). The density of *P. magnifica* in Han River was lower than that from Geum River (t value = −2.40, p = 0.017).

Table 1. Comparison of occurrence frequency, colony density, and biomass of *Pectinatella magnifica* in different sites and seasons. The density and biomass were presented as average ± standard error.

Site	Season	Occurrence frequency (%), (n)	Average number of colonies (colonies per 100 m) per site	Average total biomass (g) per site
Han River (n = 14)	June 2015	7.1 (1)	1.3 ± 1.3	318.9 ± 318.9
	October 2015	–	–	–
	June 2016	7.1 (1)	2.5 ± 2.5	341.9 ± 341.9
Nakdong River (n = 16)	June 2015	56.3 (9)	5.4 ± 2.9	1099.7 ± 1087.7
	October 2015	18.8 (3)	1.1 ± 0.8	33.1 ± 27.2
	June 2016	31.3 (5)	0.8 ± 0.4	260.1 ± 223.5
Geum River (n = 11)	June 2015	54.6 (6)	12.6 ± 7.5	652.1 ± 403.5
	October 2015	36.4 (4)	0.9 ± 0.5	202.2 ± 170.0
	June 2016	36.4 (4)	3.2 ± 1.8	871.2 ± 647.9
Yeongsan River (n = 11)	June 2015	45.5 (5)	4.4 ± 3.0	725.8 ± 556.1
	October 2015	18.2 (2)	9.4 ± 6.6	1501.4 ± 1501.4
	June 2016	36.4 (4)	1.0 ± 0.5	27.9 ± 20.5
Total		46.1 (24)	5.8 ± 2.2	367.4 ± 48.5

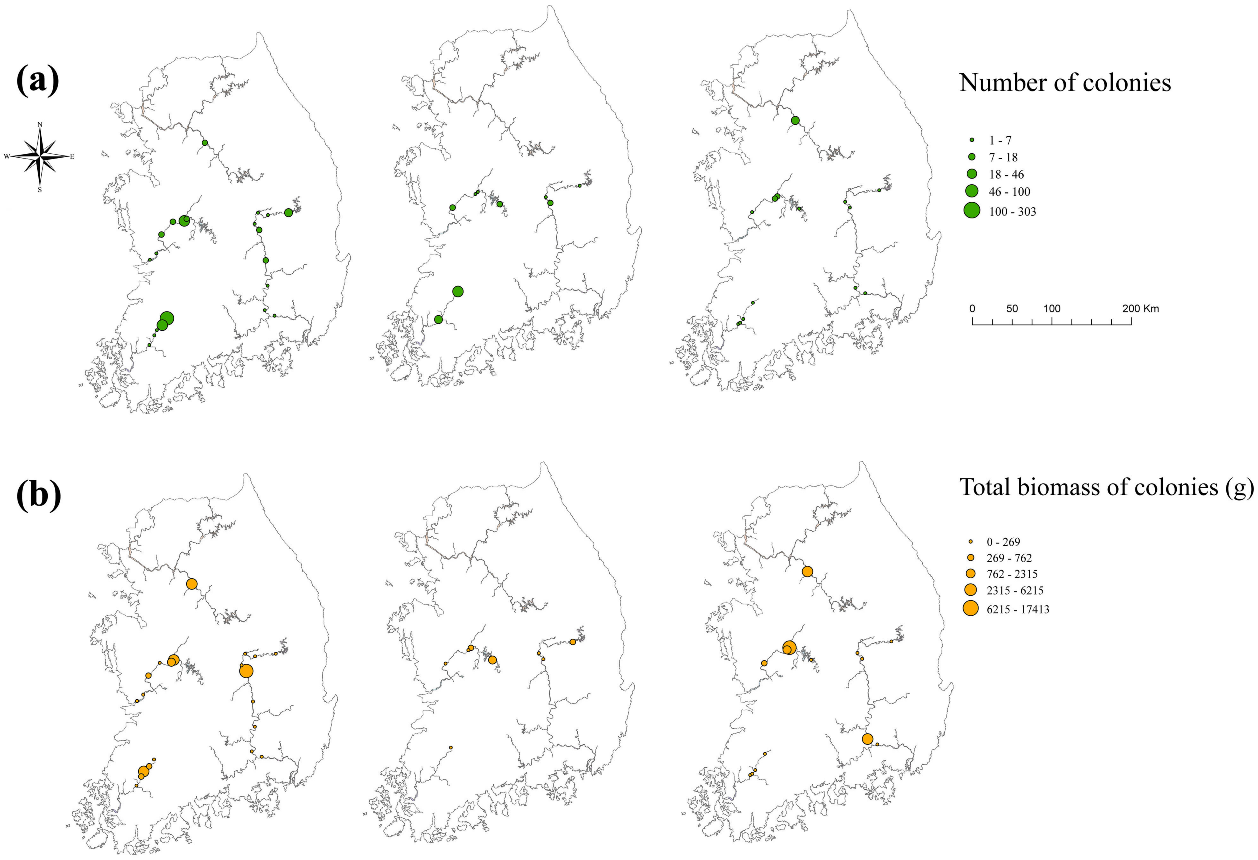

Figure 2. Temporal distribution of *Pectinatella magnifica* in June 2015, in October 2015, and in June 2016. a) number of colonies, b) total biomass of colonies.

The number of colonies decreased after monsoon periods, except for those in the Yeongsan River (Table 1, Figure 2). We identified colonies of *P. magnifica* from the upper to lower parts of the river channel (Figure 2). The biomass of *P. magnifica* showed different seasonal patterns with colony density. The biomass of colonies varied widely, from 0.001 to 17,413.8 g, and showed seasonal differences (χ^2: 29.95, df = 2, p = 0.061). The average biomass was highest during October (t value: −2.45, p = 0.014), but the biomass was not different between June 2015 and June 2016 (t value: −0.507, p = 0.613).

Table 2. Number of occurrences of *Pectinatella magnifica* in the four rivers in South Korea. Numbers in brackets represent the relative percentage (%) from the same periods.

Site	Season	Stone	Artificial substrate	Dead tree	Aquatic plant	Detached colony
Han River	June 2015	–	–	11 (61.1)	7 (38.9)	–
	October 2015	–	–	–	–	–
	June 2015	–	7 (20.0)	2 (5.7)	26 (74.3)	–
Nakdong River	June 2015	66 (76.7)	–	18 (20.9)	2 (2.3)	–
	October 2015	–	12 (85.7)	–	–	2 (14.3)
	June 2015	–	2 (15.4)	4 (30.8)	6 (46.2)	1 (7.7)
Geum River	June 2015	39 (28.1)	12 (8.6)	36 (25.9)	52 (37.4)	–
	October 2015	–	12 (63.2)	1 (5.3)	2 (10.5)	4 (21.1)
	June 2015	30 (85.7)	1 (2.9)	3 (8.6)	–	1 (2.9)
Yeongsan River	June 2015	17 (13.3)	29 (22.7)	–	82 (64.1)	–
	October 2015	–	–	1 (3.0)	32 (97.0)	–
	June 2015	3 (27.3)	–	2 (18.2)	6 (54.5)	–
	total	155 (29.2)	75 (14.1)	78 (14.7)	215 (40.5)	8 (1.5)

Water quality and substrate preference

Water temperature and DO of the surveyed sites showed seasonal differences (water temperature: $\chi^2 = 0.93$, df = 2, $p < 0.001$; DO: $\chi^2 = 0.47$, df = 2, $p = 0.013$; pH: $\chi^2 < 0.01$, df = 2, $p = 0.759$; conductivity: $\chi^2 = 0.59$, df = 2, $p = 0.356$), but we could not identify a difference in water quality between sites where *P. magnifica* was present or absent (water temperature: $\chi^2 < 0.01$, df = 1, $p = 0.546$; DO: $\chi^2 = 0.08$, df = 1, $p = 0.330$; pH: $\chi^2 < 0.01$, df = 1, $p = 0.375$; conductivity: $\chi^2 = 0.37$, df = 1, $p = 0.246$). Colonies of *P. magnifica* were observed in a wide range of water quality conditions (temperature: 16.4–29.2 °C, DO: 4.86–16.45 $mg \cdot L^{-1}$, pH: 7.05–9.93, conductivity: 44–693.4 $\mu S \cdot cm^{-1}$).

Among the five different substrates, the relative percentage of *P. magnifica* attachment was highest on the aquatic plants (40.5%), followed by stone (29.2%), dead trees (14.7%), and artificial substrate (14.1%) (Table 2). *Pectinatella magnifica* as a floating colony was rarely observed in the field (1.5%). There was no strong preference for the different substrates ($\chi^2 = 3.02$, df = 4, $p = 0.553$). However, the proportion of dominant substrates differed among the rivers. Aquatic plants constituted the largest portion in the Han (62.26%) and Yeongsan (69.77%) rivers, while the proportion of stone was highest in the Nakdong (58.41%) and Geum (35.75%) rivers.

Temporal growth of individual colonies

The initial observation of statoblasts on woody artificial substrates was 10 April (12.2 ± 6.59 statoblasts per sites; Figure 3). The number of statoblasts steadily increased on the artificial substrates until the end of May. The number of statoblasts continually increased, even after May, as the newly developed colony also produced new statoblasts; however, it was difficult to separate introduced from recently produced statoblasts. The number of colonies increased rapidly after two months from the increased attachment of statoblasts. A newly developed *P. magnifica* colony was observed on 21 May.

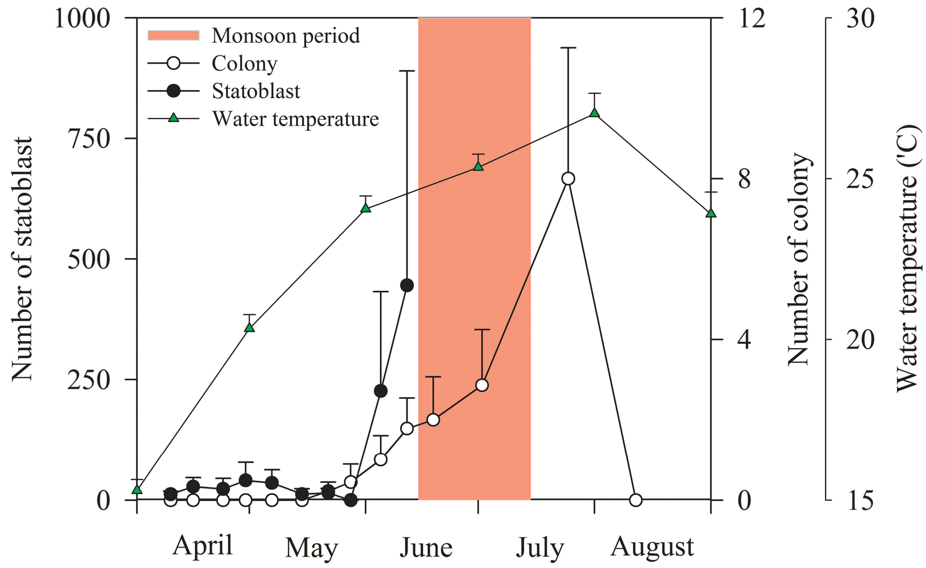

Figure 3. Temporal change of water temperature, colonies, and statoblasts of *Pectinatella magnifica* on artificial substrates from April to August 2015. Statoblasts were counted weekly until the end of May. Each symbol represents the average of each parameter and whiskers represent standard error.

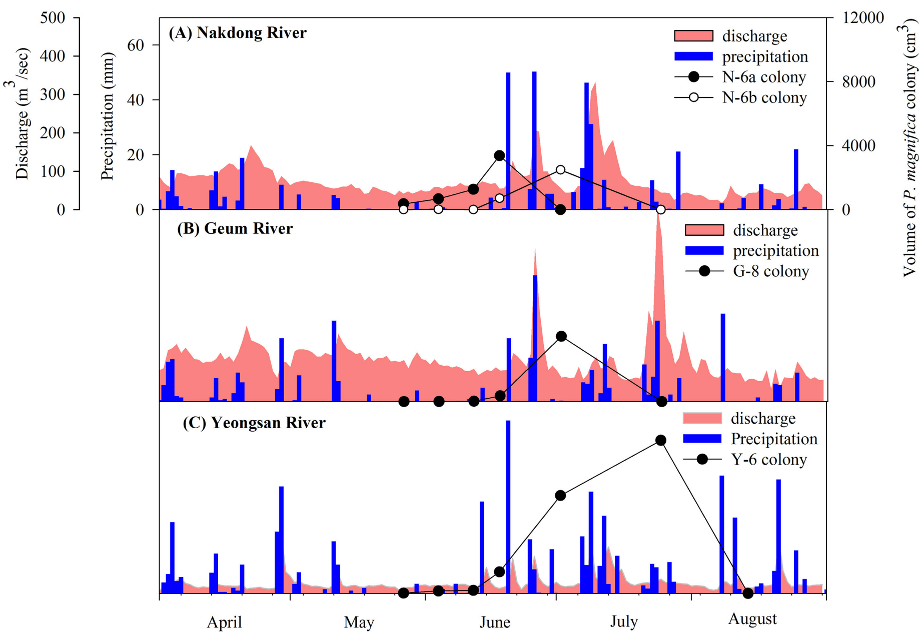

Figure 4. Volumetric changes of *Pectinatella magnifica* colonies during the growing season (April to August 2015).

The rate of increase declined slightly during the monsoon period (June). The number of colonies increased markedly at the end of July. In the middle of August, all *P. magnifica* colonies were detached from the artificial substrate.

The volumetric growth of individual colonies showed similar patterns to changes of colony density (Figure 4). On 27 May, colonies appeared near the artificial substrates in the Nakdong and Yeongsan rivers (N-6b, G-8, and Y-6). N-6a was attached to a dead tree near the artificial substrate. The initial volume of the colonies, observed at the first discovery, was 93 ± 88 cm^3

(n = 4, min = 1, max = 356). The weekly volume growth rate of *P. magnifca* ranged from a minimum of −29% (ND-6b; 25 to 7 cm^3 from June 4 to June 12) to a maximum of 10,034% (ND-6b; 7 to 709 cm^3 from June 12 to June 18). There were two strong floods (dam discharge > 4,000 $m^3 \cdot s^{-1}$) in Nakdong and Geum rivers during the monitoring periods. At the time of the first flood (between June 18 and July 3), the N-6a colony (3,374 cm^3) in the Nakdong River became detached from the substrate and disappeared (Figure 4a). During the second flood (between July 3 and July 25), both N-6b (2,490 cm^3) and G-8 (4,069 cm^3), colonies became detached from the substrate (Figure 4a, b). The final growth volume of these three colonies before detachment was 3,311 ± 457 cm^3. In the Yeongsan River, there were only weak flood events with similar amounts of rainfall during the monitoring periods (Figure 4c). The Y-6 colony, which formed the largest volume before it disappeared, survived the several weak floods, but had disappeared on August 14. The final volume of the Y-6 colony was 9,563 cm^3, which was about 3 times larger than the other monitored colonies at the sites.

Discussion

Proliferation of P. magnifica *in South Korea*

Our results showed a dynamic distribution pattern of *P. magnifica* in different rivers and seasons. Compared with recent distribution surveys of *P. magnifica* in the Nakdong River (Jo et al. 2014), only limited sites showed consistent colony occurrence (3 sites, 30%). New colonies appeared at five sites, which had not previously been colonized during the previous year. Compared with *P. magnifica* colonies in European rivers, the rate of occurrence in South Korea was much higher. The Danube River, which is used as a canal, has an average colony habitat every 250 km (total survey river stretches: 2,500 km; number of colony sites: 10; Zorić et al. 2015). However, our survey results showed colony occurrences every 102 km (total survey river stretches: 4,500 km; number of colony sites: 44). Annual colony and population fluctuations have also been observed in a diversity of freshwater bryozoans (Hill et al. 2007). It was considered that the microhabitat condition in the lotic ecosystem would be different each year when the germination conditions of statoblasts are met, or the recruitment competition with other sessile invertebrates (Sale 1977) could limit further *P. magnifica* growth. In addition, it is also possible that dredging resulted in the germination of dormant statoblasts contained in the sediment (Hill et al. 2007). As a result, abnormal proliferation occurred because of the simultaneous interactions of the external environment and statoblasts that were steadily introduced from the existing habitat.

Many *P. magnifica* studies, including our study, use the number of colonies to represent the distribution of this species (Jo et al. 2014; Zorić et al. 2015). However, as can be seen from the results of the ND-6b colony

(10,034% volumetric growth per week), we have confirmed that adjacent colonies were clustered together. This means that counting the number of colonies is likely to distort the results. Therefore, if we are to quantify *P. magnifica* for distribution, biomass can be a more accurate indicator.

Non-specific preference for water quality and substrate

We confirmed that *P. magnifica* exists in a wide range of water quality conditions. Everitt (1975) reported the preference of *P. magnifica* with slightly lower pH conditions (pH < 7.1), but our results showed that this species can also be distributed in the alkaline conditions (pH: 7.05–9.93). However, eutrophic conditions are considered not suitable for *P. magnifica* growth, because debris deposition on *P. magnifica* lophophores may cause death by limiting filter-feeding activity (Cooper and Burris 1984). Our results showed that *P. magnifica* also survived and grew in high conductivity (max: 693.4 $\mu S \cdot cm^{-1}$). These findings accurately reflect the broad adaptability of *P. magnifica* in diverse aquatic environments. Recent studies of *P. magnifica* comparing water quality between sites with and without colonies (Musil et al. 2018) have shown that oligo-mesotrophic waterbodies are most suitable for growth of *P. magnifica*. The contrasting result with that of the present study may be because of differences in the survey habitats; i.e., lentic (fishponds) versus lotic (rivers) systems. In order to overcome this problem, the factors of *P. magnifica* germination and growth should be tested experimentally.

In the rivers of South Korea, *P. magnifica* mainly grew on aquatic plants or stones, with no specific preference for certain substrates. Jeong et al. (2015) also reported dead twigs, emergent woody plants, and aquatic plants as major substrates for *P. magnifica* attachment in the Nakdong River. Substrate preference was not identified in previous studies (Bushnell 1966; Joo et al. 1992). Any substrate can be used for statoblast attachment and colony growth, but the supporting ability against water flow (i.e., flooding) could be an important factor. Colonies attached to stones were easily detached during flooding. Otherwise, aquatic plants were a good substrate to maintain colonies from monsoon floods. Colonies attached to aquatic plants mostly survived and continued growing, even after floods. The role of aquatic plants for providing microhabitat with complex physical structures for aquatic animals has been widely reported (Walker et al. 2013). The different rates of detachment during flooding events seems to be important in determining the level of proliferation of *P. magnifica* during fall in southeastern Asia, where the influence of monsoons is dominant during summer.

Monsoon flooding affects the growth of P. magnifica

P. magnifica colonies in South Korea were observed from May, and their growth period was similar to that of general freshwater bryozoans (water temperature: 15–28 °C; Wood 2014). There was a temporal lag in the increase of statoblast attachment and colony growth. Statoblasts attached to the substrate during April and May seemed to mainly originate from the previous year's statoblasts, similarly to colonies in Japan (Oda 1959, 1979, 1984, 1990). The increase in the number of statoblasts during the early colony development periods indirectly confirmed the consistent supply of statoblasts from the zooids that initially germinated. Considering that statoblasts start to germinate after 6 days at 20 °C incubation, regardless of the hibernation period (EJ Ko, *unpublished data*), and early colonies originate from overwintered statoblasts (Oda 1984; Mukai 1998), the temperature may be a cue signal for the rapid increase of statoblast attachment during spring. In North America, *P. magnifica* was also observed in the field from September to early January (Joo et al. 1992), further supporting the notion that temperature is the main cue for growth and mortality. For practical management, monitoring temporal variations of statoblasts could be used as a temporal indicator to predict blooms of *P. magnifica* colonies (Wang et al. 2017). Given the dispersal advantages of *P. magnifica*, the influx of propagules is important; however, other factors also affect their germination and growth. Indeed, the presence of colonies could represent the presence of statoblasts, but not the inverse (Jones et al. 2000).

High water temperatures during the summer result in the detachment of *P. magnifica* by accelerating the decay of gelatinous materials, or they may naturally detach from the substrate by the gas generated within the colony (Oda 1997). In East Asia, detachment of *P. magnifica* colonies could be triggered by temperature and also concentrated rainfall and flooding during the monsoon season. From the individual monitoring experiment, we could compare the influence of flooding events on the growth of *P. magnifica* during summer. Severe flooding can physically disturb *P. magnifica* colonies and affect the colony density and growth. Sites in the Yeongsan River experienced relatively weak flooding during the monsoon season, and the final biomass of *P. magnifica* was the highest among the monitored sites. In 2014, delayed monsoons provided sufficient time to grow *P. magnifica* colonies in most of the rivers, and this year recorded one of the largest *P. magnifica* proliferations in South Korea (NIER 2014). In addition to the natural climatic factors, artificial infrastructure (i.e., dams, weirs) can change the flow pattern and affect the growth of aquatic invasive species (Stromberg et al. 2007). In the present study, the Yeongsan River had a similar amount of rainfall during the monsoon season, but its flow was limited owing to reduced discharge from the dam. Therefore, the timing and amount of dam discharge can directly affect the growth of *P. magnifica* in the river channel. The response of *P. magnifica* colonies to different river flow patterns should be further evaluated to efficiently prevent and control the proliferation of bryozoans in regulated river systems.

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References

Balounová Z, Pechoušková E, Rajchard J, Joza V, Šinko J (2013) World-wide distribution of the bryozoan *Pectinatella magnifica* (Leidy 1851). *European Journal of Environmental Sciences* 3: 96–100, https://doi.org/10.14712/23361964.2015.11

Bauer C, Mildner J, Setlíková I (2010) Das Moostierchen *Pectinatella magnifica* in Österreich. *Österrichs Fishereiverband und Bundesamt für Wassewirtschaft* 63: 262–264

Bilton DT, Freeland JR, Okamura B (2001) Dispersal in freshwater invertebrates. *Annual Review of Ecology and Systematics* 32: 159–181, https://doi.org/10.1146/annurev.ecolsys.32.081501.114016

Bushnell JH (1966) Environmental relations of Michigan Ectoprocta, and dynamics of natural populations of *Plumatella repens*. *Ecological Monographs* 36: 95–123, https://doi.org/10.2307/1942151

Bushnell JH (1973) The freshwater Ectoprocta: A zoogeographical discussion. In: Larwood GP (ed), Living and fossil Bryozoa. Academic Press, London & New York, pp 503–521

Choi JY, Joo GJ, Kim SK, Hong DG, Jo H (2015) Importance of substrate material for sustaining the bryozoan *Pectinatella magnifica* following summer rainfall in lotic freshwater ecosystems, South Korea. *Journal of Ecology and Environment* 38: 375–381, https://doi.org/10.5141/ecoenv.2015.039

Cooper CM, Burris JW (1984) Bryozoans—possible indicators of environmental quality in Bear Creek, Mississippi. *Journal of Environmental Quality* 13: 127–130, https://doi.org/10.2134/jeq1984.00472425001300010023x

Everitt B (1975) Fresh-water ectoprocta: distribution and ecology of five species in southeastern Louisiana. *Transactions of the American Microscopical Society* 94: 130–134, https://doi.org/10.2307/3225540

Hill SL, Sayer CD, Hammond PM, Rimmer VK, Davidson T A, Hoare DJ, Burgess A, Okamura B (2007) Are rare species rare or just overlooked? Assessing the distribution of the freshwater bryozoan, *Lophopus crystallinus*. *Biological Conservation* 135: 223–234, https://doi.org/10.1016/j.biocon.2006.10.023

Hirose M, Mawatari SF (2011) Freshwater Bryozoa of Okinawa, Japan, with descriptions of *Rumarcanella* gen. nov. (Phylactolaemata: Plumatellidae) and two new species. *Zootaxa* 2732: 1–19, https://doi.org/10.11646/zootaxa.2732.1.1

Jeong H, Lee KL, Choi BK, Kwon H, Park HK, Joeng GY, Yu JJ (2015) Freshwater habitats of *Pectinatella magnifica* (Leidy, 1581) living in South Korea. *Korean Journal of Environmental Biology* 33: 352–359, https://doi.org/10.11626/kjeb.2015.33.3.352

Jeong KS, Joo GJ, Kim HW, Ha J, Recknagel F (2001) Prediction and elucidation of phytoplankton dynamics in the Nakdong River (Korea) by means of a recurrent artificial neural network. *Ecological Modelling* 146: 115–129, https://doi.org/10.1016/s0304-3800(01)00300-3

Jeong KS, Kim DK, Joo GJ (2007) Delayed influence of dam storage and discharge on the determination of seasonal proliferations of *Microcystis aeruginosa* and *Stephanodiscus hantzschii* in a regulated river system of the lower Nakdong River (South Korea). *Water Research* 41: 1269–1279, https://doi.org/10.1016/j.watres.2006.11.054

Jo H, Joo GJ, Byeon M, Hong DG, Gim JS, Kim JY, Choi JY (2014) Distribution pattern of *Pectinatella magnifica* (Leidy, 1851), an invasive species, in the Geum River and the Nakdong River, South Korea. *Journal of Ecology and Environment* 37: 217–223, https://doi.org/10.5141/ecoenv.2014.026

Jones KE, Marsh TG, Wood TS (2000) Surveying for phylactolaemate bryozoans by sieving lentic. In: Herrera Cubilla A, Jackson JBC (eds), Proceedings of the 11th International Bryozoology Association Conference, Panama: Smithsonian Tropical Research Institute, pp 259–264

Joo GJ, Ward AK, Ward GM (1992) Ecology of *Pectinatella magnifica* (Bryozoa) in an Alabama oxbow lake: colony growth and association with algae. *Journal of the North American Benthological Society* 11: 324–333, https://doi.org/10.2307/1467652

Kang N, An KG (2015) Statoblast ultrastructure and genetic identity of *Pectinatella magnifica* population, based on COI gene, from three different watersheds in Korea. *Animal Cells and Systems* 19: 78–84, https://doi.org/10.1080/19768354.2015.1004370

Lacourt AW (1968) A monograph of the freshwater Bryozoa-Phylactolaemata. *Zoologische Verhandelingen* 93: 1–155

Mukai H (1998) Growth and propagation of colonies of the freshwater bryozoans *Asajirella gelatinosa* and *Pectinatella magnifica* (Phylactolaemata) cultured in the natural habitat. *Science Reports of the Faculty of Education, Gunma University* 46: 47–89

Musil M, Rajchard J, Novotná K, Balounová Z, Ježková E (2018) The relationship between occurrence of invasive bryozoan *Pectinatella magnifica* (Leidy 1851) and parameters of the aquatic environment in the Biosphere Reserve Třeboňsko (Czech Republic). *Wetlands Ecology and Management* 26: 977–983, https://doi.org/10.1007/s11273-018-9624-9

NIER (2014) Studies on distribution of *Pectinatella magnifica* and water environment in the main stream of the Geum River. National Institute of Environmental Research, Incheon, South Korea, pp 1-37

Oda S (1959) Germination of the Statoblasts in Freshwater Bryozoa. *Science reports of the Tokyo Kyoiku Daigaku, Section B* 9: 90–131

Oda S (1974) *Pectinatella magnifica* occurring in Lake Shoji, Japan. *Proceedings of the Japanese Society of Systematic Zoology* 10: 31–39

Oda S (1979) Germination of the statoblasts of *Pectinatella magnifica*, a freshwater bryozoan. In: Larwood GP, Abbott MB (eds), Advances of Bryozoology, Academic Press, London & New York, pp 93–112

Oda S (1984) Hibernation of freshwater bryozoans. *Doubutsu to Shizen* 14: 17–23

Oda S (1990) Life cycle of *Pectinatella magnifica*, a freshwater bryozoan. In: Hoshi M, Yamashita O (eds), Advances in Invertebrate Reproduction, 5, Elsevier Science Publisher B.V. (Biochemical Division), Amsterdam, pp 43–48

Oda S (1997) A transition of the distribution of *Pectinatella magnifica* a freshwater bryozoan in Japan. In: Arakawa S (ed), Professor Sumio Sakagami Memorial Volume. Professor Sumio Sakagami Memorial Volume Press, Tokyo, pp 31–45

Olson J, Robertson JJ, Swannack TM, McMahon RF, Nowlin WH, Schwalb AN (2018) Dispersal of zebra mussels, *Dreissena polymorpha*, downstream of an invaded reservoir. *Aquatic Invasions* 13: 199–209, https://doi.org/10.3391/ai.2018.13.2.02

R Development Core Team (2018) R: A language and environment for statistical computing. https://www.R-project.org/ (accessed 21 March 2018)

Ricciardi A, Reiswig HM (1994) Taxonomy, distribution, and ecology of the freshwater bryozoans (Ectoprocta) of eastern Canada. *Canadian Journal of Zoology* 72: 339–359, https://doi.org/10.1139/z94-048

Rodriguez S, Vergon JP (2002) *Pectinatella magnifica* Leidy 1851 (Phylactolaemates), un bryozoaire introduit dans le nord Franche-Comte. *Bulletin francais de la Peche et de la Pisciculture* 365–366: 281–296, https://doi.org/10.1051/kmae:2002036

Sale PF (1977) Maintenance of high diversity in coral reef fish communities. *The American Naturalist* 111: 337–359, https://doi.org/10.1086/283164

Schopt TJ (1969) Paleoecology of ectoprocts (bryozoans). *Journal of Paleontology* 43: 234–244

Seo JE (1998) Taxonomy of the freshwater bryozoans from Korea. *The Korean Society of Systematic Zoology* 14: 371–381

Stromberg JC, Lite SJ, Marler R, Paradzick C, Shafroth PB, Shorrock D, White JM, White MS (2007) Altered stream-flow regimes and invasive plant species: the *Tamarix* case. *Global Ecology and Biogeography* 16: 381–393, https://doi.org/10.1111/j.1466-8238.2007.00297.x

Vuorio K, Kanninen A, Mitikka S, Sarkkinen M, Hamalainen H (2018) Invasion of Finnish inland waters by the alien moss animal *Pectinatella magnifica* Leidy, 1851 and associated potential risk. *Management of Biological Invasions* 9: 1–10, https://doi.org/10.3391/mbi.2018.9.1.01

Walker PD, Wijnhoven S, van der Velde G (2013) Macrophyte presence and growth form influence macroinvertebrate community structure. *Aquatic Botany* 104: 80–87, https://doi.org/10.1016/j.aquabot.2012.09.003

Wang B, Wang H, Cui Y (2017) *Pectinatella magnifica* (Leidy, 1851) (Bryozoa, Phylactolaemata), a biofouling bryozoan recently introduced to China. *Chinese Journal of Oceanology and Limnology* 35: 815–820, https://doi.org/10.1007/s00343-017-6052-2

Wood TS (2009) Bryozoans. In: Thorp JH, Covich AP (eds), Ecology and classification of North American freshwater invertebrates. Academic Press, San Diego, California, USA, pp 437–454, https://doi.org/10.1016/b978-0-12-374855-3.00013-3

Wood TS (2014) Phyla Ectoprocta and Entoprocta (Bryozoans). In: Thorp J, Rogers DC (eds), Thorp and Covich's freshwater invertebrates: ecology and general biology. Elsevier, Amsterdam, Netherlands, pp 327–345, https://doi.org/10.1016/b978-0-12-385026-3.00016-4

Zimmer C (1906) *Pectinatella magnifica* (Leidy) in der Oder. *Zoologischer Anzeiger* 29: 427–428

Zorić K, Szekeres J, Csányi B, Kolarević S, Marković V, Paunović M (2015) Distribution of the non-native bryozoan *Pectinatella magnifica* (Leidy, 1851) in the Danube River. *Acta Zoologica Bulgarica* 67: 241–247