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Microphytobenthos of Korean tidal flats: A review and analysis on floral distribution and tidal dynamics

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ABSTRACT

The present article presents a historical overview and key findings in the studies of microphytobenthos (MPBs) in Korea, supporting a biodiversity of the Korean tidal flats. The common internationally recognized topics relating to the tidal flat MPBs were found to be assemblages, dynamics, production, and food web etc. in chronological manner. Accordingly the review on the Korean MPBs studies was provided in the given topics, highlighting pros and cons of individual scientific efforts and data. Especially, the brief summary from the several representative works (selected based on citations) related with the corresponding topics were provided as for comparison, if applicable. The world studies of tidal flat MPBs over the past 100 years generally reflected the subjects being balanced followed by logical development of each topic. Although over 50 years of scientific gap between Korea and the European countries were evidenced historically, a rapid scientific advancement in recent 10 years would be noteworthy. A topic of floral assemblages was found to be steady issue in Korea, with documented MPBs of >400 species (ca. 10 new species) from the Korean tidal flats. As part of review, we reanalyzed our selected data from the previous and current MPBs works encompassing above 4 topics, where our key ecological findings were highlighted. Finally, future research direction was carefully discussed by comparative analysis between worldwide versus Korean studies in various aspects. Overall, the future MPBs studies in Korea would be promising to support unique biogeography in Asian tidal flats, yet with certain limitation in scientific recognition and/or methodological weakness.

1. Introduction

The Korean tidal flats as a pacific mirror of the European Wadden Sea would provide valuable ecosystem services including the supporting of primary production, such by group of the marine algae. In particular, the microphytobenthos (MPBs), namely benthic diatoms, inhabiting in the intertidal zone of shallow water system would be much ecologically important for a pelagic ecosystem as providing valuable food sources when resuspended. With many reasons including the ecological contribution by the MPBs, such through a benthic-pelagic coupling, they have long been one of the extensively studied taxonomic groups in tidal flat environments, totaling ca. 900 publications during the past 30 years (Fig. 1).

In fact, studies on the MPBs date back to the late 19th century (Fig. 2), with notable pioneering works, mainly assemblage studies though, e.g., the monumental works of Schmidt et al. (1874–1959) and Cleve (1894, 1895). Also, the work of Herdman (1921) would represent one of the first several ecological studies relating to the dynamics of MPBs on tidal flats, where a vertical migration of MPBs was documented by the phenomenon of “discoloration” of littoral sediments (Fig. 3). Such phenomenon was also intensively discussed in the work of Aleem (1950), by analyzing the daily periodicity of diatom community with various effects by light intensity, tidal conditions, and temperature etc. The very study would be of ecological significance in the following MPBs studies after the 1950s because the several key parameters influencing the MPBs production were first highlighted. With such representative works on the MPBs towards the understanding of the fundamentals in structure, the scientific concerns seemed to move demonstrating the ecological function, such as the topic of production since 1950s (Fig. 4) and later the food web study of MPBs since 1980s (Fig. 5).

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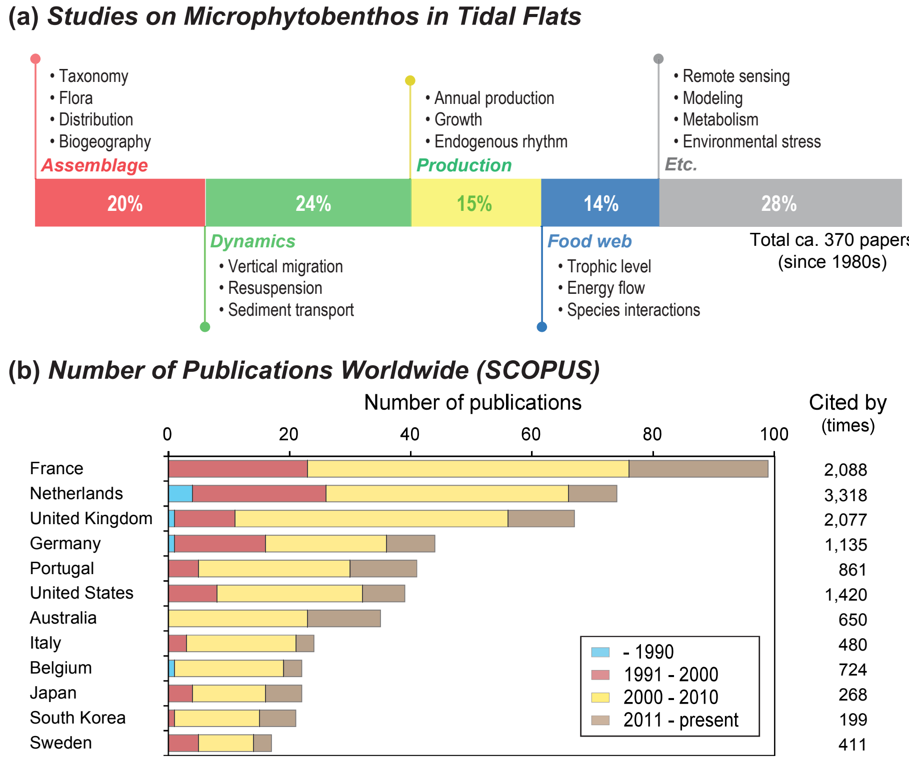

Fig. 1. Overview of studies on microphytobenthos in tidal flats, under four major topics of assemblage, dynamics, production, and food web etc., with (a) relative study efforts (%) in each category and (b) publication efforts (number of papers and citations) in top 10 ranked countries during the past 40 years, based on the literature survey (Scopus).

More recently, de Jonge et al. (2012) highlighted the possible impact of climate change on inter-annual response of MPBs biomass with accumulated MPBs data over long period of ca. 25 years (1976–99).

Meantime the ecological studies for the Korean tidal flat organisms have not been documented internationally until the late 1980s (Table 1). For example, the study of benthic macrofauna in the Gyeonggi Bay tidal flats was first reported in 1988 (Koh and Shin, 1988) and later introduced about the MPBs in the Saemangeum tidal flats (Oh and Koh, 1995). However, those early works seem to have certain technical limitation, i.e., many of the identified species during this time would have been uncritically treated as conspecific ones in Europe and/or America. Such misidentifications of the Korean species would have come from the failure to validate the appropriateness of adopting the European and/or North American taxa (Park et al., 2012a). In anyhow, more than 30 studies relating to the Korean MPBs have been reported since the first report in 1984 (Shim and Cho, 1984; in Korean), with a total of >400 species reported until now.

Based on the analysis of scientific publications on tidal flat MPBs during the past 30 years (Fig. 1a), the frequently studied topics were found to be; i) assemblages (20%), ii) dynamics (24%), iii) production (15%), iv) food web (14%), and v) other collective minor topics (28%) including remote sensing study, worldwide. While, majority of those studies have been conducted in the European countries (top five accounting for >60%), with over 200 years of scientific history, it would be noteworthy that some Asian countries including South Korea also showed relatively great scientific efforts (Fig. 1b). Although we have relatively short scientific history in tidal flat ecology compared to European countries, a growing concern on the biodiversity of tidal flat organisms including MPBs in Korea certainly dedicated a better understanding of our ecosystem of "*Getbol*", namely the Korean tidal flat (Koh and Khim, 2014).

In the present study, we aimed to present the current status of the MPBs study in the Korean tidal flats, with a brief review under several topics relating to the MPBs works worldwide. As for a comparative analysis and tracking to the scientific history of the world MPBs studies, the key findings from the series of our recent studies (Figs. 2–5), mainly after 2000s, were collectively given in the subjected topics. The four major topics highlighted in the present review were i) floral assemblages, ii) tidal dynamics, iii) primary production, and finally iv) food-web etc. of tidal flat MPBs.

2. Floral assemblages

As mentioned earlier, the European scientists pioneered the assemblages of tidal flat MPBs by contributing several atlases since late 19th century, which became to be a bible in flora studies of MPBs thereafter (Schmidt et al., 1874–1959; Cleve, 1894, 1895). In the middle of 1900s, couple of monumental works were delivered by Aleem (1950) and Brockmann (1950), highlighting mudflat diatoms in the European tidal flats. Later Amspoker (1977) first documented the assemblages of sand flat diatoms, and more recently Witkowski et al. (2000) compiled over one thousands of coastal and littoral diatom taxa, representing 130 genera from various geographic regions, being the most comprehensive reference of marine benthic diatoms at this point of time.

A Russian diatomist pioneered the study of marine diatoms in Korea, producing a report of 67 diatom taxa listed, though the majority of reported species were planktonic and only a few for benthic (Skvortzow, 1931). One year later, he also reported the diatom assemblages of the bottom sediments in the Yellow Sea and the East Sea, recording total of 83 taxa (Skvortzow, 1932). It was in 1980s when actual scientific efforts by the Korean scientists on the assemblages of MPBs began, almost 100 years of delay compared to Europe, upon the recognition of the significance of the Korean tidal flat ecosystem (Koh and Khim, 2014).

Fig. 2. Brief summary for the key findings of the representative works under the topic of floral assemblages of microphytobenthos (MPBs); as part of present study, the atlas of a biogeography of Asian tidal flat MPBs collected.

Similar to the historical concerns shown in Europe, the subject of assemblages has been received a large attention to Korean scientists compared to other topics, at the beginning state of MPBs studies in Korea (Table 1). The diatom assemblages of the Korean tidal flats were first investigated by Shim and Cho (1984), who reported 95 species and two varieties in Incheon, Gyeonggi Bay with *Paralia sulcata* and *Navicula gracilis* as dominant species. Next, Kim and Cho (1985) documented benthic diatoms in the Geum River Estuary, reporting total of 153 taxa with *Paralia sulcata* and *Cymatosira belgica* as dominant species. This work would be the first ecological work relating to the MPBs in Korea, as they investigated the seasonal changes in MPBs biomass in relation to compositional changes in sedimentary nutrients.

The study of Choi and Noh (1987) would be noteworthy in that Scanning Electron Microscopy (SEM) was first applied to identify Korean MPBs, although limited taxa were reported. Cho and Kim (1988a) reported 36 benthic diatoms belonging to three suborders of Coscinodiscineae, Auliscineae, and Biddulphineae in Korean coastal sediments, which would be one representative work in terms of first documentation of centric diatoms in Korea. Lee and Lee (1988) further improved the technical quality by combining Light Microscopy (LM) and SEM observations, by reporting six *Cyclotella* species of phytoplankton diatoms in Korean waters from wide range of locations including rivers, islands, and open bays. In the 1990s, Choi (1990) finally compiled all existing floristic reports to produce the first checklist of Korean marine benthic diatoms totaling 375 diatom taxa, with informative inclusion of local occurrence of each taxon.

However, it should be noted that those early studies conducted at the beginning stage of MPBs assemblage study has shown several limitations in technical manner. First, the diatom nomenclature and flora established in Europe and North America had been adopted and directly applied to the identification of Korean taxa without validating the applicability of the system, which means that the uncertainty in species identification might exist. For example, the species which had been identified as '*Berkeleya scopulroum*' in Korea was not identical to the original species but actually a different species of the genus *Climaconeis* (Park et al., 2007). Park et al. (2012a) has also demonstrated that many of MPBs diatoms were misidentified without conferring relevant literatures.

Second, the amount of comparative literature available at the time when these studies conducted would have been far limited, which also brought possible misidentification, if any. Such lack of diatom literatures could be further evidenced with the fact that, for

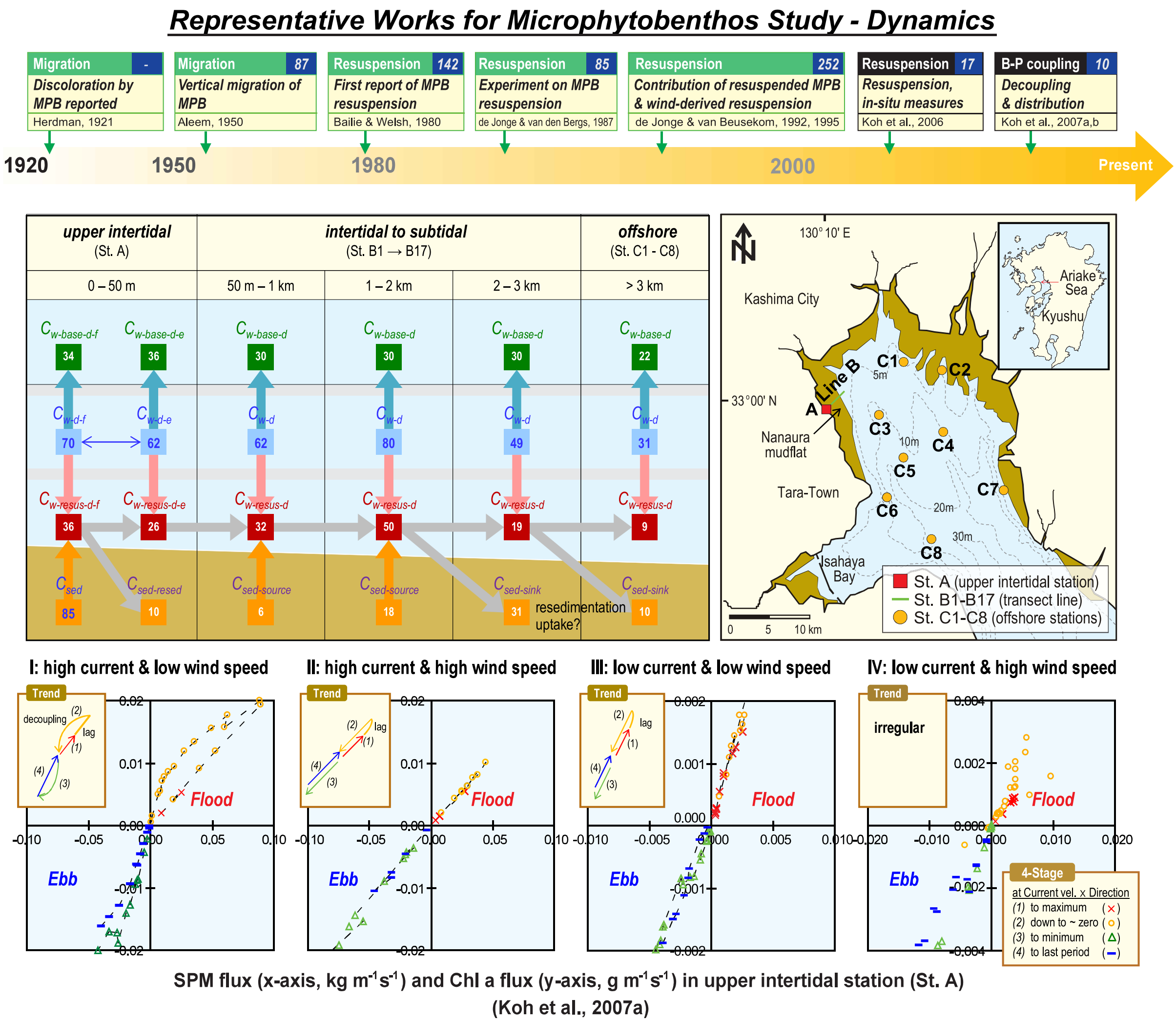

Fig. 3. Brief summary for the key findings of the representative works under the topic of tidal dynamics of microphytobenthos (MPBs); as part of present study, the schematic diagram of MPBs (Chl *a*) biomass in the intertidal area to offshore suggested and relationship between Chl *a* and SPM fluxes revisited.

the identification of MPBs diatoms, only about ten literatures have been referred in early study of Kim and Cho (1985) while about thirty referenced in Park et al. (2012a). Finally, all of the above studies were published in local journals, which resulted in a limited access to the international audience. This fact may not be necessarily critical in terms of warranting the quality of scientific work but cross-checking should be limited following potentially masking point in overall data quality.

Second phase of the Korean MPBs began in the 1990s, as the study has been far improved into the international standard quality and the subject has been extended to generally cover the topic of tidal flat ecology within the topic of MPBs1990s. For example, Oh and Koh (1995) have successfully explained the MPBs floristic characteristics against bottom sediment facies in the typical tidal flats of the Mangyeong–Dongjin River Estuary, which no longer exists due to the dike construction (completed in 2006) by the Saemangeum reclamation project (Ryu et al., 2014). Specifically, this study involved extensive sampling effort (60 locations spanning a wide range of tidal levels and sediment facies), resulting in a high number of recorded species ($n = 371$) with dominance of *Achnanthes hauckiana*, *Paralia sulcata*, and *Amphora cofeaeformis* in the order. However, 137 of reported taxa (representing over one-third of the observed species) were only identified to the genus level, thus still remained the lack of identification certainty. The unidentified taxa mainly belonged to the genera *Amphora*, *Cocconeis*, *Navicula*, and *Nitzschia*.

It was not until the late 2000s that further taxonomic progress achieved in Korea, other than simple floristic studies. For example, Park et al. (2007) made unprecedented SEM observations of *Surirella voigtii* Skvortzow, resulting in this species being transferred into the genus *Petrodictyon* under a new nomenclature of *Petrodictyon voigtii* Park & Koh. In addition, the observation of a presumably a new species of *Climaconeis* was also made. Although the authors only investigated these two diatom species, their work supported the likelihood that marine benthic diatoms in Korea exhibit a possible high biodiversity. Indeed, subsequent work has successfully shown that the diatom assemblages in the Korean tidal flats are unique because they contain many new and rarely reported diatom taxa. Park et al. (2012b) reported a new naviculoid genus viz. *Moreneis* Park, Koh & Witkowski in Korean sandflats, introducing four new species to science. Further, more recently four new species belonging to the genus *Fogedia* Witkowski, Lange-Bertalot, Metzeltin & Bafana were identified and described in the Korean sand flats (Park et al., 2013a), highlighting

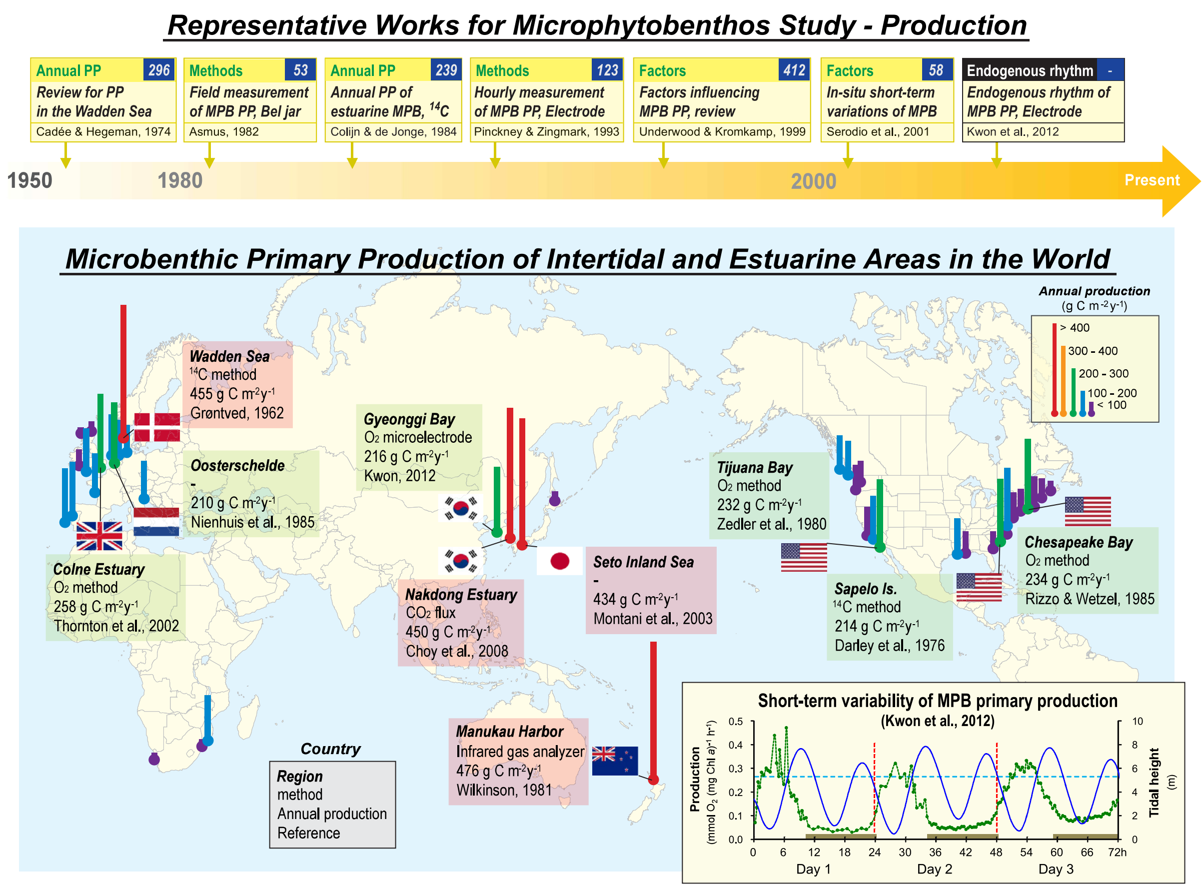

Fig. 4. Brief summary for the key findings of the representative works under the topic of primary production of microphytobenthos (MPBs); as part of present study, the production of MPBs in the intertidal and estuarine areas worldwide reviewed and a short-term variability of MPBs production in the tidal flats highlighted.

the first observation about the morphology of chloroplasts in this genus.

Typical floristic studies have also continued on other groups of the Korean diatom taxa. For example, Park and Koh (2012) recently reported the diversity in the genus *Amphora* from the Saemangeum tidal flats, documenting 23 taxa, including new records for *A. arenicola*, *A. beautifortiana*, and *A. maletractata* var. *constricta*. Pigment analysis was another approach that was introduced in the study of MPBs assemblages during the 2000s. Oh et al. (2004) investigated the biomass and community structure of MPBs in the Saemangeum tidal flats by use of High Performance Liquid Chromatography (HPLC) analysis. Later, the same technique was applied to the study of MPBs in the Gomso Bay (Lee et al., 2009) and Gwangyang Bay (Lee et al., 2012). In general, there appeared to be a strong scientific understanding on the MPBs assemblages in Korea compared to other subjects, such as dynamics, production, and food web studies, of which fact was clearly supported by the relatively large and increasing number of publications during the past 30 years (Table 1).

While a plenty of reports were available about the distribution of phytoplankton in and around Korean waters, there have been few studies reporting the distribution of the Korean MPBs until recently. The work by Oh and Koh (1995) might be the first research on this topic, as they explained diatom assemblages by addressing their spatial distribution in the tidal flats in association with several environmental parameters including sediment facies. Next, Lee (2002, 2003) investigated the distribution of MPBs assemblages on other tidal flats in Gamami and Youngkwang, Korea, respectively. In addition, Lee and Jung (2011) characterized the distribution of benthic diatoms on tidal flats in Hampyeong Bay, Korea, by examining the occurrence of MPBs in terms of temperature effect. However, it should be again noted that most of the above studies were published in a local journal (Table 1), accordingly not much influential in the international society.

The biogeography of the marine benthic diatoms in Korean MPBs study should be worthy of highlight as such topic provides fundamental biodiversity information in terms of tidal flat ecosystem service (Koh and Khim, 2014). Such study could not be warranted unless the certainty in species identification was ensured and/or extensive documentation in species archives was achieved. In the north-east Asia, Park et al. (2012a) first compiled and reported the MPBs assemblages across three countries of Korea, China, and Japan in terms of biogeography. In brief, the authors investigated the diatom assemblages on a mudflat in Nanaura, Ariake Sea (one of the representative tidal flats in Japan), and compared the co-occurrence of these assemblages with other benthic habitats in Korea, China, and Japan through a substantial critical review. In addition, the very study found a critical limitation in the former misidentifications for the north-eastern Asian benthic diatoms, and suggested the critical re-identifications. It would be also noteworthy in that they found a biogeographic similarity of Asian species. For example, *Cymatotheca weissflogii* and *Tryblioptychus cocconeiformis* are rare in the Western Hemisphere and Europe, but are widely distributed across north-east Asia.

Based on the series of our MPBs assemblages studies conducted during the past 10 years, we included herein the first report regarding the biogeography of tidal flat diatoms in north-east Northeast Asia (Fig. 3), comprising several key findings. During

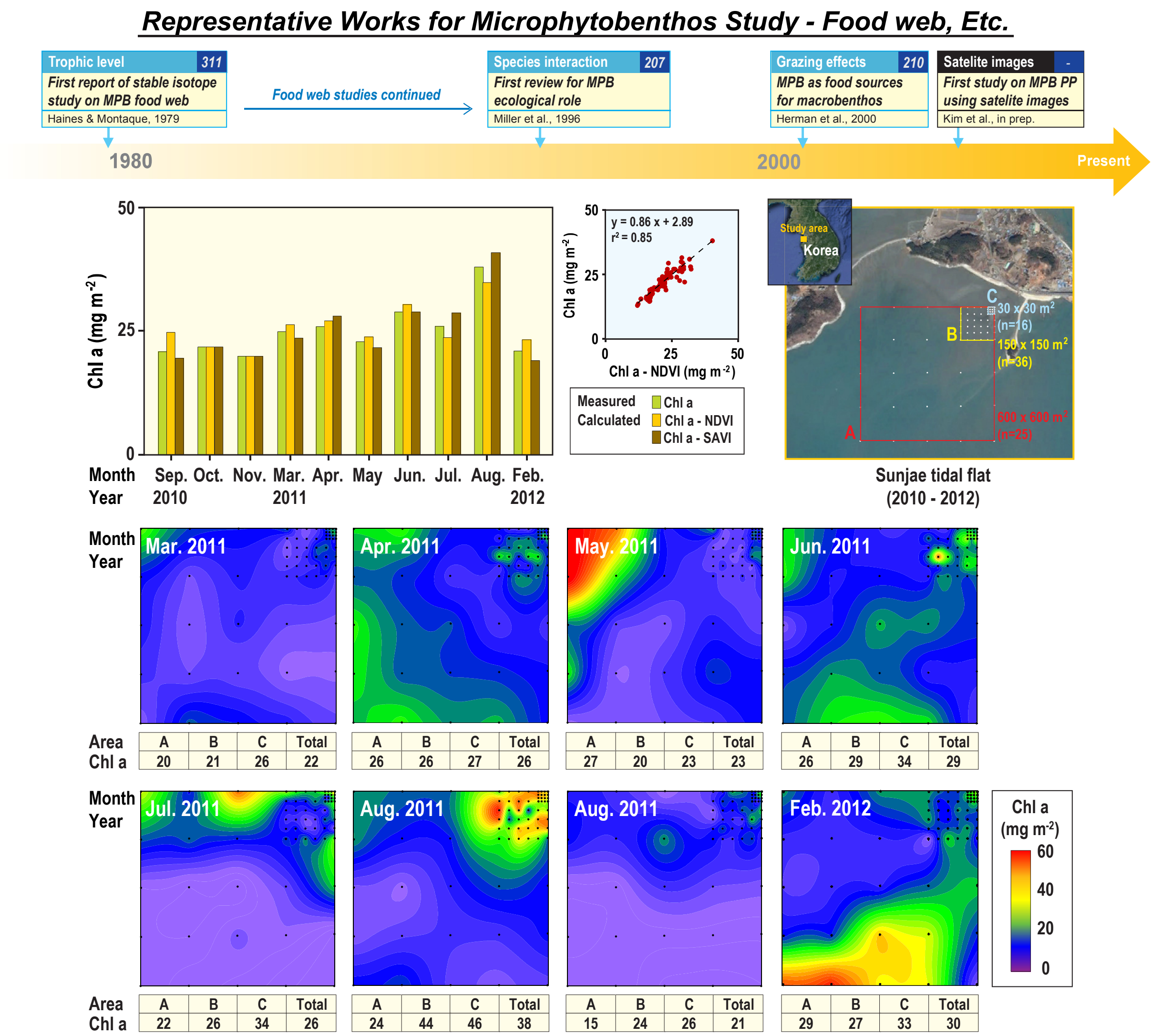

Fig. 5. Brief summary for the key findings of the representative works under the topic of food web of microphytobenthos (MPBs); as part of present study, the result relating to the application of remote sensing technique to investigate a heterogeneity of MPBs biomass distribution in the tidal flats exampled.

the study, a total of 15 locations were collectively surveyed, and the benthic diatom assemblages were analyzed; including, 6 locations in Korea, 5 locations in China, and 3 locations in Japan. Of these locations, the detailed information of MPBs assemblages in the Nanaura mudflat (Japan) has already been published (Park et al., 2012a) and diversity of the *Amphora* species in the Saemangeum tidal flats has been also documented (Park and Koh, 2012). Also, some species included in the biogeography of the Northeast Asian MPBs were described as new to science, e.g., 4 new *Moreneis* species (Park et al., 2012b) and 4 new *Fogedia* ones (Park et al., 2013a).

Of interest, in terms of biogeography, one of the four new *Fogedia* species was also observed in the tidal flats of Tianjin and Shanghai, China. Further, a number of possibly new species have been identified in several locations from the Northeast Asian tidal flats. For example, a *Petroneis* species observed in Seosan and Saemangeum areas, Korea, would be considered as new to science, along with a *Hippodonta* species, which was abundant in the diatom assemblages in the Nakdong Estuary tidal flat, Korea. We also found some rarely reported species in Korean and Japanese sandflats, say *Plagiogrammopsis crawfordii*, which has only been reported to occur in Oman and the Mississippi Delta (USA) originally (Witkowski et al., 2000), and recently in New Zealand (Harper et al., 2012). Although still remained the challenges in accumulating the diatom atlas with a fine identification, certain similarity together with broad geographical distribution of endemic Asian MPBs seemed to support a unique biodiversity of marine benthic diatoms in the Asian tidal flats.

3. Tidal dynamics

The presence of the benthic algal community in the water column has been well documented through a benthic-pelagic coupling, under the subjects of tidal resuspension and/or sediment transport. In particular, MPBs (mostly benthic diatoms) in an intertidal zone have a more significant ecological contribution in the water column, compared to phytoplankton, as resuspended algal biomass often account for a majority of total planktonic biomass (de Jonge and van Beusekom, 1992). For this reason, several subjects associated with tidal dynamics, including vertical migration, resuspension, and sediment transport, have long been of increasing concern (Figs. 1 and 3).

Table 1
List of microphytobenthos studies in Korea, by category of assemblage, dynamics, production, and food web, since the 1980s.

Category/subject	Location	Key notes	Number of taxa		Primary production	References
			Identified	Observed		
Assemblages						
Flora	Incheon	first Korean study on flora of tidal flat diatoms	83 (83%)	99	–	Shim and Cho, 1984
Flora & Biomass	Geum River Estuary	first Korean study on ecological aspect of MPBs	88 (58%)	153	–	Kim and Cho, 1985
Morphology (SEM observation)	Korean coasts	SEM observation firstly applied	NA	15	–	Choi and Noh, 1987
Flora	several locations		NA	36	–	Cho and Kim, 1988a
Morphology (SEM observation)	n.a.		NA	6	–	Lee and Lee, 1988
Flora (checklist)	Korean coasts	first compilation of Korean MPBs	NA	375	–	Choi, 1990
Morphology (SEM observation)	n.a.		NA	8	–	Noh and Choi, 1992
Flora & Distribution	Mankyung River Estuary	first international report on ecology of MPBs	NA	371	–	Oh and Koh, 1995
Flora & Distribution	Youngkwang		NA	38	–	Lee, 2002
Flora & Distribution	Gamami Beach		26	68	–	Lee, 2003
Flora (pigment analysis)	Saemangeum		NA	NA	–	Oh et al., 2004
Taxonomy (recombination)	n.a.	first taxonomic recombination of Korean MPBs	NA	2	–	Park et al., 2007
Flora & Biomass	Nakdong River Estuary		26 (67%)	39	–	Du et al., 2009
Flora (pigment analysis) & Biomass	Gwangyang Bay		NA	NA	–	Lee et al., 2009
Flora & Distribution	Hampyung Bay		NA	45	–	Lee and Jung, 2011
Flora (pigment analysis) & Biomass	Gomso Bay		NA	NA	–	Lee et al., 2012
Taxonomy (new genus)	Saemangeum	first reports of a new genus to the science	NA	4	–	Park et al., 2012b
Morphology (SEM observation)	Saemangeum		13 (57%)	23	–	Park and Koh, 2012
Taxonomy (new species)	Saemangeum	reports of four new *Fogedia* species	NA	4	–	Park et al., 2013a
Flora & Biomass	Taean		NA[a]	121	–	Park et al., 2013b
Dynamics						
Vertical migration	Nakdong River Estuary		NA	NA	–	Du et al., 2010
Vertical migration	Nakdong River Estuary		NA	NA	–	Du et al., 2012
Tidal and diel dynamics	Daebu Is.	inherent migratory rhythm of MPBs	NA	NA	~1 000 mg C m^{-2} d^{-1}	Kwon et al., in press
Production						
Primary production (with flora)	Gyeonggi Bay	first Korean study on MPBs production	119 (87%)	137	190 g C m^{-2} yr^{-1}	Cho and Kim, 1988b
Primary production	Gwanghwa	first application of oxygen microelectrode in Korea	NA	NA	0.2–11.1 mmol O_2 m^{-2} h^{-1}	Hwang and Cho, 2005
Primary production (with flora)	Gwanghwa		NA	NA	206.7 mg C m^{-2} d^{-1}	Yoo and Choi, 2005
Primary production	Nakdong River Estuary		NA	NA	546.15 g C m^{-2} yr^{-1}	Du and Chung, 2009
Primary production	Daebu Is.	first international report of microelectrode study	NA	NA	2.3–3.0 mmol O_2 m^{-2} d^{-1}	Kwon et al., 2012
Food web						
Food web	Gwangyang Bay	first reports on isotope study on Korean MPBs	NA	NA	–	Kang et al., 2003
Food web	Gwangyang Bay		NA	NA	–	Kang et al., 2006

[a] NA: not applicable.

In fact, such concerns would be developed from the phenomenon of a vertical migration of benthic diatoms as mentioned earlier (Herdman, 1921; Aleem, 1950). Later, various issues relating to the vertical migration followed by tidal dynamics of MPBs have been addressed, including the first report of the tidal resuspension of MPBs in the Branford Harbor Estuary, USA (Baillie and Welsh, 1980). Meantime, couple of studies focusing on the vertical migration rhythm of benthic diatoms have also been introduced in the Korean tidal flats (Du et al., 2010, 2012; Kwon et al., in press), but such topics have not been much highlighted in Korea, compared to other topics (Table 1).

Another key addition to the scientific understanding on tidal dynamics of MPBs would be found in the work by de Jonge and van den Bergs (1987), in which the authors performed the first laboratory experiment on resuspension of MPBs. The authors further described the physical process of MPBs resuspension in the field, where various associated parameters such as tidal currents, wind waves, and water depths were quantitatively identified as key factors in tidal resuspension of sediment associated MPBs (de Jonge and van Beusekom, 1992, 1995). However, it should be noted that the earlier studies on tidal resuspension of MPBs have not fully addressed such mechanism at a high temporal resolution until the report by Demers et al. (1987). For example, the very study reported temporal fluctuations in phytoplankton abundance within a day (four times a day) for relatively long period (148 consecutive days) addressing the influence of “wind” on sedimentary resuspension over the tidal cycles.

In general, tidal resuspension is known to be influenced by both tidal currents (particularly in a macrotidal environment, such as

Asian tidal flats) (Lee, 2010; Lee et al., 2004) and wind-induced waves (mostly in the European tidal flats) (de Jonge and van Beusekom, 1995), depending on the locality of the world. Time-series data at a high temporal resolution (say resolution of < hour) would be particularly benefit in a macrotidal environment. For example, Koh et al. (2006) first documented a time-series mooring data on MPBs biomass (Chl *a*) and suspended particulate matters (SPM) in the Nanaura mudflat, Japan, over 28 consecutive tidal cycles at intervals of 10 min, covering both flood-ebb and spring-neap periods. This study would be of ecologically significance as the authors quantified the in situ erosion threshold of the current velocity from the yet highest temporal resolution data (viz., 10 min intervals) in the field. Furthermore, within this study, several important aspects of tidal resuspension were also investigated; including, flood-ebb characteristics, spring versus neap tide variations, the relationship between resuspended algal biomass and suspended particles, and offshore transport of MPBs.

The above study was further developed into Koh et al. (2007a), where authors successfully explained the decoupling of MPBs from suspended sediments through the analysis of their fluxes by tidal phases. In addition, the series of these MPBs dynamics study further described the within-day variations of MPBs in the sediment layer and overlying water column, together with characterizing vertical migration of MPBs during daytime exposure (Koh et al., 2007b). In particular, it was observed that a significant amount of Chl *a* in the water column (up to 66%) could be derived from the bottom sediment by the mechanism of tidal resuspension.

The results from the above three studies have been collectively used to generate a conceptual, yet comprehensive, schematic diagram for the dynamics of MPBs (expressed as biomass) from the upper intertidal zone to offshore (Fig. 3). In brief, water Chl *a* (C_w) and sediment Chl *a* (C_{sed}) values were measured, and all water column Chl *a* values were depth integrated ($C_{w\text{-}d}$) by multiplying C_w and corresponding water depth. The baseline concentrations of water Chl *a* ($C_{w\text{-}base}$) were derived from the relationship between C_w and SPM in water column (C_{SPM}), of which both concentrations were measured at every ebb and flood tide over 28 tidal cycle (calculation details given in Koh et al., 2006). Finally, the resuspended Chl *a* concentrations ($C_{w\text{-}resus}$) were calculated as the difference between C_w and $C_{w\text{-}base}$.

The diagram primarily indicated that Chl *a* that is resuspended from the upper intertidal flat was transported to offshore direction, with which phenomenon was extensively discussed using indices of time-integrated fluxes for Chl *a* and SPM in our previous work (Koh et al., 2006). It was also shown that the upper to certain part of subtidal areas seemed to be the sources of Chl *a* into water column MPBs biomass, while the offshore region served to be a sink zone. Of note, the greatest amount of resuspended Chl *a* occurred in the middle of the intertidal and subtidal zone (viz., between 1 and 2 km off the coast), possibly indicating the location of the most productive zone of MPBs biomass (or production) in a shallow pelagic system.

Subsequently a detailed analysis of the mooring data has been made, by scrutinizing the fluxes of microphytobenthic Chl *a* and SPM in the water column, to explain the "segregation" of phyto-particles from sediment, over the flood and ebb tidal cycles (Koh et al., 2007a). A scatter plot of Chl *a* and SPM fluxes over the tidal period at 4 stages, divided by the differences in current direction and strength, revealed couple of characteristics; such as periods of flux-coupling, flux-lag, and flux-decoupling under the varying conditions of current and wind speed (Fig. 3). The results successfully confirmed the segregation of benthic phyto-particles from the bottom sediment, highlighting a significant contribution of benthic derived phyto-particles into overlying water column, in terms of total biomass (or production) in shallow intertidal environment.

Overall, the series of our MPBs dynamics study have collectively addressed the mechanism of in situ microalgal resuspension in tidal flat ecosystem, in terms of 1) controlling and masking factors (i.e., current versus wind), 2) flux characteristics (i.e., Chl *a* versus SPM), and 3) transport dynamics (i.e., vertical versus offshore transport). In general, the tidal flat sediment that is inhabited by MPBs plays a primary role as an algal biomass reservoir and, at the same time, contributes as a supplier for temporary pelagic biomass during submergence (i.e., over a certain period of time in a shallow water environment).

4. Primary production

Understanding the primary production of MPBs represents one of the longstanding major topics (Fig. 4), more recently as part of ecosystem function through a benthic-pelagic coupling followed by energy transfer through food web. However, it might be also interesting in that MPBs production studies seemed to have little scientific attention compared to the mainstream topics of assemblages and dynamics. The work of Cadée and Hegeman (1974) represents one notable work in MPBs production, in which the authors reported annual production of tidal flat system based on 5 years of measurements in the western Wadden Sea, the Netherlands. Following this monumental work, many studies have reported varying aspects of MPBs production by use of various in situ methods. For instance, Asmus (1982) reported the field measurement of MPBs production using the Bel Jar technique, while Colijn and de Jonge (1984) adopted the ^{14}C method to investigate annual MPBs production.

In the 1990s, more sophisticated equipment for the measure of benthic algal production was developed; for example, Pinckney and Zingmark (1993) utilized microelectrodes to address the hourly dynamics of MPBs production, while Blanchard et al. (1997) adopted photosynthetron tool to investigate the P_{max} of intertidal MPBs. Later, Underwood and Kromkamp (1999) criticized the existing techniques and the factors associated with MPBs productivity, suggesting alternative new methods, such as ^{15}N uptake and fluorescence techniques, of which review has a greater impacts on the following works (so far, 412 citations). More recently, variable fluorescence (viz., PAM method) was measured in field studies of MPBs production (e.g., Serôdio et al., 2001, 2005), which has become an established popular method.

While a number of studies on MPBs production have been conducted since 1950s worldwide, this topic has not been included in the mainstream of MPBs studies in Korea until late 1980s. Cho and Kim (1988b) investigated primary production using a benthic chamber technique, in addition to report species composition of benthic diatom assemblages in a salt marsh of the Gyeonggi Bay. Although a classical methodology was adopted, which would not be as sensitive as the contemporary ^{14}C method, this work provided a significant contribution to the studies of Korean MPBs production as a pioneering work relating to the benthic productivity in tidal flats of Korea.

After somehow long period of absence in study efforts on the MPBs, in 2005, couple of studies investigating benthic algal productivity with advanced techniques, such as Clark type microelectrodes (Hwang and Cho, 2005) and photosynthetron method coupled with HPLC analysis (Yoo and Choi, 2005) were conducted. These two studies seemingly advanced the understanding of seasonal variations in MPBs production in the Korean tidal flats. However, again, those studies have been limited to a local audience. Later, Du and Chung (2009) reported the MPBs production of tidal flats in the Nakdong Estuary, Korea, by applying the pulse amplitude modulation (PAM) method, which was the first international publication reporting the MPBs production of the Korean tidal flats.

The questions and perspectives of the most studies of MPBs production in Korea did not seem to be much advanced for 20 years of MPBs production study, the methods being used somehow advanced though. That is to say, the primary focus on the production studies in Korea has been limited to documenting the MPBs production values, sometimes combined with a floral assemblages, by space or time. Yet, the first study challenging certain ecological mechanisms related with temporal variability in MPBs production was the work by Kwon et al. (2012), where tidal and diel rhythm in benthic algal productivities were thoroughly studied.

While, many previous studies also demonstrated short-term variations in MPBs biomass and/or production, such topic was primarily addressed through the issue of vertical migration of MPBs (Consalvey et al., 2004). The work of Kwon et al. (2012) would be highlighted in that the within-day production with high time resolution (at intervals of 10 min) clearly explained diel and tidal dependent characteristics of MPBs production in terms of threshold productivity and endogenous production rhythms. Of additional interest, authors found that biomass may not be a limiting factor controlling total daily productivity, because MPB appear to have a certain unique capability in community production, even accumulated production, regardless of tidal energy condition (e.g., spring versus neap tidal condition). More recently, further questions proposed in spring-neap variations in MPBs biomass (Koh et al., 2006) or production (Kwon et al., 2012) have been addressed by simulating the MPBs production against in situ temperature and light intensity (Kwon et al., in press).

In general, the series of our MPBs production studies seemed to follow the logic and flow that have been shown in the European science, with temporal gap of ca. 30 years. In fact, the traditional methodology measuring MPBs production such as O_2 microelectrode method (1980s) and PAM technique (1990s) introduced in Europe has been adopted in Korea after 2000s. The accumulated data for MPBs production worldwide including Korea would be worthy of comparison, under the limitations of varying methodology used cross the publications or countries. Although each method has advantages and/or limitations in sensitivity and significance, the inter-comparison of annual (or daily) production at a global scale would be helpful to find geographical hot spot for MPBs production being identified.

As part of the review, we collected the MPBs production data worldwide including our data in several places around the coasts of Korea to find out geographical distribution of tidal flat productivity (Fig. 4). The highly productive spots with MPB communities were found to occur in several places, primarily those sites in well-developed estuaries (e.g., Ems-Dollard, the Netherlands) and tidal flats (e.g., the Wadden Sea, Denmark). Highly productive spots in Asia include the Nakdong River Estuary, which is one of the largest estuaries in Korea, and the Seto Inland Sea in Japan. While, the majority of sites situated in North America showed relatively low annual productivity of MPBs, however, a direct comparison between sites should be carefully discussed considering the differences in sample type, sample size, and methodology. Of note, the biomass of MPB (say Chl *a*) does not appear to be correlated with annual productivity, roughly reflecting the relationship to be site-specific.

5. Food web study etc.

Based on the literature survey on MPBs studies (Fig. 1), we found that the topics other than three main subjects (assemblage, dynamics, and production) included food web study, remote sending study, and modeling work etc. (Fig. 5). The food web study using the method of stable isotopes represented one of the most recently investigated subjects regarding the ecological role of intertidal MPBs. Since the 1970s, food-web studies have investigated the grazing effects, trophic characteristics, flow of energy and matter, and species interactions associated with MPBs. First report was made by Haines and Montague (1979), where they compiled a monumental report on this topic with high impacts (311 citations) and far later Miller et al. (1996) conducted a synthetic review on the ecological role of MPBs. More recently, Herman et al. (2000) confirmed that MPBs would contribute as major food sources for macrobenthos.

However, possibly because of methodological or instrumental limitations, the topic has not been yet flourishing and such observation follows in Korea, with only very few documented studies until now. The work by Kang et al. (2003) addressed the role of MPBs as the source of primary organic matter for macrozoobenthos community based on the food web study in the Gwangyang Bay. Kang et al. (2003) also reported the importance in the seasonal development of MPBs as an available food source for both suspension- and deposit-feeding bivalves (Kang et al., 2006). This study also highlighted the significant contribution of resuspended MPBs to total phytoplankton components, which was supported by the $\delta^{13}C$ values of the particulate organic matter. Overall, study effort on the MPBs food web remained in question; say the isotopic signature of MPBs and associated biogeochemical components are required to advance our understanding about the ecological functioning of MPBs as food sources to various feeding organisms.

Finally, as for one of the minor subjects, the remote sensing technique seems to be one promising tool to support many topics including dynamics and production of MPBs in the intertidal flat area. We have adopted the technique during the series of our MPBs study since late 2000s to investigate a large scale estimate of biomass and production of tidal flat MPBs. Our recent results indicated that significant relationship ($p < 0.05$, $r^2 = 0.85$) between in situ MPBs biomass (Chl *a*) and remote sensing index, say normalized difference vegetation index (NDVI) (Fig. 5). Interestingly, such strong correlation was consistently observed during the monthly surveys encompassing four seasons in one of the typical tidal flat, Daebu, Korea. Accordingly a rough estimate of annual production of MPBs would be promising if biomass (Chl *a*) and production are coupled in a given site, which has been fairly well documented elsewhere (Kwon et al., in press). Meantime, we also found that the average biomass (Chl *a*) of MPBs measured in three given matrix areas (A: 600×600 m^2, B: 150×150 m^2, and C: 30×30 m^2) did not greatly varied (Fig. 5), which indicated a possible measure of representative MPBs biomass with reduced uncertainty towards decrease of sampling error due to heterogeneity in the field. Overall, the alternative use of satellite imageries to MPBs biomass and/or production seemed to be promising methodology, particularly in large scale mapping of MPBs in ecological screening tool as a management purpose.

6. Future research directions

MPBs, marine benthic diatoms, are recognized as a group of marine organisms that are of ecological importance as primary food sources in intertidal flats or estuaries, and, sometimes, far offshore in the sea. MPBs studies have a long tradition in marine science, with a publication history of over 100 years worldwide existing, with mainstream topics of assemblage, dynamics, production, and food web (shown in Fig. 1). As part of the present work, the comparative analysis, between worldwide and Korean studies, on the status quo of scientific publications were provided and briefly discussed, to identify and narrow down the future research directions below. However, we analyzed the most recent ca. 40 years of international publications only to focus on recent development

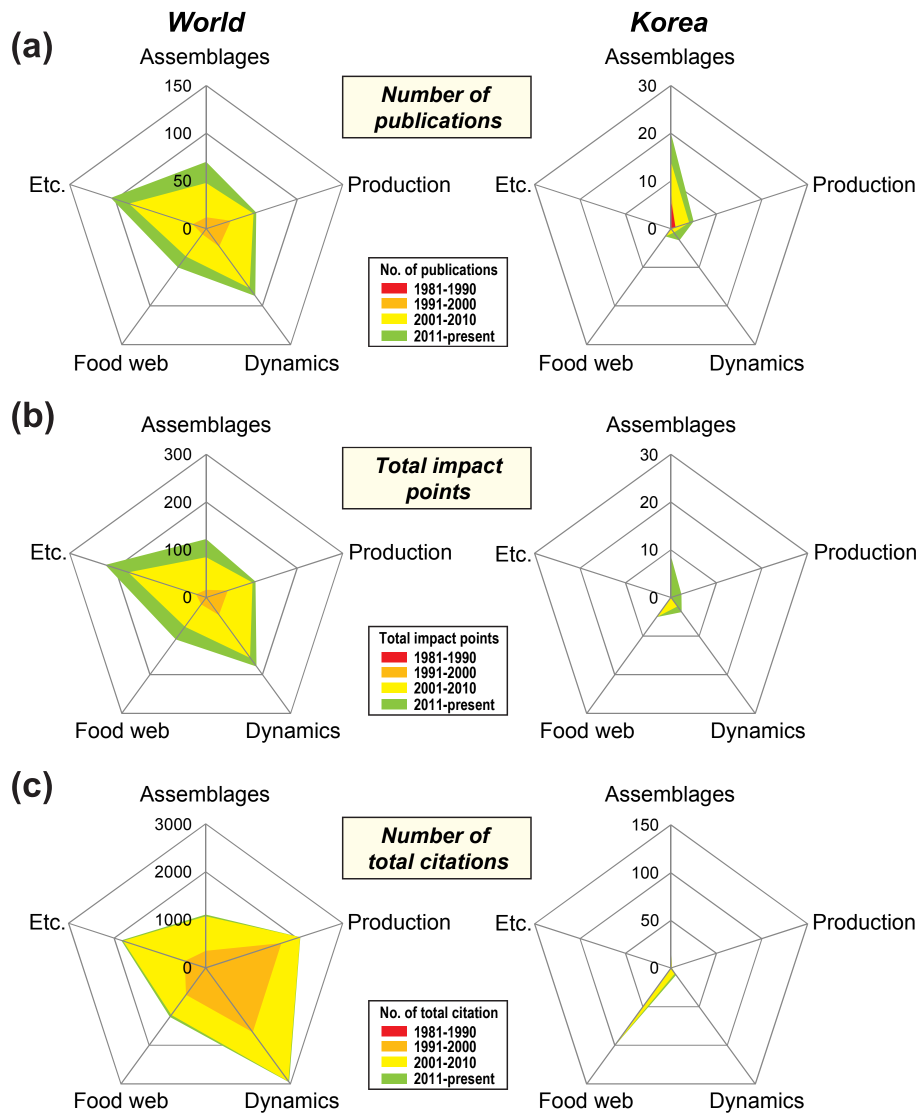

Fig. 6. Radar plots for comparison of study efforts relating to the major topics of microphytobenthos study, based on (a) the number of publications, (b) total impact points, and (c) number of total citations.

and limitations, which might be appropriate to identify future challenges in Korea.

As presented and discussed in the present review, we divided the major topics of the MPBs studies into four categories; again, assemblage, dynamics, production, and the food web etc. considering the chronological period of corresponding research. The number of publications for these topics represented about half of the total (ca. 370 papers) during the entire period of >100 years of MPBs scientific history. The four focal topics of this review were considered to be highly relevant to the ecological characteristics of MPBs, with a sufficient publication history to identify research strengths and weaknesses in both past and current efforts. Of note, other research topics associated with MPBs are also of recent scientific interest, including metabolism, material cycles, and pollution related issues; thus, indicating the broad spectrum of MPBs research in more recent years.

By simply counting the number of publications between topics the scientific efforts worldwide over the last 40 years have been fairly balanced between topics and further seemed to be developed in a sequential manner from assemblage to others. However, in Korea, the publications are highly biased toward the foundational understanding of MPBs structure, particularly floral assemblages over half of the total publications. One major weakness of MPBs studies in Korea would be a lack of scientific community with widespread but limited group(s) or individuals, and further lesser cooperation between Korean scientists compared to those in Europe and North America would have blocked the scientific development. However, individual scientific efforts in Korea since the 2000s are continuously growing with wider range of topics, in parallel to a dramatic increase in the total number of international publications.

As for additional indices of impact points or citations, which might more reflect the scientific recognition in the community, the scientific gaps between advanced countries and Korea seem to be much bigger (Fig. 6). However, such differences would be possibly decreased in the future, as majority proportion of Korean studies was published only during the past 10 years. In particular, diverse research perspectives of MPBs other than simple assemblage studies are acknowledged as future studies. For example, studies of tidal resuspension and primary production of MPBs would be still promising while food web studies are on its way to be far expanded and deepened. Applications of more advanced scientific tools such as PAM, stable isotope analysis and remote sensing technique would also strengthen and enrich when utilized complementarily. In the meantime traditional taxonomic studies are also to be continued in that Korean tidal flats have shown notable biodiversity of benthic diatoms.

In conclusion, the last 40 years of MPBs research in Korea roughly reflected the international historical trends but seemed to lose a scientific balance due to subject (or technical) preferences, indicating the need for allocation of balanced and target oriented selection of study subjects, with stimulated professional collaboration in the future.

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