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Benthic dinoflagellates in Korean waters

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The occurrence of benthic dinoflagellates, many of which are known to be toxic, is a critical concern for scientists, government officers, and people in the aquaculture, dining, and tourism industries. The interest in these dinoflagellates in countries with temperate climate is increasing because tropical or subtropical species introduced into temperate waters by currents are able to survive the winter season in the new environment owing to global warming. Recently, several species from the benthic dinoflagellate genera *Amphidinium*, *Coolia*, *Ostreopsis*, *Gambierdiscus*, and *Prorocentrum* have been reported in the waters of the South and East Sea of Korea. The advent of the benthic dinoflagellates in Korean waters is especially important because raw or slightly cooked seaweeds, which may harbor these benthic dinoflagellates, as well as raw fish, which can be potentially intoxicated by phytotoxins produced by some of these benthic dinoflagellates, are part of the daily Korean diet. The recent increase in temperature of Korean coastal waters has allowed for the expansion of benthic dinoflagellate species into these regions. In the present study, we reviewed the species, distribution, and toxicity of the benthic dinoflagellates that have been reported in Korean waters. We also provided an insight into the ecological and socio-economic importance of the occurrence of benthic dinoflagellates in Korean waters.

Key Words: *Amphidinium*; *Coolia*; epiphytic; *Gambierdiscus*; *Ostreopsis*; *Prorocentrum*; warming

INTRODUCTION

Dinoflagellates are a major component of marine ecosystems (Lessard 1991, Jeong 1999, Sherr and Sherr 2007, Terrado et al. 2009, Jeong et al. 2021b). They live in diverse environments and play diverse roles in marine food webs (reviewed by Jeong et al. 2010). Although the majority of dinoflagellates are planktonic and often form blooms in the water column (Jeong et al. 2015, 2021a), many dinoflagellate species are benthic (Tindall and Morton 1998, Kim et al. 2011). Some benthic dinoflagellates contain toxins, such as palytoxin, ciguatoxin, maitotoxin, gambierol, okadaic acid, cooliatoxin, and prorocentrolides (Litaker et al. 2010, Holmes et al. 2014, Tester et al. 2020).

Therefore, the occurrence of benthic dinoflagellates is a critical concern for scientists, government officers, and people in the aquaculture, dining, and tourism industries. Many benthic dinoflagellate species are distributed in tropical or subtropical waters, and fewer species occur in temperate waters (Besada et al. 1982, Tindall and Morton 1998, Zingone et al. 2006, Fraga et al. 2008, Hallegraeff 2010, Leaw et al. 2010, Glibert et al. 2012, Parsons et al. 2012, Larsson et al. 2019, Pavaux et al. 2020, Tester et al. 2020). However, the distribution of some benthic dinoflagellates living in tropic or subtropic waters has expanded into temperate waters owing to the elevated wa-



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ter temperatures driven by global warming (e.g., Shears and Ross 2009, Jeong et al. 2012a, 2012b).

In the last decade, several benthic dinoflagellate species have been reported from Korean waters (Kim et al. 2011, Baek 2012a, 2012b, Jeong et al. 2012a, 2012b, Kang et al. 2013, Lee et al. 2013, Lim et al. 2013, Shah et al. 2013a, 2013b, 2014a, 2014b, Jang et al. 2018, Kim and Seo 2019, Lee and Park 2020, Park et al. 2020). Most of these reported species have been found in the coastal waters of Jeju Island, which is located at the south end of Korea (33.5° N in latitude), but some species have been found in the South Sea and East Sea of Korea (~38.0° N). The toxins of some benthic dinoflagellates are known to cause illness in humans who consume seafood contaminated by the toxins bioaccumulated through food webs or when directly exposed to seawater and / or aerosol during benthic dinoflagellate blooms (Tichadou et al. 2010, Tubaro et al. 2011, Cimminiello et al. 2014, Accoroni and Totti 2016,

Pavaux et al. 2020, Tester et al. 2020). Many Koreans readily consume raw or slightly cooked macroalgae and fish. Therefore, the distribution of these benthic dinoflagellates and the presence of toxins in Korean waters are of critical concern.

The surface water temperature around Korea has been gradually increasing (Han and Lee 2020). This may allow some invasive subtropical species transported via currents or ballast waters to survive over the winter in Korea. Tropical cyclones (e.g., typhoons) occur annually in Korea (<http://www.weather.go.kr>). Strong water movements during these events may detach benthic dinoflagellates from the thalli of macroalgae (Tindall and Morton 1998, Cruz-Rivera and Villareal 2006) in Jeju waters or the South Sea and transport them to the eastern and western coasts of Korea.

In the present study, we reviewed the species, distribution, and toxicity of benthic dinoflagellates in Korean wa-

Table 1. The benthic dinoflagellates reported from Korean waters, their GenBank accession numbers, and the location, water temperature (T), and salinity (S) where the dinoflagellates were isolated or found

Species	Location	T (°C)	S	GenBank accession No.	Reference
<i>Coolia canariensis</i>	Jeju Island	14.8	33.7	FR846193–5, FR847223–4	Jeong et al. (2012b)
<i>C. malayensis</i>	Jeju Island	20.5–21.1	32.3–28.6	FR848949–50, FR847217–22	Jeong et al. (2012b)
<i>C. malayensis</i>	Jeju Island	10.9–26.3	23.6–34.8	-	Shah et al. (2013a, 2013b)
<i>Coolia</i> spp.	Jeju Island, East coast	21.0–23.6	28.9–32.5	-	Kim et al. (2011), Baek (2012a)
<i>Gambierdiscus toxicus</i>	Jeju Island	NA	NA	-	Baek (2012b)
<i>G. jejuensis</i> (previously reported as <i>G. caribaeus</i>)	Jeju Island	14.4	33.1–33.8	HE775087, MH827555–MH827562	Jeong et al. (2012a), Jang et al. (2018)
<i>G. yasumotoi</i>	Jeju Island	NA	NA	-	Shah et al. (2013a, 2014a)
<i>Gambierdiscus</i> spp.	Baek and Jeju Islands, East and South coast	13–23.6	28.9–34	-	Kim et al. (2011), Baek (2012b)
<i>Ostreopsis ovata</i>	Jeju Island	10.9–26.3	23.6–34.8	-	Shah et al. (2013a, 2013b)
<i>O. cf. ovata</i>	Jeju Island	18.6	31.2	HE793379	Kang et al. (2013)
<i>Ostreopsis</i> sp. 1	Jeju Island	15.8–18.3	33.4–34.8	MK558223–8	Kim and Seo (2019)
<i>Ostreopsis</i> sp. 6	Jeju Island	25.0–30.0	32.0–33.0	NA	Lee and Park (2020)
<i>Ostreopsis</i> spp.	Jeju and Chuja Islands, South and East coasts	18.6–29.5	28.9–35.0	-	Kim et al. (2011), Baek (2012a), Lee and Park (2018)
<i>Amphidinium carterae</i>	Jeju Island	10.9–26.3	23.6–34.8	-	Shah et al. (2013a, 2013b)
<i>A. massartii</i>	Jeju Island	22.7	33.7	HF674441–674443	Lee et al. (2013)
<i>A. operculatum</i>	Jeju Island	10.9–26.3	23.6–34.8	-	Shah et al. (2013a, 2013b)
<i>Amphidinium</i> spp.	Jeju Island, East and South coasts	21.0–23.6	28.9–32.5	-	Kim et al. (2011), Baek (2012a)
<i>Prorocentrum concavum</i>	Jeju Island	10.9–26.3	23.6–34.8	-	Shah et al. (2013a, 2013b)
<i>P. emarginatum</i>	Jeju Island	10.9–26.3	23.6–34.8	-	Shah et al. (2013a, 2013b)
<i>P. fukuyoi</i>	Jeju Island	10.9–26.3	23.6–34.8	-	Shah et al. (2013a, 2013b)
<i>P. lima</i>	Jeju Island	10.9–26.3	23.6–34.8	-	Shah et al. (2013a, 2013b)
<i>P. mexicanum</i> (previously as <i>P. cf. rhathymum</i>)	Jeju Island	14.4–20.5	33.3–33.8	HF565181–3	Lim et al. (2013)
<i>P. mexicanum</i> (previously as <i>P. rhathymum</i>)	Jeju Island	10.9–26.3	23.6–34.8	-	Shah et al. (2013a, 2013b)
<i>Prorocentrum</i> spp.	Jeju Island, South and East coast	21.0–23.6	28.9–32.5	-	Kim et al. (2011), Baek (2012a)

NA, not available.

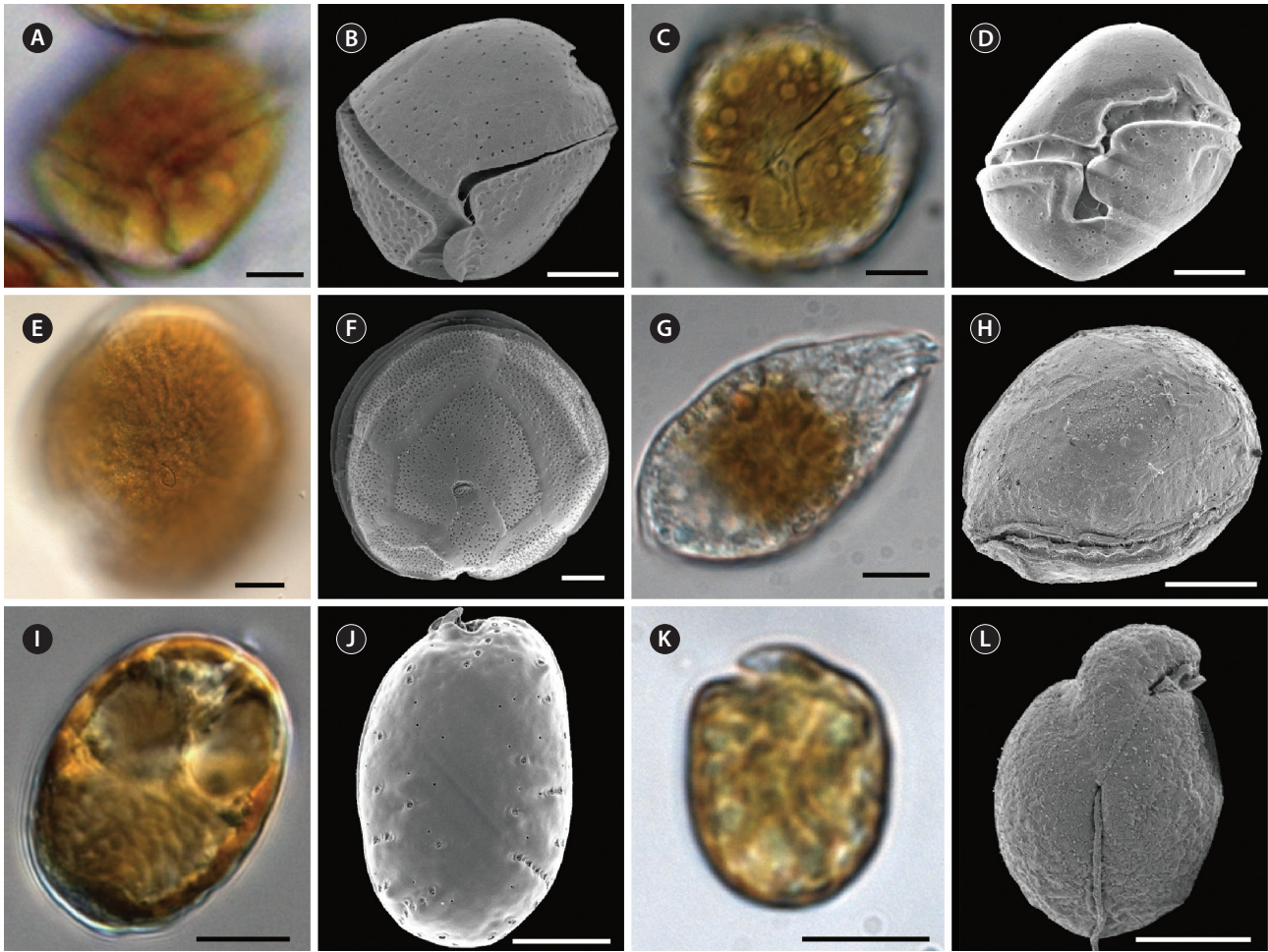


Fig. 1. Micrographs of epibenthic dinoflagellates found in Korean waters. (A & B) *Coolia canariensis* CCJJ1. (C & D) *Coolia malayensis* CMJJ1. (E & F) *Gambierdiscus jejuensis* GCJJ1. (G & H) *Ostreopsis* cf. *ovata* OVJJ1. (I & J) *Prorocentrum mexicanum* PRJJ1. (K & L) *Amphidinium massartii* AMJJ1. Micrographs in A, C, E, G, I, and K were taken using a light microscope, while those in B, D, F, H, J, and L were taken using a scanning electron microscope. Scale bars represent: A–L, 10 μ m.

ters, and also provided an insight into the ecological and socio-economic importance of the occurrence of benthic dinoflagellates in Korean waters.

TAXONOMIC COMPOSITION AND MORPHOLOGICAL AND GENETIC CHARACTERIZATIONS OF BENTHIC DINOFLAGELLATES IN KOREAN WATERS

Kim et al. (2011) were the first to report the presence of benthic dinoflagellates in Korean waters; they found five benthic dinoflagellate genera, *Amphidinium*, *Coolia*, *Gambierdiscus*, *Ostreopsis*, and *Prorocentrum*, in the coastal waters of Jeju Island in the fall of 2009 (Table 1). In their study, the dinoflagellates were identified to the

genus level based on morphological characteristics observed under a light microscope. Later, several benthic dinoflagellate species isolated in the coastal waters of Jeju Island and cultured in the laboratory were identified using both morphological and genetic analyses (Jeong et al. 2012a, 2012b, Kang et al. 2013, Lee et al. 2013, Lim et al. 2013, Jang et al. 2018) (Fig. 1). Subsequently, several studies reported the presence of diverse benthic dinoflagellate species in Jeju waters and the South and East Sea of Korea (Table 1). However, the identification of some of those species was conducted only by morphological analysis under a light microscope.

In general, the overall shapes of the Korean strains of *Coolia canariensis*, *C. malayensis*, and *Ostreopsis* spp. were similar to those of previously reported strains isolated from the waters of other countries, but the molecular

characterizations of the Korean strains were somewhat different from those of the previously described strains (Jeong et al. 2012a, 2012b, Kang et al. 2013, Kim and Seo 2019). The benthic dinoflagellate *Gambierdiscus jejuensis* isolated from the waters off Jeju Island was recently described as a new species (Jang et al. 2018). Detailed morphological and molecular characterizations of the Korean strains are provided below.

Coolia spp.

Two *Coolia* species, *C. canariensis* and *C. malayensis*, have been reported in Korean waters (Jeong et al. 2012b). These species were found in the waters off Jeju Island and were identified using both morphological and genetic analyses. The morphologies of the Korean strains of *C. canariensis* CCJJ1 and *C. malayensis* CMJJ1 and CMJJ2 were similar to those of the original Canary Islands and Malaysian strains, respectively (Fraga et al. 2008, Leaw et al. 2010, Jeong et al. 2012b). Using scanning electron microscopy (SEM), Jeong et al. (2012b) reported the exact number and shape of the sulcal plates of Korean strains of *C. canariensis* and *C. malayensis*, and reported the complete Kofoidian plate formulae as Po, 3', 7'', 6c, 6s, 5''', and 2'''' for *C. canariensis* and Po, 3', 7'', 7c, 6–7s, 5''', and 2'''' for *C. malayensis*. Moreover, these authors were the first to report the number of pores in the apical pore complex and a line of small knobs on the pore plates of *C. canariensis* and *C. malayensis*. Jeong et al. (2012b) also observed perforations within the large pores of the Korean strains of *C. canariensis* and *C. malayensis*. Perforations have been found previously in the Malaysian strains of *C. malayensis* (Leaw et al. 2010), and thus Jeong et al. (2012b) suggested that the perforations are a common feature of *Coolia* species.

Jeong et al. (2012b) reported that the large subunit (LSU) rDNA sequence of the Korean strain *C. canariensis* CCJJ1 is identical to that of the Biscayan strains, but 2–3% different from that of the Canary Islands strain VGO0775 and the Australian strain. Additionally, the sequences of the small subunit (SSU) and LSU rDNA from the two Korean strains *C. malayensis* CMJJ1 and CMJJ2 are <1% different from the Malaysian strains of *C. malayensis*, the Florida strain CCMP1345, and the New Zealand strain CAWD39 (*Coolia monotis*) (Jeong et al. 2012b). In phylogenetic trees based on LSU rDNA sequences, the Korean strains of *C. malayensis* were placed in a clade with the other strains of the same species. Jeong et al. (2012b) therefore suggested that the Korean strain of *C. canariensis* was closely related to the two Atlantic strains and the

Australian strain, whereas the Korean strains of *C. malayensis* were related to the two Malaysian strains and the Florida and New Zealand strains of *C. malayensis*.

Gambierdiscus spp.

To date, three *Gambierdiscus* species, *G. jejuensis* (previously reported as *G. caribaeus* in Jeong et al. 2012a), *G. toxicus*, and *G. yasumotoi*, have been reported in Korean waters (Baek 2012b, Jeong et al. 2012a, Shah et al. 2013a, 2014a, Jang et al. 2018). The Korean strains *G. jejuensis* GJ1703a and GCJJ1 isolated from the waters off Jeju Island were identified using both morphological and genetic analyses (Jeong et al. 2012a, Jang et al. 2018). Cells of *G. toxicus* and *G. yasumotoi* were also found in the South Sea of Korea (Baek 2012b, Shah et al. 2013a, 2014a). However, the molecular characterization of *G. toxicus* and *G. yasumotoi* is required to confirm the identification of these species.

The overall morphology of the Korean strains of *G. jejuensis* (GJ1703a and GCJJ1) isolated from the waters off Jeju Island are similar to that of the original Belize strains of *G. caribaeus* (Litaker et al. 2009, Jeong et al. 2012a, Jang et al. 2018). The depth, length, and width of living Korean *G. jejuensis* cells are comparable with those of *G. caribaeus*, whereas some morphological features, such as the length to width ratio of the Po plate and 1p plate, are different from those of *G. caribaeus*. The sequence of the SSU rDNA and those of the D1–D3 and D8–D10 regions of the LSU rDNA of the Korean *G. jejuensis* GJ1703a are 2.4–6.1% different from those of *G. caribaeus* (Jang et al. 2018). In the phylogenetic trees based on SSU and LSU rDNA sequences, the Korean strains of *G. jejuensis* formed a clade with strains of *Gambierdiscus* sp. type 2 isolated from the temperate waters of Korea and Japan. Therefore, Jang et al. (2018) proposed that the Korean strains of *G. jejuensis* and *Gambierdiscus* sp. type 2 should be classified as new species in the genus *Gambierdiscus*.

Ostreopsis spp.

Kim et al. (2011) reported the presence of some *Ostreopsis* spp. in the coastal waters of Jeju Island, and since then several other *Ostreopsis* spp. have been found (Table 1) (Kang et al. 2013, Shah et al. 2013a, 2013b, Kim and Seo 2019, Lee and Park 2020). The first *Ostreopsis* species described in detail using molecular analysis and SEM observations was *Ostreopsis* cf. *ovata* (Kang et al. 2013). The overall cell shape and plate formula of the Korean strain *O. cf. ovata* OVJJ1 are similar to those of *O. ovata* and *O.*

cf. *ovata* found in the waters of other countries. Moreover, the D8–D10 sequences of the LSU of the Korean *O. cf. ovata* OVJJ1 are 0–2.6% different from those of the Japanese strains of *Ostreopsis* sp. (Kang et al. 2013). The Korean *O. cf. ovata* OVJJ1 formed a distinct clade together with the Japanese strains of *Ostreopsis* sp. in the “*Ostreopsis* sp. 1” clade, which is one of the subclades in the *O. ovata* species complex (Sato et al. 2011, Kang et al. 2013, Kim and Seo 2019, Lee and Park 2020). Although the D8–D10 sequences of the LSU rDNA of *Ostreopsis* species in the *O. ovata* species complex show three separate genotypes, *O. cf. ovata*, *Ostreopsis* sp. 1, and *Ostreopsis* sp. 2 (Sato et al. 2011), whether the three clades represent distinct species remains uncertain (Parsons et al. 2012, Pavaux et al. 2020, Tester et al. 2020). According to Kang et al. (2013), the cell size, length of the 1p plate, and cingulum displacement of *O. cf. ovata* OVJJ1 are different from those of *O. cf. ovata* strains found in the waters of other countries (Kang et al. 2013). Therefore, if unique morphological traits, other than the aforementioned morphological characters, are discovered for *Ostreopsis* sp. 1 in future studies, the Korean *O. cf. ovata* OVJJ1 and the strains in the “*Ostreopsis* sp. 1” clade can be designated as a new species in the genus *Ostreopsis*.

In addition to the *O. cf. ovata* / *Ostreopsis* sp. 1 strains, the *Ostreopsis* sp. 6 17JJ0908 strain was recently reported from the waters off Jeju Island (Lee and Park 2020). The 19 isolates including the 17JJ0908 strain formed a distinct “*Ostreopsis* sp. 6” clade along with other strains from Japan that have been suggested to constitute a new species (Sato et al. 2011, Lee and Park 2020). Some morphological characteristics of the Korean *Ostreopsis* sp. 6 17JJ0908, such as the uniform size of the thecal pores and a body undulation of the cingulum, are similar to those of *Ostreopsis siamensis* (Schmidt 1901, Fukuyo 1981, Lee and Park 2020). However, the cell size and the shape in the lateral view of the Korean strain of *Ostreopsis* sp. 6 17JJ0908 are different from those of *O. siamensis* (Schmidt 1901, Fukuyo 1981, Lee and Park 2020). Therefore, further studies are needed to test whether the Korean strain of *Ostreopsis* sp. 6 is *O. siamensis*.

Amphidinium spp.

Kim et al. (2011) were the first to report the presence of *Amphidinium* spp. in the coastal waters of Jeju Island. Later, detailed morphological and molecular characteristics of *Amphidinium massartii* were revealed through SEM and phylogenetic analyses (Lee et al. 2013). The morphology of the Korean strain *A. massartii* AMJJ1, such

as its overall shape and body scales, coincides with that of an *A. massartii* strain isolated from Australia (Murray et al. 2012, Lee et al. 2013). Moreover, the sequences of 5.8S, ITS2, and cytochrome *b* of Korean *A. massartii* strains (AMJJ1, AMJJ2, and AMJJ3) were identical with those of the Australian *A. massartii* CS-259 (Lee et al. 2013). Recent phylogenetic and toxicity analyses conducted by Karafas et al. (2017) suggested that the strains in the non-toxic *A. massartii* clade 1 and the toxic *A. cf. massartii* clade 2, which includes the Korean strains of *A. massartii*, may be two distinct species. Nonetheless, the separation of clades 1 and 2 as two species has not been supported by unique morphological characteristics, and the status of the Korean strains of *A. massartii* remains unchanged.

Two benthic *Amphidinium* species, *A. carterae* and *A. operculatum*, have been reported in the waters off Jeju Island (Shah et al. 2013a, 2013b). Their morphological characteristics were examined only under a light microscope, and further taxonomical studies based on morphological and molecular characteristics are required for these *Amphidinium* spp.

Prorocentrum spp.

Some benthic *Prorocentrum* species such as *P. concavum*, *P. emarginatum*, *P. fukuyoi*, *P. lima*, and *P. mexicanum* (previously reported as *P. rhathymum* or *P. cf. rhathymum* in Lim et al. 2013, Shah et al. 2013a, 2013b) have been reported in the coastal waters of Jeju Island (Table 1). Except for *P. mexicanum* PRJJ1, morphological characteristics of these species have been examined only under a light microscope, while the molecular characterizations of most species are lacking.

Some morphological characteristics of the Korean strain of *P. mexicanum* PRJJ1, such as the oval-shaped cell with a smooth cell surface, a simple collar-shaped spine, and the pattern of the pores on the valves, are similar to those of the original *P. rhathymum* isolated from the Virgin Islands (Loeblich et al. 1979, Lim et al. 2013). In contrast, the LSU rDNA sequences of the Korean *P. cf. rhathymum* strains (PRJJ1, PRJJ2, and PRJJ3) are similar to those of both *P. rhathymum* and *P. mexicanum*; the Korean strains of *P. cf. rhathymum* also formed a clade with both *P. rhathymum* and *P. mexicanum* strains from different countries (Lim et al. 2013). Recently, *P. rhathymum* has been revealed as a junior synonym of *P. mexicanum* based on morphological and molecular analyses (Gómez et al. 2017). Therefore, at least five benthic *Prorocentrum* species, including *P. mexicanum*, have been reported from the Korean waters so far.

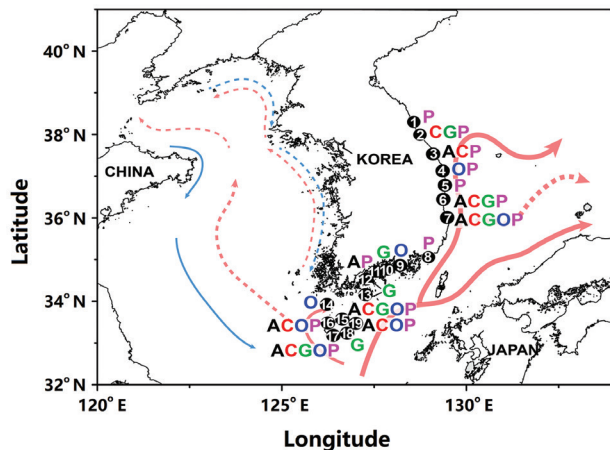


Fig. 2. Distribution of *Amphidinium* spp. (A in black), *Prorocentrum* spp. (P in pink), *Coolia* spp. (C in red), *Ostreopsis* spp. (O in blue), and *Gambierdiscus* spp. (G in green) in Korean waters. Blue lines indicate cold coastal currents and red lines indicate the warm Kuroshio Current and its branches. Sites: 1, Sokcho; 2, Yangyang; 3, Samcheok; 4, Uljin; 5, Wolsong; 6, Yeongdeok; 7, Pohang; 8, Busan; 9, Goseong; 10, Namhae; 11, Yeosu; 12, Goheung; 13, Baek Island; 14, Chuja Island; 15, Hamduck; 16, Hyupjae / Hamo; 17, Hwasun; 18, Seop Island; 19, Sinyang / Kimnyung. Data were obtained from Baek (2012a, 2012b), Shah et al. (2013a, 2013b, 2014a), and Lee and Park (2018).

GEOGRAPHICAL DISTRIBUTION OF BENTHIC DINOFLAGELLATES IN KOREAN WATERS

Prior to 2009, Korean waters were not included among the locations where benthic dinoflagellates were found (Litaker et al. 2010, Kim et al. 2011, Rhodes 2011). Since the first report of all major genera of benthic dinoflagellates, *Amphidinium*, *Coolia*, *Gambierdiscus*, *Ostreopsis*, and *Prorocentrum*, in Korean waters (Kim et al. 2011), the number of studies on benthic dinoflagellates in Korean waters largely increased (Baek 2012a, 2012b, Jeong et al. 2012a, 2012b, Kang et al. 2013, Lee et al. 2013, Lim et al. 2013, Shah et al. 2013a, 2013b, 2014a, 2014b, Jang et al. 2018, Kim and Seo 2019, Lee and Park 2020, Park et al. 2020). Species belonging to these genera have been continuously reported in the South and the East Sea of Korea, including Jeju Island (Fig. 2). The Kuroshio Current begins east of the Philippines and flows northeastward, and its branches affect the South and the East Sea of Korea (Lie and Cho 2016). These currents have likely introduced benthic dinoflagellates living in tropical waters into the Korean temperate waters and facilitated their distribution along the Korean Peninsula as a result of the east-northward range expansion (Fig. 2). Under these circumstances, it is critical to determine whether these dinoflagellates can survive and overwinter in the South and

East Sea of Korea. One of the highest latitudes at which *Coolia* spp. were found in the Pacific Ocean is in the East Sea of Korea, whereas the highest latitude at which *Coolia* spp. are found in the Atlantic Ocean is in Nieuwpoort, Belgium (51.1° N) (Leaw et al. 2016). Before the presence of *C. canariensis* and *C. malayensis* in Korean waters was confirmed by Jeong et al. (2012b), the former had been found only in the Atlantic Ocean and Australian waters (Fraga et al. 2008, Laza-Martinez et al. 2011) and the latter only in Malaysia (Leaw et al. 2010, 2016). Therefore, the discovery of these two *Coolia* species in Korean waters extended the known distribution of *C. canariensis* and *C. malayensis* into the temperate waters of the North Pacific Ocean (Jeong et al. 2012b).

HOST PREFERENCE AND ABUNDANCE OF BENTHIC DINOFLAGELLATES IN KOREAN WATERS

Amphidinium spp., *Coolia* spp., *Gambierdiscus* spp., *Ostreopsis* spp., and *Prorocentrum* spp. have been observed on the thalli of the following macroalgae collected from the South Sea and the East Sea: the chlorophytes *Cladophora wrightiana* and *Ulva pertusa* (Table 2), the phaeophytes *Chordaria flagelliformis*, *Colpomenia sinuosa*, *Dictyopteris divaricata*, *D. proliferata*, *Ecklonia cava*, *Padina arborescens*, *Sargassum horneri*, and *Sargassum* sp. (Table 3), and the rhodophytes *Chondrus ocellatus*, *Gelidium amansii*, *Martensia* sp., *Plocamium telfairiae*, and *Pterocladia capillacea* (Table 4). *Ostreopsis* species were found on most macroalgae sampled, while *Gambierdiscus* were rarely found compared with the other benthic dinoflagellate genera (Tables 2–4). Furthermore, Kim et al. (2011) reported that the highest abundance of *Ostreopsis* spp. was found on the filamentous-shaped *Derbesia* sp. (Table 2), while *Amphidinium*, *Coolia*, *Gambierdiscus*, and *Prorocentrum* were most abundant on the sheet-like *Martensia* sp. (Table 4). Many studies have examined the host preferences of benthic dinoflagellates, but no clear correlation between the two has been established (Carlson et al. 1984, Bomber et al. 1989, Yong et al. 2018, Mustapa et al. 2019, Lee et al. 2020, Park et al. 2020). For example, Bomber et al. (1989) and Carlson et al. (1984) reported the greatest abundance of *G. toxicus* on the sheet-like and slippery macroalga *Dictyota dichotoma* in waters of the Florida Keys and Virgin Islands. In contrast, Parsons and Preskitt (2007) found that *Gambierdiscus* sp. and *P. lima* preferred a filamentous host, whereas *Ostreopsis* sp. favored sheet-like macroblades.

Some macroalgae have been suggested as unfavor-

able hosts for some benthic dinoflagellates. For instance, Parsons and Preskitt (2007) reported that the rhodophyte *Tolypocladia glomerulata* may be a poor host for *O. ovata*. Similarly, the chlorophyte *Ulva rigida*, the phaeophyte *D. dichotoma*, and the rhodophyte *Rhodymenia pseudopalmeta* negatively affected the growth of *Ostreopsis* cf. *ovata* (Accoroni et al. 2015, Ben Gharbia et al. 2017). Therefore, allelopathic effects by macroalgae on certain

benthic dinoflagellate species may affect host selectivity by the latter as well as the morphology of the former. More studies on the allelopathic effects of macroalgae on benthic dinoflagellates are required to understand host selectivity by benthic dinoflagellates.

The maximum abundance of *Coolia* spp. (0.7×10^3 cells g⁻¹ wet weight [ww]) (Table 5) in Korean waters is much lower than that reported for *C. monotis* in the

Table 2. The abundance (cells g⁻¹ wet weight) of benthic dinoflagellates (*Amphidinium* spp., *Coolia* spp., *Gambierdiscus* spp., *Ostreopsis* spp., and *Prorocentrum* spp.) living on the thalli of diverse Chlorophyta collected from the coast of Jeju Island and the southern coast of Korea

Chlorophyta	Surface types	Morphology	<i>Amphidinium</i>	<i>Coolia</i>	<i>Gambierdiscus</i>	<i>Ostreopsis</i>	<i>Prorocentrum</i>	Reference
<i>Cladophora japonica</i>	H	FI	NA	NA	56.37	NA	NA	Baek (2012b)
<i>C. wrightiana</i>	H	FI	0–22	6	39	102–758	0–6	Kim et al. (2011), Shah et al. (2013b)
<i>Cladophoropsis herpestica</i>	H	FI	0	0	173	231	0	Kim et al. (2011)
<i>Codium fragile</i>	H	AR	25	0	0	21	8	Kim et al. (2011), Shah et al. (2013b)
<i>Derbesia</i> sp.	S	FI	0	0	1,595	8,660	0	Kim et al. (2011)
<i>Enteromorpha linza</i>	S	FO	14	4	0	57	25	Shah et al. (2013b)
<i>Ulva pertusa</i>	S	FO	23	3–237	0–500	52–342	8–53	Kim et al. (2011), Baek (2012b), Shah et al. (2013b)

H, hard; FI, filamentous; NA, not available; AR, arborescent; S, slippery; FO, foliaceous.

Table 3. The abundance (cells g⁻¹ wet weight) of benthic dinoflagellates (*Amphidinium* spp., *Coolia* spp., *Gambierdiscus* spp., *Ostreopsis* spp., and *Prorocentrum* spp.) living on the thalli of diverse Phaeophyta collected from the coast of Jeju Island and the southern coast of Korea

Phaeophyta	Surface types	Morphology	<i>Amphidinium</i>	<i>Coolia</i>	<i>Gambierdiscus</i>	<i>Ostreopsis</i>	<i>Prorocentrum</i>	Reference
<i>Chordaria flagelliformis</i>	S	FI	0–121	0–339	1,770	364	97	Kim et al. (2011)
<i>Champia expansa</i>	S	FO	35	30	0	48	15	Shah et al. (2013b)
<i>Colpomenia sinuosa</i>	S	FO	0–68	11	136	32–545	23	Kim et al. (2011), Shah et al. (2013b)
<i>Dictyopteris divaricata</i>	S	FO	0–37	15	0–200	12–216	6–12	Kim et al. (2011), Shah et al. (2013b)
<i>D. prolifera</i>	S	FO	33	38	1–60	43–164	0–16	Kim et al. (2011), Baek (2012b), Shah et al. (2013b)
<i>D. undulata</i>	S	FO	0	0	62	NA	0	Kim et al. (2011)
<i>Dictyota okamurae</i>	S	FO	0	0	1,000	185	0	Kim et al. (2011)
<i>Ecklonia cava</i>	S	FO	0–23	2–33	0–53	0.4–69	0–8	Kim et al. (2011), Baek (2012b), Shah et al. (2013b)
<i>Hizikia fusiformis</i>	S	AR	5	42	0	69	25	Shah et al. (2013b)
<i>Padina arborescens</i>	S	FO	0–137	0–652	8–789	583	171	Kim et al. (2011), Baek (2012b)
<i>Sargassum confusum</i>	S	AR	8	18	0	19	36	Shah et al. (2013b)
<i>S. honeri</i>	S	AR	22	24	0–1.33	57	28	Baek (2012b), Shah et al. (2013b)
<i>S. macrocarpum</i>	S	AR	11	30	0	49	23	Shah et al. (2013b)
<i>S. thunbergii</i>	S	FI	19	23	0	0.5–25	23	Shah et al. (2013b), Kim and Seo (2019)
<i>S. siliquastrum</i>	S	AR	0–6	0–17	0	37–121	0–27	Kim et al. (2011), Shah et al. (2013b)
<i>Sargassum</i> sp.	S	AR	0–10	0–121	343	434	30	Kim et al. (2011)
<i>Scytosiphon lomentaria</i>	S	FI	NA	NA	NA	1	NA	Kim and Seo (2019)
<i>Undaria pinnatifida</i>	S	FO	NA	NA	0–10	NA	NA	Baek (2012b)
<i>Zonaria diesingiana</i>	S	FO	0	0	111	44–94	0	Kim et al. (2011)

S, slippery; FI, filamentous; FO, foliaceous; NA, not available; AR, arborescent.

northwestern Mediterranean Sea (143×10^3 cells g^{-1} ww) (Table 5) (Vila et al. 2001). The maximum abundance of *Gambierdiscus* spp. ($\sim 5 \times 10^3$ cells g^{-1} ww) obtained from the waters off Jeju Island is lower than that in New South Wales, Australia (8×10^3 cells g^{-1} ww) (Table 5) (Kohli et al. 2014). The maximum abundance of *Ostreopsis* spp. ($\sim 9 \times 10^3$ cells g^{-1} ww) on *Derbesia* sp. in Korean waters is much lower than those reported in other subtropical or temperate locations (14×10^5 cells g^{-1} ww) (Table 5). The maximum abundance of *Prorocentrum* spp. ($\sim 0.3 \times 10^3$ cells g^{-1} ww) in Korean waters is lower than that in Florida (1.3×10^3 cells g^{-1} ww), but similar to that in the subtropical regions of Okinawa, Japan (Table 5). This evidence

suggests that the abundance of these benthic genera may be lower in temperate Korean waters than in subtropical and other temperate waters. Environmental conditions, such as water temperature or nutrient concentrations around Korea, may still be less favorable for these five benthic dinoflagellate genera compared with the conditions in subtropical and other temperate waters.

GRAZERS OF BENTHIC DINOFLAGELLATES IN KOREAN WATERS

Grazers are known to influence the abundance of ben-

Table 4. The abundance (cells g^{-1} wet weight) of benthic dinoflagellates (*Amphidinium* spp., *Coolia* spp., *Gambierdiscus* spp., *Ostreopsis* spp., and *Prorocentrum* spp.) living on the thalli of diverse Rhodophyta collected from the coast of Jeju Island and the southern coast of Korea

Rhodophyta	Surface types	Morphology	<i>Amphidinium</i>	<i>Coolia</i>	<i>Gambierdiscus</i>	<i>Ostreopsis</i>	<i>Prorocentrum</i>	Reference
<i>Agarophyton vermiculophyllum</i> (= <i>Gracilaria vermiculophylla</i>)	S	FI	8	14	0	52	24	Shah et al. (2013b)
<i>Amphiroa anceps</i>	H	AR	NA	NA	20	NA	NA	Baek (2012b)
<i>Ahnfeltiopsis flabelliformis</i>	S	AR	NA	NA	NA	28	NA	Kim and Seo (2019)
<i>Chondrus canaliculatus</i>	S	AR	23	8	0	49	22	Shah et al. (2013b)
<i>C. ocellatus</i>	S	FO	0–27	0–47	0–63	35–267	0–39	Kim et al. (2011), Shah et al. (2013b)
<i>Corallina pilulifera</i>	H	AR	16	7	0	40	13	Shah et al. (2013b)
<i>Corallina</i> sp.	H	AR	0	0	33–993	28–307	33	Kim et al. (2011)
<i>Galaxaura apiculata</i>	H	AR	8	26	0	48	22	Shah et al. (2013b)
<i>G. falcate</i>	H	AR	21	23	0	50	21	Shah et al. (2013b)
<i>Gelidium amansii</i>	S	AR	0–13	0–21	4–426	3–688	24–233	Kim et al. (2011), Baek (2012b), Shah et al. (2013b), Kim and Seo (2019)
<i>Gracilaria bursa-pastoris</i>	S	AR	NA	NA	NA	2	NA	Kim and Seo (2019)
<i>G. textorii</i>	S	FO	NA	NA	0–6	NA	NA	Baek (2012b)
<i>Gracilaria</i> sp.	S	AR	21	16	0	38	16	Shah et al. (2013b)
<i>Grateloupia angusta</i>	S	AR	NA	NA	0–24	NA	NA	Baek (2012b)
<i>G. asiatica</i>	S	AR	16	22	0	46	17	Shah et al. (2013b)
<i>G. filicina</i>	S	AR	NA	NA	NA	2–158	NA	Kim and Seo (2019)
<i>Hypnea charoides</i>	S	AR	12	28	0	48	20	Shah et al. (2013b)
<i>Jania pedunculata</i> var. <i>adhaerens</i>	H	AR	0.7	27	0	75	28	Shah et al. (2013b)
<i>Laurencia okamurae</i>	H	AR	NA	NA	NA	35	NA	Kim and Seo (2019)
<i>Lithothamnion</i> sp.	H	AR	0	0	25	NA	0	Kim et al. (2011)
<i>Martensia</i> sp.	S	FO	0–406	0–710	0–4,871	10–3,349	23–304	Kim et al. (2011), Shah et al. (2013b)
<i>Plocamium cartilagineum</i>	S	AR	0	0	255	255	0	Kim et al. (2011)
<i>P. telfairiae</i>	S	AR	0–13	0–24	0–1,477	50–966	0–31	Kim et al. (2011), Shah et al. (2013b)
<i>Polysiphonia morrowii</i>	S	FO	NA	NA	NA	7	NA	Kim and Seo (2019)
<i>Pterocladia capolacea</i>	S	AR	0–18	0–23	0–1,599	50–837	0–38	Kim et al. (2011), Shah et al. (2013b)
<i>Wrangelia tanegana</i>	H	AR	20	10	0	33	15	Shah et al. (2013b)

S, slippery; FI, filamentous; H, hard; AR, arborescent; NA, not available; FO, foliaceous.

thic dinoflagellates (Yoo et al. 2015, Pavaux et al. 2020, You et al. 2020). Some mixotrophic and heterotrophic dinoflagellates, ciliates, and heterotrophic nanoflagellates have been shown to feed on the Korean strains of several benthic dinoflagellates, such as *Ostreopsis* cf. *ovata*, *Coolia* spp., *G. jejuensis* (previously reported as *G. caribaeus* in Jeong et al. 2012a, 2016, Kwon et al. 2017, Lim et al. 2018, Ok et al. 2018), and *P. lima* (Table 6); the heterotrophic dinoflagellates *Gyrodinium moestrupii* and *Polykrikos kofoidii* can feed on *O. cf. ovata* OVJ1, exhibiting higher ingestion rates when feeding on *O. cf. ovata* than on other prey species (Yoo et al. 2015). *C. canariensis* CCJ1 and *C. malayensis* CMJ2 were fed by the mixotrophic dinoflagellates *Takayama helix* and *T. tasmanica* and the heterotrophic nanoflagellate *Katablepharis japonica* (Jeong et al. 2016, Kwon et al. 2017, Lim et al. 2018) (Table 6). Furthermore, *G. jejuensis* GCJ1 was fed by *T. helix* and *T. tasmanica* (Table 6). Benthic dinoflagellates, especially *Ostreopsis*, can detach easily from substrates and float in

the water column (Mangialajo et al. 2011, Pavaux et al. 2020). Korea experiences tropical cyclones almost annually (<http://www.weather.go.kr>). Thus, the vigorous water-mixing driven by tropical cyclones can release the benthic dinoflagellate cells into the water column, which temporarily increases the abundance of benthic dinoflagellates in the water column. Under these circumstances, diverse grazers can feed on benthic dinoflagellates and have a considerable impact on their populations.

TOXICITY

The Korean strains of some benthic dinoflagellates isolated from waters off Jeju Island have been revealed to have toxic compounds and show toxicity (Table 7). The *A. operculatum* HLAM2 strain exerts cytotoxicity to murine macrophage cells and human tumor cells (Table 7) (Shah et al. 2014b). The two strains *O. cf. ovata* OVJ1

Table 5. Comparison of the maximum abundances (MA, cells g⁻¹ wet weight) of benthic dinoflagellates in the genera *Amphidinium*, *Coolia*, *Gambierdiscus*, *Ostreopsis*, and *Prorocentrum* reported from the waters of temperate and subtropical-temperate regions

Species	Location	MA	Reference
<i>Coolia</i> spp.	Jeju Island, Korea	710	Kim et al. (2011)
	South-East Sea, Korea	3	Baek (2012a)
<i>C. monotis</i>	North Aegean Sea, Greece	16,000	Aligizaki and Nikolaidis (2006)
	NW Mediterranean Sea	143,000	Vila et al. (2001)
<i>Gambierdiscus</i> spp.	Back Islands, Korea	20	Baek (2012b)
	Jeju Island, Korea	56	Baek (2012b)
	Jeju Island, Korea	4,870	Kim et al. (2011)
	South-East Sea, Korea	10	Baek (2012a)
	New South Wales, Australia	8,255	Kohli et al. (2014)
<i>G. toxicus</i>	Knight key, Florida	2,279	Bomber et al. (1989)
<i>Ostreopsis</i> spp.	Jeju Island, Korea	8,660	Kim et al. (2011)
	Pohang, Korea	1,588	Lee and Park (2018)
	Jeju Island, Korea	158	Kim and Seo (2019)
<i>Ostreopsis</i> sp.	South-East Sea, Korea	140	Baek (2012a)
<i>Ostreopsis</i> spp.	Peter the Great Bay	71,000	Selina et al. (2014)
<i>Ostreopsis</i> cf. <i>ovata</i>	Jeju Island, Korea	3,204	Park et al. (2020)
<i>Ostreopsis</i> sp.	NW Mediterranean Sea	596,000	Vila et al. (2001)
<i>O. siamensis</i>	Auckland, New Zealand	1,400,000	Shears and Ross (2009)
	Knight key, Florida	308	Bomber et al. (1989)
<i>O. heptagona</i>	Knight key, Florida	394	Bomber et al. (1989)
<i>Ostreopsis</i> spp.	North Aegean Sea, Greece	405,000	Aligizaki and Nikolaidis (2006)
<i>Prorocentrum</i> spp.	Jeju Island, Korea	304	Kim et al. (2011)
<i>Prorocentrum lima</i>	South-East Sea, Korea	52	Baek (2012a)
<i>P. concavum</i>	Knight key, Florida	133	Bomber et al. (1989)
<i>P. mexicanum</i>	Knight key, Florida	844	Bomber et al. (1989)
<i>P. lima</i>	Knight key, Florida	1,379	Bomber et al. (1989)
<i>Prorocentrum</i> spp.	Kochi, Tosa Bay, Japan	29	Nishimura et al. (2020)
	Okinawa, Nakagusuku Bay, Japan	267	Nishimura et al. (2020)
<i>Amphidinium</i> spp.	Jeju Island, Korea	406	Kim et al. (2011)
	South-East Sea, Korea	2	Baek (2012a)

Bold letters indicate highest maximum abundance reported for each genus.

Table 6. Predators of the Korean strains of benthic dinoflagellates reported to date

Benthic dinoflagellate (strain)	Predator group	Predator species (strain)	Feeding	GR	Reference
<i>Ostreopsis cf. ovata</i> (OVJ1)	HTD	<i>Gyrodinium dominans</i>	Y	Negative	Yoo et al. (2015)
	HTD	<i>Gyrodinium moestrupii</i>	Y	0.862 ^a	Yoo et al. (2015)
	HTD	<i>Gyrodinium spirale</i>	N	NG	Yoo et al. (2015)
	HTD	<i>Oxyrrhis marina</i>	Y	Negative	Yoo et al. (2015)
	HTD	<i>Polykrikos kofoidii</i>	Y	0.725 ^a	Yoo et al. (2015)
	Ciliate	<i>Strobilidium</i> sp.	N	NG	Yoo et al. (2015)
	HTD	<i>Pfiesteria piscicida</i>	Y	Negative	Yoo et al. (2015)
	HTD	<i>Stoeckeria algicida</i>	N	NG	Yoo et al. (2015)
	HTD	<i>Protoperidinium bipes</i>	N	NG	Yoo et al. (2015)
	<i>Coolia canariensis</i> (CCJ1)	MTD	<i>Takayama helix</i> (CCMP3082)	Y	NA
MTD		<i>Takayama tasmanica</i> (CAWD115)	Y	NA	Lim et al. (2018)
<i>Coolia malayensis</i> (CMJ2)	MTD	<i>Takayama helix</i> (CCMP3082)	Y	NA	Jeong et al. (2016)
	MTD	<i>Takayama tasmanica</i> (CAWD115)	Y	NA	Lim et al. (2018)
	HNF	<i>Katablepharis japonica</i> (KJMS1610)	Y	NA	Kwon et al. (2017)
<i>Gambierdiscus jejuensis</i> (= previously reported as <i>G. caribaeus</i> GCJ1)	HNF	<i>Katablepharis remigera</i> (KRJH1707)	N	NG	Ok et al. (2018)
	MTD	<i>Takayama helix</i> (CCMP3082)	Y	NA	Jeong et al. (2016)
	MTD	<i>Takayama tasmanica</i> (CAWD115)	Y	NA	Lim et al. (2018)
	HNF	<i>Katablepharis japonica</i> (KJMS1610)	N	NG	Kwon et al. (2017)
<i>Prorocentrum lima</i> (DF-114)	HNF	<i>Katablepharis remigera</i> (KRJH1707)	N	NG	Ok et al. (2018)
	HTD	<i>Pfiesteria piscicida</i> (CCMP2091)	Y ^b	NA	You et al. (2020)
	HTD	<i>Oxyrrhis marina</i>	N	NA	You et al. (2020)
	HTD	<i>Gyrodinium dominans</i>	Y	-0.193	You et al. (2020)
	HTD	<i>Oblea rotunda</i>	N	NA	You et al. (2020)
	HTD	<i>Polykrikos kofoidii</i>	Y	-0.2	You et al. (2020)
	Ciliate	<i>Strombidinopsis</i> sp.	Y	NA	You et al. (2020)

GR, growth rate (d⁻¹) of each predator; HTD, heterotrophic dinoflagellate; Y, able to feed on benthic dinoflagellate; N, not able to feed on benthic dinoflagellate; NG, no growth; MTD, mixotrophic dinoflagellate; NA, not available; HNF, heterotrophic nanoflagellate.

^aMaximum growth rate.

^bAble to feed only on motionless prey cells.

Table 7. Toxicity of the strains of benthic dinoflagellates isolated from waters off Jeju Island, Korea

Species	Target for toxicity test	Toxicity / Active compound	Reference
<i>Amphidinium carterae</i> (JHWAC)	Murine macrophage cell, human promyelocytic leukemia tumor cell	NT	Shah et al. (2014b)
<i>A. massartii</i> (AMJJ1)	Brine shrimp	NT	Lee et al. (2013)
<i>A. operculatum</i> (HLAM2)	Murine macrophage cell, human promyelocytic leukemia tumor cell	Cytotoxicity	Shah et al. (2014b)
<i>A. operculatum</i> (SIAM1)	Murine macrophage cell, human promyelocytic leukemia tumor cell	NT	Shah et al. (2014b)
<i>Coolia malayensis</i> (JHACO6)	Murine macrophage cell, human promyelocytic leukemia tumor cell	NT	Shah et al. (2014b)
<i>C. malayensis</i> (JHWCO1)	Murine macrophage cell, human promyelocytic leukemia tumor cell	NT	Shah et al. (2014b)
<i>C. malayensis</i> (JHLCO6)	Murine macrophage cell, human promyelocytic leukemia tumor cell	NT	Shah et al. (2014b)
<i>Gambierdiscus jejuensis</i> (GJ1703a)	Brine shrimp	NT	Our unpublished data
<i>Gambierdiscus</i> sp.	Copepod	Mortality of nauplii	Lee et al. (2014)
<i>Ostreopsis cf. ovata</i> (OVJJ1)	Brine shrimp	Cytotoxicity / Ostreol A	Hwang et al. (2013)
<i>O. cf. ovata</i> (OVJJ1)	Hepatocarcinoma, neuroblastoma, colon cancer cells	Cytotoxicity / Ostreol B	Hwang et al. (2018)
<i>O. ovata</i> (JHAOS5)	Murine macrophage cell, human promyelocytic leukemia tumor cell	Cytotoxicity	Shah et al. (2014b)
<i>O. ovata</i> (JHWOS13)	Murine macrophage cell, human promyelocytic leukemia tumor cell	NT	Shah et al. (2014b)
<i>Prorocentrum lima</i> (Plima-YD-5)	Hepatocarcinoma, neuroblastoma, colon cancer cells	Cytotoxicity / Limaol	Yang et al. (2017), Lee et al. (2019)
<i>P. rhathymum</i> (JHWPMX1)	Murine macrophage cell, human promyelocytic leukemia tumor cell	NT	Shah et al. (2014b)

NT, non-toxic.

and *O. ovata* JHAOS5 exhibit cytotoxicity toward brine shrimp and / or cell lines (Hwang et al. 2013, 2018, Shah et al. 2014b); ostreol A and B from *O. cf. ovata* OVJJ1 were identified as new active compounds (Hwang et al. 2013, 2018). The strain *P. lima* Plima-YD-5 similarly exhibited cytotoxicity toward cell lines, and limaol was isolated from this strain (Yang et al. 2017, Lee et al. 2019). *Gambierdiscus* sp. is toxic to a copepod (Lee et al. 2014), but *G. jejuensis* GJ1703a shows no toxicity toward brine shrimp *Artemia salina* (unpublished data).

The Korean strains of *C. malayensis* (JHACO6, JH-WCO1, and JHLCO6) did not exhibit cytotoxicity toward murine macrophage cells and human tumor cells (Shah et al. 2014b), although the *C. malayensis* (previously *C. monotis*) strain isolated from other temperate regions, such as New Zealand, has been reported to have toxic effects on the larvae of *Artemia salina* and *Haliotis virginea* (Rhodes and Thomas 1997) (Table 7). Therefore, there may be differences in toxicity levels between different *C. malayensis* strains.

Among these toxic benthic dinoflagellate strains, the cultures of *P. lima* Plima-YD-5 and *O. cf. ovata* OVJJ1 were established from the cells detached from the thalli of popular edible macroalgae *Sargassum fulvellum* and *G. amansii*, respectively (Hwang et al. 2013, Yang et al. 2017, Hwang and Park 2020). Along the coastal waters of the Korean Peninsula, there are many regions where *S. fulvellum* and *G. amansii* are naturally abundant or largely cultivated (Hwang and Park 2020, Korea Fisheries Resources Agency 2020). The area along the coast of the Korean Peninsula that was covered by a seaweed aquaculture, reached approximately 21,490 ha by the end of 2019 (Korea Fisheries Resources Agency 2020). These seaweed farms may provide habitats for these benthic dinoflagellates. It is, therefore, worthwhile to monitor the toxin concentrations produced by these dinoflagellates in the waters of the eastern, western, and northern parts of Korea.

ECOLOGICAL, ECONOMIC, AND SOCIAL IMPORTANCE OF THE PRESENCE OF BENTHIC DINOFLAGELLATES IN KOREAN WATERS

Signal for an increase in the temperature of Korean coastal waters

Over several decades, the sea surface temperature (SST) around Korea has increased at an accelerated rate owing to global warming. For example, the annual aver-

age SST increased by 0.07°C for 80 years, from 1916 to 1995 (Kang 2000). A recent study reported the annual average SST increase of 1.23°C from 1968 to 2018; this increasing SST trend was particularly dominant during winter (Han and Lee 2020). The rate of change became more pronounced in recent decades than it was during the past 80 years, which implies that the coastal SST in Korea has a tendency to shift from temperate to that typical for the subtropical climate zone. Such warming in Korean coastal waters may cause the northward expansion of tropical and subtropical benthic dinoflagellate species. For example, *Coolia tropicalis* has been found only in tropical waters of Malaysia to date (Leaw et al. 2016). However, the *C. tropicalis* UTSH11D5 strain isolated from Australia can survive in temperatures as low as 10°C (Table 8) (Larsson et al. 2019). From 1984 to 2013, the average SST in the South Sea of Korea in February and December was more than 10°C and as high as 19°C around Jeju Island (Kwak et al. 2015). If this strain is accidentally introduced in the temperate waters of Korea via water currents or the ballast waters of ships, it may overwinter and survive in the Korean coastal waters. Some other tropical species such as *Coolia palmyrensis* and *Gambierdiscus ruetzleri*, which have not been found yet in Korean waters, can survive below 17°C (Tables 8 & 9). These dinoflagellates, previously not reported in Korean waters, may appear in the near future; thus, it would be worthwhile to monitor the presence of such benthic dinoflagellates regularly and to explore the conditions necessary for their survival during the winter season.

Possible risks to human health

Some *Gambierdiscus*, *Prorocentrum*, *Ostreopsis*, *Amphidinium*, and *Coolia* species are known to cause ciguatera fish poisoning, while some *Prorocentrum* species can cause diarrhetic shellfish poisoning (Ibrahim 2007, Tester et al. 2020). In some benthic dinoflagellates, such as *O. ovata* and *O. cf. ovata*, the toxin concentration per cell tends to become highest at the suboptimal temperatures, although the peak growth rate is achieved at a higher temperature (Granéli et al. 2011, Pezolesi et al. 2012). Therefore, the impact of toxins may be greater in temperate waters than in subtropical or tropical waters when toxic benthic dinoflagellates proliferate. Koreans enjoy eating raw finfish, shellfish, and seaweeds, and the seaweed aquaculture industry in Korea has expanded (Korea Fisheries Resources Agency 2020). The Ministry of Oceans and Fisheries of the Korean government reported that in 2019, the seaweed aquaculture covered an area of

90,421 ha and produced 1,812,213 tons of seaweed worth 789 million USD (Ministry of Oceans and Fisheries 2020). In addition, the shellfish aquaculture accounted for approximately 27% of all sea farming in Korea, with 527,443 tons of shellfish produced in 2019 (Ministry of Oceans and Fisheries 2020). The discovery of these potentially toxic benthic dinoflagellates in Korean waters may cause Koreans to reduce their seaweed and shellfish consumption, which may incur great financial losses for related industries. Therefore, it is worthwhile to investigate the distribution of these benthic dinoflagellates along the entire coast of Korea.

Caution is required in the establishment of underwater macroalgal forests

In 2009, the Korean government began construct-

ing marine forests to recover the marine ecosystem by providing habitats for sea animals (Korea Fisheries Resources Agency 2020). A total of 21,490 ha of macroalgal and seagrass forests were constructed along the eastern, western, and southern coasts of Korea and around Jeju Island (Korea Fisheries Resources Agency 2020). The construction of the marine forests that will cover an area of 54,000 ha is planned to be finished by 2030 (Korea Fisheries Resources Agency 2020). Macroalgal species such as *Eisenia bicyclis*, *E. cava*, *Sargassum* spp., *Undaria pinnatifida*, *Agarophyton vermiculophyllum*, *Codium fragile*, and seagrass *Zostera* spp. have been planted in these macroalgal forests; among these, only the seagrass species are non-edible (Table 10). It is likely that some of these algae will be used for human consumption. Many of the macroalgae planted in the marine forest of Korea may harbor potentially toxic epiphytic dinoflagel-

Table 8. Water temperature (T) range that allow the survival of benthic *Coolia* and *Ostreopsis* species living in the waters of Korea and other countries

Species (strain)	Climate	Location	T (°C)	Reference
<i>Coolia monotis</i>	Temperate	East Sea, Korea	16.3–35.0	Sung (2015)
<i>C. malayensis</i> (UTSMER17A5)	Temperate	Merimbula Lake, NSW, Australia	14.9–30.1	Larsson et al. (2019)
<i>C. malayensis</i> (UTSMER17A6)	Temperate	Merimbula Lake, NSW, Australia	14.5–30.2	Larsson et al. (2019)
<i>C. malayensis</i> (SKLMP_S020)	Tropical	Hong Kong, China	16.0–28.0	Li et al. (2020)
<i>C. malayensis</i> (K-0972)	Tropical	Sulu Sea, Banggi Island, Malaysia	25.0–30.0	Mohammad-Noor et al. (2013)
<i>C. monotis</i> (CM300A)	Subtropical-temperate	Knight Key, Florida, USA	21.0–35.0	Morton et al. (1992)
<i>C. monotis</i> (CAWD39)	Subtropical	Ninety Mile Beach, Northland, New Zealand	10.0–30.0	Rhodes et al. (2000)
<i>C. tropicalis</i> (UTSHI1D5)	Tropical	Heron Island Lagoon, QLD, Australia	<10.0–30.1	Larsson et al. (2019)
<i>C. tropicalis</i> (UTSHI2D4)	Tropical	Heron Island Lagoon, QLD, Australia	17.1–30.0	Larsson et al. (2019)
<i>C. tropicalis</i> (UTSHI2D1)	Tropical	Heron Island Lagoon, QLD, Australia	17.8–30.1	Larsson et al. (2019)
<i>C. tropicalis</i> (K-1156)	Tropical	Sulu Sea, Banggi Island, Malaysia	25.0–30.0	Mohammad-Noor et al. (2013)
<i>C. palmyrensis</i> (UTSHI3C5)	Tropical	Heron Island Lagoon, QLD, Australia	14.7–32.2	Larsson et al. (2019)
<i>Ostreopsis</i> sp. 1 (HJ1-4)	Temperate	Jeju Island, Korea	10.0–30.0	Kim and Seo (2019)
<i>Ostreopsis</i> sp. 1 (s0716)	Temperate	Kochi Prefecture, Japan	15.0–30.0	Tanimoto et al. (2013)
<i>O. cf. ovata</i>	Temperate	East Sea and Jeju Island, Korea	13.8–35.0	Sung (2015)
<i>O. cf. ovata</i> (s0662)	Temperate	Tosa Bay, Kochi Prefecture, Japan	17.5–30.0	Yamaguchi et al. (2012)
<i>O. cf. ovata</i> (IRTA-SMM-11-09, IRTA-SMM-11-10)	Subtropical-tropical	Catalonia, western Mediterranean Sea	19.0–28.0	Carnicer et al. (2016)
<i>O. heptagona</i> (OH 100A)	Subtropical-temperate	Knight Key, Florida, USA	16.0–31.0	Morton et al. (1992)
<i>O. siamensis</i> (OS100A)	Subtropical-temperate	Knight Key, Florida, USA	16.0–33.0	Morton et al. (1992)
<i>O. siamensis</i> (CAWD73, CAWD74, CAWD75)	Subtropical	Whatawhiwhi and Rangiputa, Northland, New Zealand	15.0–25.0	Rhodes et al. (2000)
<i>O. cf. ovata</i> (T163)	Tropical	Koh Man, Rayong, Thailand	20.0–32.5	Tawong et al. (2015)
<i>O. cf. ovata</i> (TF5OS)	Tropical	Koh Wai, Trat, South China Sea	20.0–32.5	Tawong et al. (2015)
<i>Ostreopsis</i> sp. 6 (s0587)	Subtropical	Okinawa Prefecture, Japan	17.5–30.0	Tanimoto et al. (2013)
<i>Ostreopsis</i> sp. 6 (TF29OS)	Tropical	Koh Wai, Trat, Thailand	20.0–32.5	Tawong et al. (2015)
<i>Ostreopsis</i> sp. 7 (TB30OS)	Tropical	Khao Lak, Phang-Nga, Thailand	20.0–30.0	Tawong et al. (2015)

Table 9. Water temperature (T) range that allow the survival of benthic *Gambierdiscus*, *Prorocentrum*, and *Amphidinium* species living in the waters of Korea and other countries

Species (strain)	Climate	Location	T (°C)	Reference
<i>Gambierdiscus jejuensis</i> (GCJJ1)	Temperate	Jeju Island, Korea	20.0–30.0	Jang et al. (2018)
<i>G. australes</i> (S080911_1)	Temperate	Shikoku, Japan	17.5–30.0	Yoshimatsu et al. (2014)
<i>G. carolinianus</i> (NOAA 6)	Temperate	Cape Fear, North Carolina, Atlantic Ocean	15.0–31.7	Kibler et al. (2012)
<i>G. scabrosus</i> (KW070922_1)	Temperate	Shikoku, Japan	17.5–30.0	Yoshimatsu et al. (2014)
<i>G. yasumotoi</i>	Temperate	Jeju Island, Korea	15.0–35.0	Sung (2015)
<i>Gambierdiscus</i> type 2 (M080828_2)	Temperate	Shikoku, Japan	17.5–30.0	Yoshimatsu et al. (2014)
<i>Gambierdiscus</i> type 3 (WI11G)	Temperate	Honshu, Japan	15.0–25.0	Yoshimatsu et al. (2014)
<i>G. toxicus</i> (GT600)	Subtropical-temperate	Knight Key, Florida, USA	19.5–34.0	Bomber et al. (1988)
<i>G. toxicus</i> (GT600A)	Subtropical-temperate	Knight Key, Florida, USA	19.0–35.0	Morton et al. (1992)
<i>G. belizeanus</i> (CCMP 399)	Tropical	St. Barthelemy Island, Caribbean	19.7–32.7	Kibler et al. (2012)
<i>G. caribaeus</i> (NOAA 19)	Tropical	Carrie Bow Cay, Belize, Caribbean	16.8–33.6	Kibler et al. (2012)
<i>G. caribaeus</i> (TF9G)	Tropical	Koh Wai, Trat, Thailand	20.0–35.0	Tawong et al. (2016)
<i>G. pacificus</i> (CCMP 1650)	Tropical	Moorea, Society Islands, Pacific Ocean	19.6–32.6	Kibler et al. (2012)
<i>G. ruetzleri</i> (NOAA 8)	Tropical	Carrie Bow Cay, Belize, Caribbean	16.4–33.1	Kibler et al. (2012)
<i>Gambierdiscus</i> ribotype 2 (CCMP 1655)	Tropical	Martinique, Caribbean	19.8–31.1	Kibler et al. (2012)
<i>Prorocentrum lima</i>	Temperate	Fleet Lagoon, Dorset, UK	5.0–30.0	Aquino-Cruz et al. (2018)
<i>P. lima</i> (PL 100A)	Subtropical-temperate	Knight Key, Florida, USA	19.0–35.0	Morton et al. (1992)
<i>P. concavum</i> (PC100A)	Subtropical-temperate	Knight Key, Florida, USA	19.0–33.0	Morton et al. (1992)
<i>P. mexicanum</i> (PM200A)	Subtropical-temperate	Knight Key, Florida, USA	21.0–35.0	Morton et al. (1992)
<i>P. hoffmannianum</i> (882a)	Tropical	Little Lameshur Bay, Virgin Island, USA	21.0–36.0	Morton et al. (1994)
<i>Amphidinium carterae</i>	Temperate	Jeju Island, Korea	16.8–35.0	Sung (2015)
<i>A. operculatum</i>	Temperate	Ulsan, East Sea, Korea	17.1–35.0	Sung (2015)
<i>A. klebsii</i> (AKI00A)	Subtropical-temperate	Knight Key, Florida, USA	16.0–37.0	Morton et al. (1992)

Table 10. Macroalgal and seagrass species used for establishing sea forests in Korean waters

Species	Edibility	East coast	South coast	West coast	Jeju Island	MA	Reference
Phaeophyta							
<i>Eisenia bicyclis</i>	Edible	+		+		NI	-
<i>Ecklonia cava</i>	Edible	+	+	+	+	33/53/69	Kim et al. (2011)
<i>Ecklonia cava</i> subsp. <i>stolonifera</i>	Edible	+	+	+		NI	-
<i>Sargassum horneri</i>	Edible			+		24/1/57	Baek (2012b), Shah et al. (2013b)
<i>Sargassum macrocarpum</i>	Edible	+	+			30/0/49	Shah et al. (2013b)
<i>Sargassum fusiforme</i>	Edible		+			NI	-
<i>Sargassum fulvellum</i>	Edible	+	+	+	+	NI	-
<i>Undaria pinnatifida</i>	Edible	+	+	+		NI/10/NI	Baek (2012b)
<i>Laminaria japonica</i> (= <i>Saccharina japonica</i>)	Edible	+	+	+		NI	-
Rhodophyta							
<i>Gelidium amansii</i>	Edible		+			21/426/688	Kim et al. (2011), Shah et al. (2013b)
<i>Agarophyton vermiculophyllum</i>	Edible		+			14/0/52	Shah et al. (2013b)
Chlorophyta							
<i>Codium fragile</i>	Edible		+			0/0/21	Kim et al. (2011), Shah et al. (2013b)
Seagrass							
<i>Zostera</i> spp.	Inedible		+				-

Bold letters indicate the species on which the benthic dinoflagellates have been observed. The lists of planted species in the marine forest and edible macroalgae were obtained from Han (2010), Hwang and Park (2020), and Korea Fisheries Resources Agency (2020).

MA, maximum abundance of benthic dinoflagellates reported (*Coolia* / *Gambierdiscus* / *Ostreopsis* cells g⁻¹ wet weight of macroalga); +, planted; NI, not investigated.

lates, such as *Gambierdiscus* and *Ostreopsis* (Kim et al. 2011, Baek 2012b, Shah et al. 2013b) (Table 10). Thus, the consumption of these macroalgae harboring benthic dinoflagellates may cause illness in humans. This may be prevented by monitoring the abundance of benthic dinoflagellates in marine forests.

CONCLUSION

The epibenthic dinoflagellates *Coolia* spp., *Gambierdiscus* spp., *Ostreopsis* spp., *Prorocentrum* spp., and *Amphidinium* spp. have been found in the waters off Jeju Island and along the southern and eastern coast of Korea. The occurrence of some benthic dinoflagellates in the waters off Jeju Island may be affected by the rising sea-water temperature around Korea. The presence of toxic benthic dinoflagellates may trigger Koreans to fear consuming raw seafood and edible macroalgae and eventually cause economic losses to the seafood industry. Therefore, it is important to investigate the distribution of toxic benthic dinoflagellates and continuously monitor their abundance continuously to prevent risks to human health. Molecular techniques may allow researchers to distinguish morphologically similar species and to monitor the abundance of toxic benthic dinoflagellates. All of these efforts will provide a better understanding of the epiphytic and benthic dinoflagellates in Korean waters.

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CONFLICTS OF INTEREST

The authors declare that they have no potential conflicts of interest.

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