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Biogeography of intertidal and subtidal native and invasive barnacles in Korea in relation to oceanographic current ecoregions and global climatic changes

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Abstract

The coastline of the Korean Peninsula is influenced by three major oceanographic ecoregions, including the estuarine Yellow Sea ecoregion on the west coast, the warmer and saline East China Sea ecoregion on the south coast, and the cold East Sea ecoregion on the east coast. The influence of these marine ecoregions on the distribution of intertidal barnacles has not been extensively studied. The present study examines the biogeography of thoracican barnacles from intertidal and shallow subtidal zones, along the coasts of Korea. Twenty-one species in seven families were identified, including three species of coral-associated barnacles. Species composition varied significantly in the three marine ecoregions. Multivariate analysis showed barnacle assemblages were significant among the three ecoregions, although there are large overlaps of clusters between the Yellow Sea and East China Sea ecoregions. The estuarine species, *Fistulobalanus albicostatus*, occurred mainly in the Yellow Sea ecoregion; warm-water species, *Tetraclita japonica*, and sponge inhabiting barnacles *Euacasta dofleini* were observed in the East China Sea ecoregion; and cold-water species, *Balanus rostratus* and *Perforatus perforatus*, were found in the East Sea ecoregion. Four invasive barnacle species were recorded and the European barnacle *Perforatus perforatus* expanded its range northward from its recorded distribution nine years earlier. The cold-water species, *Chthamalus dalli* and *Semibalanus cariosus*, previously recorded in the East Sea ecoregion, were absent in the present survey. A trend of increasing seawater temperatures in Korean waters may have a significant impact on the distribution of cold-water species and enhance the northward invasion of *P. perforatus*.

Introduction

In the marine environment, global climatic changes often cause a shift in the geographic distribution and abundance of species (Rivadeneira & Fernández 2005; Parmesan, 2006; Mieszkowska & Sugden, 2016; Sanda *et al.*, 2019). The fauna of the rocky intertidal zone is an excellent model to investigate the impacts of global change on biota since the ecosystem is common worldwide, although it can be patchy in the Tropical Eastern Pacific compared with temperate East Pacific regions (Fenberg & Rivadeneira, 2019). For intertidal invertebrates, the rocky shore is a harsh habitat with strong selection pressure from both physical (e.g. heat and desiccation stress) and biological (e.g. competition for space) factors (Tomanek & Somero, 2002; Helmuth *et al.*, 2006). Thus, intertidal organisms are sensitive to environmental alterations and show early responses to climate change (Helmuth *et al.*, 2006; Hawkins *et al.*, 2008, 2009). Barnacles are representative organisms on rocky shores and are an ideal model for studying biogeography of intertidal assemblages as they are sessile, highly abundant and have wide distribution along rocky shorelines (Dawson *et al.*, 2010; Chan & Lee, 2012). The geographic distribution of adult intertidal barnacles is dependent on planktonic larval for dispersal in ocean currents and range shifts are easily detected (Chan *et al.*, 2007; 2008a; Chan & Lee, 2012).

The effects of climate change on distributions of marine species have been extensively studied in the UK with the support of long-term monitoring coupled with a time-series modelling project 'Marine Biodiversity and Climate Change' (MarClim) (Mieszkowska & Sugden, 2016). In the UK, distribution patterns of intertidal communities in the Western English channel over the past 70 years show that global warming has enhanced survival, expanded ranges and abundance of warm-water species (e.g. the barnacle *Chthamalus stellatus*) and has reduced the abundance of cold-water species (e.g. the barnacle *Semibalanus balanoides*) (Southward *et al.*, 1995; Thompson *et al.*, 2002; Mieszkowska *et al.*, 2014; Mieszkowska & Sugden, 2016). In the Eastern Pacific, the intertidal owl limpet *Lottia gigantean* and the barnacle *Tetraclita rubescens* extended its northern range several hundreds of km from San Francisco, USA, due to the interaction of the migration of maladapted genes to peripheral regions and with reduced selection under environmental changes including heat waves

(Dawson *et al.*, 2010; Sanford *et al.*, 2019). Compared with the Atlantic, including the UK and the Eastern Pacific, the effect of climate change on the distribution of intertidal species in the Indo-Pacific has received relatively little attention. In the west Pacific, the acorn barnacle *Hexechamaesipho pilsbryi* has expanded its distribution into tropical waters due to increased water temperatures and a shift in ocean currents (Chan *et al.*, 2008c; Tsang *et al.*, 2011). One of the invasive barnacles from European waters, *Perforatus perforatus*, was introduced to Korean waters and it is expected its range will be expanded (Choi *et al.*, 2013). Comparable changes in species composition can affect vertical zonation, geographic distribution and gene flow among populations of intertidal organisms (Southward, 1991; Southward *et al.*, 1995; Thompson *et al.*, 2002; Helmuth *et al.*, 2006; Mieszkowska *et al.*, 2007; Yorisue *et al.*, 2019).

The Indo-West Pacific region displays the highest marine biodiversity in the world (Roberts *et al.*, 2002). The region is characterized by the presence of marginal seas and complex oceanographic current systems and the biogeography of species are affected by different hydrographic regimes and also geological events (Tsang *et al.*, 2008; Dong *et al.*, 2012; Chan *et al.*, 2014; Ni *et al.*, 2014; Yu *et al.*, 2014; Wang *et al.*, 2015; Wu *et al.*, 2015; Ma *et al.*, 2019). The Korean Peninsula is surrounded by three marginal seas; the Yellow, East China and East Seas. Kim (1973, 1977) divided the coastal waters of the Korean Peninsula into three biogeographic regions; the Yellow Sea on the west coast, the Korean Strait on the South Coast and the East Sea on the east coast in consideration of species diversity, geographic distribution and abundance patterns of intertidal assemblages. Kim (1982) and Cha *et al.* (2004) further separated Jeju Island from the Korean Strait region as a fourth biogeographic zone, based on the geographic distribution of marine crab and sea anemone assemblages. However, more recent oceanographic studies based on differences in temperature, salinity and zooplankton biomass (Rebstock & Kang, 2003; Han & Lee, 2020; Figure 1) revealed three oceanographic zones, including the Yellow Sea, East China Sea and East Sea. The division of these three oceanographic zones were also supported by Spalding *et al.* (2007) who defined Korean waters as being located in the Northern Temperate Pacific Province, with three distinct ecoregions, the Yellow Sea, the Sea of Japan (=East Sea) and East China Sea ecoregions.

Under the influence of global climatic change, seawater temperature in the world has an increasing trend of 0.05°C per decade (Intergovernmental Panel on Climate Change, 2019). In the last 51 years, an increase of 1.23°C has been recorded, with an especially prominent increase in Korean waters some 2.5 times greater than the global trend (Belkin, 2009; Han & Lee, 2020). Seawater temperature in all three ecoregions showed an upward trend from 1968 to 2018 (Han & Lee, 2020; Figure 2). It is important to survey the distribution patterns of intertidal barnacles along the coastlines of these oceanographic ecoregions. Such patterns can be compared with historical records (i.e. taxonomic records and previous literature, see Mieszkowska & Sugden, 2016) to assess changes and will provide data with which to predict future distribution changes assuming continued global climatic warming (Hawkins *et al.*, 2008).

In the present study, we conducted a survey of intertidal and shallow water barnacles at 44 locations in South Korea, following the boundary definition of the three marine ecoregions in Rebstock & Kang (2003) and Spalding *et al.* (2007). Distribution patterns of native and invasive species were displayed on oceanographic maps including sea surface temperatures, chlorophyll *a* concentrations and salinity. We hypothesize that the biogeography of barnacle species assemblages is different among different marine ecoregions in the Korean Peninsula.

Materials and methods

The Korean oceanographic ecoregions, study sites and sampling

The west and south-west coasts of the Korean peninsula are under the influence of the Yellow Sea. Spalding *et al.* (2007) considered this region as the Yellow Sea ecoregion, which is characterized by cold and saline water in winter and warm and low salinity water in summer. During the winter, the coastline bordering the Yellow Sea ecoregion is affected by the Korean Coastal Current flowing from the northern part of the Peninsula. This current brings in low seawater temperature (below 10°C in winter) (Figures 1A & 2). The Yellow Sea ecoregion shows a slightly higher chlorophyll *a* concentration than the other two ecoregions due to the influence of the coastal current. In summer, the Coastal Current is weaker due to the influence of monsoon wind stress (Jacobs *et al.*, 2000; Koh & Khim, 2014; Wu *et al.*, 2014; Lie & Cho, 2016). Further, the Yellow Sea receives a substantial input of fresh water from the Yangtze River, which can lower salinity to 31–32‰ (Figure 1C, D). The East China Sea ecoregion is affected by the Cheju and Tsushima Warm Currents which branch from Kuroshio (Nitani, 1972; Guan, 1994). As a result, this region experiences warmer seawater and high salinity (Figure 1).

The southern coastlines and Jeju Island bordering the East China Sea are affected by the Cheju and Tsushima Warm Currents. This region experiences warmer seawater and high salinity (Lim *et al.*, 2019). This ecoregion was named the East China Sea ecoregion (Spalding *et al.*, 2007). The east coast of the Korean Peninsula faces the East Sea and is influenced by the Primorye and North Korean Cold Currents from the north and the Tsushima Current from the south (hereafter named as East Sea ecoregion). The hydrography of the East Sea ecoregion is characterized by both low water temperature and high salinity. The East Sea ecoregion is affected by the cold North Korean Coastal Current from the north in both summer and winter (Figure 1E, F). Average sea surface temperatures vary from 10°C in winter to 25°C in summer (Korea Hydrographic and Oceanographic Agency, 2017, accessed online 30 March 2020; Figure 2).

Barnacles (species presence or absence data) were collected from 44 locations along all coastlines of Korea from 2016 to 2018 (Figure 3, Table 1). At each site, barnacle species were collected for >1–2 h until no additional species were found. Most of the barnacles were found on primary hard substratum. Occasional barnacle samples were also collected on the shells of limpets and gastropods. Most of the sites are natural rocky shores, which are composed of sloping platforms, large boulders and with exposures ranging from semi-exposed to exposed. There are 14 sites which are located within ports which were included to meet the aim of surveying for invasive species. At each site with rocky shores, barnacles were collected from 30–50 m stretches of rocky shore from the entire intertidal zone during low tide. Shallow water barnacles were collected with a hammer and chisel at depths of 5–20 m by scuba diving. Barnacles in ports were collected on 20–30 m long seawall surfaces, using chisels secured on a long rod and a net on a long rod for collection. Fifteen sites were in the Yellow Sea ecoregion (including eight sites which are on outlying islands without public transportation access possible, protected by the Korea Marine National Park Service, and are relatively free of anthropogenic influences). Twenty-two sites were selected along the southern coast that is influenced by the East China Sea ecoregion including four sites at Jeju Island and 14 in Marine National Park areas. Seven sites were selected along the eastern coast of Korea that borders the East Sea ecoregion. All barnacle specimens were preserved in 95% ETOH. Identification of barnacles followed Chan *et al.* (2008*b*).

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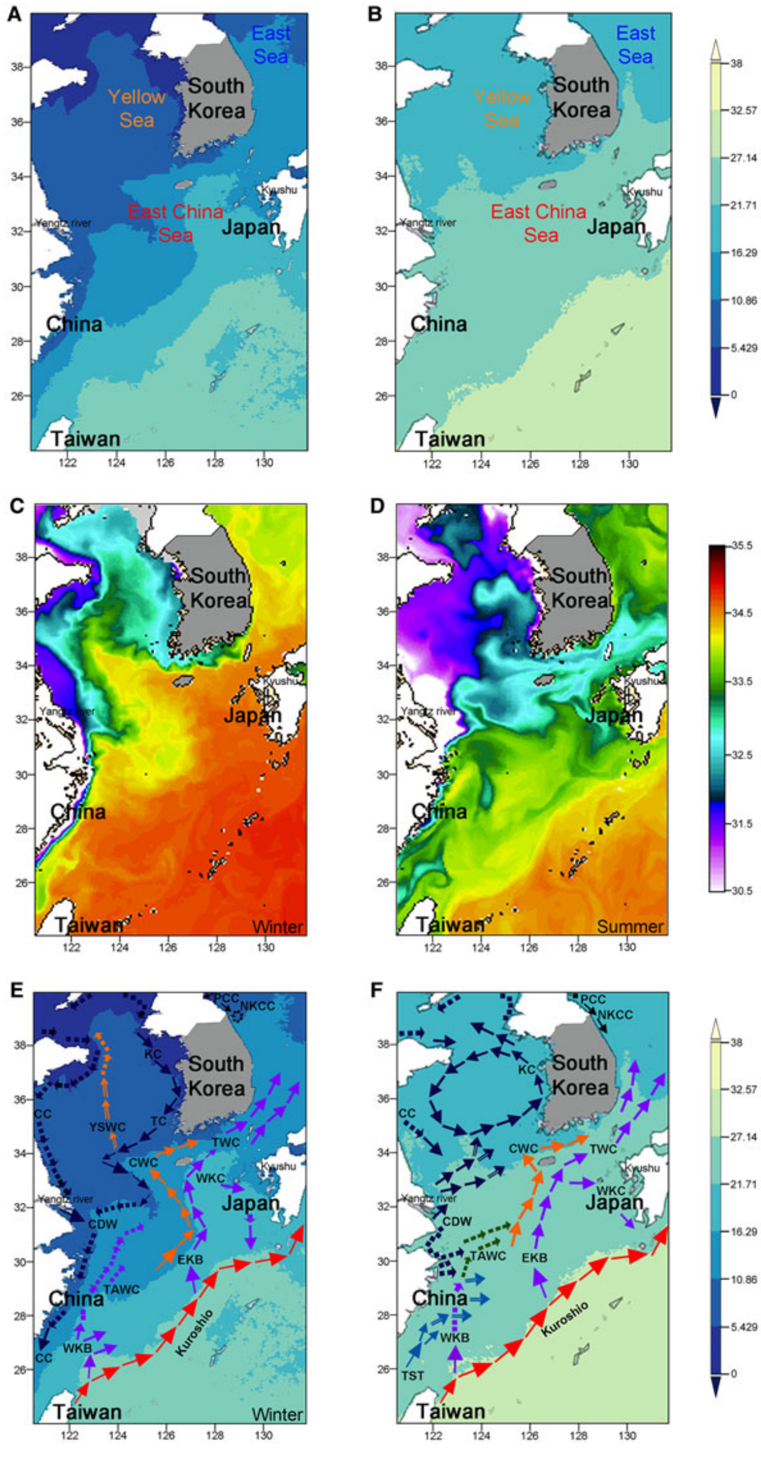

Fig. 1. Oceanographic map of the South Korea and adjacent waters, generated from the Giovanni database, NASA, USA. (A, B) Horizontal distributions of seasonal mean sea surface temperature and the contour lines of mean sea surface temperature in winter and summer in the period of 2016–2018 are shown by dashed lines; (C, D) Horizontal distributions of seasonal mean salinity; (E, F) Seasonal surface circulation for winter and summer in Korea, modified from Lie and Cho (2016). CC, Chinese Coastal Current; CDW, Changjiang Diluted Water; CWC, Cheju Warm Current; EKB, Eastern Kuroshio Branch; KC, Korean Coastal Current; TAWC, Taiwan Warm Current; TC, Yellow Sea Transversal Current; TWC, Tsushima Warm Current; WKB, Western Kuroshio Branch; WKC, Western Kyushu Current; YSWC, Yellow Sea Warm Current; PCC, Primorye Cold Current; NKCC, North Korea Coastal Current.

Barnacle species data were presented as absence or presence data in each site for subsequent statistical analysis.

Environmental factors

Oceanographic maps of average sea surface temperatures, chlorophyll *a* concentrations and salinity from December 2016 to November 2018 were derived from Giovanni and NASA databases (Giovanni database, NASA, USA, accessed online 13 December 2011). Satellite-derived sea surface temperature and remotely sensed estimates of chlorophyll *a* concentration, collected by the moderate resolution imaging spectro-radiometer (MODIS-) Aqua MODISA satellite at an estimated 4 km resolution were extracted and used to generate seasonal means for summer (from June–August) and winter (from December–February). Satellite maps of salinity were obtained from SMAP salinity maps (SMAP sea surface salinity, NASA, USA, accessed online 13 December 2018) and averaged over summers and winters from 2016–2018 (Figure 1). Seasonal variations of sea surface circulation patterns in winter and summer were modified from Lie & Cho (2016) (Figure 1E, F).

Multivariate analysis in different marine ecoregions

To investigate whether the distribution patterns of barnacle assemblages were diagnostic to different marine ecoregions, multivariate analysis (using species as variables) were performed in the PRIMER package (v6, Plymouth Routine in Multivariate Analysis, PRIMER-E Ltd; Clarke & Gorley, 2006). The site codes under the same numerical heading, i.e. (4, 4-1, 4-2), (6,

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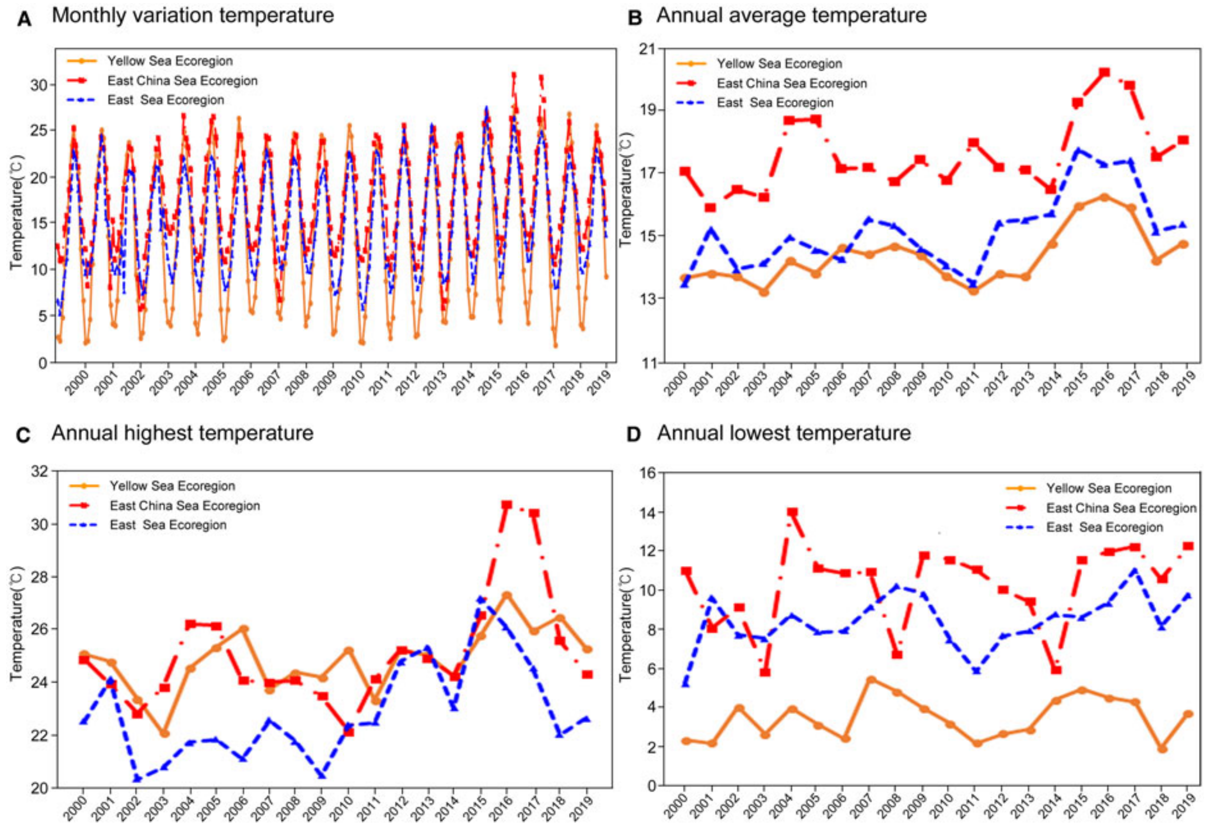

Fig. 2. Variation in sea surface temperature recorded by Korea Hydrographic and Oceanographic Agency (2017), at Incheon (Yellow Sea ecoregion), Tongyeong (East China Sea ecoregion) and Sokcho (East Sea ecoregion) sites. (A) Monthly temperature, (B) average annual temperature, (C) highest annual temperature, (D) lowest annual temperature from 2000–2017. Note there is an obvious increase in all temperature parameters from 2010–2018.

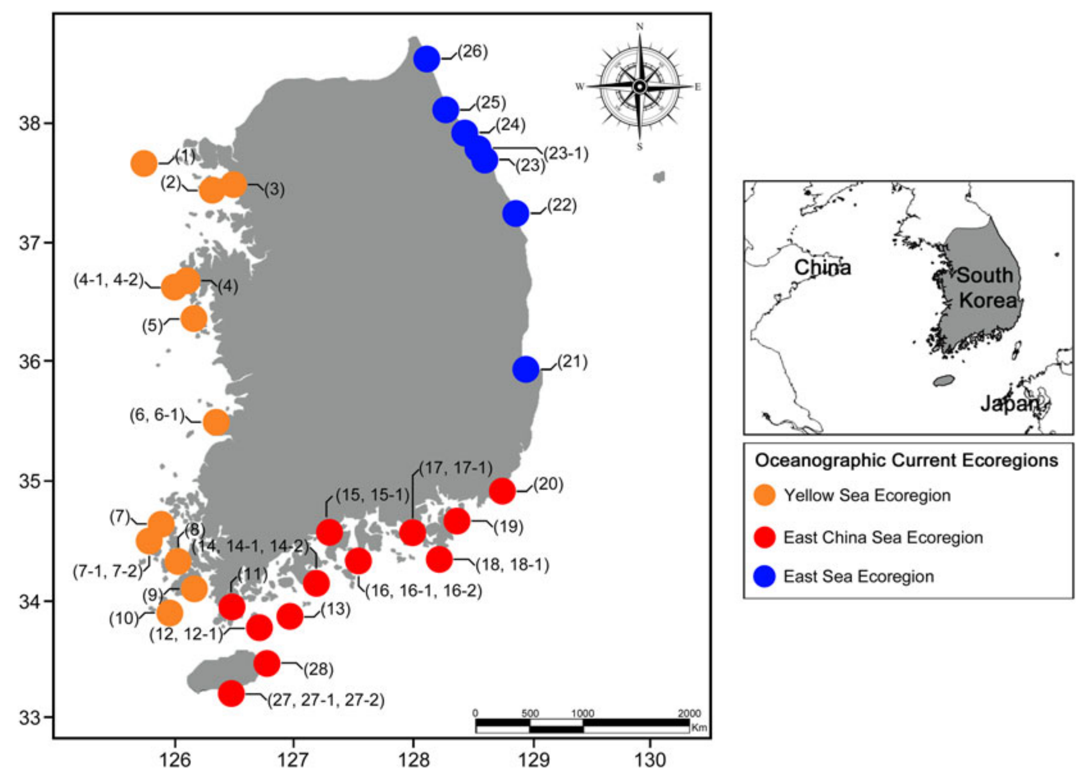

Fig. 3. Collection sites located in different oceanographic current ecoregions. Map showing the site numbers. Colour of site indicates the marine ecoregions. For details of site information, refer to Table 1.

6-1), (7, 7-1, 7-2), (12, 12-1), (14, 14-1, 14-2), (15, 15-1), (16, 16-1, 16-2), (17, 17-1), (18, 18-1), (23, 23-1), (27, 27-1, 27-2) (see Table 1) are located relatively close to each other and have the same species composition. These sites under the same numerical setting heading were pooled for the analysis. Data on species present or absent were calculated with the Sorensen similarity

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Table 1. Detailed collection sites from 2016 to 2018 in Korea

	Site code	Collection site	Latitude	Longitude	Ecoregion	Characteristics of sites
		Incheon				
1	**1**	Yeonpyeong-eup, Ongjin-gun	37°39′31.28″ N	125°40′57.94″ E	Yellow Sea ecoregion	Natural shorelines
2	**2**	Jung-gu, Incheon	37°25′54.68″ N	126°24′57.53″ E		Natural shorelines
3	**3**	Wolmi Is., Jungu	37°28′33.20″ N	126°35′50.70″ E		Ports
		Chungcheongnam-do			Yellow Sea ecoregion	
4	**4**	Sinjin Is.,Geunheung-myeon, Taean-gun,	36°40′50.5″ N	126°8′02.7″ E		Ports
5	[a]**4-1**	Ong Is., Gauidoli, Geunheung-myeon, Taean-gun	36°38′55.2″ N	126°00′28.3″ E		Natural shorelines
6	[a]**4-2**	Jeongjok Is., Gauidoli, Geunheung-myeon, Taean-gun	36°38′14.8″ N	126°05′09.1″ E		Natural boulder shores
7	**5**	Ammyeon Is., Taean-gun	36°28′15.21″ N	126°20′24.82″ E		Natural shorelines
		Jellabuk-do			Yellow Sea ecoregion	
8	[a]**6**	Chaeseokgang, Byeonsan-myeon, Buan	35°37′39.4″ N	126°28′06.4″ E		Natural boulder shores
9	[a]**6-1**	Jeokbyeokkgang, Byeonsan-myeon, Buan	35°28′15.0″ N	126°27′44.9″ E		Natural boulder shores
		Jellanam-do				
10	**7**	Aphae-eup, Sinan-gun	34°49′23.58″ N	126°4′31.32″ E		Natural shorelines
11	[a]**7-1**	Mokke, Uidodoli, Docho-myeon, Sinan-gun	34°36′09.1″ N	125°49′43.0″ E		Natural shorelines
12	[a]**7-2**	Seongchon beach,Uidodoli, Docho-myeon, Sinan-gun	34°37′06.2″ N	125°49′47.2″ E	Yellow Sea ecoregion	Natural shorelines
13	**8**	Seomanghang, Jindo-gun	34°21′50.9″ N	126°07′56.5″ E		Ports
14	[a]**9**	Hyeol Is., Jodomyeon, Jindo-gun	34°31′0.21″ N	126°5′11.75″ E		Natural boulder shores
15	[a]**10**	Gwanmae Is., Jodomyeon, Jindo-gun	34°14′37.49″ N	126°3′6.61″ E		Natural boulder shores
16	[a]**11**	Soan-myeon, Wando-gun	34°10′19.47″ N	126°38′59.35″ E	East China Sea ecoregion	Ports
17	[a]**12**	Cheongsan Is., Cheongsan-myeon, Wando-gun	34°11′16.94″ N	126°54′41.88″ E		Natural boulder shores
18	[a]**12-1**	Yeoseli, Cheongsan-myeon, Wando-gun	33°59′03.1″ N	126°56′00.4″ E		Natural boulder shores
19	**13**	Geomun Is., Samsan-myeon, Yeosu-si	34°2′51.85″ N	127°18′41.02″ E		Natural boulder shores
20	[a]**14**	Geumo Is., Nam-myeon, Yeosu-si	34°31′38.96″ N	127°43′51.68″ E		Natural shorelines
21	[a]**14-1**	Ando beach, Andoli, Nam-myeon, Yeosu-si	34°29′22.8″ N	127°48′51.9″ E		Natural shorelines
22	[a]**14-2**	Jikpo beach, Dumoli, Nam-myeon, Yeosu-si	34°30′28.9″ N	127°44′21.7″ E		Natural shorelines
		Gyeongsangnam-do				
23	[a]**15**	Wolgokli, Seolcheon-myeon, Namhae-gun	34°55′25.3″ N	127°51′29.0″ E		Natural boulder shores
24	[a]**15-1**	Geumeumli, Seolcheon-myeon, Namhae-gun	34°55′23.4″ N	127°55′40.5″ E		Natural boulder shores
25	[a]**16**	Sangjubeach, Sangjuli, Sangju-myeon, Namhae-gun	34°43′03.8″ N	127°59′28.1″ E		Natural shorelines
26	[a]**16-1**	Sejon Is., Sangjuli, Sangju-myeon, Namhae-gun	34°29′57.4″ N	128°04′58.3″ E	East China Sea ecoregion	Natural boulder shores
27	[a]**16-2**	Yangali, Sangju-myeon, Namhae-gun	34°43′42.5″ N	127°57′07.4″ E		Ports
28	**17**	Pungwhali, Sanyang-eup, Tongyeong-si	34°49′10.0″ N	128°22′56.3″ E		Ports
29	**17-1**	Yeonwhali, Sanyang-eup, Tongyeong-si	34°46′04.1″ N	128°24′26.7″ E		Ports

(*Continued*)

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Table 1. (*Continued.*)

	Site code	Collection site	Latitude	Longitude	Ecoregion	Characteristics of sites
30	**[a]18**	Hansan Is.,Hansan-myeon, Tongyeong-si	34°46′59.71″ N	128°30′19.99″ E		Natural boulder shores
31	**[a]18-1**	Hong Is., Hansan-myeon, Tongyeong-si	34°32′17.3″ N	128°43′48.8″ E		Natural boulder shores
32	**[a]19**	Irun-myeon, Geoje	34°48′06.1″ N	128°42′53.2″ E		Natural boulder shores
33	**20**	Haeundae-gu, Busan	35°5′58.76″ N	129°7′19.05″ E		Natural boulder shores
		Gyeongsangbuk-do				
34	**21**	Guryongpo-eup, Pohang	36°0′47.0″ N	129°28′04.1″ E	East Sea ecoregion	Natural boulder shores
		Gangwon-do				
35	**22**	Janghohang-gil, Geundeok-myeon, Samcheok-si	37°17′20.44″ N	129°19′3.10″ E		Ports
36	**23**	Changhae-ro, Jumunjin-eup, Gangneung-si	37°46′20.028″ N	128°57′5.922″ E		Ports
37	**23-1**	Jumumli, Jumunjin-eup, Gangneung-si	37°54′22.9″N	128°49′48.5″E		Ports
38	**24**	Susangil, Sonyang-myeon, Yangyang-gun	38°04′44.5″ N	128°40′49.0″ E		Ports
39	**25**	Yongho-gil, Ganghyeon-myeon, Yangyang-gun	38°08′08.4″ N	128°37′18.4″ E		Ports
40	**26**	Daejinhang-gil, Hyeonnae-myeon, Goseong-gun	38°30′00.2″ N	128°25′36.8″ E		Ports
		Jeju Island				
41	**27**	Beophwan-dong, Seogwipo-si	33°13′25.72″ N	126°30′57.45″ E	East China Sea ecoregion	Natural boulder shores
42	**27-1**	Bomok-dong, Seogwipo-si	33°13′53.43″ N	126°35′50.43″ E		Natural boulder shores
43	**27-2**	Seogwi-dong, Seogwipo-si	33°14′10.6″ N	126°34′06.5″ E		Ports
44	**28**	Udo Is., Jeju-si	33°30′7.97″ N	126°56′35.33″ E		Natural boulder shores

[a]Marine National Park areas of Korea protected by Korea Marine National Park Service.

index for the 21 species and sites as replicates within the three marine ecoregions (N = 10 in the Yellow Sea, N = 12 in the East China Sea, N = 6 in the East Sea). Non-metric Multidimensional Scaling (nMDS; Clarke, 1993) was conducted to generate two-dimensional plates on the species composition in all sites. Analysis of Similarity (ANOSIM) and Global *R* tests was used to test the similarity of the three marine ecoregions. Analysis of similarity percentage (SIMPER) was used to identify the species primarily providing the average per cent dissimilarity in the contribution of barnacle assemblages among the ecoregions.

Results

Native species composition and diversity

A total of 21 barnacle species belonging to 14 genera were recorded in the study site from all marine ecoregions in Korea. The diversity of barnacles was variable among oceanographic current ecoregions. Twelve species were recorded in the Yellow Sea ecoregion and 18 species were recorded in the East China Sea ecoregion (Table 2). Between the two current ecoregions, overlap in the distribution of 10 species was detected. The stalked barnacle *Capitulum mitella* and the acorn barnacle *Tetraclita japonica* were common in the mid-littoral zone in the Yellow Sea and East China Sea ecoregions; these species are rare on the eastern coast inside the East Sea ecoregion. The mangrove barnacle *Fistulobalanus albicostatus* was also recorded in the Yellow Sea (90% of the sites) and East China Sea (60% of the sites) ecoregions but absent from the East Sea ecoregion. This species is mainly attached to the rocks or on other marine crustacean shells of intertidal mudflats. The barnacles *Striatobalanus amaryllis* and *Amphibalanus reticulatus* were only recorded in the Yellow Sea ecoregion. These species are distributed from the low intertidal zone to shallow water (up to 15 m depth). Three coral associated barnacles, *Cantellius arcuatus*, *Cantellius* sp. and *Pyrgomina oulastreae* were recorded only in the East China Sea ecoregion. In the East Sea ecoregion, seven species were recorded (Table 2). Of these, the cold water species *Hesperibalanus hesperius hesperius* and *Amphibalanus improvisus* were found attached on the surfaces of molluscan shells.

There are four common barnacles that are present in all marine ecoregions of Korea: *Chthamalus challengeri*, *Balanus rostratus*, *Balanus trigonus* and *Megabalanus rosa*. The intertidal barnacle, *C. challengeri*, is common from the mid-littoral to the supra-littoral zones of the rocky shore. The remaining three species were found not in the intertidal zone but attached to buoys or on the surfaces of molluscan shells.

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Table 2. Summary of presence and absences of barnacle species collected in the different ecoregions of Korea (+:presence, –:absence)

Species	Yellow Sea ecoregion	East China Sea ecoregion	East Sea ecoregion
Capitulum mitella (Linnaeus, 1758)	+	+	–
Chthamalus challengeri Hoek, 1883	+	+	+
Tetraclitella chinensis (Nilsson-Cantell, 1921)	–	+	–
Striatobalanus amaryllis (Darwin, 1854)	+	–	–
Tetraclita japonica Pilsbry, 1916	+	+	–
Euacasta dofleini (Kruger, 1911)	+	+	–
Cantellius arcuatus (Hiro, 1938)	–	+	–
Cantellius sp.	–	+	–
Pyrgomina oulastreae (Utinomi, 1962)	–	+	–
Fistulobalanus albicostatus (Pilsbry, 1916)	+	+	–
Fistulobalanus kondakovi (Tarasov and Zevina, 1957)	+	+	–
Amphibalanus amphitrite (Darwin, 1854)	+	+	–
Amphibalanus eburneus (Gould, 1841)	–	+	–
Amphibalanus improvisus (Darwin, 1854)	–	+	+
Amphibalanus reticulatus (Utinomi, 1967)	+	–	–
Balanus rostratus Hoek, 1883	+	+	+
Balanus trigonus Darwin, 1854	+	+	+
Megabalanus rosa (Pilsbry, 1916)	+	+	+
Megabalanus volcano (Pilsbry, 1916)	–	+	–
Perforatus perforatus (Bruguière, 1789)	–	+	+
Hesperibalanus hesperius hesperius (Pilsbry, 1916)	–	–	+
Total	12	18	7

Presence/absence of species in relation to different marine ecoregions

The non-metric multidimensional scaling (nMDS) ordination plots of the species abundance in relation to different current ecoregions using the Sorensen similarity index formed distinct clusters. The Yellow Sea and East China Sea ecoregions formed overlapping clusters, but the clusters of the East Sea ecoregion were distinct and clearly separated from other ecoregions (Figure 4).

The ordination patterns in the nMDS plots were statistically supported by the ANOSIM analysis, which showed significant differences in barnacle assemblages among the current ecoregions ($R = 0.503$, $P < 0.001$). In the nMDS plot, there are relatively large overlaps of the clusters between the Yellow Sea and East China Sea ecoregions, while the clusters in the East Sea were separate from the other two ecoregions. In pairwise ANOSIM comparisons, all current ecoregions were statistically discriminant from one another. Yellow Sea ecoregion *vs* East China Sea ecoregion, $R = 0.25$, $P < 0.08$; Yellow Sea ecoregion *vs* East Sea ecoregion, $R = 0.78$, $P < 0.001$; East China Sea ecoregion *vs* East Sea ecoregion, $R = 0.66$, $P < 0.001$, suggesting that barnacle assemblages are associated with ecoregions.

From the cluster analysis, the similarity of the barnacle assemblages between the Yellow Sea and East China Sea mingled together. Based on a criteria of <20% similarity, only two main clusters were identified: the Yellow Sea + East China Sea ecoregions and East Sea ecoregion. This means the composition of barnacle species in the East Sea ecoregion is strongly different (Figure 5).

From the similarity percentage analysis (SIMPER), the average dissimilarity between pairs of current ecoregions ranged from 65.06% (Yellow Sea *vs* East China Sea ecoregion), 79.88% (East China Sea *vs* East Sea) and to 90.98% (Yellow Sea *vs* East Sea ecoregion). *Fistulobalanus albicostatus*, *Balanus trigonus*, *Euacasta dofleini*, *T. japonica* and *Chthamalus challengeri* contributed a total of 46.3% dissimilarity between the Yellow Sea and East China Sea ecoregions. *Euacasta dofleini* and *Balanus trigonus* are more abundant in the East China Sea ecoregion and contribute to reduced abundance in the Yellow Sea ecoregion. By comparing the Yellow Sea and East Sea ecoregions, *F. albicostatus*, *Perforatus perforatus*, *B. rostratus*, *C. challengeri* and *B. trigonus* contributed a total of 68.3% dissimilarity. *Perforatus perforatus*, *C. challengeri*, *B. rostratus*, *B. trigonus* and *F. albiscostatus* contributed 48.8% of the dissimilarity between the East China Sea and East Sea ecoregions (Table 3, Figure 6).

Invasive barnacles

Four barnacle species are invasive in Korean waters: *Amphibalanus amphitrite*, *Amphibalanus eburneus*, *Amphibalanus improvisus* and *P. perforatus* (Kim, 1998; Choi *et al.*, 2013; Park *et al.*, 2017). *Amphibalanus amphitrite*, a successful marine invader worldwide, was found at six sites located in the Yellow Sea and East China Sea ecoregions. *Amphibalanus eburneus* was introduced to the Pacific from the North-west Atlantic Ocean and was found attached to buoys or on the bottoms of ships in two sites (Tongyeong and Geoje) in the East China Sea ecoregion (Figure 7A, B). *Amphibalanus improvisus*, was found at five sites on a seawall inside a port and on molluscan shells. Two sites are located at Namhae (Yellow Sea ecoregion), one at Busan (East China Sea ecoregion) and two sites at Yangyang (East Sea ecoregion). *Perforatus perforatus* was mainly found at six sites, Busan and Pohang (East China Sea ecoregion) and four sites at important international shipping ports (East Sea ecoregion) (Figures 7C, D & 8).

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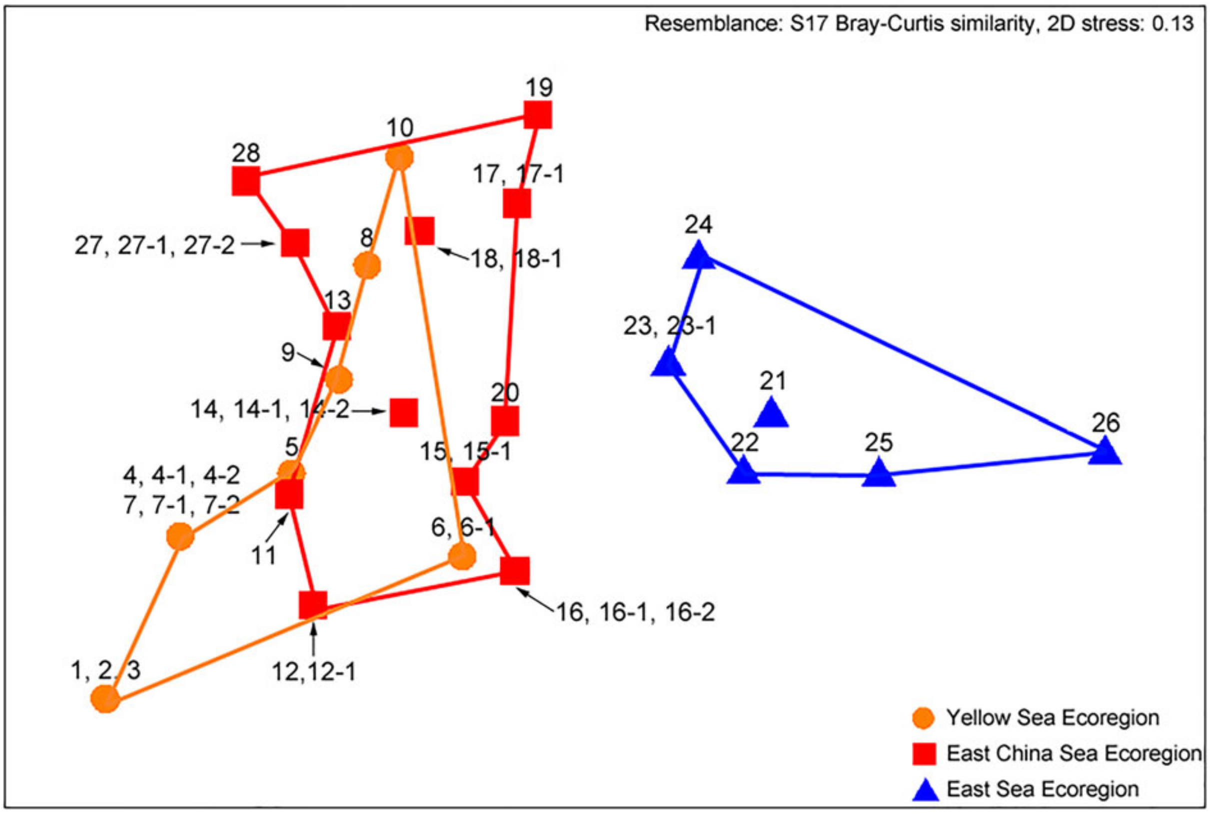

Fig. 4. Non-metric nMDS plots on the species compositions in all collecting sites from different current ecoregions in Korea. The site code under the same numerical heading, i.e. (4, 4-1, 4-2), (6, 6-1), (7, 7-1, 7-2), (12, 12-1), (14, 14-1, 14-2), (15, 15-1), (16, 16-1, 16-2), (17, 17-1), (18, 18-1), (23, 23-1), (27, 27-1, 27-2) (see Table 1) are located relatively close to each other and have the same species composition. These sites under the same numerical heading were pooled for the analysis and represent one site ordination in the nMDS plot. Note the ordination of sites from 1 to 3 and 4 and 7 overlapped due to same species composition.

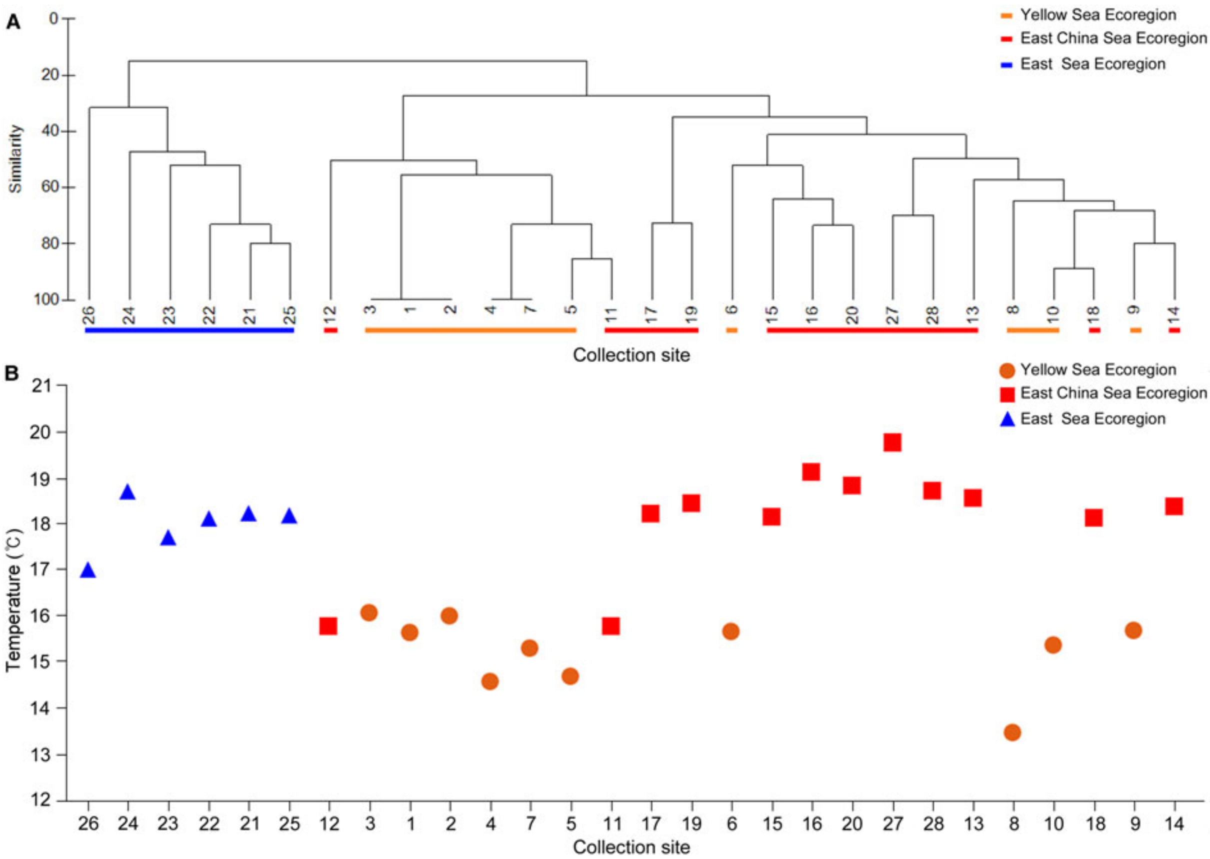

Fig. 5. (A) Cluster dendrogram showing the similarity based on the species compositions at all collecting sites from different marine ecoregions. Some sites were marked with a representative number due to same species composition between number and sub-numbers; (B) average sea surface temperature in all the collection sites during 2016–2018 from Korea Hydrographic and Oceanographic Agency (2017).

Table 3. SIMPER analysis results from pairwise comparisons of three different ecoregions based on between group dissimilarity for each pairwise combination of ecoregions

Between group dissimilarity	Dissimilarity (%)	Species	Average dissimilarity	Contribution (%)
Yellow Sea and East China Sea ecoregions	65.06	*Balanus trigonus*	8.17	12.56
		Tetraclita japonica	5.95	9.15
		Euacasta dofleini	5.45	8.37
		Fitulobalanus albicostatus	5.39	8.29
		Chthamalus challengeri	5.36	8.25
Yellow Sea and East Sea ecoregions	90.98	*Fitulobalanus albicostatus*	15.7	17.26
		Perforatus perforatus	15.34	16.86
		Balanus rostratus	14.03	15.42
		Chthamalus challengeri	9.9	10.88
		Balanus trigonus	7.2	7.91
East China Sea and East Sea ecoregions	79.88	*Perforatus perforatus*	9.54	11.95
		Chthamalus challengeri	7.93	9.93
		Balanus rostratus	7.49	9.38
		Balanus trigonus	7.32	9.17
		Fitulobalanus albicostatus	6.76	8.47

Discussion

Species assemblages of intertidal and shallow water barnacles in Korean waters vary among the three marine ecoregions. Such variation in assemblages is also reported in intertidal hermit crabs and their parasitic rhizocephalan barnacles (Jung *et al*., 2018, 2019). From multivariate nMDS plots, there is a large degree of overlap of the clusters from the Yellow Sea and East China Sea ecoregions, suggesting there are large groups of species shared between these two ecoregions. ANOSIM analysis suggest the variations in the species clusters among the three ecozones is significant. From pairwise ANOSIM analysis, R value of the pairwise comparison between Yellow Sea and East China Sea ecoregions is 0.25, indicating there is a large degree of overlap of the clusters. Cluster analysis show the barnacle species of these two systems fall in the same group, based on 80% differences in the criteria. However, the *P*-value of this pairwise ANOSIM comparison reached 0.018, suggesting there are still some species that are diagnostic between these two ecoregions. A common barnacle in the Yellow Sea ecoregion is *Fistulobalanus albicostatus*, which was abundant in estuary sites on the west coast of Korea. *Fistulobalanus* is often found in estuarine-intertidal habitats and mangroves in Japan, Okinawa and Taiwan (Chang *et al*., 2017). This genus appears to prefer low salinity regions. The East China Sea ecoregion is characterized by higher seawater temperatures and salinity than the other two ecoregions. *Balanus trigonus* is a common species in the East China Sea ecoregions, probably because of the high salinity and warmer water in this ecoregion. Sponges and coral reefs are present in this ecoregion, especially around Jeju Island, located off the southern coast of Korea. Jeju Island is the northern-most limit of scleractinian corals (only eight species of zooxanthellae-containing scleractinian corals have been recorded; Sugihara *et al*., 2014). The common sponge-inhabiting barnacle, *Euacasta dofleini*, is common in the East China Sea ecoregion, but it is absent from the Yellow Sea ecoregion and East Sea ecoregion. The presence of this species is likely related to the Cheju Warm Currents (CWC). Three species of coral-inhabiting barnacles (*Cantellius arcuatus*, *Cantellius* sp. and *Pyrgomina oulastreae*) were identified exclusively from five scleractinian corals at Jeju Island within the East China Sea ecoregion (also see Chan *et al*., 2018). These barnacle species did not contribute to the significant species assemblage between the Yellow Sea and East China Sea ecoregion because they are only recorded in Jeju Island within the East China Sea ecoregion. At the same latitude on the Pacific Ocean side of Japan, ~30 coral-inhabiting barnacles and 100 hard coral species have been reported (Chan *et al*., 2018). The warm Kuroshio in the East China Sea ecoregion is relatively weak, resulting in reduced diversity of scleractinian coral species. The barnacle *P. oulastreae* was recorded further north (waters close to the south coast of the Korean peninsula) where zooxanthellae-bearing scleractinian corals become very rare. In this region, *P. oulastraea* were found on the cold-water, non-zooxanthellae-containing coral *Dendrophyllia cribrosa*. *Pyrgomina oulastreae* is a cold-water tolerant coral barnacle species that can define the extreme fringe of coral distribution.

The acorn barnacle *Tetraclita japonica* and the stalked barnacle *Capitulum mitella* are tropical to subtropical species and occur mid-shore in the Yellow Sea and East China Sea ecoregions. The presence of these two species decreased along the east coast in the East Sea ecoregion. The natural northern limit of both species is around Pohang (in the East Sea ecozone) at about 36°06′N. In this region, *T. japonica* and *C. mitella* became sparse and occurred occasionally with *Chthamalus challengeri*, which is still the predominant intertidal species in this region. The absence of *T. japonica* and *C. mitella* in the northern part of the East Sea ecoregion is probably due to poor survival in low water temperatures in winter. *Chthamalus challengeri* is a cold-water species that also tolerates a wide range of salinity. This barnacle is common in all intertidal ecoregions along the Korean Peninsula and is the major occupier of space in mid to high intertidal zones. Due to its long larval dispersal period and greater tolerance to low salinity, *C. challengeri* has a wide geographic distribution in almost all coastlines of Japan and Korea, and is now considered as an invasive species in Zhoushan waters, close to the southern region of Shanghai (Cheang *et al*., 2012; Liu *et al*., 2015). Additionally, a common species in the Yellow Sea ecoregion, *F. albicostatus*, is absent from the East Sea ecoregion, probably because high salinity, low winter temperatures and stronger wave action do not

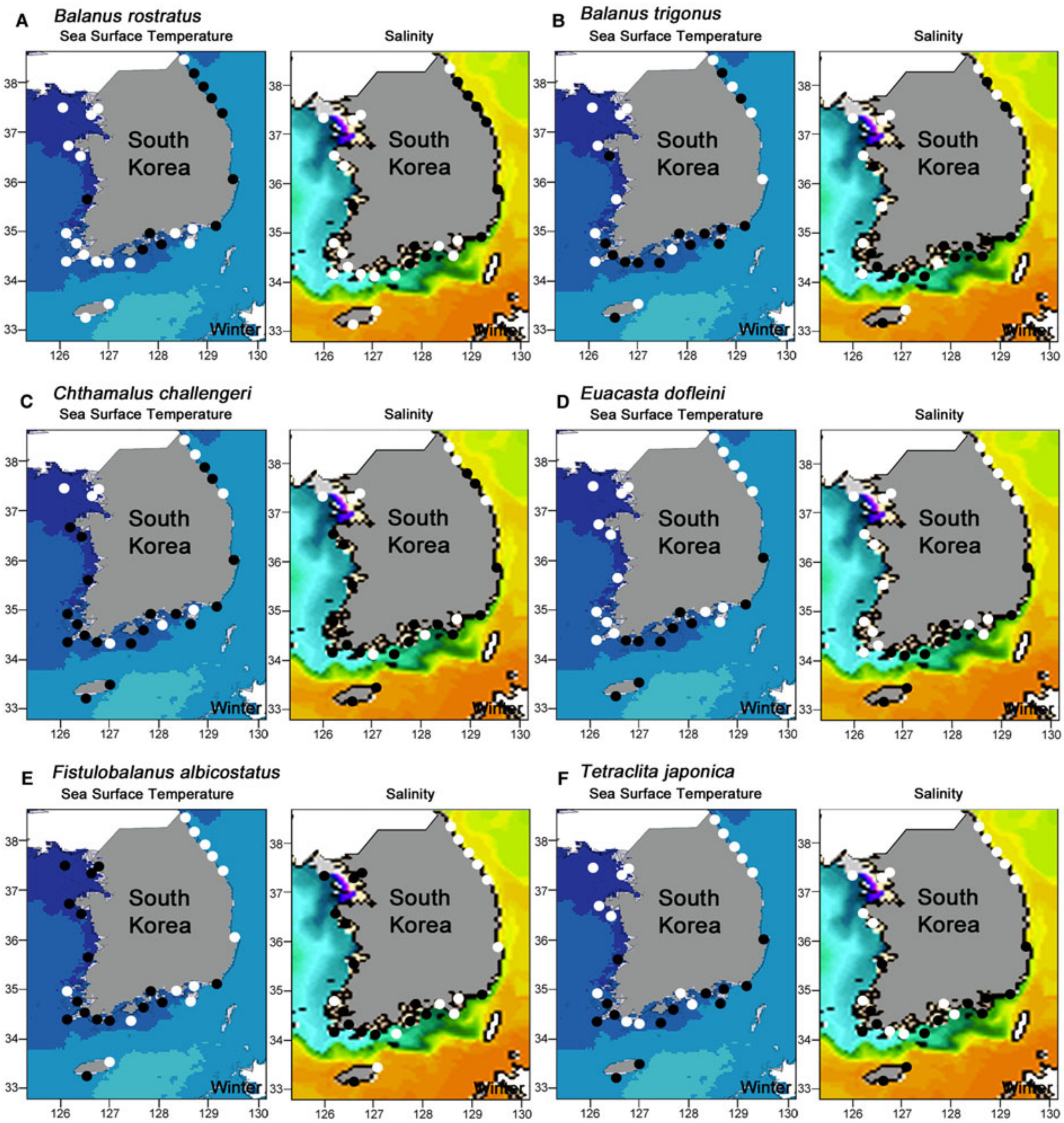

Fig. 6. Distribution pattern of the diagnostic species among oceanographic ecoregion identified from SIMPER analysis. (A) *Balanus rostratus*, (B) *Balanus trigonus*, (C) *Chthamalus challengeri*, (D) *Euacasta dofleini*, (E) *Fistulobalanus albicostatus*, (F) *Tetraclita japonica*, which contribute to the dissimilarity among different current ecoregions. Black circle: present, white circle: absent.

provide a suitable habitat. In contrast, *Hesperibalanus hesperius hesperius* and *Balanus rostratus* are cold-water barnacles, being present in the East Sea ecoregion but absent from the other two ecoregions. Distribution of these species is influenced by low sea surface temperature resulted from the Liman Cold Current (LCC) from the north.

One recent invasive barnacle species, *Perforatus perforatus*, has rapidly expanded its northern range along the east coast of Korea when compared with distribution records from 2008 (Choi *et al.*, 2013) and 2013 (Park *et al.*, 2017). *Perforatus perforatus* was first identified as an invasive species on the SE coast of Korea in 2008 (Choi *et al.*, 2013). The distribution of the species was similar in 2008 and 2013; northern limits did not exceed 38°N and the southern limit was not below 35°N in 2008 and 2013. In the present study, the northern limit of *P. perforatus* has reached 38°30′N and the southern limit did not change from 2008 and 2013 (Figure 7D). Choi *et al.* (2013) conducted modelling on the distribution of *P. perforatus* and predicted that this species would expand its range southward, but not northward along the east coast. Since 2008, *P. perforatus* has certainly migrated northward along the east coast (Figure 8B). One reason may be increases in seawater temperature in the last 10 years in the East China Sea and East Sea ecoregions (Figure 2). The east coast of Korea is experiencing a northward flow of the Tsushima Warm Current throughout the year, and this current may be responsible for northward dispersal of *P. perforatus* larvae.

The cold-water invasive species, *A. improvisus*, originating from western shores of Atlantic coasts, is common in estuaries and has a significant tolerance for low salinity environments (Wrange *et al.*, 2016). In the present study, small numbers of *A. improvisus* were found in both Yellow and East Sea ecoregions (Figure 7C). The distribution of *A. improvisus* shrinks within the range previously reported by Kim (1998) and Park *et al.* (2017) (Figure 8A). The warm-water invasive species, *A. eburneus*,

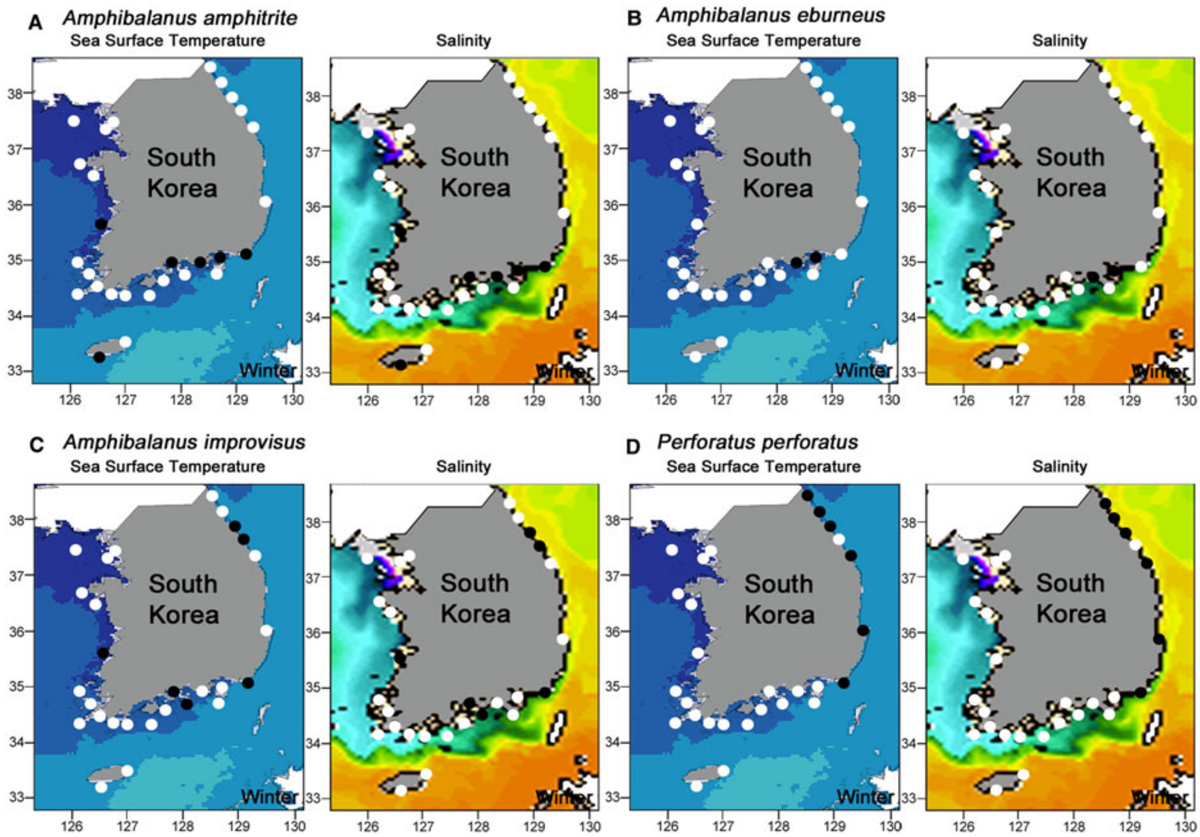

Fig. 7. Distribution of invasive barnacle species (A) *Amphibalanus amphitrite*, (B) *Amphibalanus eburneus*, (C) *Amphibalanus improvisus*, (D) *Perforatus perforatus* on oceanographic maps of sea surface temperature and salinity in summer and winter. Black circle: present, white circle: absent.

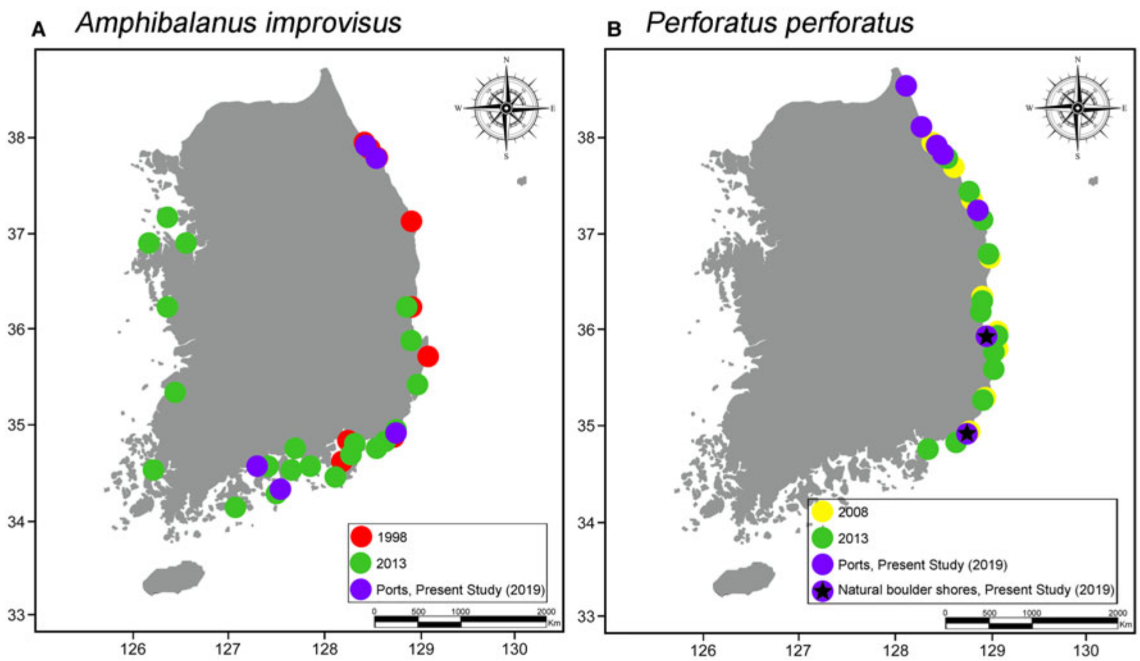

Fig. 8. Comparing the previous records (1998, 2008, 2013) of invasive barnacle species distribution with the data obtained in the present study. (A) *Amphibalanus improvisus*, (B) *Perforatus perforatus*. 1998 data were retrieved from Kim (1998), 2008 and 2013 information was obtained from Choi *et al*. (2013) and Park *et al*. (2017) respectively. Refer to Figure 2 for the increasing trend of seawater temperature in these three ecoregions for the last 20 years.

which tolerates low salinity (Southward, 1962; Henry & McLaughlin, 1975), was present in the East China Sea ecoregion and absent in the East Sea ecoregion in the present study (Figure 7B). The present distribution of *A. eburneus* is similar to the range reported in Kim (1998). Park *et al.* (2017), however, reported the presence of *A. eburneus* along all Korean coastlines because all collection sites were in shipping ports. *Amphibalanus eburneus* commonly occurs inside ports but is not present on natural shores in most Korean waters. Similarly, *A. amphitrite*, a dominant fouling organism, is well established

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especially in ports all around Korean waters as reported previously by Park *et al.* (2017). However, in the present study, this species was not found in natural intertidal habitats of southern and western coasts and its distribution along the southern coast may be limited to ports (Figure 7A).

Increases in ocean warming have already affected species' geographic distribution in Britain (Mieszkowska & Sugden, 2016). Southern species in the UK, including the trochoid gastropods *Osilinus* and *Gibbula*, expanded their range (Mieszkowska *et al.*, 2007). In Korean waters, seawater temperatures have increased in the last 50 years (Han & Lee, 2020; Figure 2). The highest and lowest recorded temperatures in all three ecoregions increased gradually with time (Figure 2). The cold-water species, *Semibalanus cariosus* and *Chthamalus dalli*, which were recorded in the NE coast of Korea (East Sea ecoregion) by Kim (1998), were absent in the present collection. Kim (1998) described *C. dalli* as rare and *S. cariosus* as common on bivalve shells. The absence of cold-water adapted species, *C. dalli* and *S. cariosus*, in the present study likely results from increases in water temperatures over the last 10–20 years. Some impacts of natural climatic oscillation, like the impacts of the Atlantic Multidecadal Oscillation on the distribution of *Semibalanus* and *Chthamalus* species in the UK, might also have occurred (Mieszkowska *et al.*, 2014). As water temperature increases, changes in species distribution in the East Sea ecoregion are expected to become more obvious than changes in the East China Sea and Yellow Sea ecoregions because the East Sea ecoregion supports exclusively cold-water species. The northern limits of *T. japonica* and *C. mitella* on the east coastline may shift further north and the abundance of *P. perforatus* may increase to the point that the species becomes a dominant space occupier along intertidal shores of the East Sea ecoregion in Korea. To further address such changes in the biogeography of intertidal species, sustained long-term monitoring of data, in a manner like the MarCLIM project, should be developed in the Pacific region. The protocol of the MarCLIM project can guide data collection to monitor intertidal species in the Pacific and subsequently the data can be comparable to the Atlantic counterparts.

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