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The distribution of the red-throated ascidian *Herdmania momus* shifts northwards in association with ocean warming in the Korean Peninsula

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Abstract

Climate change poses a major threat to marine ecosystems, with its effects felt worldwide. A major effect of climate change on marine ecosystems is the rise in water temperature, leading to a northward expansion of habitats for marine organisms. *Herdmania momus*, a species of ascidians (sea squirts), originally found in tropical and subtropical regions, was introduced to the Korean Peninsula. In this study, we examined the habitat of *H. momus* along the southeastern coast of the Korean Peninsula between 2016 and 2022. We found that *H. momus* settlements were observed across the entire survey area, with confirmed habitation in Busan in 2016, Ulsan in 2021, and Gyeongju (the northernmost location) in 2022. The observed habitation trend indicates a rapid geographical expansion, occurring approximately 79 years earlier than previously predicted. These observations demonstrate that marine organisms are undergoing a more rapid geographical expansion than previously projected. These unexpected findings should inform government policies related to proactive measures and strategies for managing the impact of climate change on marine ecosystems.

Introduction

Marine biodiversity in temperate seas faces several threats, including climate change and invasive species (Halpern *et al.*, 2008). The increasing global temperatures associated with climate change have led to notable shifts in the distribution ranges of marine species, often pushing them towards higher latitudes (Gervais *et al.*, 2021). Additionally, anthropogenic changes in marine ecosystems can introduce invasive species, resulting in changes in species composition and thresholds in ecosystems such as intertidal rocky shores, temperate and tropical reefs, estuaries, and pelagic systems (Bulleri *et al.*, 2020). Such transformations in marine ecosystems can result in complex adverse interactions (Council of Europe, 2008).

Unlike terrestrial organisms, marine species tend to exhibit more pronounced geographic expansion in response to climate change. Planktonic larvae, in particular, can readily spread to new environments because of their transportability within turbulent boundary layers (Eckman, 1990; Pinsky *et al.*, 2020). Pinsky *et al.* (2020) reported two major trends in the geographical distribution of warm-water marine organisms in the Northern Hemisphere: (1) a northward expansion in their range and (2) a shift into deeper waters. Numerous warm-water organisms have extended their geographical habitats from lower to higher latitudes (Rubenstein *et al.*, 2023). For example, the Korean Peninsula has witnessed the northward movement of species such as perforated barnacles (*Perforatus perforatus*) and Korean top shells (*Turbo sazae*) due to the recent increase in seawater temperature along the East Sea (Kim *et al.*, 2020; Son *et al.*, 2020).

The precise prediction of ecological responses, including alterations in habitat range due to climate change, has become a pressing challenge (Bennett *et al.*, 2019). Geographical information system (GIS) technology combined with species distribution modelling has shown that the rate of invasive species entering and spreading into new habitats has been accelerating globally (Maravelias and Reid, 1997; Tittensor *et al.*, 2009; Capinha *et al.*, 2012; Tyberghein *et al.*, 2012; Assis *et al.*, 2018; Park *et al.*, 2020). The 5th Assessment Report of the Intergovernmental Panel on Climate Change (IPCC, 2014) provided long-term climate change projections, termed representative concentration pathways (RCPs), defined by different carbon dioxide emission assumptions. In IPCC RCP4.5 scenario, technological developments enable substantial stabilisation of atmospheric carbon dioxide concentrations and a consequent deceleration of seawater warming. Conversely, the IPCC's RCP8.5 depicts unmitigated atmospheric carbon dioxide concentration increases and sharp temperature rises. Multiple studies have explored marine species distribution based on these IPCC RCP scenarios (e.g. Jones and Cheung, 2015; Allyn *et al*., 2020; Fabri-Ruiz *et al*., 2020).

The red-throated ascidian *Herdmania momus* is an invasive, solitary sea squirt species (Class: Ascidiacea) that is globally distributed in tropical and subtropical marine habitats (Palomares and Pauly, 2023). Recent GIS-based species distribution analysis has predicted range shifts for warm-water species along the Korean Peninsula (Park *et al*., 2020). The results showed that *H. momus*, which was first observed along the coast of Jeju Island in 1969 (Rho, 1971), has spread throughout Jeju and reached parts of Busan. According to Park *et al*. (2020) and the RCP8.5 scenario, the habitat range of *H. momus* is projected to expand from Busan to Ulsan by 2100. Due to its short lifespan (between 10 and 12 months) and rapid growth, *H. momus* can readily extend its habitat range in response to environmental changes (Yi and Kim, 2016; Park *et al*., 2020). However, it may face spatial competition with perennial seaweeds (e.g. *Sargassum* spp. and *Ecklonia cava*) and/or corals (e.g. scleractinian corals and *Alveopora japonica*) in its introduced habitat.

The aim of this study was to examine the extent of northward expansion of the *H. momus* habitat in line with Park *et al*.'s (2020) predictions based on IPCC RCP scenarios. *H. momus* habitat was assessed via qualitative scuba diving surveys conducted at nine stations in Busan, Ulsan, and Gyeongju between 2016 and 2022.

Materials and methods

Study area

The study area is located along the coastal region from Busan to Gyeongju, Korea (Figure 1), including the northernmost points where *H. momus* habitat has been confirmed or predicted previously by Park *et al*. (2020). Observations were made at nine rocky subtidal stations within the geographically interconnected Busan–Ulsan–Gyeongju area, including three stations in Busan (BS-1, BS-2, and BS-3), four stations in Ulsan (US-1, US-2, US-3, and US-4), and two stations in Gyeongju (GJ-1 and GJ-2) (Figure 1). Three stations, BS-1, BS-3, and GJ-2, were among the National Marine Ecosystem Monitoring Program (rocky ecosystem) Project (NMMP) study sites. The remaining six stations were selected arbitrarily while considering the requirement for maintaining a consistent distance among study stations for this research (Table 1). The water depths of each study site were between 5.0 and 39.0 m, with US-2 and US-3 being shallower compared to the other stations, while GJ-1 and GJ-2 were deeper (Table 1).

Field survey

To document the distribution of *H. momus* and co-occurring ascidians, a field survey was conducted by underwater scuba

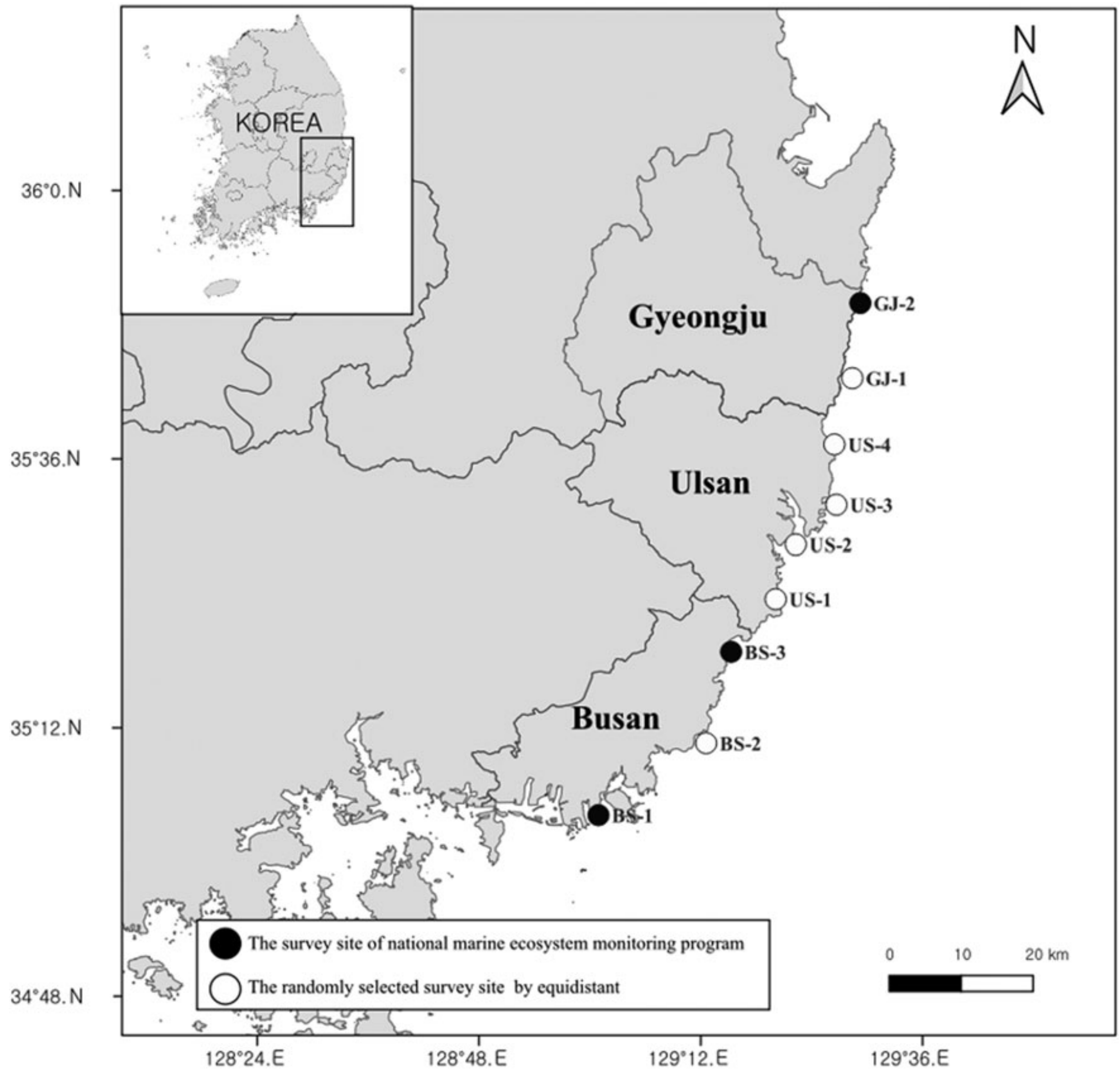

Figure 1. Locations of study sites (nine stations) for observing the presence of solitary ascidians via scuba observations from 2016 to 2022. Black symbols indicate three NMMP stations and open symbols are additionally selected stations.

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Table 1. Characteristics of the study sites

Location	Station	Latitude	Longitude	Water depth (m)
Busan	BS-1	35°03′41.5″N	129°01′13.6″E	13.5–14.8
	BS-2	35°10′09.2″N	129°13′02.8″E	19.0–26.5
	BS-3	35°17′56.5″N	129°15′23.1″E	20.0–30.0
Ulsan	US-1	35°23′03.3″N	129°20′46.4″E	5.0–28.0
	US-2	35°28′49.3″N	129°22′00.4″E	5.5–11.0
	US-3	35°30′16.8″N	129°25′01.2″E	8.5–12.0
	US-4	35°36′23.3″N	129°27′35.3″E	23.5–39.0
Gyeongju	GJ-1	35°42′36.5″N	129°28′09.9″E	18.0–32.0
	GJ-2	35°48′43.1″N	129°30′33.1″E	11.0–33.0

diving at the nine study stations in rocky subtidal zones to water depths of 1-20 m. In accordance with the NMMP framework, quantitative samples were collected according to the Protocol of National Survey on Marine Ecosystems (MOF and KOEM, 2022). Photographs were taken to identify solitary ascidians during the survey. As the present study focused on the latitudinal trends of solitary ascidians, the presence or absence of *H. momus* was identified by analysing high-resolution underwater images in a laboratory. At all stations, two professional divers moved approximately 20 m in a zigzag pattern while remaining at a distance of 2–5 m from each other. They photographed a number of the individual images encountered during their movement, which lasted approximately 30 min overall.

Field surveys were conducted between 2016 and 2022, except in 2019 when the sites were not surveyed. The three NMMP stations were examined twice a year (May and August), whereas observations at the other six stations were conducted once a year (between May and June).

We collected surface water temperature data from Marine Environment Monitoring stations operated by the Korea Marine Environment Management Corporation to understand the factors affecting the spatial distributions of ascidians (https://www.meis.go.kr/portal/; accessed 10 February 2024).

Species identification and historical distribution

Solitary ascidians photographed from field surveys were identified to the species level based on various taxonomic references (e.g. Bae *et al.*, 2022; Shenkar *et al.*, 2023). Species identifications for each ascidian species were conducted by two or more researchers and then double-checked from expert ascidian taxonomists in Korea. The occurrence of each ascidian species as well as their geographical location and time were also recorded. The species identified by image analysis were initially annotated according to their Korean names based on the National List of Marine Species II: Marine Invertebrates (MABIK, 2022; MOF and KOEM, 2022), and their scientific names were confirmed in accordance with the World Register of Marine Species (WoRMS, 2023).

For *H. momus*, the current observations recorded on the southeastern coast of Korea were compared with previous global records from the biological databases of the Global Biodiversity Information Facility (GBIF, 2023).

Results

Sea surface water temperatures (SSTs) gradually decreased from southern to northern stations, but SSTs tended to increase over time across the entire study area (Figure 2). In May, SSTs remained below 16°C at all stations except for the southernmost station BS-1, but there was a notable increase in SSTs at middle latitude station BS-3 beginning in 2018, followed by a widespread increase in SSTs at most of the stations between 2021 and 2022. While in August, SSTs remained consistently above 23°C at three stations located in Busan coast (BS-1, BS-2, and BS-3); significant increases in SSTs were observed at all stations in Ulsan and Gyeongju during 2017, 2018, and 2021.

Seven solitary-type ascidian species were identified across all nine stations, with *Styela clava* being the most frequently observed and *Pyura sacciformis*, the least common. The stations with the highest diversity of solitary ascidians were BS-3 and US-4, where six species were observed. The remaining stations showed the presence of between four and five ascidian species. In 2020, five of the seven species, with the exception of *Boltenia echinata* and *P. sacciformis*, were consistently observed at the southernmost station (i.e. BS-1) since 2016. The most common *S. clava* occurred

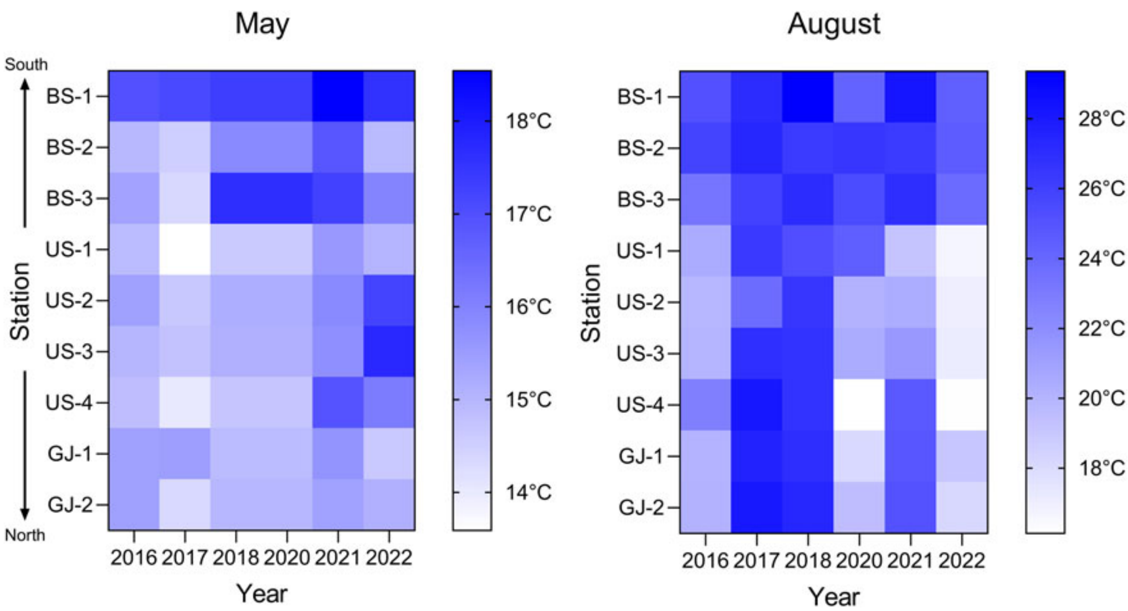

Figure 2. Heat map showing SSTs at nine study stations over 6 years between 2016 and 2022 on the southeastern coast of the Korean Peninsula.

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at Busan and Ulsan stations during the study period, but not at the Gyeongju station.

The presence of *H. momus* was confirmed at five stations (BS-1, BS-3, US-3, US-4, and GJ-2). Notably, *H. momus* was observed only at the southernmost station, BS-1, from 2016 to 2020. However, their presence was observed for the first time at more northern stations, US-3 and US-4, in 2021, and their habitats expanded to GJ-2, the northernmost station within the study area by the last year of the survey (Table 2).

Discussion

In the present study, seven solitary-type ascidian species were observed in nine study locations from 2016 and 2022. Most of the ascidians were subtropical or tropical species except for *B. echinata* and *Halocynthia roretzi* (Palomares and Pauly, 2023). Their lifespans were largely different from 1 to 4 years depending on the species, showing shorter lifespans in tropical species including *Ciona savignyi*, *H. momus*, and *Styela plicata* (Svane and Lundälv, 1982; Nomaguchi *et al.*, 1997; Lambert and Lambert, 1998; de Barros *et al.*, 2009; Yi and Kim, 2016). Generally, short-lived species take advantage of new opportunities to settle and colonise quickly in new marine environments by maximising population growth through high fecundity, rapid development, and a large investment in reproduction (Heppell *et al.*, 2005). Among ascidians recorded in this study, tropical species, including *H. momus*, have relatively shorter longevity, and thus, they may have an advantageous edge for inhabiting newly settled temperate reef habitats (Figley, 2003).

The main finding of the present study was the poleward extension of *H. momus*' habitat from the southernmost (35°03′41.5″N) to the northernmost (35°48′43.1″N) stations within our study area between 2016 and 2022. This finding indicates that by the end of the study period, the entire Busan–Ulsan–Gyeongju region had become part of the habitat range of *H. momus*. The rising seawater temperatures caused by global climate change have had a direct effect on the recruitment and habitat expansion of invasive species along the Korean Peninsula (Raitsos *et al.*, 2010; Son *et al.*, 2020; Hong *et al.*, 2022). These invasive species are expanding into other habitats through various routes, and their recruitment is progressing faster than predicted (Lee *et al.*, 2008; Capinha *et al.*, 2012).

H. momus is a typical tropical and subtropical species found primarily in the Indo-West Pacific Ocean, Atlantic Ocean, and Mediterranean Sea (Palomares and Pauly, 2023). According to the GBIF database (Figure 3), the northernmost recorded distribution of *H. momus* in the West Pacific was at 35°03′30″N in 2015, along the Busan coast of Korea (GBIF, 2023).

Except for this record, the northern distribution limit of the species is approximately 35°N or lower latitudes in the Northern Hemisphere, whereas the southern distribution limit reaches approximately 43°S (GBIF, 2023). Therefore, our study presents a new northernmost record of *H. momus*, implying *ca.* 50′ poleward expansion in species distribution since the mid-2010s.

The use of GIS analysis coupled with species distribution modelling has significantly improved our ability to observe and predict the climate change-associated expansion of various taxa (Guinotte *et al.*, 2006; Januario *et al.*, 2015; Assis *et al.*, 2018). Our present findings build upon previous observations of the northward expansion of the *H. momus* habitat range (Park *et al.*, 2020). According to the IPCC (2014) RCP4.5 scenario, which involves some mitigation of carbon dioxide concentrations, the habitat range of *H. momus* is projected to expand from the already established coastal habitats on Jeju Island to certain areas of the southern Korean Sea by 2100. In contrast, the worst-case RCP8.5 scenario predicts that the distributional expansion of *H. momus* will encompass the eastern part of the southeastern coast of the Korean Peninsula, including our study area. Park *et al.* (2020) deduced that the most influential environmental factor affecting *H. momus* expansion was the maximum seawater temperature, which accounted for 77.1% of the expansion observed.

Since 2016, the habitat range of *H. momus* observed by Park *et al.* (2020) has primarily included Jeju Island and some areas on the Busan coast. The observations we present in this study extend far beyond the habitat range of the RCP4.5 scenario, which predicted the habitat range of *H. momus* to remain

Table 2. Summary of Ascidiacea observation data from 2016 to 2022 by station

	Stations								
	Busan			Ulsan			Gyeongju		
Year	BS-1	BS-2	BS-3	US-1	US-2	US-3	US-4	GJ-1	GJ-2
2016	**C**, F	A	A, F	D	A, F	G	B, D, G	B	D
2017	**C**	D, E	B, F	B, F, G	B, F	F	D	D	
2018	B, **C**		F		B, F	B, F	D, G	A, B	G
2020	B, **C**, D	G	D, G	B, F		G	A	E	A, B, D
2021	–	F	–	D	E	**C**, F	**C**, F, G	B, D	–
2022		D, G	**C**	F	G				B, **C**
Number of species	4	5	6	4	5	4	6	4	5

A: *B. echinata*, B: *C. savignyi*, C: *H. momus*, D: *H. roretzi*, E: *P. sacciformis*, F: *S. clava*, G: *S. plicata*

						
A	B	C	D	E	F	G

Grey shadings indicate the presence of *H. momus*.
Note: The labels A–G correspond to arbitrarily assigned alphabetical designations used by the authors for species classification purposes. A blank space indicates that there no observed occurrences, while '–' indicates that no examination of the site.

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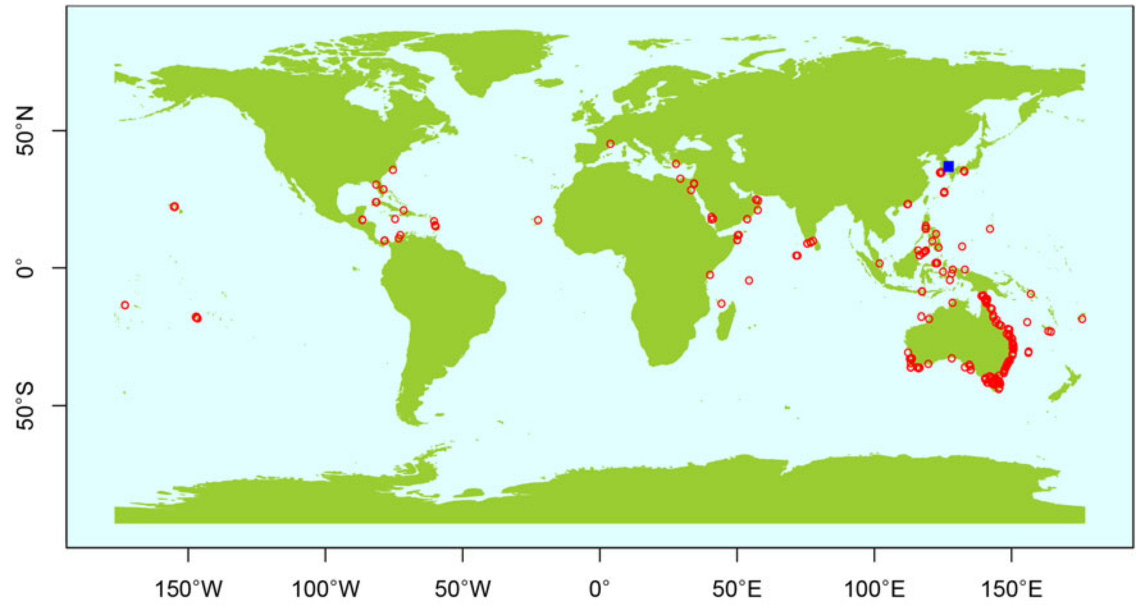

Figure 3. Distributional records of *H. momus*, showing historical records (red circles) from the Global Biodiversity Information Facility (GBIF, 2023) and the new record (blue square) off southeastern coast, South Korea.

relatively stable throughout 2100 (Park *et al.*, 2020). Moreover, our observations of *H. momus* in the waters off Ulsan in 2021 indicate that the species has spread more rapidly than was predicted in the RCP8.5 scenario of unmitigated climate change, wherein it was anticipated to expand from Busan to Ulsan by 2100 (Park *et al.*, 2020). This accelerated northward expansion of *H. momus* occurrences, beyond previous predictions, is likely due to the recent sharp increase in water temperatures in the East Sea (Lee and Park, 2019). Compared with global trends, sea surface temperatures around the Korean Peninsula, as well as the eastern coast of North America, are rising relatively quickly (Fasullo and Gent, 2017; Widlansky *et al.*, 2020). Therefore, continuous monitoring is required to better predict the habitat expansion of warm-water species and assess the impact of subtropical marine species on temperate marine ecosystems (Batten *et al.*, 2006).

In conclusion, our study's findings suggest that the poleward habitat expansion of subtropical marine species entering the Korean Peninsula due to climate change outpaces previous predictions, at least in the case of *H. momus.* Although the IPCC's RCP scenarios are broadly used to predict future changes in marine ecosystems, it is difficult to apply them to specific regions experiencing rapid localised temperature increases, such as the Korean Peninsula. These scenarios are based on only four representative pathways and consider global socioeconomic, political, and policy factors, which limits their accuracy in predicting local marine ecosystem changes. Effectively addressing marine ecosystem changes in the Korean Peninsula will require the development of governmental policies that incorporate proactive measures and strategies to mitigate eventualities that exceed even the most recent predictions.

Data availability statement. Data availability is not applicable to this article as no new data were created or analysed in this study.

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Author's contribution. Choul-Hee Hwang: conceptualisation, data curation, methodology, formal analysis, and writing of the original draft. Su Jin Lee, Hyeong Ju Seok, and Hyun-Jung Kim: methodology and formal analysis. InSeo Hwang: conceptualisation, data curation, and supervision. Min Gu Kang: methodology, visualisation. Joo Myun Park: methodology, software, visualisation, writing – review, and editing.

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Competing interests. None.

Ethical standards. Because this study conducted a field survey using non-disturbing scuba observations, an ethical review by the Statement Animal Experiment Committee was not required.

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