

## Research Article

# Spatiotemporal dynamics of *Watersipora subtorquata* in Korean coastal harbors: effect of water temperature and salinity on percent cover

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## Abstract

The colonial bryozoan *Watersipora subtorquata* is a globally distributed non-indigenous species (NIS), posing increasing threats to marine biodiversity and coastal industries through biofouling and competition with native biota. In South Korea, despite its recognition as a harmful marine organism, few studies have addressed its ecological behavior under varying environmental conditions. This study investigated the spatio-temporal dynamics of *W. subtorquata* percent cover in four Korean harbors—Yangpo, Tongyeong, Bieung, and Jeju—over a 39-month period (April 2021 to July 2024). Standardized acrylic settlement plates and in-situ measurements of water temperature and salinity were used to evaluate percent cover patterns. Generalized Additive Models (GAMs) revealed temperature was significantly associated with percent cover across all four harbors, while salinity played a key role in Bieung. A significant interaction effect between temperature and salinity was observed in Jeju. These results provide novel insights into the environmental sensitivity of *W. subtorquata*, highlighting the importance of multi-regional and long-term monitoring to guide site-specific management of invasive species, while underscoring the need for higher-resolution environmental time series to assess climate-related implications more directly.



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**Key words:** Artificial substrates, biofouling, environmental monitoring, generalized additive models, harmful marine organism, non-indigenous species

## Introduction

Bryozoans are a diverse and widespread group of colonial marine invertebrates, with over 6,500 species worldwide and 260 species recorded from Korea (National Institute of Biological Resources 2026; WoRMS Editorial Board 2026). Among them, *Watersipora subtorquata* (d'Orbigny, 1852) has garnered increasing scientific and policy attention due to its rapid global spread and negative ecological impacts. This species was thought to be native to the tropical Southwestern Atlantic and Indo-West

Pacific (Vieira et al. 2014). However, it is now recorded throughout the world, including Europe, East Asia, the Americas, and Australasia (Mead et al. 2011; Ryland et al. 2011). Its success as an invasive marine species stems from its high reproductive capacity, environmental tolerance, and preference for artificial substrates such as vessel hulls, aquaculture infrastructure, and harbor walls (Cohen 2011; Bakran et al. 2023).

Invasive biofouling organisms such as *W. subtorquata* pose increasing risks to coastal ecosystems by altering community structures, competing with native species, and causing substantial economic damage to aquaculture and maritime industries (Park et al. 2017; Kim et al. 2021). For example, Japan has developed localized protocols for early detection of *W. subtorquata* in high-risk harbors (McLachlan 2017) and Australia has deployed anti-fouling strategies using targeted coatings and rapid response frameworks (Dunstan and Johnson 2004; Glasby et al. 2007). In South Korea, *W. subtorquata* has been designated as one of the 18 Harmful Marine Organisms (HMOs) under the national Act on Conservation and Management of Marine Ecosystems (Ministry of Oceans and Fisheries 2023). However, while regulatory recognition exists, detailed ecological data across multiple Korean regions remain scarce.

To date, most research studies concerning *W. subtorquata* have focused on taxonomy (Seo 2010; Mackie et al. 2012; Vieira et al. 2014), larval morphology (McLachlan 2017), or antifouling control methods (Bae et al. 2022; Liang et al. 2022). Few studies have investigated the influence of abiotic factors on percent cover dynamics in natural harbor environments over extended periods (Azevedo et al. 2020; Jewett et al. 2022). Furthermore, studies tended to focus on individual harbors or single-season snapshots, lacking a nationwide, multi-year perspective that could assess ecological drivers over time and space. This gap in knowledge hinders our ability to design predictive models or formulate effective policy measures tailored to specific environmental conditions.

Water temperature and salinity are widely recognized as key drivers of recruitment, growth, and survival of marine sessile invertebrates (Boyd et al. 2002; Kinlan and Gaines 2003; Dunstan and Johnson 2004). For *W. subtorquata*, optimal recruitment has been observed within water temperatures of 12–27 °C and salinity ranges of 25–37 PSU (Boyd et al. 2002), although tolerance limits and recruitment responses may differ among regional populations. Environmental variability—especially in semi-enclosed or inner bay environments—can modify recruitment patterns and survival rates, contributing to different degrees of invasiveness among localities (Bullard et al. 2007; Glasby et al. 2007). In Korean waters, that are characterized by diverse salinity regimes and pronounced temperature variability, it remains unclear how these factors can shape the spatial distribution and seasonal patterns of *W. subtorquata* communities. In this study, we quantify spatiotemporal variation using percent cover as an integrated measure of colony establishment and growth.

Long-term warming trends have already led to species range shifts, with non-indigenous species (NIS) expanding into previously unsuitable areas (Ricciardi and MacIsaac 2000). For biofouling organisms such as *W. subtorquata*, rising sea temperatures might lower thermal barriers, facilitate overwintering survival, and extend colonization windows, particularly in temperate regions such as the Korean Peninsula. Thus, understanding how *W. subtorquata* responds to subtle changes in temperature and salinity is essential for forecasting future invasion scenarios and informing the design of adaptive management frameworks.

To address these gaps, this study investigated the spatiotemporal dynamics of *W. subtorquata* percent cover across four distinct harbor regions in South Korea—Yangpo, Tongyeong, Bieung, and Jeju—between April 2021 and July 2024. Using standardized field deployments and Generalized Additive Models (GAMs), we explored independent and interactive effects of temperature and salinity on percent

cover variability. Our findings offer critical insights into environmental sensitivities of *W. subtorquata* and provide a scientific basis for developing ecosystem-based control measures amid increasing anthropogenic pressures and climate-induced change.

## Methods

### Study sites and monitoring period

This study was conducted over a period of 39 months, from April 2021 to July 2024, across four representative coastal harbors in South Korea: Yangpo (East Sea), Tongyeong (Korea Strait), Bieung (Yellow Sea), and Jeju (offshore Jeju Island). These sites were selected to capture regional variations in oceanographic conditions and harbor characteristics (Fig. 1). Yangpo (East Sea) represents an open-coast harbor setting on the Korean east coast, where coastal hydrography is strongly influenced by the East Korea Warm Current (a branch of the Tsushima Warm Current) and associated alongshore variability (Pak et al. 2023; Lee et al. 2024). Tongyeong (Korea Strait) is located in a relatively sheltered, semi-enclosed southern-coast embayment with extensive harbor infrastructure and high vessel activity; hydrography in this region is strongly affected by Kuroshio-derived warm currents entering through the

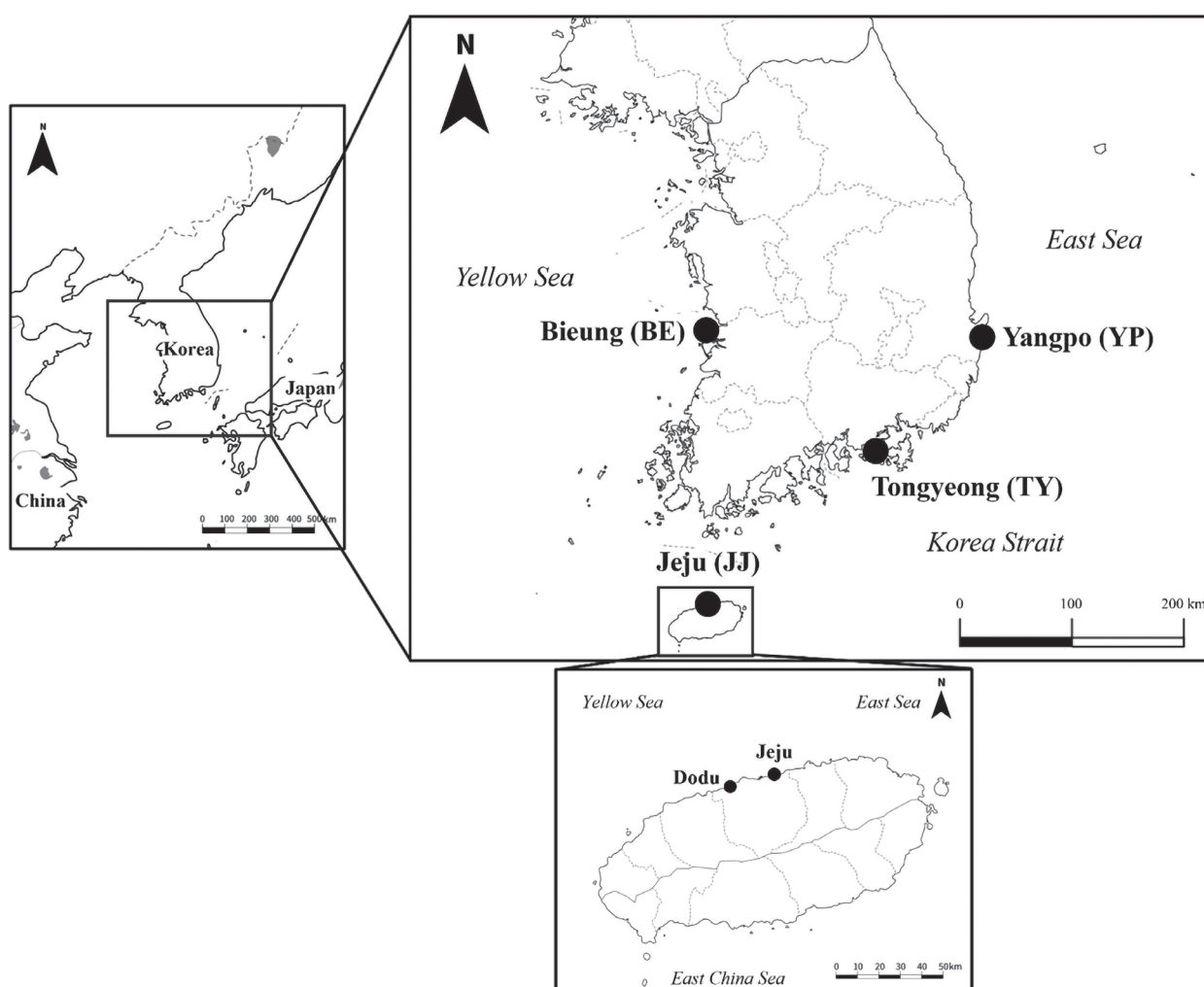


**Figure 1.** Geographical distribution of the four monitoring harbors in Korea: Yangpo (East Sea), Tongyeong (Korea Strait), Bieung (Yellow Sea), and Jeju (offshore Jeju Island).

Korea Strait and seasonally varying stratification (Jiang et al. 2023; Kang et al. 2024). Bieung (Yellow Sea) represents a macrotidal, well-mixed west-coast environment where strong barotropic tides and tidal mixing can increase turbidity and drive short-term variability in nearshore conditions relevant to settlement (Lin et al. 2021; Du et al. 2022). Jeju (offshore Jeju Island) reflects a more oceanic island setting influenced by warm, saline Tsushima/Jeju Warm Current pathways and energetic tidal currents around the Jeju Strait, which can create pronounced spatial variability in temperature and salinity (Cha and Moon 2020; Kim et al. 2022; Kim and Choi 2024).

## Percent cover monitoring using settlement plates

At each site, artificial settlement substrates were deployed to quantify percent cover of *Watersipora subtorquata* as an integrated measure of colony establishment and growth on the plates. Substrates consisted of square acrylic plates (300 mm × 300 mm × 5 mm), a material commonly used in harbor infrastructure. Plates were grouped in sets of ten and suspended vertically using polypropylene ropes, with adjacent plates spaced 30 cm apart, spanning approximately 1–4 m depth along the water column (uppermost to lowermost plates). Plates were redeployed in the same vertical configuration after each survey and were not intentionally reassigned among depths between sampling events. Because plates were deployed as standardized vertical arrays rather than as fixed-depth experimental treatments, percent cover values were interpreted as an integrated response across this representative 1–4 m near-surface depth range, and depth was therefore not included as an independent predictor in the GAM analyses. Three deployment points were established per site. Points were selected in areas with high vessel berthing and traffic, and were positioned closer to the seaward side of each harbor (near the harbor mouth) rather than nearshore inner sections, to better represent conditions experienced by floating and fixed harbor infrastructure. These plates remained submerged for a standardized exposure period that was consistent across all sites; only plates with a minimum exposure duration of 6 months were included in the analysis. Plates were deployed at least 6 months prior to the first survey (i.e., before April 2021), and the monitoring period (April 2021–July 2024) represents repeated observations of already established assemblages on these plates. Therefore, all observations used in the analyses corresponded to plates with a minimum immersion time of 6 months. Surveys were conducted in April, July, and October in 2021; in April, June, August, and October in 2022; in April, July, and October in 2023; and in April and July in 2024. Within each survey cycle, all four sites were sampled within approximately 2 weeks of each other (not necessarily on the same day) to ensure temporal comparability among sites (Table 1). During each field survey, plates were retrieved to the surface and photographed out of the water on shore using a digital camera (Olympus Tough TG-5, Japan), after which they were redeployed. These images were later analyzed using ImageJ software (Schneider et al. 2012) to determine the percent cover of *W. subtorquata* calculated as the percentage of the plate area covered by the species.

$$\text{Percent cover(\%)} = \left( \frac{\text{Number of pixels in the area occupied by the target species}}{\text{Number of pixels in the total area of the attachment plate}} \right) \times 100$$

## Species identification

Colonies of *Watersipora subtorquata* observed on settlement plates were identified in the field based on colony morphology and diagnostic characters. Identification followed the taxonomic keys and illustrated guides for bryozoans in Korean waters

**Table 1.** Summary of sampling dates and seasonal distribution of surveys.

| Year  | Survey count | Survey dates |    |    |        |           |    |    |        |           |    |    |        |
|-------|--------------|--------------|----|----|--------|-----------|----|----|--------|-----------|----|----|--------|
|       |              | Spring       |    |    |        | Summer    |    |    |        | Autumn    |    |    |        |
|       |              | YP           | TY | BE | JJ     | YP        | TY | BE | JJ     | YP        | TY | BE | JJ     |
| 2021  | 3            | Apr 19–22    |    |    | Apr 29 | Jul 19–22 |    |    | Jul 15 | Oct 18–21 |    |    | Oct 25 |
| 2022  | 4            | Apr 18–20    |    |    | Apr 22 | Jun 20–21 |    |    | Jul 15 | Oct 17–18 |    |    | Oct 20 |
|       |              |              |    |    |        | Aug 22–23 |    |    | Aug 26 |           |    |    |        |
| 2023  | 3            | Apr 10–12    |    |    | Apr 17 | Jul 10–11 |    |    | Jul 14 | Oct 10–12 |    |    | Oct 16 |
| 2024  | 2            | Apr 16–18    |    |    | Apr 30 | Jul 15–17 |    |    | Jul 12 | –         |    |    |        |
| Total | 12           |              |    |    |        |           |    |    |        |           |    |    |        |

(Seo 2005; Seo 2010) and was cross-checked against relevant taxonomic literature. To strengthen taxonomic reliability, identifications were additionally reviewed through consultation and collaboration with a Ph.D.-level taxonomic specialist in the field.

## Environmental data collection

Water temperature and salinity were measured at each survey site using a multi-parameter water quality meter (Pro Plus, YSI, USA). Measurements were taken simultaneously with plate retrieval to ensure temporal consistency between biological and environmental data. Water temperature and salinity were measured at approximately 2 m depth adjacent to the plate arrays during each survey. Because these measurements were collected at discrete survey times rather than continuously, they represent contemporaneous conditions during each sampling event. Site-specific summaries of observed temperature and salinity across surveys are provided in Suppl. material 1, and temporal changes in water temperature and salinity at each harbor are shown in Suppl. material 4. Because these measurements were collected only at the time of each survey, they do not represent integrated environmental histories prior to sampling. Accordingly, potential lagged effects of temperature and salinity on percent cover were not evaluated in this study.

## Data processing and outlier management

Outliers in plate percent cover were identified and corrected using the Interquartile Range (IQR) method. For each sampling event at each site, plate-level percent cover values were pooled across plates (within the same location and survey cycle) to compute the IQR and identify outliers. Following Tukey's rule, values above the upper fence ( $Q3 + 1.5 \times \text{IQR}$ ) were winsorized (i.e., capped rather than removed) by replacing them with the upper fence value (Tukey 1977). Values  $\leq 0$  were set to 0.01 to allow model fitting under a log link. To improve transparency of the raw observations and the extent of zero values and outlier handling, we provide a site-specific scatter plot of plate-level *W. subtorquata* percent cover over the monitoring period (Suppl. material 2). Observations flagged as outliers using Tukey's IQR rule within each harbor  $\times$  survey month (values  $> Q3 + 1.5 \times \text{IQR}$ ) are indicated in the figure. Raw zero values are shown as 0 in Suppl. material 2; however, for Gamma GAM fitting under a log link, zeros were replaced with 0.01 as described above. For statistical modeling, plate-level percent cover values were summarized to a single mean percent cover for each harbor and survey date after outlier treatment. Thus, although outlier detection and correction were performed on plate-level observations, the response variable used in the GAM analyses was the survey-event mean percent cover rather than individual plate values.

## Statistical analysis

Generalized Additive Models (GAMs) were fitted separately for each harbor to evaluate the relationships between environmental conditions and *W. subtorquata* percent cover. For each harbor and survey date, plate-level percent cover values were first summarized to a single mean value, and the corresponding water temperature and salinity measured during that survey were used as predictors. Therefore, the statistical unit in the GAM analyses was the harbor-by-survey event rather than individual plates. No lagged environmental covariates were included; therefore, the GAMs were designed to evaluate associations between percent cover and temperature/salinity measured contemporaneously at each survey event. Analyses were conducted in R using the mgcv package (R version 4.4.1) (Zuur et al. 2009; Wood 2017). Because summarized percent cover values were positive and right-skewed, models were fitted with a Gamma error distribution and a log link. When necessary for model fitting under the log link, zero values were replaced with 0.01. For additive effects, the site-specific model was: percent cover  $\sim$  s(water temperature,  $k = 10$ ) + s(salinity,  $k = 10$ ), where smooth terms were represented using thin-plate regression splines. To assess the temperature–salinity interaction, we additionally fitted a tensor-product smooth model for each harbor: percent cover  $\sim$  te(water temperature, salinity,  $k = 3$ ). Smoothness parameters were optimized automatically in mgcv. Model performance was evaluated using adjusted R-squared and deviance explained (%), and the statistical significance of smooth terms was assessed using F-statistics and associated p-values ( $\alpha = 0.05$ ). Because each harbor was represented by repeated survey events over time, the GAM results are interpreted as survey-event-level associations rather than as independent plate-level responses.

## Visualization

Results were visualized using the ggplot2 package in R (Wickham 2016). Smooth term plots were used to illustrate the individual effects of environmental factors, and contour plots were generated to display temperature–salinity interaction patterns across continuous gradients. The supplementary materials include site-specific environmental summaries (Suppl. material 1), raw plate-level percent cover observations by survey month, with zero values and IQR-identified outliers highlighted (Suppl. material 2), temporal variation in mean percent cover (Suppl. material 3), and temporal variation in water temperature and salinity (Suppl. material 4).

## Results

A total of 12 field surveys were conducted over a 39-month period (April 2021 to July 2024) across four harbor locations (Fig. 1). *Watersipora subtorquata* percent cover had considerable temporal and spatial variations across sites, showing marked differences in both magnitude and environmental response patterns. Accordingly, the GAM results should be interpreted as relationships with contemporaneous conditions measured at the time of each survey.

### Yangpo Harbor

Percent cover of *W. subtorquata* in Yangpo Harbor demonstrated marked seasonal and interannual variability, reflecting strong environmental modulation over the study period. The annual average percent cover ranged from 0.86% in 2021, peaking at 2.48% in 2022. It then decreased to 0.90% in 2023 before it slightly

increased again to 1.76% in 2024. Percent cover was particularly elevated during spring seasons. April 2022 had the highest percent cover (7.87%), followed by April 2021 (1.83%) and July 2024 (2.64%), indicating that higher percent cover was observed during several spring sampling events, particularly under the contemporaneous conditions recorded during those surveys (Suppl. material 3: fig. S3A).

Environmental monitoring recorded mean water temperatures of  $18.0 \pm 5.0$  °C, with seasonal extremes ranging from 8.1 °C in April 2023 to 25.9 °C in July 2021. Salinity showed a moderate fluctuation, averaging  $31.7 \pm 1.7$  PSU (range, 28.9 PSU in July 2024 to 34.3 PSU in April 2022) (Suppl. material 1).

GAM modeling identified a statistically significant negative linear effect of water temperature on percent cover (EDF = 0.9731,  $F = 0.5750$ ,  $p = 0.0318$ ), suggesting that percent cover decreased modestly with increasing temperatures (Table 2, Fig. 2A). However, salinity exhibited no significant influence on percent cover (EDF = 2.4825,  $F = 19.1478$ ,  $p = 0.6151$ ) despite its nonlinear relationship shape (Fig. 2B).

Additionally, the interaction between temperature and salinity was not significant (EDF = 2.1458,  $F = 0.7076$ ,  $p = 0.1065$ ), indicating independent environmental effects in this harbor (Table 3, Fig. 3A).

### Tongyeong Harbor

Percent cover in Tongyeong Harbor followed a bimodal seasonal trend, showing elevated cover during both early spring and mid-summer. The highest monthly percent cover occurred in April 2021 (2.08%) and July 2023 (1.39%). However, annual averages showed a general decline from 1.09% in 2021 to 0.21% in 2024, suggesting reduced percent cover over time (Suppl. material 3: fig. S3B).

Water temperatures varied from 14.3 °C to 23.7 °C, with a mean of  $19.4 \pm 3.4$  °C. Salinity ranged from 28.4 PSU to 34.0 PSU, with an average of  $31.5 \pm 1.9$  PSU (Suppl. material 1).

**Table 2.** Site-specific GAM results for the additive effects of water temperature and salinity on the percent cover of *W. subtorquata* across four harbors. Separate GAMs were fitted for each harbor: percent cover ~ s(water\_temperature) + s(salinity) (Gamma distribution, log link). Values shown are EDF, F-value, and  $p$ -values for each smooth term, along with adjusted  $R^2$  and deviance explained.

| Harbor    | Water temperature |          |            | Salinity |         |            | Adjusted $R^2$ | Deviance explaining |
|-----------|-------------------|----------|------------|----------|---------|------------|----------------|---------------------|
|           | EDF               | F-value  | $p$ -value | EDF      | F-value | $p$ -value |                |                     |
| Yangpo    | 0.9731            | 0.5750   | 0.0318     | 2.4825   | 19.1478 | 0.6151     | 0.672          | 58.7%               |
| Tongyeong | 7.7853            | 300.5334 | 0.0426     | 0.0000   | 0.0000  | 0.4223     | 0.927          | 97.6%               |
| Bieung    | 3.5402            | 4.2444   | 0.0453     | 0.8088   | 0.6952  | 0.0251     | 0.656          | 59.6%               |
| Jeju      | 0.7255            | 0.5383   | 0.0230     | 0.5923   | 0.2719  | 0.0625     | 0.411          | 51.4%               |

**Table 3.** Site-specific GAM results for the temperature–salinity interaction effect on the percent cover of *W. subtorquata* across four harbors. Separate GAMs were fitted for each harbor: percent cover ~ te(water\_temperature, salinity) (Gamma distribution, log link). Values shown are EDF, F-value, and  $p$ -values for the tensor-product smooth, along with adjusted  $R^2$  and deviance explained.

| Harbour   | Water temperature, Salinity |         |            | Adjusted $R^2$ | Deviance Explained |
|-----------|-----------------------------|---------|------------|----------------|--------------------|
|           | EDF                         | F-value | $p$ -value |                |                    |
| Yangpo    | 2.1458                      | 0.7076  | 0.1065     | 0.365          | 41.3%              |
| Tongyeong | 0.2435                      | 0.0394  | 0.3142     | 0.035          | 5.2%               |
| Bieung    | 0.3654                      | 0.0946  | 0.1635     | 0.087          | 7.2%               |
| Jeju      | 1.5439                      | 1.2334  | 0.0141     | 0.346          | 50.6%              |

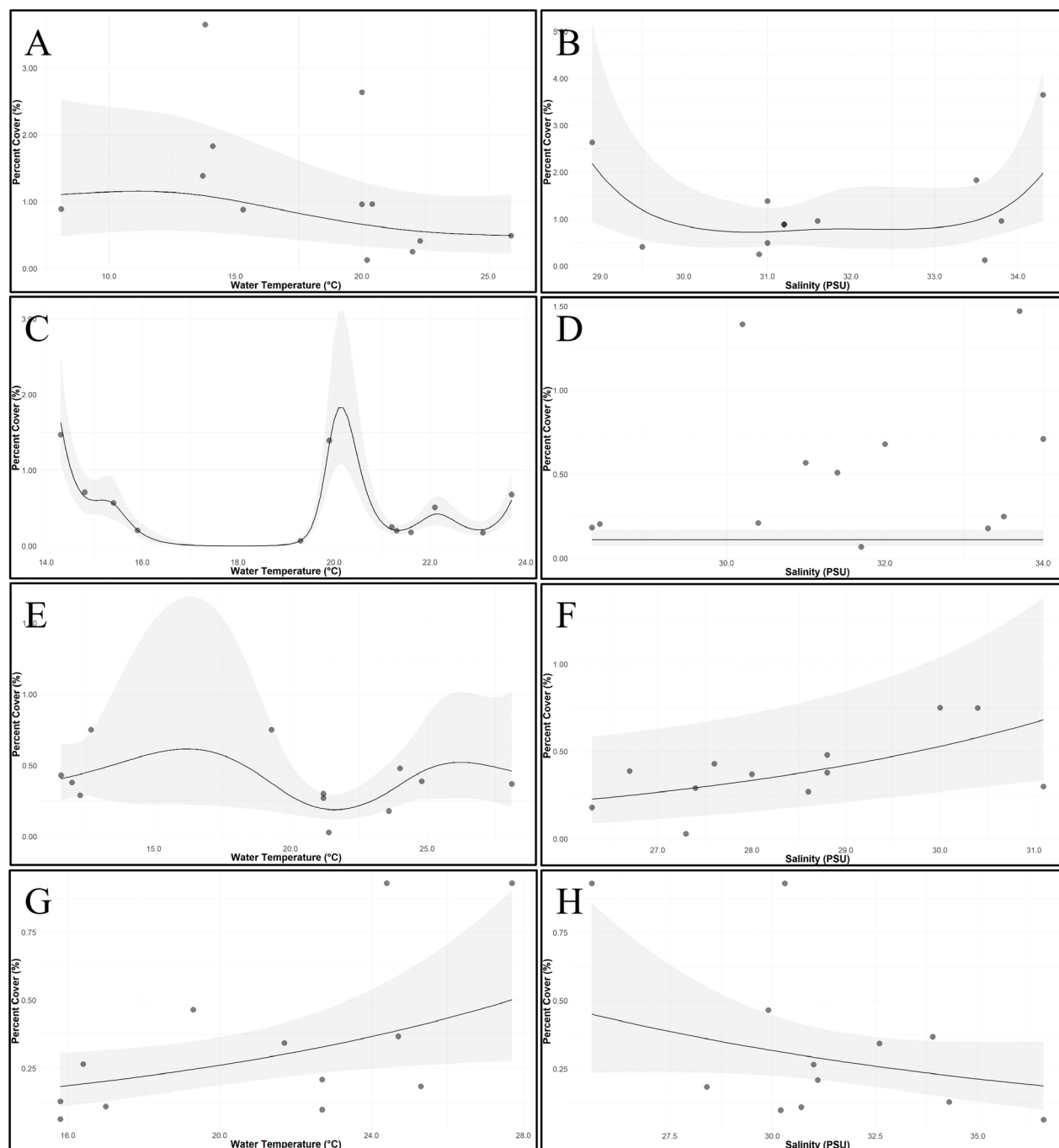


**Figure 2.** GAM results showing effects of environmental factors on percent cover of *W. subtorquata* across four Korean harbors from April 2021 to July 2024: Yangpo (A, B), Tongyeong (C, D), Bieung (E, F), and Jeju (G, H). A, C, E, G. Effect of water temperature with constant salinity; B, D, F, H. Effect of salinity with constant water temperature. Shaded bands represent 95% confidence intervals ( $\pm 1.96$  SE) around the fitted GAM smooths.

GAM analysis (Table 2) revealed a significant nonlinear effect of temperature (EDF = 7.7853,  $F = 300.5334$ ,  $p = 0.0426$ ) on percent cover, exhibiting a U-shaped percent cover response with higher percent cover observed at temperatures below 16 °C or above 21 °C (Fig. 2C). In contrast, salinity exhibited no significant effect (EDF = 0.0000,  $F = 0.0000$ ,  $p = 0.4223$ ), indicating that variation in salinity did not influence percent cover patterns at this site (Fig. 2D).

Additionally, no statistically significant interaction was found between temperature and salinity (EDF = 0.2435,  $F = 0.0394$ ,  $p = 0.3142$ ), suggesting that the

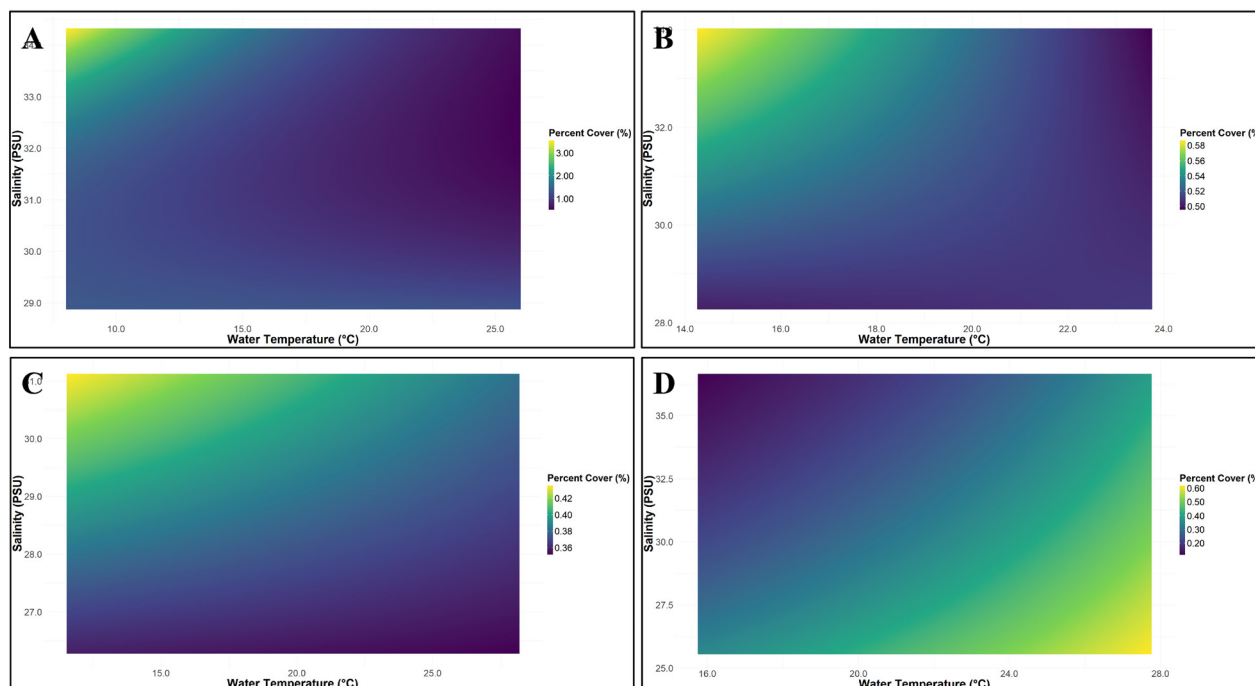


**Figure 3.** Contour plots of the GAM-predicted percent cover of *W. subtorquata* as a function of water temperature and salinity in four Korean harbors: **A.** Yangpo; **B.** Tongyeong; **C.** Bieung, and **D.** Jeju. Warmer colors indicate higher predicted values.

effect of each variable was independent in Tongyeong (Table 3, Fig. 3B). These findings suggest that Tongyeong's *W. subtorquata* population is very sensitive to specific temperature windows but insensitive to salinity variations, possibly reflecting its local adaptation or physiological tolerance.

### Bieung Harbor

Percent cover at Bieung Harbor was the lowest among the study sites. Monthly percent cover seldom exceeded 0.84%, often remaining under 0.40%. Despite low averages, localized seasonal peaks were observed in April 2022 (0.84%) and October 2022 (0.75%), suggesting episodic increases in cover under specific conditions (Suppl. material 3: fig. S3C).

Water temperatures in Bieung ranged from 15.5 °C to 27.0 °C, with an average of  $21.4 \pm 3.2$  °C across the monitoring period. Salinity in Bieung ranged from 29.7 PSU to 34.5 PSU with a mean of  $31.2 \pm 1.6$  PSU (Suppl. material 1), and showed a slightly wider fluctuation than in other sites.

GAM results (Table 2) revealed that both water temperature and salinity had statistically significant effects on percent cover in Bieung Harbor. Water temperature showed a significant nonlinear effect (EDF = 3.5402,  $F = 4.2444$ ,  $p = 0.0453$ ), indicating that percent cover varied nonlinearly across the observed temperature range (Fig. 2E). Salinity also had a statistically significant positive effect on percent cover (EDF = 0.8088,  $F = 0.6952$ ,  $p = 0.0251$ ), suggesting that higher salinity levels in this semi-enclosed estuarine setting were associated with higher percent cover of *W. subtorquata* (Fig. 2F).

Additionally, no significant interaction between temperature and salinity was observed (EDF = 0.3654,  $F = 0.0946$ ,  $p = 0.1635$ ) (Table 3, Fig. 3C), indicating that both temperature and salinity contributed to variation in percent cover in Bieung, although their interaction was not significant. Although temperature and salinity showed significant additive associations with percent cover in Bieung,

the explanatory power of models based only on these variables remained limited, suggesting that additional unmeasured factors may also contribute to temporal variation in percent cover at this site.

## Jeju Harbor

Jeju Harbor exhibited the greatest variability in percent cover and environmental conditions among the four study sites. Percent cover increased over the study period, with the highest monthly value reaching 1.45% in July 2024. Annual averages of percent cover increased from 0.21% in 2021 to 0.78% in 2024. However, because temperature and salinity were measured only at discrete survey times, this temporal increase should not be interpreted as direct evidence of ocean-warming effects (Suppl. material 3: fig. S3D).

Environmental conditions were notably dynamic, with water temperature fluctuating between 15.8 °C and 27.7 °C (mean:  $21.1 \pm 4.1$  °C) and salinity ranging from 25.6 PSU to 36.6 PSU (mean:  $31.2 \pm 2.9$  PSU). These broad ranges are characteristic of offshore sites exposed to variable oceanographic processes (Suppl. material 1).

GAM results (Tables 2, 3) showed that temperature had a statistically significant positive effect on percent cover (EDF = 0.7255,  $F = 0.5383$ ,  $p = 0.0230$ ), indicating that higher percent cover was associated with higher contemporaneous temperatures under the salinity conditions observed at this site (Fig. 2G–H). Although salinity alone was not significant (EDF = 0.5923,  $F = 0.2719$ ,  $p = 0.0625$ ), its interaction with temperature was significant (EDF = 1.5439,  $F = 0.2334$ ,  $p = 0.0141$ ), indicating a synergistic effect between salinity and temperature under specific environmental thresholds (Fig. 3D).

Percent cover was maximized when temperatures exceeded 25 °C and salinity remained within 25–27.5 PSU, revealing a narrow but optimal environmental window associated with higher percent cover of *W. subtorquata* in Jeju. These findings suggest that percent cover was highest under a relatively narrow range of contemporaneous temperature–salinity conditions in Jeju, although future expansion cannot be inferred directly from these snapshot measurements alone.

## Summary of environmental effects

The influence of water temperature and salinity on percent cover varied by location. Results are summarized in Table 4. While temperature showed significant effects across all four harbors, salinity played a meaningful role only in Bieung Harbor. Notably, a statistically significant interaction between the two variables was only observed in Jeju Harbor.

**Table 4.** Summary of environmental effects on percent cover of *W. subtorquata* across four harbors based on GAM analysis (O indicates statistically significant relationships at  $p < 0.05$  and X indicates non-significance).

| Harbor    | Temperature effect       | Salinity effect          | Interaction effect                                              |
|-----------|--------------------------|--------------------------|-----------------------------------------------------------------|
| Yangpo    | O (Negative association) | X (Not significant)      | X (Not significant)                                             |
| Tongyeong | O (Nonlinear (U-shape))  | X (Not significant)      | X (Not significant)                                             |
| Bieung    | O (Positive association) | O (Positive association) | X (Not significant)                                             |
| Jeju      | O (Positive association) | X (visible trend only)   | O (Significant interaction)<br>( $> 25.0$ °C and 25.0–27.5 PSU) |

## Discussion

### Site-specific effects of temperature and salinity

Percent cover of *Watersipora subtorquata* differed among the four harbors (Friedman test across 12 survey cycles:  $\chi^2 = 9.70$ ,  $df = 3$ ,  $p = 0.0210$ ), although values were generally low at all sites. This variation appears to reflect differences in local temperature and salinity. Temperature showed a significant association with percent cover across sites. Percent cover slightly decreased with increasing temperature in Yangpo. In Tongyeong, there was a more complex response, with higher percent cover at both low and high temperatures. In Bieung, percent cover also varied significantly with temperature, showing a nonlinear response across the observed range. In Jeju, the relationship was statistically significant, although the trend was relatively stable. These associations were broadly consistent with previously reported temperature ranges under which *W. subtorquata* has been observed to perform well (Boyd et al. 2002). However, because temperature and salinity were measured only at the time of each survey, our data do not allow direct inference about growth or recruitment processes, and the observed relationships should be interpreted as associations with contemporaneous conditions rather than as evidence of integrated seasonal drivers. These associations should therefore not be interpreted as evidence of causal environmental drivers of percent cover variability. Salinity effects were less consistent among harbors. At most sites, no strong association was found. However, in Bieung, percent cover increased with salinity, suggesting that local salinity variability may help explain cover dynamics at this site. At the same time, these results should be interpreted cautiously, because temperature and salinity alone are unlikely to capture all of the drivers of percent cover variability. In this more enclosed setting, additional factors such as local hydrodynamics, turbidity, propagule supply, and substrate-related differences may also contribute to variation in percent cover. Similar patterns have been noted for other fouling organisms in estuarine systems (Dunstan and Johnson 2004). Interpretation of these site-specific patterns should also consider differences in local harbor settings that can influence propagule delivery and colony development. For example, open-coast versus semi-enclosed geomorphology can alter water residence time and the retention of larvae near plate surfaces, and differences in harbor infrastructure and vessel traffic may modify substrate availability and introduction pressure among sites.

### Site-specific interaction effects and their ecological interpretation

A significant interaction between temperature and salinity was only observed in Jeju. In Jeju, the predicted temperature–salinity response surface indicated higher percent cover under warmer temperatures (e.g.,  $> 25.0^\circ\text{C}$ ) combined with relatively lower salinity (approximately 25.0–27.5 PSU) within the observed range (Fig. 3D), consistent with a significant interaction between the two variables. However, this interaction should be interpreted cautiously because environmental variables were measured as snapshot conditions and do not reflect continuous environmental exposure. The relatively open coastal structure and stable conditions around Jeju might have contributed to this pattern. These findings are in line with studies showing that certain invasive species respond strongly to specific combinations of environmental factors (Ricciardi and MacIsaac 2000). In contrast, other sites showed no significant interaction effects possibly due to reduced environmental variability or stronger physical isolation from open water. In Yangpo and Tongyeong, both of which are open-coast harbors, interaction signals may have been harder to detect due to the limited sampling frequency and the relatively narrow ob-

served range of one or both variables during the survey windows. Differences in connectivity and nearshore larval delivery among harbors may also affect whether interaction signals are detectable, particularly if establishment is supply-limited or episodic at some sites. A further consideration is potential cryptic diversity within *Watersipora*. Mackie et al. (2012) reported latitudinal segregation among *Watersipora* lineages (“new sp.” and additional clades) and suggested that lineage occurrence can be correlated with temperature. Because our identifications were based on morphology, we cannot fully exclude the possibility that percent cover responses at some sites reflect contributions from a different lineage. Future work integrating morphometric and DNA-based identification would help resolve lineage-specific cover–environment relationships.

## Implications for monitoring and management

These results highlight the need for site-based monitoring strategies. Jeju appears particularly suitable for *W. subtorquata* establishment under certain conditions, and ongoing warming may be consistent with increased risk, although this cannot be directly inferred from the present data. Bieung also warrants attention given its sensitivity to salinity variability, as changes in estuarine inputs or circulation could alter establishment patterns. We did not use satellite-derived products because coastal harbor environments are strongly influenced by local circulation and freshwater inputs, and satellite pixels may not reliably represent nearshore conditions at the spatial scale of the deployment sites. A limitation of this study is that temperature and salinity were measured intermittently during field surveys rather than continuously, and thus may not fully capture short-term variability. In addition, because environmental covariates were measured only at the time of sampling, our analyses do not account for lagged effects or prior environmental exposure that may also influence percent cover. In addition, the present models considered only temperature and salinity, and therefore did not explicitly incorporate other potentially important drivers such as hydrodynamic conditions, turbidity, propagule pressure, or substrate-related variation. Another limitation is that plates spanned an approximately 1–4 m depth range and were analyzed as an integrated vertical array, so potential fine-scale depth effects within this near-surface window were not evaluated explicitly. A further limitation is that each harbor was represented by a relatively small number of repeated survey events over time and thus potential temporal autocorrelation among observations was not explicitly modeled in the present analyses. Future studies using high-frequency temperature–salinity loggers, denser temporal sampling, and plate-specific depth records would better resolve percent cover dynamics, lag effects, within-array depth variation, and temporal autocorrelation.

## Conclusions

This study provides the first long-term, multi-site assessment of *Watersipora subtorquata* percent cover in South Korean coastal harbors, examining how water temperature and salinity could shape its cover dynamics. Across four sites—Yangpo, Tongyeong, Bieung, and Jeju—percent cover exhibited clear spatial and temporal variability largely influenced by temperature, with salinity effects varying by location. Temperature significantly affected percent cover in all four harbors, although the nature of response differed among sites, reflecting both linear and non-linear patterns. Salinity, in contrast, played a key role only in Bieung. However, a significant interaction between temperature and salinity was observed in Jeju, suggesting

that percent cover was highest within a relatively narrow range of combined environmental conditions. These findings highlight that *W. subtorquata* percent cover was associated with site-specific temperature and salinity conditions across Korean harbors. However, because environmental measurements represented snapshot conditions at the time of sampling, the results should not be interpreted as direct evidence of climate-driven expansion. Rather, by combining long-term field observations with flexible statistical modeling, this study provides a baseline for site-specific monitoring and localized management of *W. subtorquata* in Korean coastal harbors, and highlights the need for future studies incorporating higher-frequency environmental time series to better resolve environmental drivers of percent cover dynamics.

### Author contribution

Seongjae Kim: Conceptualization, Data Curation, Formal analysis, Investigation, Methodology, Resources, Software, Validation, Visualization, Writing – Original draft;

Taekjun Lee: Conceptualization, Data Curation, Methodology, Writing – Review and Editing, Supervision;

Jeounghye Lee: Conceptualization, Funding Acquisition, Methodology, Project administration, Supervision, Visualization, Writing – Review and Editing.

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### Conflicts of interest

The authors have no conflicts of interest to disclose.

### Ethics and permits

This research did not involve any human participants or vertebrate animals. No ethical approval was required. All procedures involving sampling complied with institutional and national guidelines.

### Data availability

Monitoring data and recruitment records of *Watersipora subtorquata* used in this study were collected under the supervision of the Ministry of Oceans and Fisheries (MOF), Republic of Korea. Due to national regulatory constraints on harmful marine species data sharing, datasets are not publicly accessible. However, data might be available from the corresponding author upon reasonable request and with permission from the MOF.

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## Supplementary material 1

Site-specific summary of water temperature and salinity measured during field surveys at four Korean harbors from April 2021 to July 2024

Authors: Seongjae Kim, Taekjun Lee, Jeounghee Lee

Data type: docx

Explanation note: Values are summarized as mean  $\pm$  SD and range (min–max) for water temperature and salinity at Yangpo, Tongyeong, Bieung, and Jeju. Measurements were collected at discrete survey times and represent contemporaneous conditions rather than continuous environmental records.

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Link: <https://doi.org/10.3391/ai.2025.21.3.199579.suppl1>

## Supplementary material 2

Raw plate-level observations of *Watersipora subtorquata* percent cover (%) on settlement plates plotted against survey month for each harbor (YP, TY, BE, and JJ)

Authors: Seongjae Kim, Taekjun Lee, Jeounghee Lee

Data type: jpg

Explanation note: Points represent individual plates; raw zeros are indicated by triangles. Values identified as outliers using Tukey's IQR rule within each harbor  $\times$  survey month ( $Q3 + 1.5 \times IQR$ ) are highlighted (see Methods); outliers were winsorized for statistical analyses, whereas this figure shows the untransformed raw observations.

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Link: <https://doi.org/10.3391/ai.2025.21.3.199579.suppl2>

## Supplementary material 3

Temporal variation in percent cover of *W. subtorquata* across four Korean harbors from 2021 to 2024

Authors: Seongjae Kim, Taekjun Lee, Jeounghee Lee

Data type: jpg

Explanation note: **A.** Yangpo; **B.** Tongyeong; **C.** Bieung, and **D.** Jeju.

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## Supplementary material 4

### Temporal variation in water temperature and salinity across four Korean harbors from April 2021 to July 2024

Authors: Seongjae Kim, Taekjun Lee, Jeounghee Lee

Data type: jpg

Explanation note: Panels show water temperature and salinity measured at each survey event: A–B, Yangpo; C–D, Tongyeong; E–F, Bieung; and G–H, Jeju. Values represent contemporaneous field measurements rather than continuous environmental records.

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