

Article

Population Dynamics of the 'Golden Tides' Seaweed, Sargassum horneri, on the Southwestern Coast of Korea: The Extent and Formation of Golden Tides

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Abstract: Since 2015, troublesome masses of floating Sargassum horneri have been introduced via ocean currents and winds to the southwestern coastline of Korea, including Jeju Island. These massive mats have caused considerable damage to the aquaculture industry, tourism, and the marine ecosystem. Most previous studies of *S. horneri* have focused on cultivation, the development of gene markers, and photosynthetic activity, but few data on population dynamics are available. We investigated the population dynamics of native S. horneri off the southwestern coast of Korea with the aim of predicting the formation of golden tides. Populations at two sites had obligate annual life cycles. Thalli were recruited during the period September–November, grew during the period December–April, and senesced by July. This pattern reflected seasonal trends in water temperature. Specific growth rates and heights of the thalli at Munseom were significantly higher than those at Jindo. The greatest environmental difference between the two sites is probably the degree of exposure to wave action. Mortality density (thalli lost per unit area) in the Munseom population was highest during the period December–January (i.e., 2–3 months after recruitment) and in March. Most thalli in the Jindo population died off in July when water temperatures increased. The maximum average biomass of S. horneri thalli detaching from the substrata reached 1.6 kg fresh weight m^{-2} during January and March. Thus, large-scale drifting mats were formed by S. horneri detachment from the substrata. Despite the differences in space and environment between China and Korea, our findings will enable quantitative assessments of the overall floating Sargassum biomass in the East China and Yellow Seas.

Keywords: Sargassum horneri; golden tides; population dynamics; mortality; detached biomass

1. Introduction

Massive floating macroalgal blooms (so-called seaweed tides) of increasing frequency, magnitude, and severity have been reported from coastal regions around the world [1,2]. 'Green tides' formed by blooms of species of the genus *Ulva*, and 'golden tides' formed by blooms of *Sargassum* species

are exemplars of seaweed tides globally. These tides have been linked to coastal eutrophication resulting from inorganic nutrient inputs [3,4]. A few recent studies have emphasized the role of high water temperature during winter (a result of global climate change) as a factor in the formation and magnitude of seaweed tides [2,5]. Floating seaweed mats provide essential habitats for a variety of fish, and they serve as hotspots for biodiversity and productivity [6–8]. However, they wash ashore along the coastline, causing serious environmental, ecological, and economic problems [1,4,9].

Golden tides (mainly Sargassum fluitans and S. natans) have occurred periodically during the summer along the coastlines of the Gulf of Mexico, with recent range extensions across the central Atlantic Ocean from the Dominican Republic to Ghana [2,10]. Large-scale drifting S. horneri mats originating off the Chinese coast have been observed regularly in the East China Sea, where the magnitude has been increasing since the first decade of this century [5,11,12]. In 2017, massive Sargassum mats were observed at the Pyropia farms in the offshore region of Jiangu Province, and they led to an economic loss of at least \$70 million in the nori industry of Dafeng in Jiangsu Province, China [12,13]. In 2015, a massive drifting mat of *S. horneri* released from Zhejiang Province, China, was transported by ocean currents and wind to the southwestern coasts of Korea, including Jeju Island [14]. During the period 2015–2018, hundreds of thousands of tons (wet weight) of *S. horneri* were observed on the southwestern coasts of Korea, including Jeju Island. The removal of about 33×10^3 t fresh weight from beaches, ports, and aquaculture farms involved 30,000 people at an estimated cost of ₩2.8 billion (\approx \$2.55 million). This estimate did not include losses incurred by the fishing and tourism industries (unpublished data). Golden tides led to an economic loss of W0.8 billion (\approx \$0.73 million) by seaweed aquaculture operations along the coast (unpublished data). Consequently, golden tides have received considerable attention in Korea due to their detrimental effects on the local economy and coastal ecosystems.

Most relevant studies have focused on the transportation, formation, and distribution of golden tides and on the genetic origins and diversity of floating populations [5,11–15]. Several studies have examined the attachment strength, life history traits, photosynthetic activity, and reproduction of *S. horneri* [16–19]. The extent of golden tides formed by thalli detached from rocky coastal shores of the East China Sea is affected by the density of benthic *S. horneri* populations along the Chinese coast [20]. The duration of the floating period depends on the reproductive state of thalli when they detach from the substratum [21]. Demographic parameters are clearly relevant to the development of golden tides, but few studies have focused on recruitment, biomass, growth, density, and mortality on rocky shores of the northwestern Pacific [18,21]. The dearth of population dynamics data for attached *S. horneri* thalli has prevented predictive modeling of golden tide formation.

Sargassum horneri (Turner) C. Agardh, which is widely distributed along northwestern Pacific coastlines, is a native brown seaweed species with an annual life cycle [22]. This species functions as an ecosystem engineer; it provides habitat, spawning sites, and nursery grounds for a diverse assemblage of marine organisms in coastal ecosystems [23,24]. *S. horneri* was first introduced to Long Beach Harbor, California, in 2003 [25]. More recently, it has spread aggressively throughout southern California, the USA, and into Baja California, Mexico [26]. *S. horneri* has an important role in the biofiltration of enriched inorganic nutrients in mainland effluent discharges. The large biomasses that develop during the growing season help maintain and improve water quality [16]. This species has been considered a particularly suitable candidate for reforestation of kelp zones in East Asia, and it has been transplanted to natural and artificial reefs at kelp deforestation sites [24,27,28].

Our study aimed to investigate the population dynamics of *S. horneri* on the southern coast of Korea in order to improve understanding of the magnitude and formation of golden tides. We postulated that (i) the population dynamics of *S. horneri* are affected by local habitat conditions, and (ii) the size of the drifting biomass of *S. horneri* is strongly associated with detachment of *S. horneri* populations. To test these postulates, we examined the morphology, density, recruitment, mortality, growth rate, and biomass of natural *S. horneri* populations in exposed and semi-sheltered sites on the southern coast of Korea. Data were collected monthly by Scuba diving from November 2017 to October 2018.

This study should provide valuable information for a better understanding of the extent and formation of golden tides.

2. Materials and Methods

2.1. Study Area

This study was conducted at two sites, Jindo (34°22′37″ N, 126°18′28″ E) and Munseom (33°13′38″ N, 126°34′04″ E), which are on the southwestern coast of Korea (Figure 1). The Jindo site was located in Supumhang Harbor; it is a sheltered area with a substratum comprising boulders and stones overlaid with muddy sand. The macroalgal community was dominated primarily by large brown algae (*Sargassum horneri, S. thunbergii, S. fulvellum,* and *Undaria pinnatifida*) and ephemeral green algae (*Ulva* spp.). In particular, *S. horneri* formed dense assemblages at 4–7 m water depth. In contrast, the Munseom site, located on Jeju Island, is very exposed to wave action originating in the East China Sea. *S. horneri* dominated water depths of 5–8 m at Munseom. Kim et al. provided a detailed description of macroalgal assemblages at Munseom [29]. The tidal cycle on the coast is semi-diurnal, and the system is classified as mesotidal, with a maximum tidal range during spring tides of about 3.0 m at Jindo and 2.7 m at Munseom (Tide Tables for the Coast of Korea, National Oceanographic Research Institute of Korea).



Figure 1. Study sites at Jindo and Munseom, off the southwestern coast of Korea.

2.2. Sampling Design

Observations were made monthly at the two sites using Scuba diving in the period from November 2017 to October 2018. In November 2017, we established permanent quadrats at the two sites at water depths in which *S. horneri* formed dense assemblages. Quadrat sizes were selected according to population densities. Five 1.0 m² quadrats and four 0.25 m² quadrats were set at Jindo and Munseom, respectively. Quadrats were spaced at three-meter intervals. All thalli in each quadrat were tagged

with surveyors' flagging tape and individually numbered for sequential observations on individuals. We marked 100 and 150 thalli at Jindo and Munseom, respectively.

2.3. Data Collection

The height, density, mortality, biomass, and growth rates of individuals at each site were recorded monthly in the field from November 2017 to October 2018. Heights were measured as the lengths of the main shoots of undamaged thalli. The main shoot is typically the longest; however, lateral branches may be longer than the main axis when it has been severed by wave action [30]. When this was the case, we used the length of the longest lateral branch as a measure of thallus height. Thallus elongation was calculated using the following formula:

where L_0 is the initial length (cm) of the main shoot axis, L_t is the length (cm) of the main axis after t days, and t is the observation period (days). The growth rates of individuals were calculated using the following equation [31]:

Growth rate of thallus (% day⁻¹) =
$$[(L_t - L_0)^{1/t} - 1] \times 100\%$$
. (2)

The density of thalli was estimated by counting all individuals in the quadrats. The density was converted to units of individuals per m². Densities (individuals per m²) and rates (%) of monthly mortality were estimated from the number of tagged individuals that disappeared each month. The total biomass of thalli per unit area (m²) was estimated by summing the individual predicted weights of thalli in each quadrat. To estimate the individual weights, we collected 60 thalli with a range of main axis lengths monthly from each of the sites to determine the allometric relationship between thallus height (cm) and individual weight (g dry weight). The main axis lengths of all undamaged and damaged thalli in each of the quadrats were measured monthly and converted to dry weights using allometric relationship equations. *Sargassum horneri* usually grows attached to rocks, and it also continues to grow while free-floating. Unfortunately, we were unable to measure elongation in the floating population. Therefore, we assumed that rates of elongation were identical in attached and floating populations. The weights of detached thalli were estimated using the allometric relationship equations per unit area (m²) was estimated using the allometric relationship enditions in the floating populations. The weights of detached thalli were estimated using the allometric relationship equations per unit area (m²) was estimated using the individual predicted weights of thalli that detached in each quadrat.

We measured water temperature at the two sites every 15 min using HOBO Pendant temperature/light data loggers (Onset Computer Corporation, Bourne, MA, USA). Salinity was measured on each sampling occasion using a YSI salinometer (YSI model 63, YSI incorporated, USA). To determine dissolved inorganic nutrient concentrations (NH_4^+ , NO_3^- , NO_2^- , and PO_4^{3-}) in the water column, we collected four replicate surface water samples each month through the experimental period. Water samples were placed on ice in the field and frozen until analyzed. Water column nutrient concentrations were determined using standard colorimetric techniques following the procedures of Parsons et al. [32]. The sum of NH_4^+ -N, NO_3^- -N, and NO_2^- -N concentrations was recorded as total dissolved inorganic N (DIN). PO_4^{3-} concentrations were used as a measure of total dissolved inorganic phosphate (DIP).

2.4. Statistical Analyses

Significant differences in height, density, elongation, growth rate, biomass, detached biomass, mortality, mortality rate of thalli, and water column nutrients (DIN and DIP) among sampling times and between sites were identified by two-way ANOVA. A two-way ANOVA without replication was performed to test for significant differences in daily mean water temperature between the two study sites. Data were tested for normality and homogeneity of variance prior to analysis to determine whether they met the assumptions of parametric statistics. If these assumptions were not satisfied, data were

square root transformed (height, density, biomass, detached biomass, mortality, and elongation) or arcsine transformed (mortality rate and growth rate). When significant differences were detected by ANOVA, we performed Student–Newman–Keuls (SNK) post hoc tests to identify significant pairwise differences between means. An alpha level of 0.05 was used for statistical tests. All statistical analyses were performed using IBM SPSS Statistics ver. 20.0 software (IBM Corporation, Armonk, NY, USA).

3. Results

3.1. Environmental Factors

Water temperature at both sites had distinct seasonal patterns, ranging from 4.6 °C and 14.6 °C in February 2017 to 27.3 °C and 28.4 °C in August 2018 at Jindo and Munseom, respectively (Figure 2A). Water temperature was significantly higher (p < 0.001) at Munseom than at Jindo. While water temperatures during fall, winter, and spring were higher at Munseom than at Jindo, there was no difference in water temperature between the two sites during late spring–summer. Notably, water temperatures during the late August–early September period decreased temporarily at Munseom following the passage of typhoon Soulik. Salinity was relatively constant throughout the study period, with averages of 31.9 and 30 Practical Salinity Unit (PSU) at Jindo and Munseom, respectively (Figure 2B).

Water column DIN concentrations at both study sites varied significantly (p < 0.001) with sampling time (Figure 2C). The DIN concentrations at Jindo were significantly higher (p < 0.001) than those at Munseom. The average DIN concentrations at Jindo and Munseom were 8.8 and 1.8 μ M, respectively. Water column DIP concentrations at both sites were usually less than 1.0 μ M during the study period (Figure 2D).



Figure 2. Seasonal variations in water temperature (**A**), salinity (**B**), water column dissolved inorganic nitrogen (DIN) (**C**), and dissolved inorganic phosphate (DIP) (**D**) concentrations at Jindo and Munseom on the southwestern coast of Korea. The values of DIN and DIP are mean \pm SE (n = 4).

3.2. Density and Mortality

Sargassum horneri had a clear annual density cycle. Recruitment occurred in the fall (Figure 3A). Thallus density at Munseom was significantly higher (p < 0.001) than that at Jindo (Table 1). The species

had the highest densities during late fall and early winter (November/December), 1–3 months after recruitment; thereafter, densities decreased. All *S. horneri* thalli had completely disappeared by July. The patterns of mortality density (i.e., thallus losses per unit area) and mortality rate differed markedly between the two sites (Figure 3B,C). The mortality density at Munseom was significantly higher (p < 0.001) than that at Jindo due the differences in density between the two sites (Table 1). The mortality rate at Munseom fluctuated greatly with time; it was highest during the periods December–January, March–April, and June–July. The mortality rate of the Jindo population gradually increased over time, with the highest values in April and the period June–July.



Figure 3. Seasonal variations in total density (**A**), individuals lost per unit area (mortality density) (**B**), and mortality rate (**C**) of *Sargassum horneri* thalli at Jindo and Munseom. Values are mean \pm SE (n = 4–5).

Table 1. Summary ANOVA tables for height, density, elongation, growth rate, biomass, detached biomass, individuals lost per unit area (mortality density), and mortality rate of *Sargassum horneri* at Jindo and Munseom. All data were either square root transformed (density, mortality density, height, elongation, biomass, and detached biomass) or arcsine transformed (mortality rate and growth rate) prior to analysis to meet the assumptions of parametric statistics. DF, degrees of freedom; mortality density, individuals lost per unit area.

Parameter	Source	DF	MS	F-ratio	<i>p</i> -value
Density	Site	1	96.660	70.664	< 0.001
	Time	11	58.254	42.587	< 0.001
	Site \times Time	11	18.271	13.357	< 0.001
Mortality density	Site	1	59.968	53.806	< 0.001
	Time	7	4.347	3.901	=0.002
	Site \times Time	7	6.295	5.648	< 0.001
Mortality rate	Site	1	0.614	23.220	< 0.001
	Time	7	2.020	76.386	< 0.001
	Site \times Time	7	0.090	3.401	=0.004
Height	Site	1	1670.037	151.698	< 0.001
	Time	6	1885.748	171.292	< 0.001
	Site \times Time	6	888.421	80.700	< 0.001
Elongation	Site	1	110.785	294.097	< 0.001
	Time	4	12.143	32.236	< 0.001
	Site \times Time	4	11.902	31.595	< 0.001
Growth rate	Site	1	0.380	192.995	< 0.001
	Time	4	0.059	30.065	< 0.001
	Site \times Time	4	0.039	19.674	< 0.001
Biomass	Site	1	1253.824	17.002	< 0.001
	Time	11	2441.508	33.106	< 0.001
	Site \times Time	11	258.725	3.508	< 0.001
Detached biomass	Site	1	3032.415	67.151	< 0.001
	Time	11	924.001	20.462	< 0.001
	Site \times Time	11	393.697	8.718	< 0.001

3.3. Height, Growth and Biomass

The seasonal fluctuations in thallus height differed greatly between sites (Figure 4A). Thallus height at Munseom dramatically increased from November to April, when thalli reached a maximum length (857 cm). The heights at Jindo gradually increased over the study period, reaching a maximum of 137 cm in April. After May, the apices of all thalli were damaged or severed by wave action. Elongation varied significantly (p < 0.001) between sites (Figure 4B; Table 1). During the growth period, the elongation rate at Munseom was significantly higher (p < 0.001) than that at Jindo (Table 1). The highest elongation rate, 12.7 cm day⁻¹, occurred during February at Munseom. The elongation rate was very low at Jindo (<0.5 cm per day). The growth rate was also significantly higher (p < 0.001) at Munseom than at Jindo. The highest rate at Jindo occurred in January, and the lowest rate during the period March–April (Figure 4C; Table 1).

Thallus biomass also varied significantly (p < 0.001) by season, and patterns differed between sites (p < 0.001) (Figure 5A; Table 1). The biomass of the Munseom population increased during fall and winter and decreased during spring and early summer. The biomass of the Jindo population also increased during fall and early winter (September–December), was almost constant from December to April, and decreased between mid-spring and summer (April–July). The maximum population biomasses at Jindo and Munseom were 925 and 3100 g fresh weight m⁻², respectively. The biomass of detached thalli at Munseom varied significantly (p < 0.001) with sampling time but did not track a clear seasonal trend (Figure 5B; Table 1). The detached biomass of the Jindo population increased gradually through the study period (Figure 5B). The biomass of detached thalli was highest during January and March (average: 1600 g fresh weight m^{-2}) at Munseom and lowest during April and July (average: 250 g fresh weight m^{-2}) at Jindo.



Figure 4. Seasonal changes in height (**A**), elongation (**B**), and growth rate (**C**) of *Sargassum horneri* thalli at Jindo and Munseom. Values are means \pm SE (n = 10–150).



Figure 5. Total biomass (**A**) and detached biomass (**B**) of *Sargassum horneri* thalli at Jindo and Munseom. Values are mean \pm SE (n = 4–5). FW, fresh weight.

3.4. Relationship between Water Temperature and Thallus Biomass

The biomass of the Jindo population was highest at a water temperature of ca. 5–12 °C between December and early April; thereafter, it decreased with increasing water temperature (Figure 6A). Elongation peaked at temperatures of about 8–12 °C in January and during the period March–April, but slowed during May when water temperatures exceeded 16 °C (Figure 6C). Thallus biomass at Munseom was highest at temperatures ca. 14–16 °C between January and early April, and decreased thereafter with increasing water temperatures (Figure 6B). The peak elongation in the Munseom population occurred at a temperature of about 15 °C in February, but it fell when temperatures exceeded 16 °C (in May (Figure 6D).



Figure 6. Seasonal trends in water temperature (solid lines) and in biomass (**A** and **B**) and elongation (**C** and **D**) of *Sargassum horneri* thalli at Jindo (**A** and **C**) and Munseom (**B** and **D**). The values of biomass (n = 4-5) and elongation (n = 10-150) are mean \pm SE. FW, fresh weight.

2017

2018

4. Discussion

2017

4.1. Population Dynamics of S. horneri Populations

2018

The present study showed that two *S. horneri* populations on the southwestern coast of Korea had obligate annual life cycles. The demographic parameters of both populations exhibited strong seasonal variation: Recruiting during September–November, growing and maturing during November–April, and disappearing during July. These patterns reflected seasonal changes in water temperatures, which have conspicuous impacts on the growth of S. horneri. Seasonal trends in S. horneri populations (increasing during fall and spring and decreasing during spring and early summer) have been reported for the northwest Pacific coasts [30,33,34]. Water temperature is a vital driver of seasonal variation in Sargassum spp. biomasses within the seaweed beds at Ningaloo [35]. We found that S. horneri at both study sites had maximum biomass and elongation at temperatures in the range 5–15 °C during winter and spring, although two sites had different seasonal trends in water temperature. This finding was similar to those of previous studies on persistent S. horneri beds along the coast of Japan; the optimal temperature for *S. horneri* growth in Japan ranged between 10 and 15 °C [30,33,36]. In our study, the growth rate of the two populations was highest at water temperatures within the 5–15 $^{\circ}$ C range during the winter-spring period, similar to the findings of Yu et al., who showed that the specific growth rates for length and weight in S. horneri increased when water temperature rose from 5 °C to 20 °C [37]. Thus, we showed that water temperature can be considered a major factor controlling the growth and maturation of *Sargassum* spp. [33,38].

The two populations we studied exhibited obviously different trends in height, density, biomass, and mortality. The height, density, biomass, elongation, and growth rate at Munseom were 5–10 times higher than those at Jindo. Nutrient availability influences the growth, productivity, and community structure of seaweeds [39,40]. The growth patterns of kelp species are strongly affected by local nutrient availability [41]. Nitrogen enrichment enhances the specific growth rates of length and weight in *S. horneri* and promotes high biomass accumulation of drifting thalli [37]. The water column DIN and DIP concentrations at Jindo were significantly higher than those at Munseom. It is likely that

the ambient nutrient level at Jindo provided adequate nutrients for *S. horneri* growth. Nevertheless, the Jindo population had lower height, density, biomass, elongation, and growth rate than the Jeju population. Therefore, the difference in growth between the two populations cannot be attributed to differences in nutrient availability.

The variability in the growth rate and morphology of *S. horneri* has been linked to water temperature [36]. Warming promotes higher *Sargassum* growth rates by increasing rates of metabolism and photosynthetic activity before the thalli decay [42]. During winter, *S. horneri* thalli exposed to high water temperatures have increased growth rates and lengths, and earlier maturation than those in cooler waters [30]. The average water temperature at Munseom (16.2 °C) was higher than at Jindo (8.9 °C) during the growing season (December–April). After January, the Munseom thalli grew more rapidly and reached larger sizes than the Jindo thalli. Thalli with receptacles were found in Munseom during early March; receptacles were first observed on Jindo thalli in mid-April (S.R. Park, personal observation).

Wave action is also considered an important factor in the growth of large brown algae when there are minimal differences in other environmental factors between sites, such as light, temperature, and nutrients [43]. Wave action has an impact on the growth and productivity of macroalgae [44,45]. The morphology and survival of seaweeds is related to water flows created by waves or currents [18,46]. Thus, wave activity or wave-induced water motion is considered an important controlling factor in algal community structure and composition [47,48]. Munseom is located on the southern coast of Jeju Island, where it is directly open to the East China Sea. Thus, the Munseom population was likely exposed to higher wave activity than the Jindo population. The degree of exposure to wave action may account for the large differences in morphology, density, biomass, and mortality that we observed between the two populations. Therefore, wave exposure and warmer water temperatures during the winter season were probably key drivers of *S. horneri* growth.

4.2. Contribution of Mortality to the Formation of Golden Tides

Since the early years of the current century, massive drifting mats of *S. horneri* have been frequently observed along the East China Sea coast. They have aggressively spread along the length of the southwestern coast of Korea (including Jeju Island) and the western coast of Japan [11,49–51]. Floating S. horneri rafts originated from attached thalli in the subtidal zones of islands off Zhejiang Province, China, and were transported northeastwards with oceanic currents and wind [5,11,13,14]. The floating S. horneri biomass therefore depends on the biomass of the attached source populations. The biomass of attached benthic populations of S. horneri off Gouqi Island, China, where the massive drifting S. horneri rafts in the East China Sea originated, ranged from 0.54 kg fresh weight m⁻² in August to 4.42 kg fresh weight m⁻² in June [52]. The maximum biomass of attached *S. horneri* in Obama Bay, Japan, averaged 555 g dry weight m^{-2} (ca. 2.8 kg fresh weight m^{-2} , using a dry weight: fresh weight ratio of 0.2) [33]. In contrast, non-native populations of S. horneri in Todos Santos Bay, Mexico, had very low biomass, ranging from 3 g dry weight m^{-2} (ca. 15 g fresh weight m^{-2}) to 78 g dry weight m^{-2} (ca. 390 g fresh weight m^{-2} [53]. S. horneri biomass at Munseom and Jindo ranged from 0.6 kg fresh weight m^{-2} to 3.1 kg fresh weight m^{-2} during the growing season (December–May); this range was similar to those measured in S. horneri populations in China and Japan [33,52]. The maximum biomasses of S. horneri fragments detached from attached thalli at Munseom were 1.5 ± 0.4 and 1.7 ± 0.5 kg fresh weight m⁻² in January and March, respectively, when mortality was high. The floating *S. horneri* biomass in the East China Sea was ca. 2 kg fresh weight m⁻². The estimated floating biomass of *Sargassum* in the Florida straits and the Gulf of Mexico ranged from 1.26 kg fresh weight m⁻² to 6.74 kg fresh weight m⁻², averaging 3.34 kg fresh weight m⁻² [10,20]. Given that detached *S. horneri* thalli continue to grow during the floating period [21], our estimates of floating biomass are similar to those reported for the East China Sea, the Florida Straits, and the Gulf of Mexico [10,20]. Our results provide a quantitative assessment of the overall floating Sargassum biomass.

Similar to those around the islands off Zhejiang Province, the S. horneri population at Munseom was exposed to high wave action and had high mortality rates and densities during the December-January period and March, suggesting that large drifting seaweed rafts may be produced by detaching thalli. When high mortality occurs around the islands off Zhejiang Province and floating S. horneri mats form in the Yellow Sea and East China Sea, drifting S. horneri rafts can be observed in the southern part of Jeju Island, Korea, within approximately a month [51]. Large mats of drifing *S. horneri* were introduced to the Korean coasts by the Kuroshio Current and Taiwan Warm Current in the late January-February and April-early May periods of 2015–2019. These rafts accumulated along the southern coast of Korea, including Jeju Island [14,54]. High mortality rates and/or densities likely also occurred among the islands off Zhejiang Province during the December-January period and March. If so, this would strongly support our second postulate, namely that the biomass of drifting S. horneri is strongly associated with mortality in attached *S. horneri* populations. Unfortunately, there are few data for the S. horneri populations among the islands off Zhejiang Province, China, which severely limits more detailed interpretation of the extent and formation of golden tides in the East China Sea. Therefore, further studies of the populations among the islands off Zhejiang Province are required to better understand the extent and formation processes of drifting S. horneri mats.

5. Conclusions

Recently, massive *S. horneri* mats have resulted in devastating impacts on the local economy and coastal ecosystems in Korea. A dangerous combination of wave and tide conditions can exacerbate economic losses due to *Sargassum* beaching events. Thus, predicting the timing and extent of golden tides will provide early-warning of *Sargassum* beaching. The results of this study confirm that *S. horneri* had a clear annual life cycle and exhibited seasonal variations in density, which reflected seasonal changes in water temperature. Furthermore, the difference in height, density, growth, and mortality between the two sites may be affected by the degree of exposure to wave action. High mortality density at the study site was observed during the December-January period and in March. The detached thalli had an effect on the extent and formation of floating *S. horneri* mats. This result showed that the biomass of *S. horneri* thalli detached from substrata was approximately 1.6 kg fresh weight m⁻² during high mortality periods. This will help us to estimate the extent and formation timing of golden tides. However, most seaweeds show inter-annual variation in their biomass, and environmental conditions were temporally not constant. Thus, long-term monitoring, with more study sites, is needed to fully predict the extent and formation timing of drifting *S. horneri* mats.

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