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# Carbon Reduction Associated with Sediment Reworking through Burrows of the Thalassinid Mud Shrimp *Laomedia* sp. (Crustacea: Laomediidae) from Korean Intertidal Sediments

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**Abstract:** This study evaluated the biotic and abiotic factors influencing the sediment reworking rate (SRR) of *Laomedia* sp. through in situ measurements and assessed the organic carbon reduction by comparing carbon concentrations between particles collected from the water column and reworked sediments. The SRR was significantly correlated with the duration of submergence at high elevation, whereas it showed a stronger correlation with mound height than with the duration of submergence at low elevation. The organic carbon content of suspended particles was reduced by 68% by the sediment reworking of *Laomedia* sp., with a mean organic carbon reduction of 0.01 gC ind.$^{-1}$ d$^{-1}$. This reduction resulted from particle selection by the inhabitant and by accumulation along the burrow walls. The estimated annual organic carbon reduction associated with the sediment reworking was 12.8 gC m$^{-2}$ yr$^{-1}$. The transport of organic carbon from the burrows into the water column was comparatively high relative to other species. These findings suggest that *Laomedia* sp. plays a significant role in enhancing the carbon cycle as an important bioturbator, with its burrows acting as carbon sinks by trapping organic carbon in intertidal sediments. Therefore, bioturbation by macroinvertebrates should be considered when evaluating carbon sequestration in intertidal sediments.

**Keywords:** bioturbation; *Laomedia* sp.; sediment reworking; carbon reduction; intertidal sediments

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## 1. Introduction

Thalassinidean mud shrimps are among the most common deep-burrowing benthic macroinvertebrates. Their burrows protect the animals from desiccation and predation and have large effects on biogeochemical processes in intertidal sediments [1,2]. The construction and maintenance of these burrows involve continual mixing of sediment between deeper and shallower layers, resulting in significant sediment movement that is influenced by changes in organic matter content and grain size [3–5]. The burrow environment of thalassinidean shrimp is distinct from both the surface sediment and its surroundings. Burrow walls often contain organic matter with varying reactivities, influenced by factors such as its source, chemical composition, structure, and age [6,7]. The low diffusivity through the burrow lining restricts the movement of solutes between the sediment and the burrow interior, while the irrigation activity of the animal enhances the flow of nutrients and oxygen across burrow walls [7,8].

Bioturbation has only recently been considered important for organic carbon dynamics in coastal wetland sediments, with growing evidence that large benthic bioturbators may alter sediment carbon stocks [9–12]. Increased remineralization of sediment carbon may occur when bioturbation increases soil oxygen supply, whereas burial of plant detritus into deep anoxic sediment layers by benthic fauna may increase organic carbon sequestration [9,13,14]. The physical activities of macrofauna can have major impacts on coastal carbon cycling and sequestration due to their influence on sediment properties and their

relationship with sediment microbes [15–20]. Direct impacts include mechanical reworking of sediment, which disperses carbon-rich deep sediment onto the sediment surface, in contact with oxygenated water. Indirect impacts include feeding processes that alter the microbial community within the deeper parts of the burrow [14]. According to the definition proposed by Kristensen et al. [15], which is adopted here, bioturbation encompasses all of these activities, including the process of bio-irrigation or burrow ventilation. Bioturbators can act as a physical catalyst for sediment metabolism via incorporation of organic matter (e.g., seagrass detritus) into burrow walls and introduction of oxygen into an otherwise anoxic environment [21,22].

The thalassinidean mud shrimp *Laomedia* sp. is found in upper tidal flats along the western coast of Korea. The burrows of *Laomedia* sp. are huge and complex, featuring several funnel-shaped openings through which seawater flows, along with a single bell-shaped mound through which burrow water containing sediments is discharged, driven by shrimp irrigation activity during the submerged period [23,24]. To date, there have been few studies on how Laomedia sp. bioturbation affects biogeochemical processes in intertidal sediments. As part of evaluating this impact, we previously measured the sediment reworking rate (SRR) of this species and analyzed factors influencing this process in the upper tidal flat of Gomso Bay, on the west coast of Korea [25]. The SRR of *Laomedia* sp. was estimated to be 40 g ind.$^{-1}$ d$^{-1}$ and the annual SRR was 72.2 kg m$^{-2}$ yr$^{-1}$, based on the density in this study area. The SRR increased with submergence duration and mound height, but the effects of sediment reworking by this species on the carbon cycle in intertidal sediments remain unclear. The intensity of sediment reworking depends on various habitat environmental factors, such as tidal condition, food availability and organic matter contents [26–28]. Therefore, assessing the factors that influence the SRR of *Laomedia* sp. is crucial for estimating the ecological function of this species on the carbon cycle in intertidal sediments.

The aim of this study is to evaluate the influencing factors of the SRR of *Laomedia* sp. to identify site-specific differences in biotic and abiotic factors, and to estimate the carbon reduction associated with sediment reworking through burrows of this species in order to assess their ecological functions as a carbon sink. We evaluated biotic and abiotic factors influencing the SRR of *Laomedia* sp. through in situ measurements and assessed the organic carbon reduction by comparing carbon concentrations between particles collected from the water column and reworked sediments.

## 2. Materials and Methods

### *2.1. Study Area*

This study was conducted in the upper tidal zone of Anmyeon Island, on the west coast of Korea (36°34′33.44″ N 126°21′59.94″ E, Figure 1 and Figure S1). The mean tidal range is 4.3 m, with spring and neap tide at 6.0 m and 3.0 m, respectively. The sediment in the study area consists primarily of silt, with a mean grain size of 5.92 ∅, and is positioned 2.3 m above mean sea level (MSL). The study area includes a wide upper intertidal zone, where *Laomedia* sp. inhabits at a high density, with a mean density of 8 ind. m$^{-2}$. Moreover, this area provides a suitable condition by which to evaluate the influence of elevation on the sediment reworking of this species, given that *Laomedia* sp. habitats have an elevation gradient.




**Figure 1.** Location and layout of the study site in the Anmyeon Island tidal flat, located on the western coast of Korea. The red square represents the study area; the gray area represents tidal flats.

### 2.2. Quantification of Reworked Sediments

The amount of reworked sediment released from *Laomedia* sp. burrows was measured during the spring tide in October 2022 using a direct entrapment method. A sediment trap, consisting of a cylindrical plastic container (25 cm in diameter and 20 cm in height), was placed over the mound. The container had a plastic wrap with a 1 cm hole at the center bottom, aligning with the mound opening. These traps were placed over five mounds at three different elevations (E1: 1.83 m, E2: 1.49 m, and E3: 1.27 m from MSL) as shown in Figure 2 and Figure S2. Each trap was inserted 3 cm into the sediment, with the plastic wrap firmly attached to the mound surface to prevent floating. Additionally, an artificial mound (25 × 25 × 15 cm, W × L × H) resembling a *Laomedia* sp. mound, but without a hole, was constructed as a control at each elevation. A sediment trap was placed over each control mound to measure natural sedimentation from the water column during submersion (Figure S2).

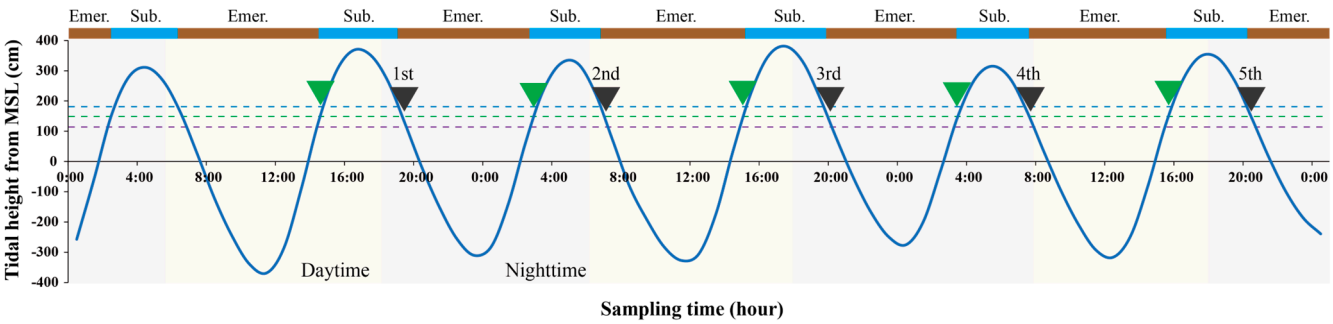



**Figure 2.** Sampling times for collection of suspended particles and reworked sediments as well as tidal height from MSL. Seawater collection was conducted during the submerged period (green triangles), and reworked sediment collection was conducted during the emerged period (black triangles). Blue, green, and purple dotted lines represent tidal heights at E1, E2, and E3, respectively. Emer.: emergence, Sub.: submergence.

Immediately after the mound was exposed by the receding tide, reworked sediments within the sediment traps were collected using a syringe containing seawater and transferred to a plastic bottle. This process was repeated five times consecutively at each submergence period during the spring tide; the duration of submergence varied with tidal height (Figures 2 and 3). The reworked sediments within the sediment traps were collected from a different mound at each sampling time and elevation. A salinity logger (U24-002-C, HOBO, Bourne, MA, USA) was installed to determine the durations of submergence and emergence at each elevation, with salinity recorded at 1 min intervals. The duration of submergence and emergence at each elevation was estimated based on changes in salinity. The wet weight of the reworked sediments was measured using an electronic scale after allowing the samples to settle for 72 h to separate the seawater from the sediments. The SRR was calculated based on the wet weight of the reworked sediment and adjusted according to the natural sedimentation rate observed in the control (artificial mound).

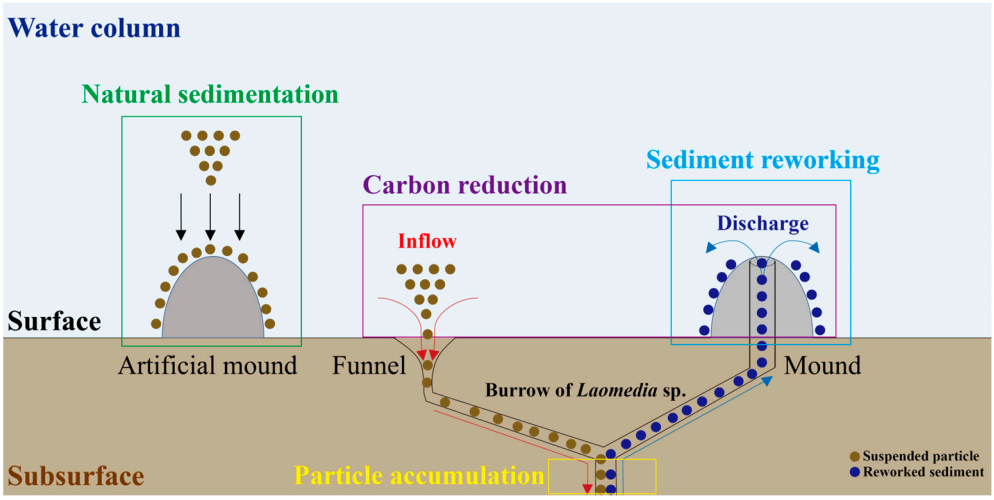



**Figure 3.** Schematic diagram of the quantification of the natural sedimentation, SRR, and estimation of carbon reduction and particle accumulation.

### *2.3. Organic Carbon Concentration Analysis*

Bottom seawater was collected using a water sampler immediately after (less than 1 min) submergence of all mounds to estimate the carbon reduction associated with burrow of *Laomedia* sp. via comparison of carbon concentration between suspended particles collected from the water column and those from reworked sediments (Figures 2 and 3). This process was repeated five times consecutively at each submergence period during the spring tide. Seawater was filtered using a 0.45 µm filter (GF/F, Whatman, Maidstone, UK), and the filtered particles were homogenized after freeze-drying. The organic carbon concentration was then determined using an elemental analyzer (Flash EA1112, Thermo Fisher Scientific, Waltham, MA, USA). The organic carbon reduction was calculated based on the difference in carbon concentrations between suspended particles and reworked sediments.

### *2.4. Grain Size Distribution Analysis*

The grain size distributions of suspended particles and reworked sediments were analyzed using a standard sieving method [29] for the sand fraction and a particle size analyzer (Sedigraph 5100; Micromeritics, Atlanta, GA, USA) for the mud fraction at 0.5-∅ intervals. The sand and mud fractions were separated by wet sieving through a 4 ∅ sieve after removal of organic matter and carbonates with 10% $H_2O_2$ and 0.1 N HCl, respectively. The sand fraction was sieved again for 15 min using a Ro-Tap sieve shaker fitted with 0.5 ∅ sieves, and weight percentages were calculated for each particle size class. The inclusive graphic method was used to determine the sediment type and mean grain size [30].

### 2.5. Burrow Wall Characteristics Analysis

The burrow wall sediments and ambient sediments were collected at spring tide in October 2023 within an in situ observatory (Figure 4). The burrow wall sediments were obtained six times from a depth of 10–30 cm below the surface in the *Laomedia* sp. burrows adjacent to the observatory wall, with the ambient sediments collected in equal amounts at the same depth as the burrow wall sediments. The burrow wall corresponding to a thickness of 1 to 2 mm was carefully collected using a spatula, and then the ambient sediments were obtained away from the burrow wall. The organic carbon concentration of burrow wall sediments and ambient sediments were determined using an elemental analyzer after freeze drying and homogenization. The grain size distributions of both samples were analyzed using the same method as described in Section 2.4.




**Figure 4.** Images of the *Laomedia* sp. burrows and ambient sediments within the in situ observatory.

### 2.6. Statistical Analysis

The relationship between the SRR and factors such as duration of submergence, mound height and elevation were assessed by regression analysis. The relationship between SRR and duration of submergence at each elevation was evaluated using SRR and duration of submergence for each sampling time. The overall SRRs over the entire sampling period for all elevations were used to evaluate the relationship between SRR and elevation as well as between SRR and mound height. Differences in mean mound diameter, mean mound height, mean duration of submergence, mean duration of emergence, mean mass of reworked sediments, and mean SRR among the elevations were assessed using non-parametric analysis of variance (Kruskal–Wallis test) due to the heteroscedasticity of the data. The two-sample t-test was used to identify differences in organic carbon concentration and grain size distribution between suspended particles and reworked sediments as well as between burrow wall sediments and ambient sediments. The results were considered statistically significant at $p < 0.05$.

## 3. Results

### 3.1. Biotic and Abiotic Factors

The tidal conditions and morphometric data for mounds of *Laomedia* sp. are presented in Table 1 and Table S1. The mean mound diameter was greatest at E3, followed by E1 and E2, while the mean mound height was highest at E3, followed by E1 and E2. As elevation increased, the mean duration of submergence decreased, while the mean duration of emergence increased.

**Table 1.** Comparison of morphometric data of *Laomedia* sp. mounds and tidal conditions among elevations (mean ± standard deviation). Different superscripts indicate the significant differences at 0.05.

| | Mean Mound Diameter (mm) | Mean Mound Height (mm) | Elevation from MSL (m) | Mean Duration of Submergence (min) | Mean Duration of Emergence (min) |
|---|---|---|---|---|---|
| E1 | 7.6 ± 2.1 $^{a}$ | 34.0 ± 10.7 $^{a}$ | 1.83 | 238 ± 23 $^{a}$ | 532 ± 23 $^{a}$ |
| E2 | 7.3 ± 1.2 $^{a}$ | 29.2 ± 3.6 $^{a}$ | 1.49 | 267 ± 18 $^{ab}$ | 503 ± 18 $^{ab}$ |
| E3 | 8.5 ± 1.9 $^{a}$ | 34.9 ± 8.3 $^{a}$ | 1.27 | 257 ± 31 $^{b}$ | 513 ± 31 $^{b}$ |

### 3.2. SRR

The reworked sediment mass was highest during the fourth sampling at E2 and tended to increase, except for the fifth sampling (Table 2). The mass of the reworked sediments increased gradually with longer duration of submergence, except for a decrease during the fourth sampling, followed by a shar decrease in the fifth sampling (Table 2). Specifically, the mass of reworked sediment was relatively high during the fifth sampling among the sampling periods at E3 (Table 2). The mean reworked sediment mass at E1 was highest, followed by E2 and E3, but these differences were not significant (Table 2). In this study area, the individual SRR and annual SRR for *Laomedia* sp. based on the reworked sediment mass and density were estimated as 78 g ind.$^{-1}$ d$^{-1}$ and 100.3 kg m$^{-2}$ yr$^{-1}$, respectively.

**Table 2.** Comparison of reworked sediment mass and SRR among the elevations (mean ± standard deviation). Different superscripts indicate the significant differences at 0.05.

| | Reworked Sediments over the Entire Sampling Period (g) | | | | | Overall Mean Reworked Sediments (g) | Overall Mean SRR (g min$^{-1}$) |
|---|---|---|---|---|---|---|---|
| | 1st | 2nd | 3rd | 4th | 5th | | |
| E1 | <0.1 | 213.0 | 116.9 | 110.4 | 31.6 | 94.4 ± 83.2 $^{a}$ | 0.58 ± 0.58 $^{a}$ |
| E2 | <0.1 | <0.1 | <0.1 | 90.3 | 4.3 | 18.9 ± 40.1 $^{ab}$ | 0.10 ± 0.14 $^{ab}$ |
| E3 | 0.34 | 2.6 | 1.5 | 0.0001 | 3.3 | 1.5 ± 1.4 $^{b}$ | 0.01 ± 0.02 $^{b}$ |

The mean SRR was significantly correlated with the duration of submergence at E1 ($p < 0.05$), whereas the correlation coefficients between these factors at E2 and E3 were relatively small ($p > 0.05$, Figure 5 and Table S2). The mean SRR was positively correlated with mound height at all elevations, and the regression coefficient was largest at E3 ($p < 0.05$), followed by E1 and E2 ($p < 0.05$, Figure 6 and Table S2). Throughout the study period, the SRR ranged from 0.01 to 1.44 g min$^{-1}$. Specifically, the mean SRR at E1 was the highest at 0.58 g min$^{-1}$, followed by E2 at 0.10 g min$^{-1}$, and E3 at 0.01 g min$^{-1}$. There was a significant difference in mean SRR between E1 and E3 ($p < 0.05$), but no significant differences were found between E1 and E2, or between E2 and E3 (Table 2). Furthermore, the mean SRR showed positive correlations with both elevation and mound height ($p < 0.05$, Figure 7 and Table S2).

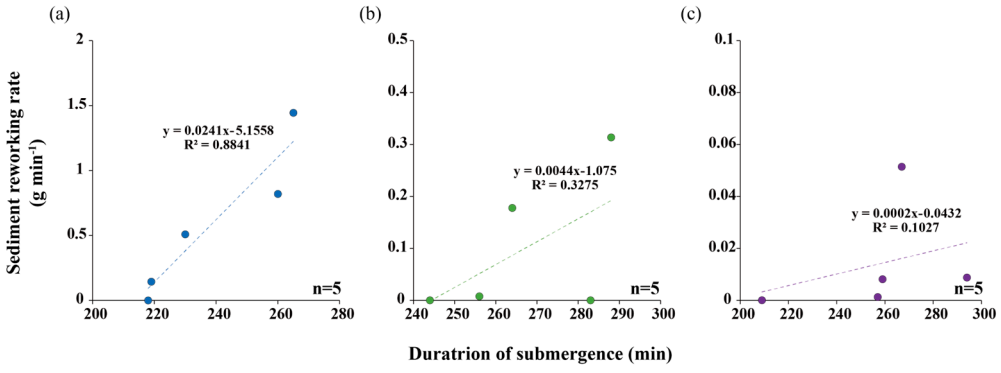



**Figure 5.** Comparison of relationship between mean SRR and mean duration of submergence over the entire study period at various elevations: (**a**) E1, (**b**) E2, and (**c**) E3.

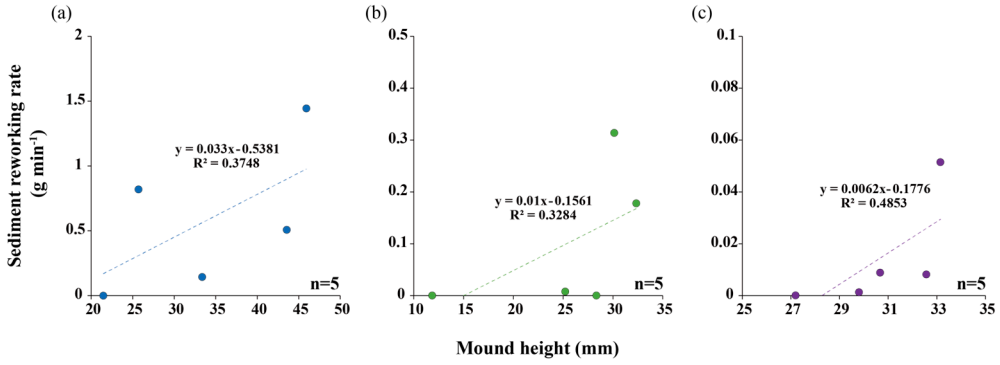



**Figure 6.** Comparison of relationship between the mean SRR and mound height over the entire study period at various elevations: (**a**) E1, (**b**) E2, and (**c**) E3.

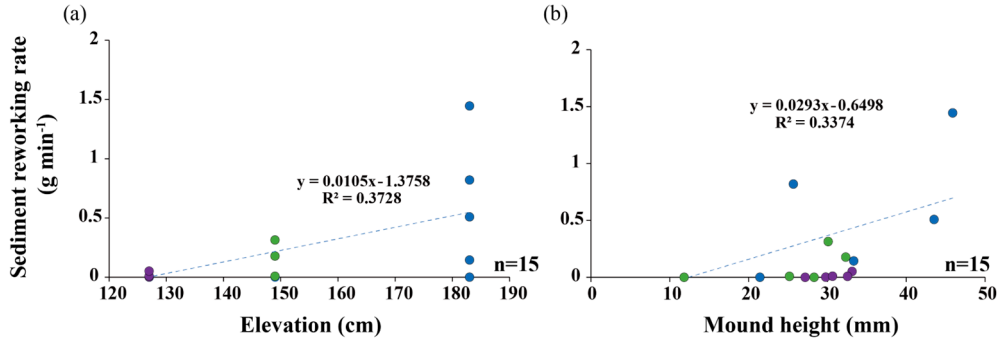



**Figure 7.** Comparison of relationship between the (**a**) mean SRR and elevation and (**b**) mean SRR and mound height. Blue, green, and purple circles represent E1, E2, and E3, respectively.

### *3.3. Grain Size Distribution*

The sediment composition differed between suspended particles and reworked sediments (Table 3). The sand content was significantly higher for reworked sediments than suspended particles, whereas higher silt and clay contents were observed in suspended particles than reworked sediments. The mean grain size was significantly finer for suspended particles than reworked sediments, with mean values of 7.0 and 4.9 ∅, respectively.

**Table 3.** Comparison of the grain size distribution between suspended particles and reworked sediments (mean ± standard deviation). Significant differences based on the t-test at $p < 0.05$.

| | Composition (%) | | | Mean Grain Size (∅) |
|---|---|---|---|---|
| | Sand | Silt | Clay | |
| SP | 4.0 ± 1.6 | 67.9 ± 6.1 | 28.1 ± 6.6 | 7.0 ± 0.5 |
| RS | 32.9 ± 16.9 | 57.6 ± 14.8 | 9.4 ± 2.6 | 4.9 ± 0.6 |
| *p* value | <0.05 | >0.05 | <0.05 | <0.05 |

SP: suspended particles, RS: reworked sediments.

### *3.4. Organic Carbon Reduction*

The organic carbon concentration of suspended particles ranged from 5.32 to 9.94 mg $g^{-1}$, whereas that of reworked sediments ranged from 1.95 to 2.42 mg $g^{-1}$ over the entire study period (Table 4). The organic carbon reduction ratio was highest during the first sampling period, at 76%, whereas the lowest ratio was observed during the fourth sampling period, at 61%. The mean organic carbon concentration was significantly lower for reworked sediments than suspended particles during all sampling periods, with a mean reduction of 68%.

**Table 4.** Comparison of the organic carbon concentration between suspended particles and reworked sediments (mean ± standard deviation). Significant differences based on the *t*-test at $p < 0.05$.

| | Organic Carbon Concentration over the Entire Sampling Period (mg $g^{-1}$) | | | | | Mean Organic Carbon Concentration (mg $g^{-1}$) |
|---|---|---|---|---|---|---|
| | 1st | 2nd | 3rd | 4th | 5th | |
| SP | 9.94 | 6.29 | 5.32 | 6.17 | 7.16 | 6.98 ± 1.78 |
| RS | 2.42 | 2.09 | 1.95 | 2.41 | 2.20 | 2.22 ± 0.20 |
| *p* value | | | | | | <0.05 |

SP: suspended particles, RS: reworked sediments.

### 3.5. Burrow Wall Characteristics

The sediment composition varied between the burrow wall sediments and the ambient sediments (Table 5). The sand content was significantly higher for ambient sediments than burrow wall sediments. Conversely, higher silt and clay contents were observed in burrow wall sediments than ambient sediments. The mean grain size was slightly finer for burrow wall sediments than ambient sediments, with mean values of 4.6 and 4.4 ∅, respectively ($p < 0.05$). The mean organic carbon concentration was significantly higher in the burrow wall sediments compared to the ambient sediments ($p < 0.05$).

**Table 5.** Comparison of the grain size distribution and the organic carbon concentration between the burrow wall sediments and the ambient sediments (mean ± standard deviation). Significant differences based on the *t*-test at $p < 0.05$.

| | Composition (%) | | | Mean Grain Size (∅) | Mean Organic Carbon Concentration (mg $g^{-1}$) |
|---|---|---|---|---|---|
| | Sand | Silt | Clay | | |
| BS | 20.1 ± 4.4 | 72.7 ± 2.6 | 7.2 ± 2.5 | 4.6 ± 0.2 | 4.15 ± 0.93 |
| AS | 25.5 ± 0.7 | 69.2 ± 0.5 | 5.3 ± 0.8 | 4.4 ± 0.1 | 3.02 ± 0.91 |
| *p* value | <0.05 | <0.05 | >0.05 | <0.05 | >0.05 |

BS: burrow wall sediments, AS: ambient sediments.

## 4. Discussion

Differences in elevation reflect varying periods during which shrimp burrows are submerged in seawater, allowing for the deposition of nutritive detritus from the water column. Consequently, burrows at lower elevations, which remain underwater for longer periods, tend to have higher food content [31–33]. The SRRs of two callianassids, *Callianassa filholi* and *Callianassa subterranea*, increased with elevation, suggesting that rapid sediment reworking is necessary to process large volumes of sediment and meet energy demands [33–35]. In our study area, the duration of emergence increased with elevation, implying that shrimp living at high elevations had less opportunity to actively irrigate their burrows compared with shrimp at low elevations. The SRR of *Laomedia* sp. increased with longer submergence time, which were shorter at higher elevations. Furthermore, the correlation between the SRR and duration of submergence was stronger at higher elevation (E1) than lower elevations (E2 and E3). These findings suggest that shrimp living at high elevations require larger volumes of sediment to optimize their energy intake. Therefore, the insufficient duration of submergence at high elevations is an important factor regulating the SRR of this species.

In the present study, the SRR of *Laomedia* sp. was significantly correlated with mound height. A correlation between body size and SRR in thalassinidean shrimp has been reported in previous studies. Berkenbusch and Rowden [33] found that larger individuals of *C. filholi* expelled significantly more sediment than smaller shrimp. Similarly, Rowden et al. [34] observed a significant correlation between SRR and shrimp size in the thalassinidean *C. subterranea*. These studies suggest that shrimp size is an important biotic factor determining the SRR of thalassinidean shrimp. However, capturing the inhabitants of each *Laomedia* sp. burrow was not feasible, as their burrows can extend up to 2 m below the sediment surface and feature complex structures [24]. Consequently, the direct evaluation

of the correlation between SRR and shrimp size was not possible in this study. Nonetheless, the opening dimension of macroinvertebrate burrows can be used as a proxy to estimate the body size and biomass of the inhabitants [35]. Our previous research confirmed that the mound diameter of *Laomedia* sp. has no significant correlation with shrimp body size, while a significant correlation was observed between mound height and body size (unpublished data). This relationship suggests that mound height is indicative of the size of the inhabitant. The SRR of *Laomedia* sp. at the higher elevation (E1) was found to be strongly correlated with the duration of submergence. Meanwhile, the SRR was found to be more strongly correlated with mound height than duration of submergence at lower elevations. Therefore, shrimp size is a more important factor than the duration of submergence in determining the SRR of *Laomedia* sp. in areas at low elevation with sufficient submergence time. In this study, the SRR of *Laomedia* sp. was found to be influenced by elevation and height, consistent with our previous research findings, with no site-specific differences [25]. However, we found that the factors influencing the SRR of this species vary depending on the elevation of habitat, which had not been clearly examined in previous study. Given that the SRR is influenced by various biotic and abiotic factors, such as tidal cycles, organic matter contents, and life cycles, conducting monthly or at least seasonal surveys is essential to accurately establish correlations between the SRR and these influencing factors. Therefore, more comprehensive studies involving longer time series and more frequent sampling are necessary to fully evaluate the relationship between the SRR of *Laomedia* sp. and its influencing factors.

The burrows of thalassinidean shrimp function as traps for fine sediment and thus help limit the outflow of carbon and nitrogen from tidal flats [36]. Burrows of *Laomedia* sp. in the study area are plastered with a smooth red or brown layer with a finer grain composition than the ambient sediment (Table 5 and Figure 4), as has been reported previously for other thalassinidean burrows [5,37,38]. This observation suggests that this species is capable of sorting sediment grains; that selected fine particles are incorporated into the burrow wall to stabilize the burrow structure. Although particle selection by *Laomedia* sp. has not yet been evaluated, this mechanism is employed by other thalassinidean shrimps [39,40]. Thalassinideans, particularly *Biffarius arenosus* and *Trypaea australiensis*, sort sediment particles prior to ejection from the burrow, preferentially removing grains with particle diameters of 125–250 µm [41,42]. Various other thalassinideans have been reported to line their burrows with fine sediment [2,40,43]. The thalassinidean mud shrimp *Upogebia* retains fine-grained sediment in order to coat its burrow walls with fine mud [44,45]. The mean grain size of the burrow wall sediments of *Laomedia* sp. was finer than that of the ambient sediments, with a higher proportion of silt and clay (Table 5), suggesting that fine sediments transported from the water column accumulate on the burrow walls of this species. This process is consistent with other studies demonstrating accumulation of organic matter in the burrows of thalassinideans. Thalassinideans actively facilitate the adherence of organic matter to the burrow walls by pumping overlying water through their burrow systems during irrigation. Therefore, the carbon reduction associated with the burrows of *Laomedia* sp. results from particle selection by the inhabitant and accumulation along the burrow walls. The mean organic carbon concentration of burrow wall sediments was 37% higher than that of ambient sediments due to the accumulation of fine particles (Table 5). This indicates that the organic carbon accumulation on the burrow wall of *Laomedia* sp. is 1.4 times higher than in non-burrowed sediments. Our findings suggest that *Laomedia* sp. burrows function as traps for organic carbon and can be considered potential carbon sinks.

The organic carbon content of suspended particles was reduced by 68% by the sediment reworking of *Laomedia* sp., with a mean organic carbon reduction of 0.01 gC ind.$^{-1}$ d$^{-1}$. Coastal wetlands, including mangroves, seagrasses, and salt marshes, are considered important carbon sinks due to their carbon storage function in coastal ecosystems. Global mean organic carbon burial rates in coastal wetlands have been reported as 174 gC m$^{-2}$ yr$^{-1}$ for mangroves, 151 gC m$^{-2}$ yr$^{-1}$ for salt marshes, and 40 gC m$^{-2}$ yr$^{-1}$ for seagrass meadows [46–48]. Recently, Lee et al. [49] demonstrated that bare tidal flats in Korea can function as po-

tential carbon sinks despite their relatively small organic carbon stocks compared with mangroves, seagrasses, and salt marshes. They have reported that the organic carbon sequestration rate on tidal flats in Korea was 71,383 MgC $yr^{-1}$, and that the mean sedimentary organic carbon sequestration rate in Garolim Bay, adjacent to the present study area, was 1.4 gC $m^{-2}$ $yr^{-1}$ [49]. Bioturbation by macroinvertebrates has only recently been considered important for organic carbon dynamics in coastal wetlands, and growing evidence indicates that bioturbators may increase or decrease carbon stocks [9–12]. Increased remineralization of sediment carbon may occur when bioturbation increases the soil oxygen supply, whereas burial of organic matter into deep anoxic sediment layers by benthic fauna may increase organic carbon stocks [9,13,14]. In this study, the annual organic carbon reduction associated with the sediment reworking of *Laomedia* sp., based on their observed density, was estimated as 12.5 gC $m^{-2}$ $yr^{-1}$. This value is relatively low compared with previous reports of organic carbon sequestration rates in coastal wetlands [46–48] but is higher than the rate observed in bare tidal flats [49]. Therefore, our findings suggest that bioturbation by macroinvertebrates should be considered when evaluating carbon sequestration in intertidal sediments. Nonetheless, the residence time of carbon in the burrow is considered one of the most important factors for accurately assessing the actual impact of carbon reduction by burrows on the global cycle. Therefore, a follow-up study is needed to assess the residence time of carbon within the burrows to accurately evaluate carbon reduction through the burrows in this species.

The sediment reworking of macroinvertebrates transports soil and organic matter from deep layers to the surface, accelerating carbon cycling [50,51]. The transport of organic carbon from the burrows of *Laomedia* sp. into the water column through the sediment reworking varied depending on tidal conditions associated with the duration of submergence. Based on the SRR and duration of submergence, the organic carbon transport was estimated to be 0.61 gC $ind.^{-1}$ $d^{-1}$ at E1, followed by 0.12 gC $ind.^{-1}$ $d^{-1}$ at E2, and 0.01 gC $ind.^{-1}$ $d^{-1}$ at E3, showing a nearly 60-fold difference between E1 and E3. These findings suggest the importance of considering factors that influence the sediment reworking when evaluating carbon transport by in this species. In this study, the mean organic carbon transport rate from the burrows of *Laomedia* sp. into the water column was estimated to be 12.1 gC $m^{-2}$ $d^{-1}$. This value is significantly higher than those reported for other species. For example, Wang et al. [52] and Gutierrez et al. [53] estimated the carbon transport of burrowing crabs, *Helice tridens tientsinensis*, *Sesarma dehaani*, *Sesarma plicata*, and *Uca arcuata*, by in situ quantification of sediment ejected from their burrows. They reported the carbon transport rate for these crab species of 7.33 gC $m^{-2}$ $d^{-1}$ and 10.28 gC $m^{-2}$ $d^{-1}$, respectively. As carbon transport is influenced by a range of biotic and abiotic factors, including species, size, population density, tidal conditions, and organic matter content, direct comparisons among species are inappropriate. Nonetheless, the carbon transport of *Laomedia* sp. is relatively high compared with other species. Our findings suggest that this species plays a crucial role in carbon cycling as a bioturbator in this study area.

## 5. Conclusions

We estimated the SRR by quantification of reworked sediments ejected from the burrows of *Laomedia* sp. and assessed the organic carbon reduction of this species by comparing carbon concentrations between particles collected from the water column and those from reworked sediments. The SRR was significantly correlated with the duration of submergence at high elevation, whereas it had a stronger correlation with mound height than with the duration of submergence at low elevation. The organic carbon content of suspended particles was significantly reduced due to particle selection by the inhabitant and by the accumulation along the burrow walls. The organic carbon reduction ratio associated with the sediment reworking of *Laomedia* sp. was relatively low compared with those reported in coastal wetlands. Conversely, the carbon transport linked to sediment reworking is relatively greater than that of other species. Our findings suggest that *Laomedia* sp. plays a

crucial role in enhancing the carbon cycle as an important bioturbator, with its burrows acting as carbon sinks by trapping organic carbon in intertidal sediments.

**Supplementary Materials:** The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/w16131806/s1, Figure S1: The zoomed-in locations of the sediment traps spaced along a gradient of the varying elevation relative to MSL; Figure S2: Sediment trap for quantifying reworked sediments and suspended particles in seawater (a) before submergence, (b) after submergence and (c) control (artificial mound); Table S1: Duration of submergence and duration of emergence at each elevation over the entire sampling period; Table S2: Comparison of correlation coefficient, coefficient of determination, and p value between SRR and influencing factors derived from regression analysis.

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**Data Availability Statement:** The data presented in this study are available in article and Supplementary Materials.

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