# Size Variation and Survival after Transplantation of the Tropical Box Marine Mussel *Septifer bilocularis* on the Three Coastal Sites of North Sulawesi, Indonesia

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## ABSTRACT

Box mussels exhibit patchy distribution patterns across intertidal and subtidal zones, where environmental contrasts strongly influence their physiology and ecology. Intertidal box mussels experience frequent air exposures, variable salinity, acidity, and turbidity during low tide, whereas subtidal mussels generally experience more stable conditions. However, with rising sea temperatures related to global climate change, these stressors may intensify, disrupting the mussel's activities. Consequently, their roles in marine ecosystems may change, yet knowledge of box mussel responses to environmental change remains limited. This study investigated the effects of site, time (monthly intervals), and position (intertidal vs. subtidal) on mussel growth and survival. Box mussels were transplanted to intertidal and subtidal seabeds at three sites in North Sulawesi: Tiwoho, Tongkaina, and Blongko, from August to November 2023. Shell length and survival rates were analyzed using a three-way ANOVA, with site, time, and position as main factors. The results showed that mean shell length was significantly influenced by all three factors. The box mussels grew rapidly from August to September, followed by slower growth from October to November. The final mean size was higher at Tongkaina compared to Blongko, while Tiwoho did not differ significantly from Tongkaina. Survival declined steadily, averaging 22–40% by November, and was influenced by time and position but not by site. Ascidians were observed attaching to the cages in November. Seawater temperature, ascidian presence, and food availability may influence mussel size and survival. Finally, although the tropical mussel, *S. bilocularis*, exhibits higher thermal tolerance, it remains vulnerable to ocean warming.

**Keywords:** Aggregation, Box mussels, Patch, Restoration, Transplantation

## INTRODUCTION

Box mussel populations form aggregations or patches called mussel beds, which create habitats for various organisms and enhance local biodiversity, providing benefits to ecosystem function. However, the abundance of mussel beds has globally declined because of environmental stressors, including water temperature, pollution, habitat destruction, coastal erosion, climate change, and unsustainable harvesting methods (e.g., zu Ermgassen *et al*., 2013; Petraitis and Dudgeon, 2020; van den Bogaart *et al*., 2023). These impacts have triggered habitat restoration interventions and transplantation.

The tropical box mussel, S*eptifer bilocularis* (Linnaeus, 1758), colonizes the intertidal zone (Wagiu *et al*., 2021) and subtidal coral habitats (Zelin and Latipov, 2006; Morton *et al*., 2020). In North Sulawesi, the species is found abundantly on the west coast (Palit *et al*., 2021; Ompi *et al*.,

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2023a; 2023b). Under favorable conditions, larvae attach to various hard substrata, such as dead coral reefs and rocks, forming mussel beds (e.g. Soria *et al*., 2022; Ompi *et al*., 2023a). These beds become habitats for many species, including infauna and epifauna. Infauna live in the sediments between mussels, while epifauna larvae attach to mussel shells (e.g. People, 2006; Soria *et al*., 2022; Ompi *et al*., 2023b). A fully developed mussel bed thus becomes a feeding- and nursery area for many commercial species (e.g. Commito *et al*., 2019; Seitz *et al*., 2014). Mussel beds facilitate trophic interactions and subsequently provide food sources for higher trophic levels, such as fish (Nauta *et al*., 2022). The presence of feeding fish within mussel beds attracts artisan fishers, potentially affecting overall ecosystem health (e.g. McLeod *et al*., 2019; People, 2006; Nauta *et al*., 2022; Soria *et al*., 2022).

At the investigated mussel beds in North Sulawesi, Indonesia, the density of box mussels in the tidal zone of Tongkaina previously varied between 10 and 20 individuals per 20 $cm^2$ before the beds disappeared entirely (Ompi, 1997; Ompi *et al*., 2023b). The main reason for the loss was the extensive accumulation of sediment covering the mussel beds. A similar decline was observed in Vanphong Bay (Khanh Hoa Province), reported by Zelin and Latipov (2006).

Several European countries have reduced the practice of bottom dredging as a harvesting method because of its negative impact on the seabed and benthic ecosystems (e.g. van den Bogaart *et al*., 2023). Restoring mussel beds and their ecological function can be achieved by reducing human impacts (Bridger *et al*., 2022; Nauta *et al*., 2022), but it might take a long time to recover. Transplantation of mussels as artificially created aggregations and patches may therefore be considered to support the development and re-establishment of the mussel bed ecosystem (e.g., Schotanus *et al*., 2020; van den Bogaart *et al*., 2023).

After the decline of the tropical box mussels on the coast of northern Sulawesi (Ompi and Lumingas, 2019; Palit *et al*., 2021; Ompi *et al*., 2023a), re-establishment by transplantation has been undertaken. Recent studies have shown that site placement, positioning, and substrate type influence mussel settlement. Specifically, site and position within the patch, and substrate type, significantly affected settlement density and initial sizes of recruits (Ompi *et al*., 2023b). Heavier, thicker, and larger mussels were found in a small patch rather than in a larger patch (Ompi and Lumingas, 2019). Similar studies in other mussel species have highlighted the importance of physiological and environmental interactions (Fernandes-Reiriz *et al*., 2016; Kamermans and Saurel, 2022; Benjamin *et al*., 2024). Mussels also vary in response to intertidal submersion levels and exposure, which may affect their sizes through changes in growth, survival, metabolism, and reproduction. This study focused on the size and survival of mussel transplants, with the effects of sites, times, and positions (tidal zone) as the major factors. We hypothesized that different sites, times, and positions dictate mussel size and survival. This research will provide information for an optimal strategy, such as transplantation site and timing, and the choice of tidal zones to enhance mussel restoration.

## MATERIALS AND METHODS

*Sites*

The research was conducted in the coastal areas of Tiwoho, Tongkaina, and Blongko, in North Sulawesi, as shown in Figure 1. Tiwoho is located at 1°35'41.7"N 124°50'10.7"E; Tongkaina at 1°34'9.71"N 124°48'6,18"E; and Blongko at 1°11'13.55"N 124°28'37.66"E. The coastal areas of Tiwoho and Tongkaina have extensive tidal flats, whereas Blongko has a relatively short tidal zone. The bottom at each site comprises dead coral debris and coral boulders over sandy sediments. During low tide, these areas are exposed to the air.

*Field experiments*

Box mussel populations were observed on the coast of Tiwoho, were absent along the coast of Tongkaina, and were present in declining numbers on the coast of Blongko (Ambarak *et al*., 2021; Ompi *et al*., 2023b). Since mussels were absent in

Tongkaina and were declining in Blongko (Ompi *et al*., 2023b), mussels were carefully sampled from Tiwoho by detaching them from their substrata and cutting the byssus threads. Fifteen individuals with lengths ranging from 9 to 12 mm were selected and inserted evenly onto two nylon fiber ropes. Each rope measured 15 cm in length and 1.5 mm in diameter, serving as a substratum. These substrata were fixed to the bottom of a cage (15 cm long, 10 cm wide, and 5 cm high), which was covered with a 1-cm mesh net.

A recent study showed that environmental conditions rather than mussel density influence mussel growth for the green mussel, Perna viridis (Rahim *et al*., 2025). Therefore, the same number of mussels with similar shell sizes was used in this experiment to minimize density effects. The mussels were expected to show similar growth and survival responses to environmental factors during the early phase of the experiment.

The cages were placed overnight in a plastic container filled with seawater to stimulate the production of byssus threads for attachment to the nylon fibers. Eighteen cages were then secured to a concrete breakwater and distributed across the bottom of the intertidal zone and the subtidal zones (5 m depth) at Tiwoho, Tongkaina, and Blongko. Three replicates were placed in each zone, spaced 1 m apart to minimize interference while ensuring spatial replication.

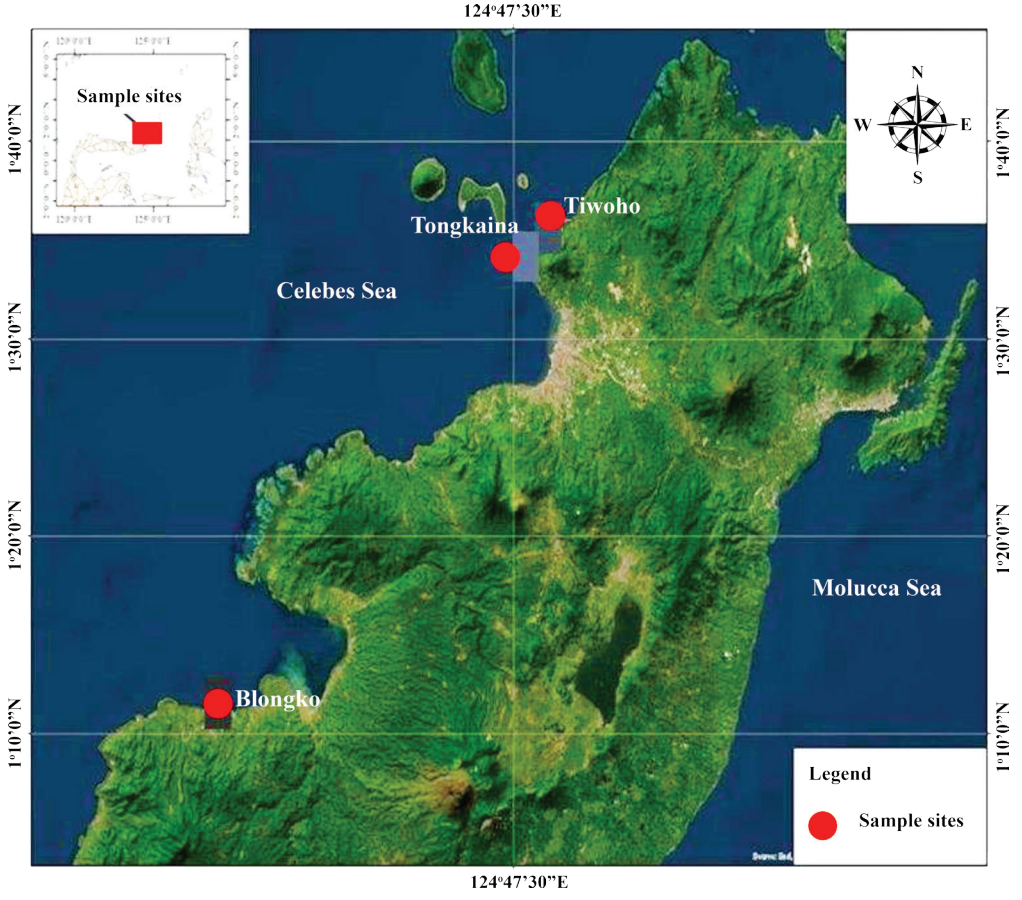



Figure 1. Sampling sites (study locations) on the coast of Tiwoho, Tongkaina, and Blongko in North Sulawesi. Source: GCS_WGS_1984, WKID: 4326, Authority: EPSG, Google Earth.

At the end of each month (August, September, October, and November), the number of mussels in the cages was counted, and shell length was measured using a caliper with an accuracy of ± 1 mm. During transplantation, seawater temperature was measured using a Horiba instrument. Seawater temperature was recorded during low tide from 12:00 and 13:00.

*Data analysis*

The data were analyzed using the statistical computer package MYSTAT. To fulfill the assumptions of analysis of variance (ANOVA), the shell length and survival data were tested for homogeneity of variance using Levene's test. Because these assumptions were not fully met, the data were transformed prior to analysis. Shell length data were log-transformed because the variance of shell length data was larger than the mean (Fowler *et al*., 1998). For survival data, the arcsine transformation was applied. A three-way ANOVA was then performed, with site, time (monthly interval), and position (intertidal and subtidal) as the main factors. When the test showed a significant effect of the main factors, post hoc comparisons were performed using the Student-Newman-Keuls (SNK test).

## RESULTS

*Effect of site, time, and position*

The results of the three-way ANOVA on shell length, with site, time, and position as main effects are shown in Table 1. A significant effect of site, time and position was found ($p<0.05$, Table 1). Significant interactions were found between site × time ($p = 0.002$) and between site × position ($p = 0.003$, Table 1), but not between time × position ($p = 0.171$), or among site × time × position ($p = 0.125$) (Table 1). The interaction pattern was driven by an increase in shell size at Blongko in October, which declined in November (Figure 2). An inconsistent size increment of mussels in the intertidal cages from October to November was found (Figure 2).

*Effect of site*

The mean shell length increment varied among sites (Figure 3). Significantly higher mean shell lengths were found in Tongkaina than in Tiwoho (SNK test: $p<0.05$) and Blongko as well (SNK test: $p<0.05$). No significant difference in mean shell length between mussels in Tiwoho and Blongko was evident (SNK test: $p>0.05$). Because of the large statistical variation causing significant interaction between sites, the result should be treated cautiously.

*Effect of time*

An increase in shell length with time was observed (Figure 4). The pattern of increase was pronounced from August to October but leveled off during October to November (Figure 4). The statistical analysis showed a significant effect of time on shell length with no interactions (Table 2; Figure 4). SNK tests showed significant differences between August, September and October (SNK test: $p<0.05$) but no difference between October and November (SNK test: $p<0.05$).

*Effect of position*

A significant effect of position was found (Table 1; Figure 5). Mussels living in the intertidal had significantly greater mean shell length than those living in subtidal areas (SNK test: $p<0.05$; Figure 5).

*Survival*

Survival of box mussels differed across site, time, and position (Figure 6, Table 2). However, survival was not significantly affected by sites ($p = 0.438$). In contrast, survival varied significantly with sampling time ($p = 0.000$) and between positions (intertidal vs. subtidal ($p = 0.018$). No significant two-way or three-way interactions among site, time, and position were detected (all $p>0.05$; Table 2).

Table 1. Results of the three-way ANOVA for shell length of *Septifer bilocularis*, with site, time, and position as the main effects.

| Sources | SS | DF | MS | F | p-value |
|---|---|---|---|---|---|
| Site (S) | 0.575 | 2 | 0.287 | 5.136 | 0.043 |
| Time (T) | 67.252 | 3 | 24.043 | 265.759 | 0.000 |
| Position (P) | 0.702 | 1 | 0.702 | 7.751 | 0.006 |
| S*T | 1.931 | 6 | 0.322 | 3.554 | 0.002 |
| S*P | 1.044 | 2 | 0.522 | 5.765 | 0.003 |
| T*P | 0.456 | 3 | 0.152 | 1.678 | 0.171 |
| S*T*P | 0.911 | 6 | 0.152 | 1.677 | 0.125 |
| Error | 43.653 | 482 | 0.091 | | |

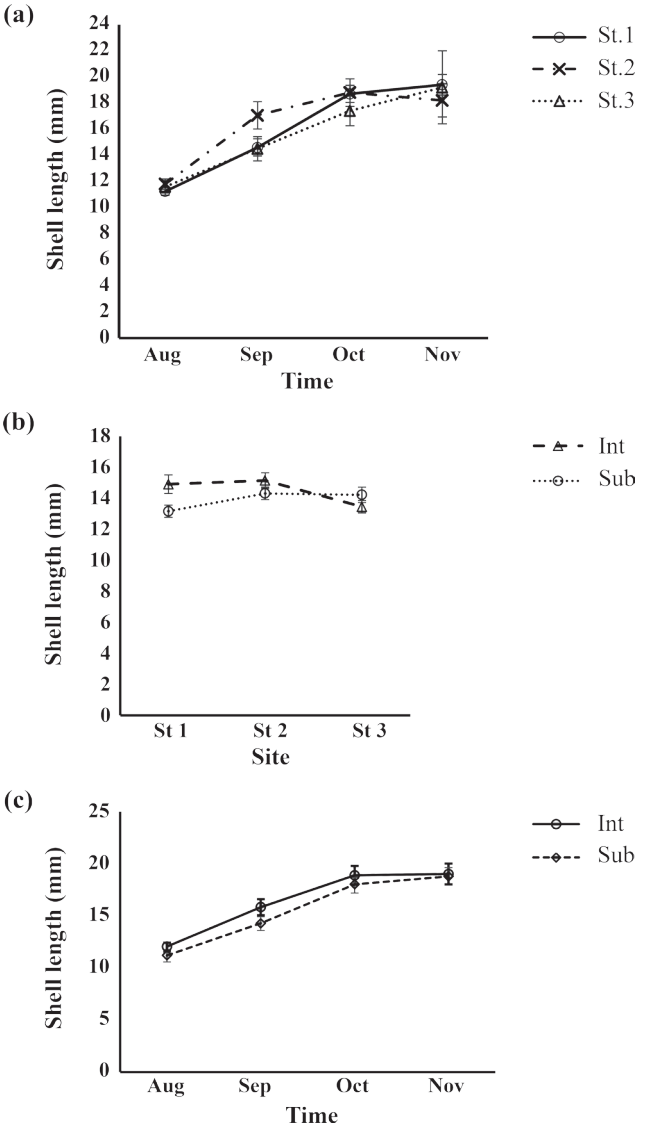



Figure 2. Interaction plots from a three-way ANOVA of shell length in *Septifer bilocularis*: (a) Site × Time; (b) Site × Position; (c) Time × Position. Bars indicate 95% confidence intervals (CI).

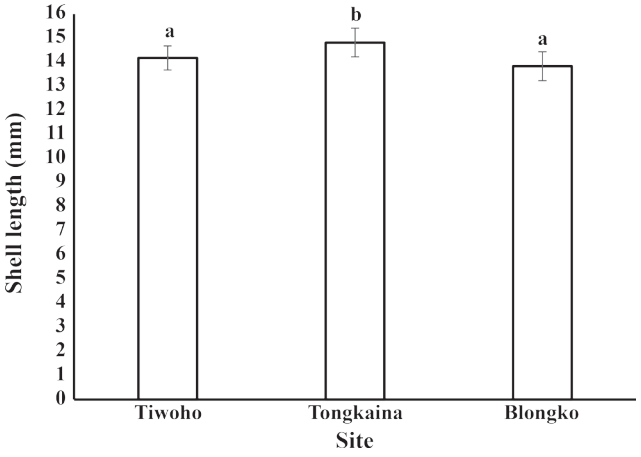



Figure 3. Mean shell length of *Septifer bilocularis* sampled at Tiwoho, Tongkaina, and Blongko. Bars indicate 95% confidence interval (CI).

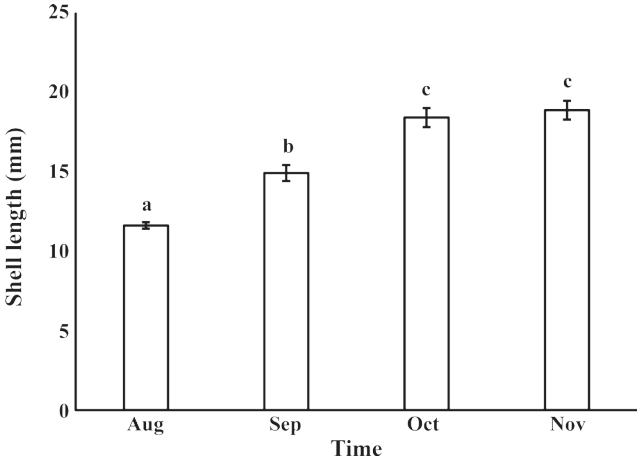



Figure 4. Mean shell length of *Septifer bilocularis* over time. Bars indicate 95% confidence interval (CI).

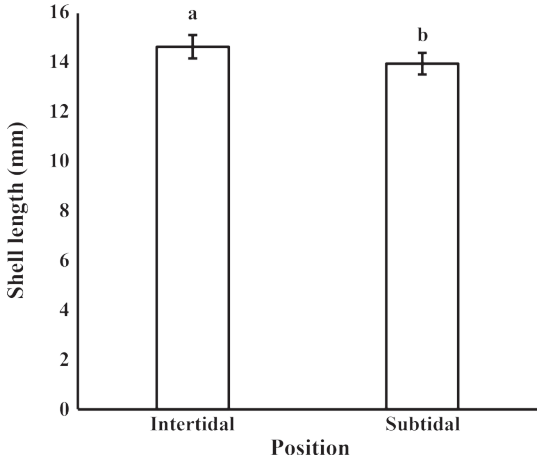



Figure 5. Mean shell length of *Septifer bilocularis* by position (intertidal vs. subtidal). Bars indicate 95% confidence interval (CI).

Table 2. Three-way ANOVA of mean survival of box mussels, with time, position, and sites as main effects.

| Sources | SS | DF | MS | F | p-value |
|---|---|---|---|---|---|
| Site (S) | 3.253 | 2 | 1.627 | 0.839 | 0.438 |
| Time (T) | 53.264 | 3 | 17.755 | 9.162 | 0.000 |
| Position (P) | 11.642 | 1 | 11.642 | 6.008 | 0.018 |
| S*T | 3.781 | 6 | 0.749 | 0.387 | 0.884 |
| S*P | 2.108 | 2 | 1.054 | 0.544 | 0.584 |
| T*P | 5.772 | 3 | 1.924 | 0.993 | 0.404 |
| S*T*P | 4.389 | 6 | 0.732 | 0.378 | 0.890 |
| Error | 93.018 | 48 | 1.938 | | |

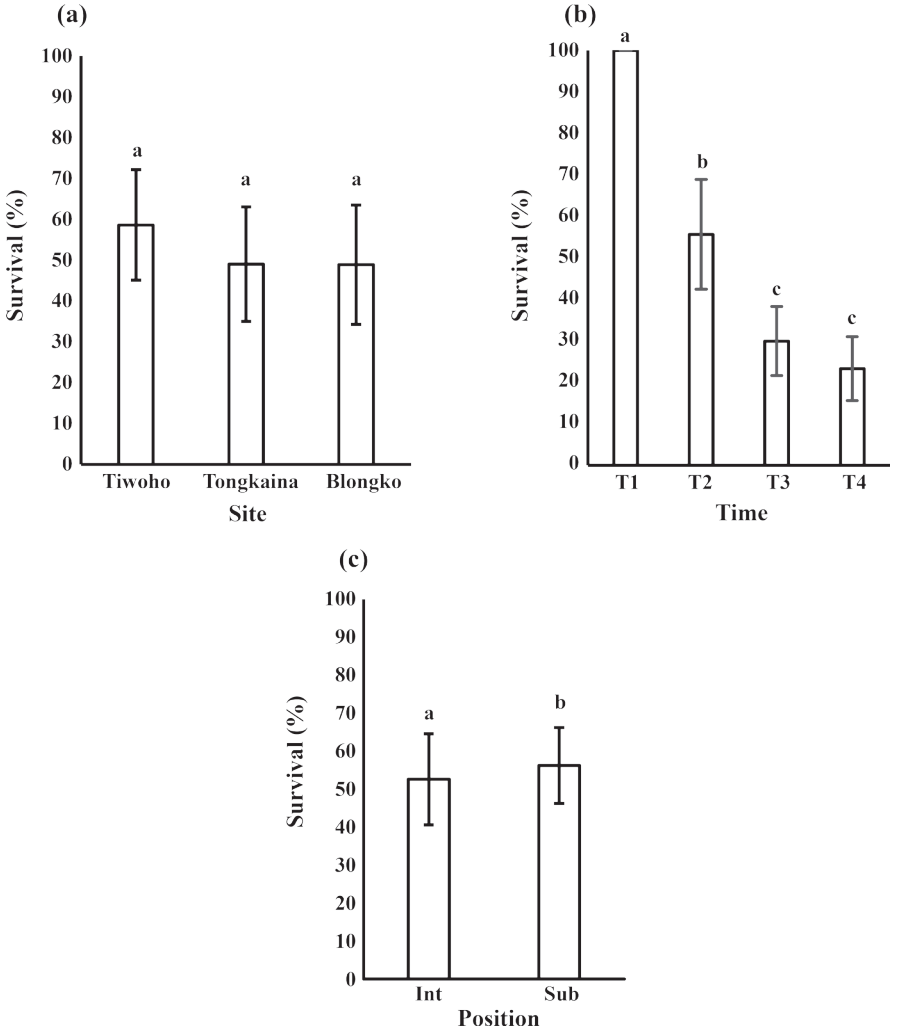



Figure 6. Mean survival of *Septifer bilocularis* by: (a) Site (Tiwoho, Tongkaina, Blongko); (b) Time (August, September, October, and November); and (c) Position (Intertidal zone (Int) and Subtidal zone (Sub). Bars indicate 95% confidence interval (CI).

Mussel survival decreased significantly from August to September to September (SNK test, $p<0.05$; Figure 6b) and decline further from September to October (SNK test: $p<0.05$). In contrast, survival did not differ significantly between October and November (SNK test: $p>0.05$) (Figure 6b). Survival was also significantly higher in the subtidal zone than in the intertidal zone (SNK test: $p<0.05$, Figure 6c).

*Seawater temperature*

Seawater temperature showed spatial and temporal variation across sites and positions (Table 3). In August, it reached 36 °C at the intertidal zone of all sites (Tiwoho, Tongkaina, and Blongko) and 31 °C at the subtidal zones. In September, intertidal temperatures decreased to 32 °C, while subtidal temperatures were 30 °C across sites. A further decline was observed in October, with 31 °C at the intertidal zone, and 29 °C at the subtidal zone of Tiwoho and Tongkaina, decreasing to 28 °C in Blongko. By November, seawater temperature had decreased to 29 °C at the intertidal zones and 28 °C at the subtidal zones across sites (Table 3).

Table 3. Seawater temperature (°C) observed in the intertidal (Int.) and subtidal (Sub) zones across sampling time.

| Sites | Months/Positions | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | August | | September | | October | | November | |
| | Int. | Sub. | Int. | Sub. | Int. | Sub. | Int. | Sub. |
| Tiwoho | 36 | 31 | 32 | 30 | 31 | 29 | 29 | 28 |
| Tongkaina | 36 | 31 | 32 | 30 | 31 | 29 | 29 | 28 |
| Blongko | 36 | 31 | 32 | 30 | 31 | 28 | 29 | 28 |

## DISCUSSION

*Effect of sampling sites*

Many studies have shown that mussels respond to environmental changes, including increased shell length (e.g. Kamermans and Saurel, 2022), shell shape and thickness (e.g. Telesca *et al*., 2018), and behaviour (e.g. Jaatinen *et al*., 2020). In this study, we showed for the first time how the tropical box mussel responded at different sites, times, and positions. Our study showed that site affected mussel growth. Mussel growth was higher in the intertidal area than in the subtidal area. Mussel size increased from August to October but decreased from October to November.

Mussel shell length was used in this study as a measure of growth because it was easy to measure directly every month. Shell length has been used as a representative measurement for the growth of many marine bivalves, such as mussels and oysters (e.g., Kamermans and Saurel, 2022).

*Effect of temperature*

Many studies have shown that increasing seawater temperatures affect the growth of mussels (e.g. Benjamin *et al*., 2024). Rising seawater surface temperatures have been observed because of global climate change (nasa.gov), for example, in the South China Sea (Williams *et al*., 2019), and Indonesia (Kusuma *et al*., 2017). The Indonesian seawater surface temperature varies (https://seatemperature.net/country/indonesia), and is affected by the Indonesian Through Flow (ITF) (Iskandar *et al*., 2023).

In this study, the seawater temperature reached 36 °C at low tide in the three intertidal sites, while it was 28–32 °C at 5-m depth at each subtidal site. These seawater temperature variations may explain the variation in the shell length of our tropical box mussel in this study. According to Gosling (1992), mussels, particularly adult blue mussels, tolerate increasing seawater temperatures up to 29 °C. In this study, seawater temperature

at the intertidal zone was higher than this upper tolerance limit, but not at 5-m depths in the subtidal. Here, the seawater temperature was probably within an optimal level or within the ecological range (e.g., Matoo *et al*., 2021). Previous studies have shown that mussels might stop feeding and growth, and instead allocate energy to maintain physiological homeostasis, when the sea temperature reached or exceeded their thermal tolerance limits (e.g., Matoo *et al*., 2021; Ibarrola *et al*., 2022). However, increased air temperature during low tide did not appear to affect the box mussel directly in this study. Exposure to elevated aerial temperatures at low tide may enhance mussel filtration activity during immersion, leading to greater particle uptake from the water column at high tide.

During immersion, food particle concentration appeared higher across intertidal flats at the surface than in the adjacent subtidal water column, providing mussels in the intertidal habitats with greater feeding opportunities, which affected their growth patterns (see Seed and Suchanek, 1992).

Rising seawater temperatures to the upper tolerance limit in the subtidal habitat down to 5-m depths might stimulate mussel pumping rates and enhance the filtration of suspended particles (e.g. Jørgensen *et al*., 1990; Kittner and Riisgård, 2005). The presence of food particles in the water column may increase clearance rates (e.g., Kamermans and Saurel, 2022) and elevate metabolic demands (Menge *et al*., 2008). Thus, mussels occupying subtidal environments may exhibit growth, though typically not to the same extent as conspecifics inhabiting the intertidal zone.

Seawater temperatures varied among sites in the latter part of this study, particularly in the last two months of 2023, when it decreased from 36 °C to 31 °C in October and continued to decrease to 28 °C in November at both sites of Tiwoho and Tongkaina. At the same time, the seawater temperature was 28 °C at the subtidal zone of Blongko in October, and then it was consistently 28 °C in November. This variation in seawater temperature could be driven by local conditions, such as suggested by Barbosa *et al*. (2021), Kamermans and Saurel (2022), and Wang *et al*. (2022). Tropical mussels were placed on the coast of Blongko, which has a short and steep reef, where cool seawater from deep water might affect the seawater temperature. In contrast, Tiwoho and Tongkaina, with wide sloping reefs, may be less influenced by cool deep-water inputs, which leads to seawater temperature at the intertidal zone being 31 °C in October, and then down to 29 °C in November. Consistently high seawater temperatures might lead to elevated pumping rates, leading to higher food intake (Bayne *et al*., 1989). As a result, mussels in Tiwoho and Tongkaina might have absorbed more food particles than those in Blongko. This process might explain the larger mussel size observed in Tiwoho and Tongkaina than in Blongko.

Growth rates are often faster in younger mussels, and slower later in life (e.g., Chelyadina and Popov, 2020; Clements *et al*., 2020). It is assumed that box tropical mussels show a similar pattern of slowing growth rates as large sizes, such as *Mytilus galloprovincialis* (e.g. Chelyadina and Popov, 2020). However, no data on growth are available for the box mussel. In this study, early mussel sizes varied from 9 to 12 mm. The box mussel had a sharp increase in shell length increment from August to September, and then to October. Then, slower growth from October to November occurred (Figure 3).

The proportion of small shell length individuals could explain the fast-increasing mussel shell length observed at the three sites in this study. This pattern might be in line with many previous studies, such as those reported by Steffani and Branch (2003) and Clements *et al*. (2020), smaller mussels grew faster than larger mussels. In this study, slow growth of large mussels might occur during October–November, compared to small mussels during August to October (Figure 3).

*Associated fauna*

The ascidian, *Didemnum molle* (Herdman, 1886), was first recorded in November, when it was abundantly attached to the outer nets at all three sites. Similar to mussel and gastropod larvae, ascidian larvae remain in the water column for some time before settling on suitable substrates for attachment (e.g. Ompi and Svane, 2018; Ompi *et al*., 2023b; 2024). Ascidian larvae were likely abundant in the water column in October, after which they settled on the cage net and developed. Ascidians are a group of Chordata (Tunicata) and are filter feeders (e.g. Petersen and Svane, 2002; Conley *et al*., 2018). The presence of ascidians attached to the outside of all nets suggests that food competition might occur by lowering particle concentration in the nets and affecting water flow. Food competition could explain the slow growth of mussels in the period from October to November.

*Survival*

Marine benthic species such as mussels experience regular periods of aerial exposure in the intertidal zone, where subtidal species remain continuously submerged, even during low tide. Benthic mussels are subjected to abiotic stresses, with thermal stress being a major factor that can affect their physiological performance and survival (e.g. Collins *et al*., 2020). The survival of the tropical box mussel was first shown to vary among sites, times, and positions in this study. After 4 months of transplantation, the results showed that mussel survival was higher in the subtidal zone at 5 m than in the intertidal zone. Temperature fluctuations in the intertidal zone might affect the transplanted mussel's survival rates. During low tide, the intertidal zone is exposed to air, as observed in the South Island of New Zealand (Benjamin *et al*., 2024). This zone is also subject to wave action and turbidity (e.g. Helmuth *et al*., 2002). In contrast, the subtidal zone remains consistently covered by seawater, even during low tide.

Previous studies have shown that mussels vary in their tolerance to temperature depending on site and species. For example, the Asian green-lipped mussel, *Perna canaliculus* (Gmelin, 1791) in New Zealand waters has an optimum temperature limit of about 25 °C (Benjamin *et al*., 2024). A similar thermal tolerance limit has been reported for temperate species such as *Mytilus edulis* Linnaeus, 1758 and *M. galloprovincialis* Lamarck, 1819 (e.g. Kamermans and Saurel, 2022). In contrast, the Asian green mussel, *P. viridis* has shown a wider thermal tolerance, ranging from 20 to 29 °C in Guayacan Venezuela (Arrieche *et al*., 2020), and from 26–32 °C in Maradu Bay, Malaysia (Soon and Ransangan, 2016). Yuan *et al*. (2016) observed that *Perna viridis* (Linneaus, 1758) survived at a wide range of seawater temperature (9–35 °C) when salinity was 35–37‰.

This study was the first to describe that the tropical box mussel after 4 months of transplantation, reached lower average survival in the intertidal zone than in the subtidal zone. A significantly higher decline in survival occurred from August to September, when seawater temperature reached 36 °C in the intertidal zone. The mussel survival declined slowly from October to November when the seawater temperature in the intertidal zone dropped to 31 °C in October and 29 °C in November. In the subtidal zone, seawater temperature was 28 °C in November. This study suggested that the box mussel has a high optimum tolerance to seawater temperature compared to other Asian mussel species such as *P. viridis, P. canaliculus*, and two temperate species.

This study showed that the tropical box mussel exhibited strong biological and ecological sensitivity to climate-driven impacts, particularly to temperature fluctuations and associated stressors. These stressors included differences between sites, vertical positions (intertidal and subtidal zones), time (monthly intervals), and additional pressure from ascidian competition. Such environmental influences were reflected in measurable changes in mussel growth and survival. Prioto *et al*. (2020) similarly reported that variations in mussel sizes and survival are closely linked to environmental factors. Collectively, these findings contribute to the prediction of long-term ecological trends, consistent with the observations of Marshall *et al*. (2021).

## CONCLUSIONS

This study revealed that spatial and temporal factors influence mussel size and survival. Mussel size was significantly affected by site, time, and position, with rapid early development and the largest sizes observed at Tongkaina. Mussel survival, however, declined steadily over time and was strongly influenced by time and microhabitat position rather than site differences. These findings suggest that while a favourable site can promote faster growth, long-term survival is constrained by broader environmental pressures. The relatively high thermal tolerance of the tropical box tropical mussel, *S. bilocularis*, compared with other Asian and temperate species, may still constrain its resilience in warming seas, despite its tolerance to other environmental stressors.

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