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Research Article

Settlement of the Tropical Box Mussel, *Septifer bilocularis*: Effects of Site, Position, and Substratum

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The box tropical mussel *Septifer bilocularis* lives attached to a hard substratum, forming a dense aggregation or patch. The aggregation occurs at the time of larvae settlement in response to different cues. Larvae may have a positive response whereas larvae may settle and attach to the substratum, while in a negative response, postpone settling occurs. Byssus threads are produced and attached to the substratum, and for some reason, they are affected by many variables. We studied whether the attachment was affected by sites, position in the patch, and substratum. Large and small patches of mussel beds were selected arbitrarily, each in 3 replicates. Substrata of palm, coconut, polypropylene fibres, and mussel shells with byssus threads, each in 4 replicates, were distributed randomly into a PVC plate with 16 holes. The PVC plates with experimental substrata were placed along the edge and in the middle of large and small patches. A three-factorial ANOVA was then performed on samples of sites, position in patches, and substratum as main effects. A significant effect of sites, position within patches, and substratum as well were found. A significantly high number of new settlers in small patches than in other positions within patches occurred. The larger number of new settlers was found on coconut, palm, and polypropylene fibres, while low numbers on the mussel shells with byssus threads were found. The new settlers of *S. bilocularis* (<1 mm) with transparent shells were observed attached to coconut, palm, and polypropylene fibres. In contrast, the new settlers ranged from >1 mm to 3 mm with dark green shells attached to mussel shells with byssus threads. This study suggests that early settlement occurs when mussels' larvae first settle and attach to coconut, palm, and polypropylene fibres before reattaching to adult shells with byssus threads.

1. Introduction

Beds of the tropical box mussels are a common feature in the intertidal habitat of North Sulawesi [1]. The distribution is patchy similar to the North European *Mytilus edulis* Linnaeus 1758 [2]. Patches of mussels vary in size. In this study, a small patch has a diameter of 0.25 meters, while a large patch can reach a diameter of more than 2 meters [1]. In temperate marine waters, mussel beds, such as blue mussels, *M. edulis*, a large patch, can reach a diameter of more than 9 meters [2, 3].

The size and dynamics of a mussel patch are determined by settlement into established patches. Mussel larvae become photonegative and descend to the sea bottom and search for a suitable substratum for settlement when the larval stage ends (e.g. [4, 5]. At this stage, the larvae swim and crawl on surface surfaces to search for a suitable substratum. If a larva gets a stimulus from a substratum, it will respond by secretion of byssal threads. Mussel larvae use proteinaceous secretions of their foot glands, the byssus, to attach themselves to the substratum (e.g. [6, 7]. If no stimuli, a larva swims and crawls continuously on the bottom or swims back into the water column (e.g., [4, 8]. When searching for suitable substratum, mussel larvae may also be flushed away by tidal currents because of a weak and passive swimming behaviour. The larvae will continue to search for an attractive substratum with an increased risk of mortality (e.g. [9].

The first attachment occurs when a larva finds a suitable substratum by the release of a byssus thread and attaches to it

[10]. More and more byssus threads were produced and attached to the substrates when mussels grew [11]. The attachment was secured by the subsequent addition of more byssus threads [11]. A number of studies have shown that attachment strength was enhanced when mussels were exposed to predators [7, 11] and waves [11–13]. However, mussel attachment might be disrupted for various reasons [14], due to the influence such as hydrodynamics forces [13, 15, 16]. In the study of wave action that limits crowding in an intertidal mussel, Gutiérrez et al. [12] suggested that the mussel's attachment was dislodged when wave forces acting on the organisms exceeded the strength to which they were attached.

Mussel beds are habitats for various associated infauna and epifauna which may affect settlement, recruitment, and survival within a patch [2, 17–19]. The mussels are effective filter feeders and depend on the availability of plankton. Large beds can completely remove plankton, including mussel larvae (e.g., [20] from the water column, leading to interspecific competition [21]. As a result, the number of new settlers may be affected when settlement occurs [20, 22].

Other threats to new settlers in mussel beds can be siltation caused by changes in currents and habitat. The consequence is the development of anaerobic conditions within patches leading to increased mortality for new recruits and mussel adults as well [23, 24].

Along the coast of North Sulawesi, many box mussel beds are lost due to increased development and subsequent erosion which constitutes a threat to biodiversity and habitat structure. Maintaining the box mussel beds is important for the ecological function and stability of the coastal habitats. Destruction of beds is comparable to the loss of mangroves due to the development of prawn farms [25]. Accordingly, an understanding of the function and distribution of the box mussel beds is important for mitigation and protection.

In this study, we focus on the effects of mussel settlement in relation to patch size. Larval function at settlement for temperate mytilids is well understood [4, 7, 8, 14] but less so for the tropical box mussel. The question raised in this study is whether settlement of the box mussel is affected by two natural fibres (coconut and palm fibres), one artificial fibre (polypropylene fibres), and conspecific adult mussel shell with byssus threads as a function of patch size, position in the patch, at two different sites. The aim was to understand settlement preferences and further explore suitable substrata to enhance settlement by artificial means.

2. Materials and Methods

2.1. Sites. This study was performed in two sites with intertidal mussel beds, Tiwoho, North Minahasa, at the position of 1°35′20″N and 124°49′22″E, and Blongko, South Minahasa, at the position of 1°131′39″N and 124°21′19″E, North Sulawesi, Indonesia (Figure 1). The mussel bed of Tiwoho is found in a wide intertidal area, 950 meters, measured as the distance from the edge of the mangrove to the edge of the dry at low tide. The mussel beds are situated in the middle of the intertidal areas on rocks and coral rubble. Mangroves are separating the mussel beds from the mainland. Marine algae, such as *Halimeda* sp, *Hypnea* sp, *Padina* sp, seagrasses, *Enhalus* sp, and *Thalasia* sp, are found between the mussel beds. Echinoids such as *Echinometra* sp. and Ophiuroids such as *Ophiomastix* sp., *Ophiactis* sp., *Ophiocoma* sp. are found within the mussel beds.

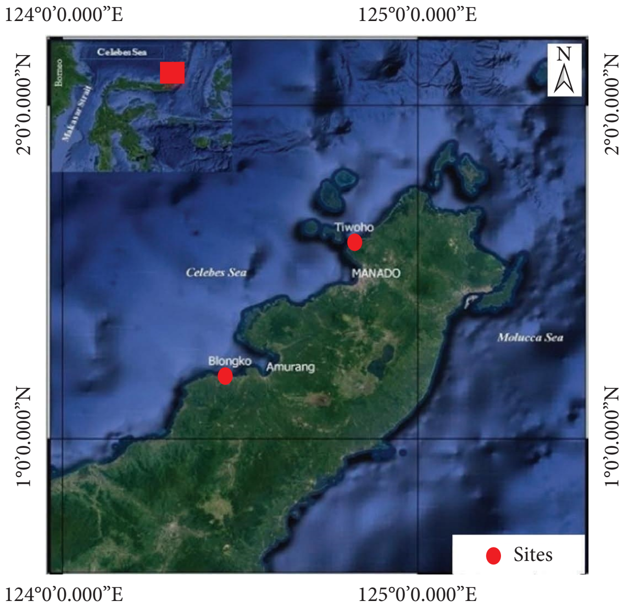


Figure 1: Map showing North Sulawesi with the two study locations of sampling indicated by cycles of red colour and then the position of north Sulawesi on Celebes Island indicated by red rectangle colour.

Unlike in Tiwoho, Blongko has a short intertidal zone, 600 meters wide, measured from the edge of the mangrove to the edge of the dry at low tide. The area is covered by hard substrata with boulders, coral rubbles, and dead hard corals. Mussel beds are found in the centre of the intertidal zone with mangroves between the mussel beds and the mainland. At low tide, seagrass, *Enhalus* sp., and *Thalasia* sp. and algae, such as *Halimeda* sp., *Hypnea* sp., and *Padina* sp., as well as echinoid and ophiuroids were observed within and between the mussel beds.

2.2. Field Experiments. Four different substrata were chosen. Two were the natural palm fibres from the sugar palm tree, *Arenga pinnata,* and coconut fibres from the common coconut tree, *Cocos* nucifera [26]. Another one was a conspecific substratum of the adult mussel shell with byssus threads, and the last one was the polypropylene fibres. Each substratum was replicated four times. Except for the mussel shell with byssus threads, all three fibres were woven together by hand to form a rope.

All types of substrata were arranged in a random pattern on PVC plates (20 cm × 20 cm). Each plate was divided into 16 squares of 1.25 × 1.25 cm. A 1.2 cm diameter hole was drilled in the centre of each of the 16 squares. Bundles of the coconut fibres, palm fibres, and polypropylene fibres were fit into each hole by using small pointed tweezers until they were about level with the plate. The shell with byssus threads was obtained from live adults carefully removed from their substratum. The live mussel shell with byssus threads was cleaned, and a small part of the closed shell from the hinge to the umbo was glued into a drilled hole in a PVC plate.

At each site, two patch sizes, each in three replicates, were arbitrarily chosen. The patch sizes were measured as the largest distance from edge to edge and constituted a large patch (±2 m) and a small patch (±0.3 m). A PVC plate was placed at the middle and the edge, each of the large patches and the middle of each of the small patches. To avoid PVC floating, each PVC plate was tied down to the cement brick. A total of 18 PVC plates fitted with substrata were deployed in two mussel beds, 9 PVC plates in Tiwoho and another 9 PVC plates in Blongko (Figure 1). The PVC plates were deployed for 6 weeks from May to June 2022. After six weeks, all plates were collected, labelled and in plastic bags transported to the laboratory, and frozen before analysis. Each PVC plate was transferred to a plastic tray for 1 hour before analysis under a compound microscope.

2.3. Data Analysis. Data on the number of settlers as a function of the site, position in the patch, and substratum were analyzed using a three-way ANOVA. A square root transformation was used to obtain the homogeneity after using the *F*-max test [27]. Post hoc comparisons were then performed using the Tukey test when the ANOVA test shows significant treatment effects [27]. All statistical analyses were applied using the computer program MYSTAT.

3. Results

3.1. Observations. Settlement of the box mussel, *S. bilocularis*, occurred on palm, coconut, and polypropylene ropes. The size of new settlers attached to these substrata was <1 mm (Figures 2(a)–2(c)). The settlers on these three substrata had thick, smooth, transparent shells with white longitudinal stripes from the umbo to the edge. In comparison, the settlers attached to conspecific mussel shells with byssus threads ranged in size from 1 to 3 mm (>1 mm). These settlers had a white-green colour at the umbo and dark green colour shells (Figure 2(d)).

3.2. Effect of Site. The mean number of settlers of box mussels is significantly different between the two sites, Tiwoho and Blongko (3-way ANOVA, df = 1, $F = 10.721$, $P < 0.05$, Table 1). The graphic depiction of the settlement between Tiwoho and Blongko is shown in Figure 3. The mean number of new settlers in Blongko (b) was significantly greater than in Tiwoho (a) (Tukey test: $P < 0.05$, Figure 4).

3.3. Effect of Position in the Patch. A significant effect of position in the patch on the settlement was found (3-Way ANOVA, df = 2, $F = 10.154$, $P < 0.001$, Table 1). The post hoc test reveals that in Tiwoho, the mean number of new settlers in the small patch was significantly greater than in the edge and middle of large patches (Tukey test: $P < 0.05$, Figure 4). However, no significant mean number of new settlers was recorded between the middle and the edge of the large patch (Tukey test: $P < 0.05$, Figure 4). In Blongko, the mean number of new settlers in the small patch was significantly greater than in the edge of the large patch (Tukey test: $P < 0.05$, Figure 4), but there were no differences in the mean number of new settlers between the edge and the middle of the large patch (Tukey test: $P < 0.05$).

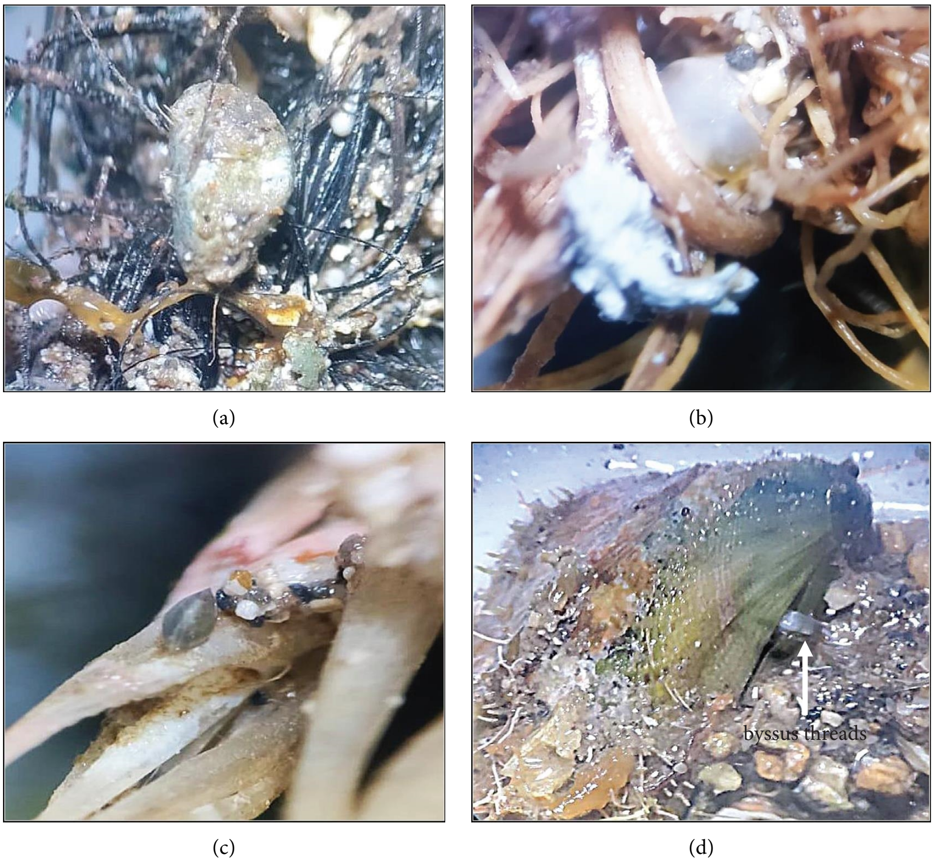
3.4. Effect of Substratum. The number of new settlers varied among substrata. A significant effect of the substratum was evident (three-way ANOVA, df = 3, $F = 10.704$, $P < 0.001$, Table 1). A significant interaction between the position in the patch and substratum (Table 1) indicates that the effects are not consistent between substrates. In Tiwoho, a significant difference in new settlers between coconut fibre and mussel shells with byssus threads and between polypropylene fibre and mussel shells with byssus threads occurred (Tukey test: $P < 0.05$, Figure 5). However, no significant difference in new settlers between palm, coconut, and polypropylene fibre occur ((Tukey test: $P < 0.05$, Figure 5). In Blongko, the mean number of new settlers in polypropylene fibre was significantly greater than in mussel shells with byssus threads (Tukey test: $P < 0.05$, Figure 5). However, no significant differences in the mean number of new settlers was recorded between palm and coconut fiber, as well as mussel shells with byssus threads (Tukey test: $P < 0.05$, Figure 5).

3.5. Interactions. The number of new settlers varied considerably between site, position in the patch, and substratum. The results of the interactions of the statistical test using a 3-factor ANOVA are shown in Table 1. It shows the nature of the interaction, where a significant interaction between the position and substratum occurred (df 6, $F = 3.242$, $P < 0.05$). The patterns of interaction are mainly caused by the number of new settlers in coconut, polypropylene fibre, and shells with byssus threads showing interference. The interaction plots are shown in Figure 6.

4. Discussion

4.1. Sizes and Colour. This study showed that the newly settled box mussels varied in size and colour. The settlers of three substrata had thick, smooth, transparent shells with white longitudinal stripes from the umbo to the edge. Settlers attached to conspecific mussel shells with byssus threads ranged in size from 1 to 3 mm (>1 mm). These settlers had a white-green colour at the umbo and dark green colour shells (Figure 2 D).

A possible explanation for the result of the differences in size and colour of new settlers could simply be caused by different times of settlement. In the laboratory study, the growth rate of new settlers varied among species such as 21 μm/day for *Perna canaliculus* [28], 25 μm/day for *M. edulis* [29], and 32 μm/day for *M. galloprovincialis* [4]. Many mussel larvae settle about 300 μm in length, and at the same time, metamorphosis occurs, such as *Mytilus edulis*



(a) (b)

(c) (d)

Figure 2: New settlers of *S. bilocularis* on (a) palm fibres, (b) coconut fibres, (c) polypropylene fibres, and (d) mussel shell with byssus threads.

Table 1: Three-factorial ANOVA, settlement of the box mussel, *S. bilocularis*, with site, positions in the patch, and substratum as the main effects.

Sources	SS	df	Mean squares	F-ratio	P value
Sites	3.457	1	3.457	10.721	0.001*
Positions in patches	6.548	2	3.274	10.154	<0.001**
Substratum	10.354	3	3.451	10.704	<0.001**
Sites ∗ positions in patches	0.133	2	0.067	0.207	0.813$^{\text{n.s}}$
Sites ∗ substratum	0.421	3	0.140	0.435	0.758$^{\text{n.s}}$
Positions ∗ substratum	6.663	6	1.045	3.242	0.004*
Sites ∗ positions ∗ substratum	0.663	6	0.110	0.342	0.914$^{\text{n.s}}$
Error	85.129	264	0.322		

**: $P < 0.001$; $^{*}P < 0.05$; n.s.: not significant.

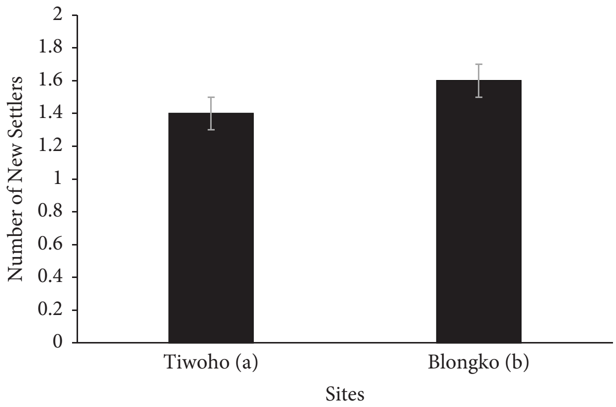


Figure 3: The mean settlement of *S. bilocularis* in mussel beds in Tiwoho (a) and Blongko (b). Bars: 95% confidence interval.

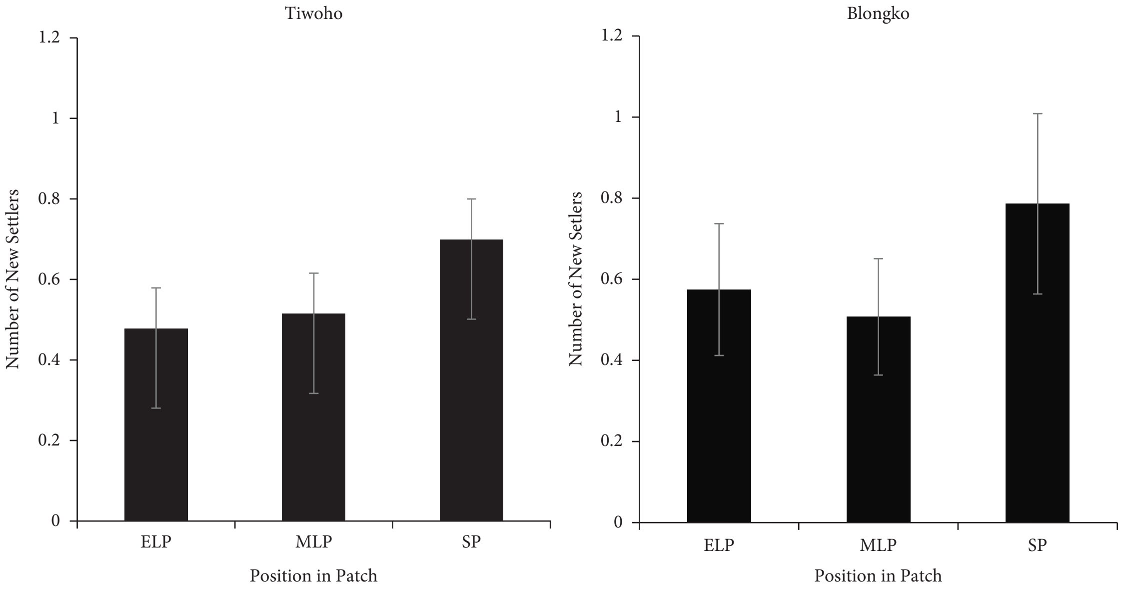


Figure 4: The mean number of new settlers of box tropical mussels, *S. bilocularis,* in the position of the patch in both Tiwoho and Blongko. MLP = middle large patch, ELP = edge large patch, and SP = small patch. Bars indicate 95% confidence interval.

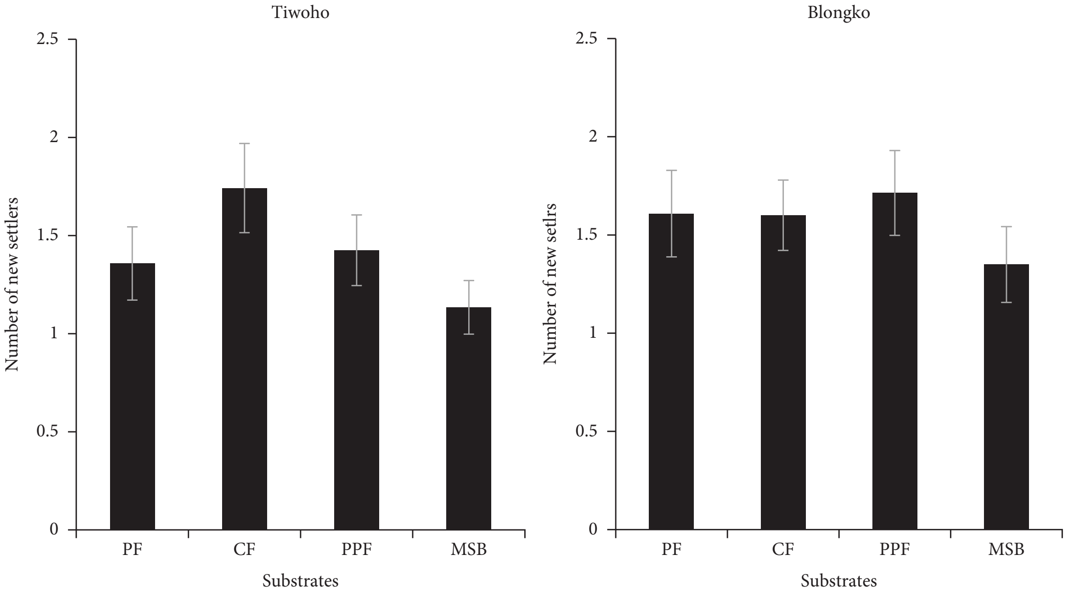


Figure 5: The mean number of new settlers in the mussel's bed of Tiwoho and Blongko. PF = palm fibre; CF = coconut fibres; PPF = polypropylene fibres; and MSB = mussels shells with byssus threads. Bars = 95% confidence interval.

[30], *Perna canaliculus* [28], *M. galloprovincialis* [4, 8], as well as *Brachidontes rostratus* and *Trichomya hirsutus* [8]. At these growth rates of 21–32 μm/day, such as any primary mussel settlement with size 300 μm in length attached on substrata provided, could reach 594–748 um after 14 days (2 weeks) and then 882–1175 um in length after 35 days (5 weeks).

In this study, the early settlers of box mussels were after 5 weeks >1 mm in length with blue and dark green colour, while the latest settlers, after 2 weeks, had <1 mm in length with transparent colour. The changes in size and colour are a part of settlement and metamorphosis characteristics similar to adult mussels [4, 9, 31, 32].

A possible explanation for the result of the differences in size and colour of new settlers could be what is called resettlement. Understanding factors that trigger resettlement might not be clear, where it could occur due to various factors such as chemical cues [33, 34], substrata stability, predation, and food competition (South et al. [35]). Here, first settlement larvae might grow and then have the capability to detach the byssus thread from the original substrates. Then, the mussel moved and finally

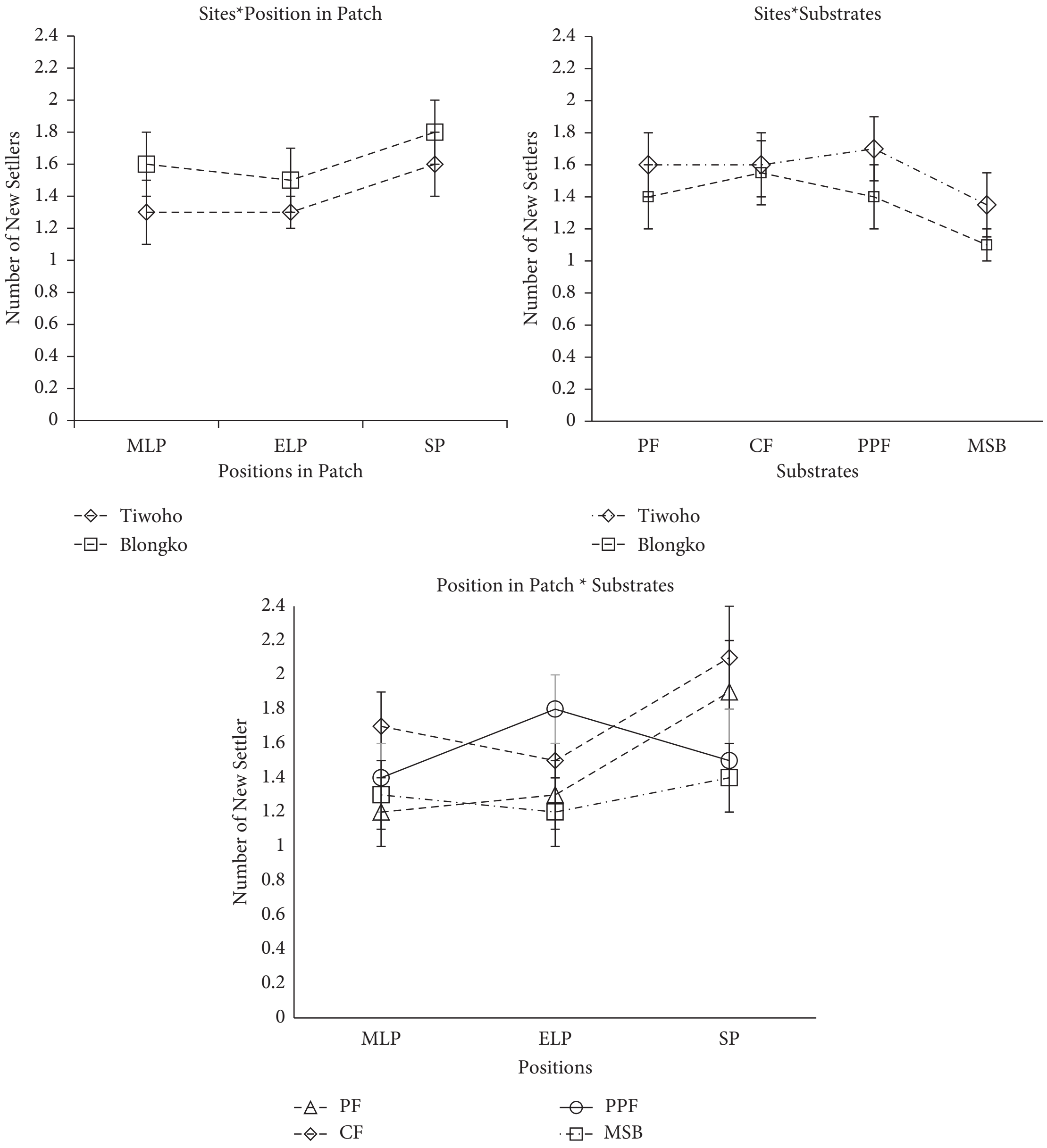


Figure 6: Interaction plots of a three-factorial ANOVA of the number of new settlers of The tropical box mussels of *S. bilocularis* at two sites (Tiwoho and Blongko), positions within patches (middle and edge of the large patch and small patch), and substratum (fibre of palm, coconut, polypropylene, and mussel shells with byssus threads) as main effects. MLP = middle large patch; ELP = edge large patch; SP = small patch; PF = palm fibres, CF = coconut fibres, and PPF = polypropylene fibres; MSB = mussel shell with byssus threads. Bars: 95% confidence interval.

resettled and attached to the mussel shell with byssus threads provided. New settlers might move or crawl using their foot along a byssus thread and then produce new byssus to attach to adult mussels' shells. A drifting sticky mucus thread might also be produced by box mussel larvae as reported by Protopopescu and Beal [36]. Here, it might facilitate mussels to move and attach to the mussel shell provided in this study. Lastly, a changing position within a patch might occur. In this study, a box mussel <3 mm might move from a mussel bed to neighbour substrates and then attach to mussel shells with byssus threads within a patch through active dispersal by crawling.

The changing position of movement (resettlement) was also reported such as by Hunt and Scheibling [3]; Protopopescu and Beal [36]; South et al. [35]. In the study of *Perna canaliculus*, South et al. [35] reported that new settlers at size >1 mm were highly mobile and migrated among substrata. Resettlement could occur several times where the mussels varied in length from 0.5 to 2 mm [29], 2 mm [37], more than 3 mm [38], 6 mm [35], and 7 mm [28, 39].

4.2. *Effect of Sites.*

The differences in the number of new settlers between the two sites in this study might be due to exposure time as suggested by Hunt and Scheibling [3]. It was observed in this study that Blongko has a shorter intertidal area than Tiwoho. The intertidal of Blongko might be covered by seawater faster than Tiwoho when high seawater occurred. As a result, the mussel bed of Tiwoho might open to solar energy more times than in Blongko. The seawater temperature here in Tiwoho could be drastically increased during low tide compared to the seawater temperature in Blongko. Generally, benthic organisms can experience a variety of abiotic stressors, such as thermal stress that are known to affect organisms' performance and survival (e.g., [40]). In the study of intertidal mussels, *Mytilus galloprovincialis*, Collins et al. [41] reported that mussels had thermal stress when exposed to air. In this study, the new settlers attached to substrata in Tiwoho might have more stress than those in Blongko, which might affect new settler mortality. As a result, a lower number of new settlers in Tiwoho (a) than in Blongko (b) were observed (Figure 2).

New settlers in both sites of Tiwoho (a) and Blongko (b) might depend on the larval mussel supply in the water column as reported by Navarrete et al. [42]; South [43]; Wilcox et al. [44]. Tropical mussels may release eggs and sperm all the year [8], which supply larvae in the water column all the year. However, increased development along the coast including Tiwoho (a) and surrounding areas may bring sediment particles into the water column. In this study, sticky soft sediment was observed on the PVC plates in Tiwoho. The sticky sediment particles on the PVC plates might indicate that coagulation particles were formed in the water column before falling down and stuck on PCV plates. Particle sediments might create problems for mussels' larvae in the water column when sediment particles were abundantly in the water column. Mussels larvae might die before settlement took place. Mortality of larvae in the water column might affect the larval supply, as more reason, where a lower number of new settlers in Tiwoho (a) than in Blongko (b) occurred in this study.

4.3. Effect of Position in the Patch.

4.3. Effect of Position in the Patch. This study showed that the settlement varied with positions in the patch, with a higher number of settlers on the small patches rather than on the middle and the edge of the large patch (Figure 5). Cannibalism might explain a lower number of settlements in any position in the large patch than in the small ones. Here, the larvae might be exposed to filter-feeding by adult box mussels. At the end of the larvae stage, the larvae go close to the bottom where, together with particles above the mussel bed, they might be filtered by the adult box mussels (e.g. [21]. Several studies have shown a lower number of settlers with an increasing density of adult suspension feeders [20, 22, 35, 45]. It has been shown that larvae die when entering the filter system of mussels and then pass through the ingesting system [20, 22]. As a result, a lower number of new settlers were found in the middle and at the edge of a large patch than in a small patch as observed in this study.

Instead of cannibalism, predators might also affect the settlement larvae in the position of the patch. In this study, both echinoid and ophiuroid species were dominantly observed within large patches rather than in small patches. Both associated faunas have a wide range of food resources. For example, echinoids feed on various foods, such as algae, sponges, corals, and molluscs [46, 47]. Similarly, ophiuroids feed on molluscs, crustaceans, polychaetes, sipunculids, ascidians, and other echinoderms [48]. New settlers within the large patch might be food sources for the associated fauna and therefore is a consistently lower number of new settlers within the large patch than in the small patch at both stations.

Mussel beds can be sediment traps [49]. We observed thick sedimentation on plates with substrata placed at the edge and middle of large patches than at the small patches. Mussels mortality caused by sedimentation might occur as shown by Dame et al. [24]; Lummer et al. [50]; Emilio et al. [23]. In this study, the filter system of new settlers along the edge and middle of a large patch might be blocked and affect new settler mortality when sediment particles were affecting the capacity of filtering.

4.4. Substratum Preferences. The box mussel larvae, *S. bilocularis,* show a higher settlement on the substrata of coconut, palm, and polypropylene fibre rather than the conspecific box shell. Substratum structure complexity could be one explanation for the preferences. Studies have shown that complex substratum structures provide more surface area than noncomplex substrata (e.g. [4, 36]. Forming united fibres into rope could create more space area than a single fibre. In this study, new settlers were not only attached to the surface of the palm, coconut, and polypropylene fibres but also among fibres within the rope of each substratum. Here, the settlement pattern appeared attractive with more surface area and subsequent protection for new settlers, as reported for *M. galloprovincialis* [4]; *M. edulis* [36]; *Perna perna* and *M. galloprovincialis* [5]. Over time, more byssus threads might be produced, and as a result, a secure and strong attachment to substrates occurred [7, 11–13].

Many studies have shown that artificial filamentous substrata are effective for the settlement of mussels (e.g. [5, 36]. In this study, all fibres formed into a rope have a similar filamentous structure. It might be one more factor that explains why more new settlers attached to palm, coconut, and polypropylene fibres rather than on mussel shells with byssus threads. Aside from this, palm, coconut, as well as polypropylene fibres contain organic material that becomes one of the favourite components that stimulate invertebrates' larvae to settle and metamorphosis (e.g., [9, 38]). The chemical composition of substrata may play an important role in the mussel's attachment, as reported by Brenner and Buck [33]. Polypropylene fibres can absorb water which might be required for the attachment of byssus threads [34]. The chemical composition of the polypropylene fibres might explain the relatively high number of new settlers attached as was observed in this study.

5. Conclusion

This study has shown that box mussel settlement was affected by site, position in the patch, and substrata. In our study, a large number of new settlers attached consistently on substrata in small patches rather than in large patches at both sites. Our study also showed for the first time that the tropical box mussel, *Septifer bilocularis*, in the field can choose and attach to fibres of coconut, palm, and polypropylene in the varied positions of patches. A consistently larger number of new settlers attached to coconut and polypropylene fibres rather than on mussel shells with byssus threads were found. We suggest that resettlement of box mussels on adult byssus threads after first being attached to substrata of coconut, palm, and polypropylene in the mussel beds is likely to have occurred.

Data Availability

The (Mussel Settlement Data_Medy_31032023) data used to support the findings of this study have been deposited in the (shorturl.at/nGSV2).

Conflicts of Interest

The authors declare that they have no conflicts of interest.

Acknowledgments

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