

Article

Larval Dispersal Modelling of the Blue Swimming Crab *Portunus pelagicus* (Linnaeus, 1758) from the Crab Banks along the Coast of Trang Province, Southern Thailand

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Abstract: In Thailand, the populations of a commercially important crab *Portunus pelagicus* (Linnaeus, 1758) have been decreasing due to overfishing, raising concerns about the conservation efforts of this crab species. The Crab Bank Project has recently been established to restore crab populations by releasing crab larvae from each crab bank station. However, the fate of crab larvae after the release is poorly understood. Here, we assessed the dispersal and settlement patterns of the larvae *P. pelagicus* released from crab banks along the coast of Trang Province, Southern Thailand. The Lagrangian particle tracking model was employed to simulate the larval dispersal and settlement patterns after release from the crab banks during the inter-monsoon, southwest monsoon, and northeast monsoon. Our simulation revealed that virtual larvae were predominantly retained within inshore areas after the release for 14 days, regulated by tidal-driven currents, wind-induced currents, and local coastal topography. Monsoon periods affected the larval dispersal, with some larvae being transported into estuaries due to the SW monsoonal effects. After the 14-day release period, our modelled simulations suggested that the crab larvae arrived at numerous seagrass meadows along the coast, indicating potential settlement and growth. This result highlights the connectivity of sources and sinks for crab larvae after release from crab banks. Moreover, significant implications for conservation efforts and the fishery management of *P. pelagicus* were also discussed based on our modelled simulations.

Keywords: Andaman Sea; particle tracking model; crab larvae; recruitment; conservation



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1. Introduction

The blue swimming crab *Portunus pelagicus* (Linnaeus, 1758) is one of the portunid crab species found in coastal areas throughout the Indo-West-Pacific regions [1]. These crabs predominantly inhabit intertidal to shallow-coastal areas, including seagrass meadows, near reefs, shallow bays, and outer parts of estuaries and mangroves [1,2]. In Southern Thailand, a previous study reported that berried females of *P. pelagicus* are mostly found during two periods, March–April and August–September [2]. When the eggs develop into an early-releasing stage, berried females migrate to offshore-coastal areas to release their eggs into the water column [3,4]. After the eggs are released, eggs immediately hatch into the first zoeal stage and larvae moult through four zoeal stages until metamorphosing into one megalopa and the first crab star, respectively [5]. The young crabs (approximately 2.5–3.0 mm in carapace width) and juveniles prefer shallow-water areas, such as seagrass beds, while the larger crabs are likely to migrate to offshore areas [2,6].

P. pelagicus is commonly considered a commercial crab species in many Asian countries, including Thailand, due to its high demand from seafood markets and industries [1,7,8]. In Thailand, the blue swimming crab fishery is a major part of small-scale fisheries in many areas along the coasts of the Andaman Sea and the Gulf of Thailand. Thailand is one of

the leading marine producers in the world, exporting approximately 42.2 million tons of *P. pelagicus* per year with a value of USD 35 million [1,7]. However, the total landing and export of *P. pelagicus* in Thailand have been decreasing over the previous decades due to declining crab populations caused by overexploitation [1,9]. Illegal fishery gear and collecting ovigerous crabs, as well as unregulated crab fisheries, are also proposed as the key factors, leading to a rapid decrease in the crab populations [10]. The decrease in crab populations not only negatively affects commercial fisheries but also poses a significant threat to their reproductive capacity and population structure.

To deal with the decrease in crab populations, the National Research Council of Thailand, in collaboration with various government agencies and educational institutions under the Crab Bank Project, has embarked on a mission to protect and recover *P. pelagicus* to reach sustainable exploitation and fishery management. For this active restoration activity, berried female crabs are provided by local fishermen and held in the closed cultivation system until the crabs release their eggs. After eggs hatch into the first zoeal stage, the crab larvae are collected and released into shallow-coastal areas during a spring tide period. This activity is expected to be powerful method for enhancing the restoration of *P. pelagicus* populations along the coasts of Thailand. However, there are no studies and evidence on larval biology, habitat use, survival rates, and recruitments of the crab larvae after release from the crab banks. Hence, an understanding of crab larval dispersal and its patterns is highly needed to improve further conservation strategies and restoration of *P. pelagicus*.

Investigating the larval dispersal and settlements is crucial to understanding larval ecology, recruitments, and ecological connectivity across habitats, especially in open seas and coastal areas [11]. However, one of the primary challenges for studying marine larval dispersal and population connectivity lies in interpreting larval biology in the context of physical oceanographic processes. As meroplankton during early life stages, the dispersal and transport of larvae are influenced by various hydrodynamic factors, such as coastal topography, stratified water columns, tidal-induced currents, surface waves, wind-induced currents, and variability in the speeds and directions of currents due to monsoons [12]. For *P. pelagicus*, the dispersion of crab larvae has been investigated through field observation. The results have shown that the crab zoeal and megalopa individuals prominently colonised and completed their development in mid-shore and offshore areas [13,14]. The larval dispersal of *P. pelagicus* is significantly regulated by some hydrological parameters, particularly water density and currents. Wind-induced currents are primarily considered the key drivers, determining the abundance and dispersal of the crab larvae *P. pelagicus* [15]. Additionally, monsoon-driven currents also participate in regulating the dispersal patterns of the crab larvae [14]. However, the effects of monsoons and hydrodynamic factors on the crab larvae *P. pelagicus* remain insufficient studies.

A numerical model, including a particle tracking model, is an effective tool to predict patterns of larval transport and the dispersal and settlements of marine invertebrates and fishes [16,17]. In general, there are two main types of biophysical modelling, including active and passive larval modelling. Active modelling includes survival rates and biological traits of larvae to enhance the ecological relevance of the simulation while passive larval modelling neglects those biological parameters. The results based on simulating models are very useful for assessing the population dynamics and connectivity of marine animals, whose early-life stages are drifting organisms [18,19]. Based on laboratory and field observations, marine larvae as meroplankton can move vertically and horizontally in the water column. Nevertheless, approximately 56% of previous studies [11] still used passive larval modelling, assuming that the larvae movement was passive over their development. This may be due to difficulty in observing and determining larval motion and movement in the fields and the laboratory observation might not reflect the realistic behaviours of larvae in relation to natural conditions. Hence, this can demonstrate that larval dispersal simulation using numerical models is an effective tool; this method could be applied for investigating the larval dispersal and settlements of *P. pelagicus*.

In Trang Province, located on the coast of the Andaman Sea, Southern Thailand, there are more than 23 crab banks along the coastline associated with many seagrass meadows. At least 10 large seagrass meadows have been reported along the Trang coastline with the percent coverages ranging from 0.136 to 20.89 km³ [20]. There are seven genera and twelve species of seagrasses found in the Andaman Sea, including Trang coastal areas [21]. Most seagrass beds experience natural variations influenced by environmental conditions while some seagrass areas face threats from human activities, such as fishery activities and coastal constructions [20]. In terms of ecosystem services, seagrasses play various ecological roles in coastal ecosystems, such as trapping sediments, reducing wave energy, regulating nutrient cycling, and providing nursery grounds and habitats for various marine invertebrates and fishes [22–24]. Importantly, seagrass beds serve as key nursery areas and habitats for many swimming crabs, particularly *P. pelagicus*. Upon completing the development of their planktonic larvae, megalopae *P. pelagicus* are transported back to inshore areas and settle in shallow-water areas, including seagrass beds, and grow up into juveniles and larger crabs [6,15]. As described above, it highlights the potential role of seagrass meadows as settlement areas and nursery grounds for larvae and juveniles of *P. pelagicus* released from the crab banks along the Trang coastline.

To enhance our comprehension of larval transport once released from the crab banks along the Trang coastline, this study aimed to investigate the larval dispersal of *P. pelagicus* using a passive larval tracking approach with the Delft3D-PART model. The larval arrival over seagrass areas after the release and the effects of monsoon periods on the larval dispersal were also characterised. The data derived from this study will provide valuable information for decision making and the development of effective strategies working toward conservation and sustainable fishery management of blue swimming crabs in the future.

2. Materials and Methods

2.1. Study Area

This study was conducted in the Trang coastal areas, situated along the Andaman Sea in Southern Thailand. The region is characterised by extensive seagrass beds, mangroves, and coral reefs, providing crucial ecological services in coastal ecosystems, such as serving as nursery grounds, offering shelter for marine organisms, and serving as artisanal fishery grounds for local communities. The coastal geomorphology is quite complex, including various islands, semi-enclosed bays at the northern and southern coast, large river mouths, and tributaries nearby the coastline. The water depth ranges from 2 to 16 m, relying on semidiurnal tidal rhythms. The tidal range during the spring tides is approximately 3 m and the water depth is 1 m during the neap tides. Due to the tidal rhythms, water currents are directed toward the coastline during the high tide period while the currents move toward the southern part of the coastline. The water circulation is regulated by monsoon wind patterns, climatic conditions, riverine runoffs from the Trang river mouth, and brackish water tributaries [25]. According to a previous study, the water circulation along the Trang coastline dominantly depends on tidal currents. The study area is influenced by the northeast and southwest monsoon wind patterns. The southwest monsoon occurs from May to October, resulting in heavy precipitation and high wave action. The mean current velocity is directed from the southwest to the northern part of the coastline and, clockwise, moves toward the southern part. This current is then mixed with the currents from the Malacca Strait, resulting in the net current being directed toward the southeast part. The effects of the northeast monsoon can be detected during the end of the October to February period, resulting in less precipitation and lower wave action in comparison to the southwest monsoon period. The mean current velocity at the surface is directed from the northern to the southern part of the coastline with a clockwise pattern. The currents encounter the Malacca Strait's current, resulting in the net current moving toward the southeast. Overall, this indicates that the circulation in the Trang coastline is mainly

regulated by the currents from the Malacca Strait, accompanied by the local oceanographic conditions, such as monsoon wind patterns and tidal currents [26].

The Trang coastline is renowned as one of the prominent seagrass ecosystems in Southern Thailand, featuring more than 10 large seagrass meadows, as illustrated in Figure 1. These include Pak Klong Kalasae, Ban Laem Sai, Ban Pak Klong-Koh Phi, Ao Boon Kong, Ao Kham, Koh Mook, Pak Klong Chao Mai, Koh Nok, North Koh Libong, and Ao Thung Chin. The seagrass bed in Ao Thung Chin exhibits the highest coverage (20.89 km^3), followed by Koh Mook (15.83 km^3) and North Koh Libong (5.27 km^3) in descending order [20]. Across all seagrass meadows along the Trang coastline, seven genera and twelve species of seagrasses can be found in all seagrass meadows in the Trang coastline, within which the dominant species are *Halophila ovalis*, *Enhalus acoroides*, and *Cymodocea serrulate* [20,21].

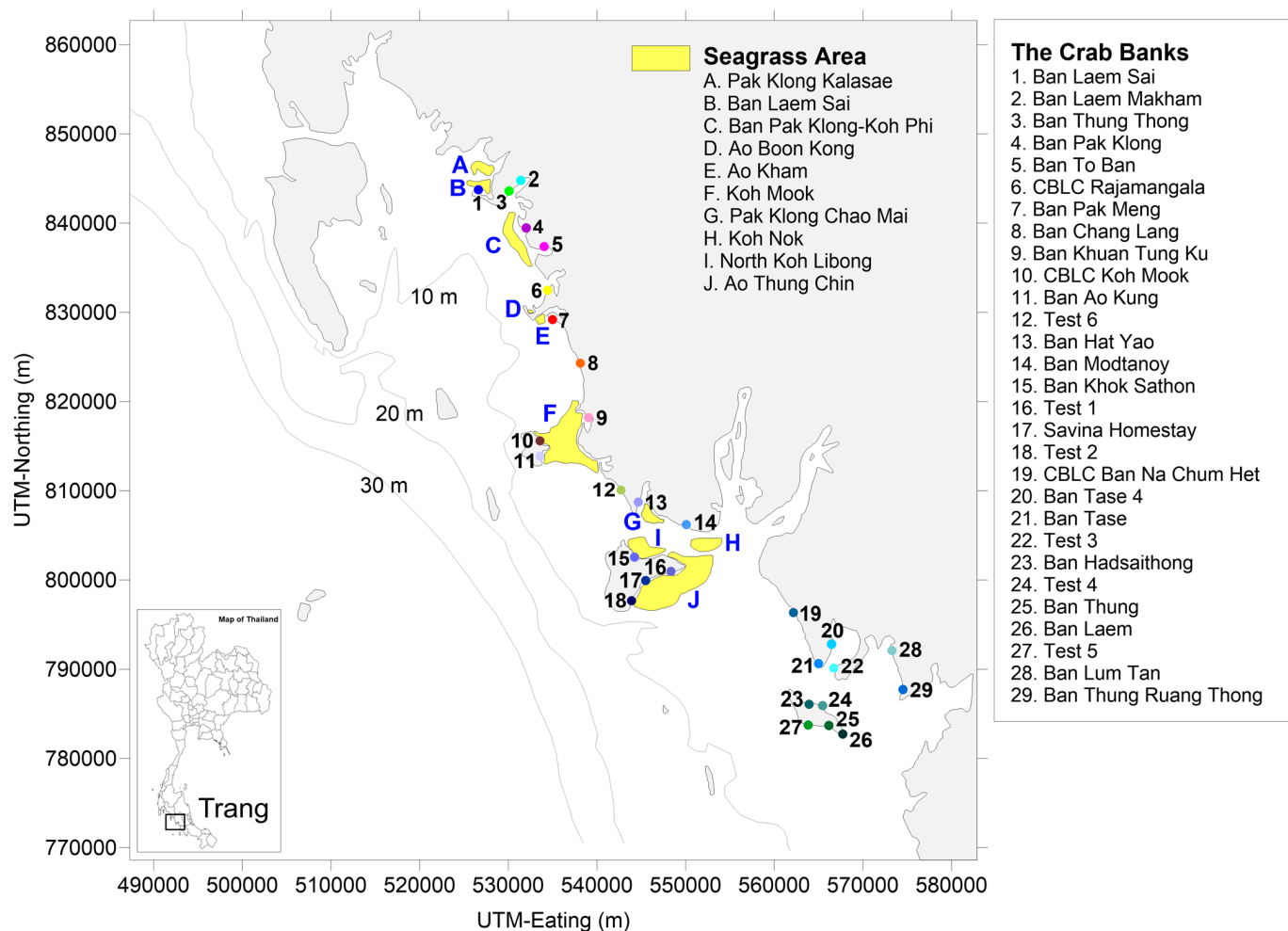


Figure 1. A map demonstrates the locations of the blue swimming crab banks and seagrass meadows along the coastline of Trang Province, Southern Thailand. The coloured dots with numbers represent the locations of blue swimming crab banks along the coast of Trang Province. The yellow areas indicate seagrass beds.

There are 23 crab banks situated along the coastal areas, accompanied by 6 additional crab bank stations, termed Tests 1–6, which have been planned to be established in the near future (Figure 1). As part of the routine activities associated with the crab banks, berried females of *P. pelagicus* exhibiting eggs with yellow, brown, and grey colours were collected by local fishermen. These berried crabs were kept in a hatchery until they released their eggs into the water column. Throughout the egg incubation period, the crabs were individually held in a plastic container filled with 15–20 L of

seawater at salinities of 27–35 PSU. The seawater temperature was in the range of 26–32 °C. Dissolved oxygen and pH levels of seawater were 6.0–7.2 mg/L and 7.5–8.5, respectively. These environmental conditions are conducive for berried crabs to release their eggs. Upon observation of berried females releasing eggs, the eggs immediately hatch into the 1st zoeal larvae. Subsequently, the larvae were collected and released into shallow-coastal waters during the spring tide period.

2.2. Three-Dimensional Modelling of *P. pelagicus* Larval Dispersal

2.2.1. Particle Tracking Modelling Experience

In this study, the Delft3D-PART model [27] was employed to simulate the passive dispersal of *P. pelagicus* crab larvae. This simulation was based on two primary assumptions: firstly, a 100% survival rate for crab larvae during their dispersal phase is assumed and, secondly, both the vertical and horizontal swimming of the larvae were neglected. This passive larval modelling was applied to estimate larval dispersal and settlement patterns of *P. pelagicus* as these crab larvae lack the ability to swim against horizontal currents. Along the Andaman Sea coastline, horizontal current speeds were generally greater than 1 cm/s while the zoeae of *P. pelagicus* exhibited a vertical movement with velocities ranging from 0.44 to 0.93 cm/s [28]. This suggests that the transport of crab larvae is passive and regulated by physical oceanographic parameters.

The Delft3D-PART model is a particle tracking model that seamlessly integrates advection and diffusion processes. Notably, the advective component is a crucial aspect, resolved using an analytical integration procedure. This procedure involves integrating a linearly interpolated hydrodynamic velocity field, ensuring the mass conservation of water. Additionally, it also effectively manages closed (land) boundaries where velocities asymptotically vanish; particles crossing open (water) boundaries are excluded from the calculation.

The analytical integration procedure is given by Equation (1):

$$x(t + \Delta t) = x(t) + \int_0^{\Delta t} \left(\frac{dx}{dt} \right) dt \quad (1)$$

where x is the distance depending on streamline distance function $s(t)$, t is the time, and $\frac{dx}{dt}$ is the velocity. The equation calculates the position of a particle at time $(t + \Delta t)$ based on its position at time t and its velocity over the time interval Δt .

The velocity $\frac{dx}{dt}$ is given by Equation (2):

$$\frac{dx}{dt} = \frac{ds}{dt} (\alpha_x x(s) + \beta_x) \quad (2)$$

where α_x and β_x are constants that depend on the flow field and $\frac{ds}{dt}$ is the rate of change of the streamline distance.

The constants α_x and β_x are defined in Equations (3) and (4):

$$\alpha_x = C(\sigma) \left(\frac{Q_+ - Q_-}{V} \right) \quad (3)$$

$$\beta_x = C(\sigma) \left(\frac{Q_{+/-}}{V} \right) \quad (4)$$

where $Q_{+/-}$ is the flow through the upwind or downwind surface of the grid cell, V is the volume of the grid cell, and $C(\sigma)$ is the distance between the velocity points in the hydrodynamic grid. The term $\frac{Q_{+/-}}{V}$ represents the inverse of the travel time of the grid cell with this $Q_{+/-}$.

For the implemented numerical integration, the path acceleration is neglected and the rate of change of the streamline distance is assumed to be constant:

$$\frac{ds}{dt} = 1 \quad (5)$$

The flow field employed in our simulation is directly linked to the hydrodynamic flow field (Delft3D-FLOW) and satisfies certain conservation conditions, as described in Equation (6):

$$\frac{\partial}{\partial x}(\alpha_x x + \beta_x) = 0 \quad (6)$$

The dispersion component of our simulation was resolved using a Euler-type numerical scheme. This scheme addressed both horizontal dispersion and vertical settling, with boundary conditions being purely reflective. Dispersion in both the horizontal and vertical directions was driven by a white noise process, characterised by Equation (7):

$$\Delta s = \sqrt{6D\Delta t} \quad (7)$$

where Δs is the maximum displacement, D is the dispersion coefficient, and Δt is the Lagrangian time step:

$$D = at^b \quad (8)$$

where a and b are the constant coefficients and, in this study, a and b are set to be 1 and 0.01, respectively.

To validate our particle tracking model, we released 10,000 particles from 29 crab banks during the low tide of spring tides when the water depth was approximately 1 m. Input parameters for the Delft3D-PART model, including water velocity, temperature, and salinity, were extracted from a simulated hydrodynamic model, termed Delft3D-FLOW [29]. The particle tracking model was simulated over a 14-day duration, considering the influence of tidal patterns, prevailing winds, and meteorological variability within the study area. The 14-day simulation period was chosen because the crabs exhibit planktonic behaviour within this time frame [5,15].

To elucidate the impacts of monsoon periods on the larval dispersal model, 3 different monsoon periods, including inter-monsoon (March–April), southwest monsoon (May–September), and northeast monsoon (November–February), were taken into consideration. Further details, including the simulated timeframe and wind regimes, are provided in Table 1 and Figure 2.

Table 1. Simulation periods for Delft3D-PART to investigate the larval dispersal.

Wind Regime	Release Time at Crab Bank	End of Simulation Period	Duration (Days)
Inter-monsoon	1 April 2022 12:00	14 April 2022 11:00	14
Southwest monsoon	1 June 2022 13:00	14 June 2022 12:00	14
Northeast monsoon	8 November 2022 15:00	21 November 2022 14:00	14

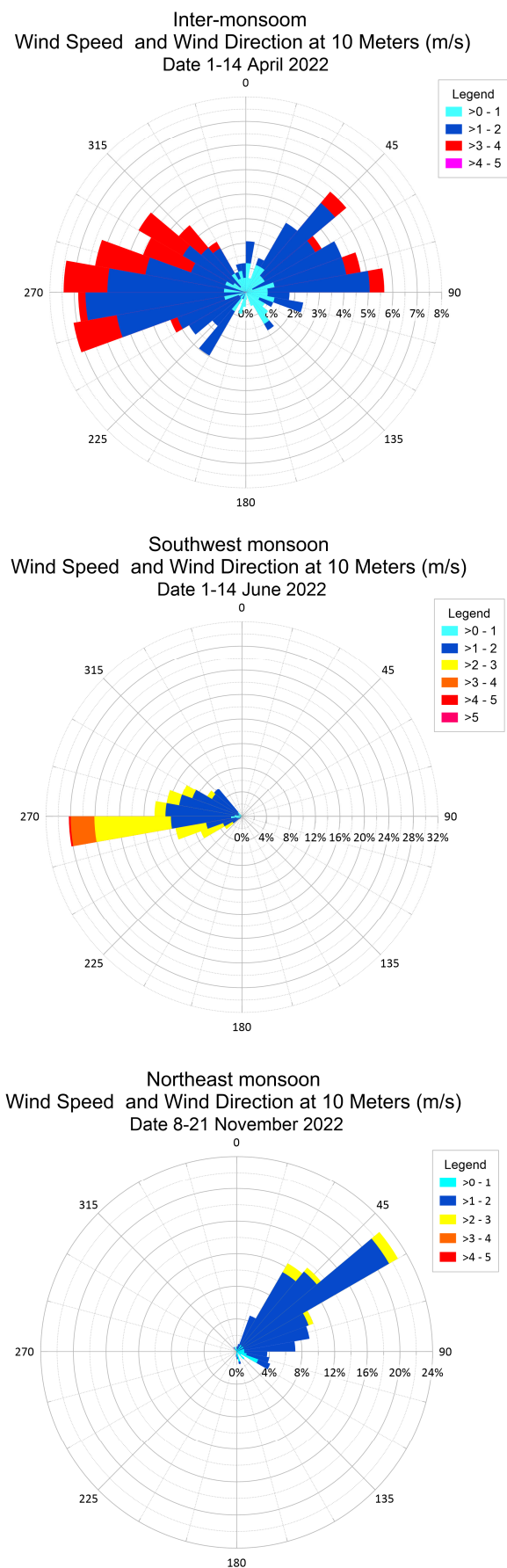


Figure 2. A schematic diagram shows the wind direction and speeds (m/s) that occur in the study area in each monsoon period.

2.2.2. Laboratory Experiments for Producing the Crab Larvae

All animal procedures in this study were approved by the Animal Care and Use Committee of the Faculty of Science, Chulalongkorn University (protocol number 2223009). A total of 20 berried females of *P. pelagicus* exhibiting eggs with a yellow colour were caught by local fishermen from coastal waters using gill nets. The crabs were then transported to the laboratory at the crab bank at Ban Hadsaithong (Figure 1; Station 23). During transportation, the crabs were placed in plastic containers containing seawater from the collecting site with aeration. In the laboratory, all berried crabs were held individually in a plastic cast that was submerged in a plastic experiment tank filled with seawater. The seawater temperature was in a range of 26–28 °C and a natural light–dark cycle was implemented. A salinity level was maintained in a range of 28–30 PSU. To prevent an accumulation of nitrogenous waste, 25% of the seawater in the tank was changed daily. The period of egg incubation, during which the eggs changed from a yellow to dark grey colour was approximately 4 days. The berried crabs were starved throughout the egg incubation period. The berried crabs carrying eggs with a dark grey colour released their eggs within a day. After the female crabs spawned their eggs, the eggs promptly hatched into the 1st zoeal larval stage. Subsequently, the zoeal larvae were collected for field experiments.

2.2.3. Validation of Models with Buoy Release and Larval Sampling

The Delft3D-PART model was used to simulate the zoeal dispersal patterns from 16 May 2022 at 2.00 p.m. to 17 May 2022 at 3.00 p.m. after their release from Sukorn Island (Station Test 4). To assess the accuracy of the larval dispersal simulation, a current-tracking buoy was deployed. The crab zoeae collected from the laboratory were carried to the released station (Test 4, as shown in Figure 1) located at Sukorn Island. Approximately 4 million crab zoeae collected from the laboratory (as described above) and a buoy were released from the released station during the spring tide period in the daytime (on 16 May 2022; releasing time at 2.00 p.m.). After the release of both larvae and the buoy, the trajectory of the buoy was monitored using a GPS tracking device attached to the buoy (GPS-ULTRA) to validate the trajectories simulated by our modelled simulations.

Throughout the buoy tracking, a zooplankton net (with a mesh size of 103 microns and a diameter of 30 cm) equipped with a flow meter was employed to collect crab zoeae in the water column. The sampling was conducted every hour at both a surface level (0.5 m from the water surface) and a bottom level (2 m from the water surface) at each designated point based on the buoy's position. The boat's velocity during sampling was approximately 0.33 m/s. All zoeae samples were preserved in 4% neutral formalin for subsequent species identification in the laboratory. The zoeae of *P. pelagicus* were observed and identified under a light-compound microscope, following the key identification of [30]. The abundance of crab zoeae at each sampling point and each water depth was calculated (individual per m³).

2.3. Three-Dimensional Modelling of a *P. pelagicus* Larval Settlement and Its Validation

The Delft3D-PART model was simulated from 20 May 2023 to 2 June 2023 to investigate the larval settlement after their release from the crab bank. A total of 20 berried female crabs of *P. pelagicus* were collected from local fishermen. All protocols of the crab transport, egg incubation, and collecting the zoeal larvae were the same as described in the previous section, Section 2.2.2. The laboratory-reared larvae were released from the Rajamangala blue swimming crab bank learning centre (CBLC), hereafter Rajamangala CBLC (Station 6 in Figure 1), on 20 May 2023 during low tides in the daytime (1.00 p.m.). The model study was employed to simulate the settlement sites of 10,000 virtual megalopae after 14 days of the release.

To validate the settlement points of the megalopae after the release for 14 days, the crab megalopae were collected using collectors (Figure 3), adapted from [31,32] in a coastal area adjacent to the Rajamangala CBLC (Station 6 in Figure 1). This location was selected based on the model prediction of the larval dispersal model generated by Delft3D-PART. The megalopa collectors ($n = 20$) were submerged and left at a water depth of 0.5 m above

the seabed for 24 h prior to Day 14. On Day 14 (2 June 2023 at 2.00 p.m.), the collectors were retrieved and megalopa samples were obtained by washing the traps with freshwater. All collected megalopa-stage larvae were preserved in 4% neutral formalin. Identification of megalopae *P. pelagicus* obtained from the collectors was conducted under a light microscope, following the identification key provided by [30].

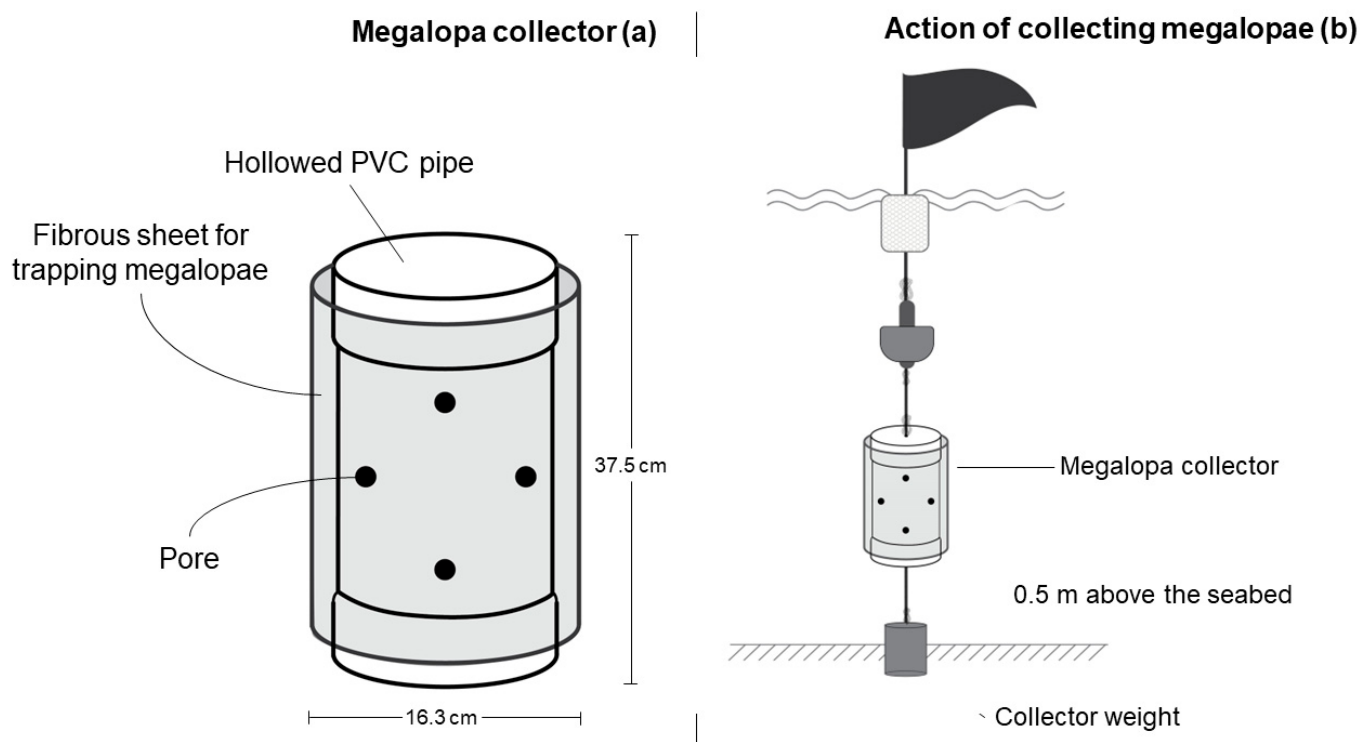


Figure 3. An illustration demonstrates the megalopa collectors used in this study (a) and the action of collecting megalopae using the collectors at sampling sites (b). The megalopa collector (a) is made from a hollowed polyvinyl chloride (PVC) pipe. The PVC pipe is drilled into numerous pores, allowing water to flow through the collector. The collector encloses a fibrous sheet as a settlement area for crab megalopae. The diameter and length of the collector, which includes a fibrous sheet, are 16.3 cm and 37.5 cm, respectively. For collecting megalopae in each sampling site, the collectors are placed above the seabed for 0.5 m (as shown in (b)), attached to a weight, a sub-surface, and a surface buoy.

3. Results

3.1. Modelled Simulations of Larval Dispersal Patterns

Following the simulation of crab larvae, our results showed that the crab larvae dispersed along the coastline. After the 14-day release period, the crab larvae were prominently retained within inshore areas, with some being transported into offshore areas, estuaries, and near-shore tributaries. The larva dispersal patterns were primarily regulated by tide-driven currents and wind-induced currents, resulting in variations in dispersal patterns dependent on monsoon periods and release locations. Regarding the influences of tides on dispersal patterns, the larvae showed a cycle of an inshore–offshore movement pattern. The larvae were transported out away from inshore areas during the low tide by ebb currents while they were returned to inshore areas by flood currents during the high tide period. Due to the semi-diurnal tide in this area, this tidal pattern retained most of the crab larvae, causing them to disperse within inshore areas near the coastline.

In addition to the tidal regulation of larval dispersal patterns, our findings also revealed that the crab larvae exhibited different dispersal patterns, relying on monsoon periods. These results demonstrated that monsoonal wind patterns had significant effects, controlling the dispersal pattern of larvae *P. pelagicus* after release from crab banks. Overall, our results suggested that the dispersal patterns following the release from each station can

be grouped into three main regions: Region a (northern coast), Region b (middle coast), and Region c (southern coast). During the inter-monsoon period (in April), when the wind direction exhibited more variability compared to the southwest and the northeast monsoon periods (Figure 2), there was a greater larval transport toward offshore areas. The 5.33% of crab larvae transported out to offshore areas was higher than during both the southwest and northeast monsoon periods (Figure 4). Approximately 82.10% of the crab larvae widely dispersed in mid-shore to inshore areas while 12.57% of the larvae travelled into estuaries and brackish water tributaries (Table 2). During the inter-monsoon, the virtual crab larvae released from Stations 1–12 dominantly flowed toward the northern coast, aggregating within Region a. Some of the larvae released from Stations 7–11 were transported out to offshore areas. The virtual larvae derived from Stations 12–18 were dominantly colonised within Region b at the middle part of the coastline. The majority of virtual larvae released from Stations 19–29 were transported toward the southern coast, concentrating their dispersal within Region c.

During the southwest monsoon period, the winds were directed from the southwest to the northeast (Figure 2), which exerted the most virtual larvae (75.14%) to retain their dispersion within inshore areas. Additionally, 23.45% of the larvae were transported into river mouths and near-shore tributaries while 1.41% of the larvae moved toward offshore areas (Figure 5 and Table 2). The virtual crab larvae released from Stations 1–12 (Region a) aggregated to the northern coast while a minor proportion of crab larvae (from Stations 10–11) was transported out to offshore areas (Figure 5). The virtual larvae from Stations 13–19 (Region b) were located in the middle part of the coastline while the larvae released from Stations 20–29 (Region c) retained their dispersion within the southern coast near their released stations. During this monsoon period, the virtual crab larvae that were released from stations close to river mouths and near-shore tributaries were dispersed into estuaries and brackish tributaries, driven by southwest monsoon wind-induced currents. The virtual larvae released from Stations 2, 3, 13, 14, and 22 showed greater proportions of larvae transporting into estuaries and brackish tributaries compared to other stations along the coast (Table 2).

During the northeast monsoon period, the winds were directed from the northeast to the southwest (Figure 2). This wind direction regulated larval dispersal patterns to disperse within inshore areas (89.51% of crab larvae) greater than the southwest monsoon period. The larvae were transported offshore (2.20% of crab larvae), higher than during the southwest monsoon, while some of the virtual larvae (8.30% of crab larvae) moved into estuaries and brackish tributaries, lower than during the southwest monsoon. The virtual larvae released from Stations 1–12 were transported toward the northern part of the coastline, as shown in Region a, while minor proportions of the larvae released from Stations 10 and 11 were transported out to offshore areas. Most virtual larvae released from Stations 13–19 tended to aggregate at the middle part of the coast, as found in Region b. The larvae derived from Stations 20–29 moved toward the southern coastline and retained their dispersal within Region c (Figure 6 and Table 2).

Overall, the dispersal patterns of virtual larvae released from each region are still retained near their released stations, similar to the southwest monsoon period.

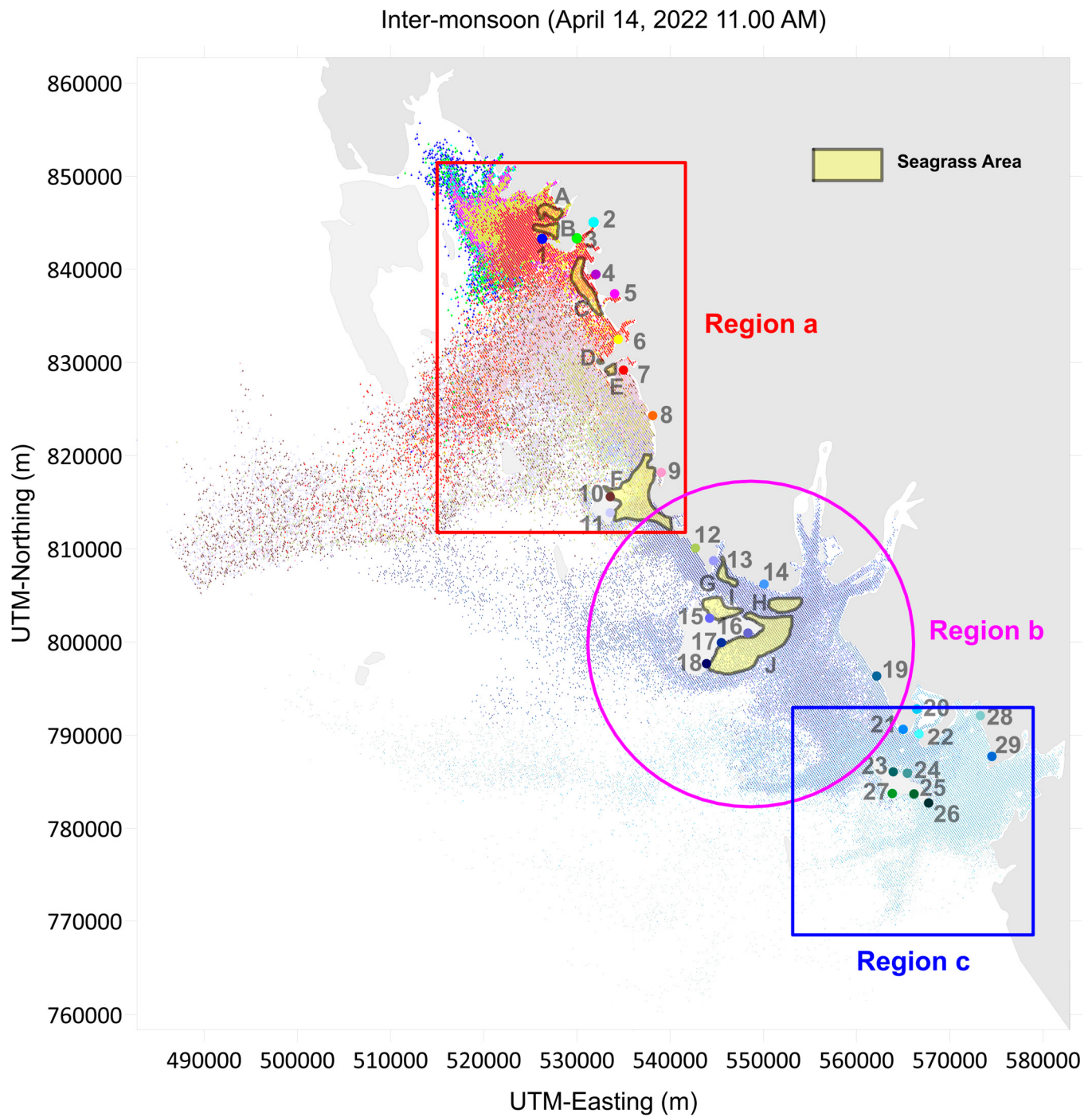


Figure 4. The modelled simulation demonstrates the dispersal patterns of virtual crab larvae released for 14 days (10,000 individuals per released point). These releases took place at coordinates from the 29 stations of crab banks on 1 April 2022, during the spring tide period at 12:00 p.m. The coloured dots represent the positions of the virtual crab larvae on 14 April 2022 at 11:00 a.m. after release from the crab banks. The different colours of the dots indicate the sources (release station) of the virtual larvae.

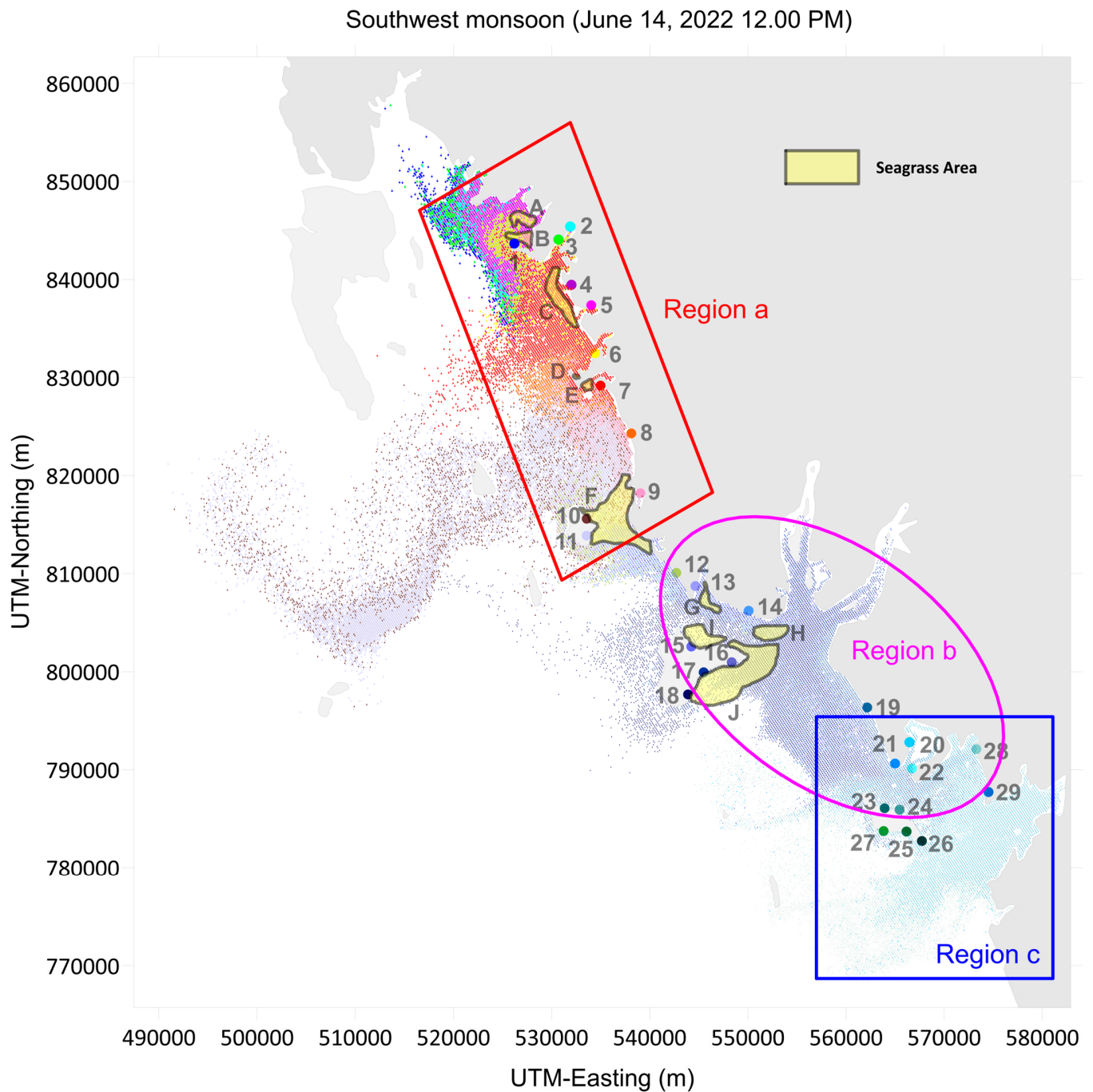


Figure 5. The modelled simulation illustrates the dispersal pattern of virtual crab larvae released for 14 days (10,000 individuals per released station) during the southwest monsoon. These releases took place at 29 stations, originating from the crab bank coordinates, on 1 June 2022, during the spring tide at 1:00 p.m. The coloured dots represent the positions of the virtual crab larvae on 14 June 2022 at 12:00 p.m. after release from the crab banks. The different colours of the dots indicate the sources (release station) of the virtual larvae.

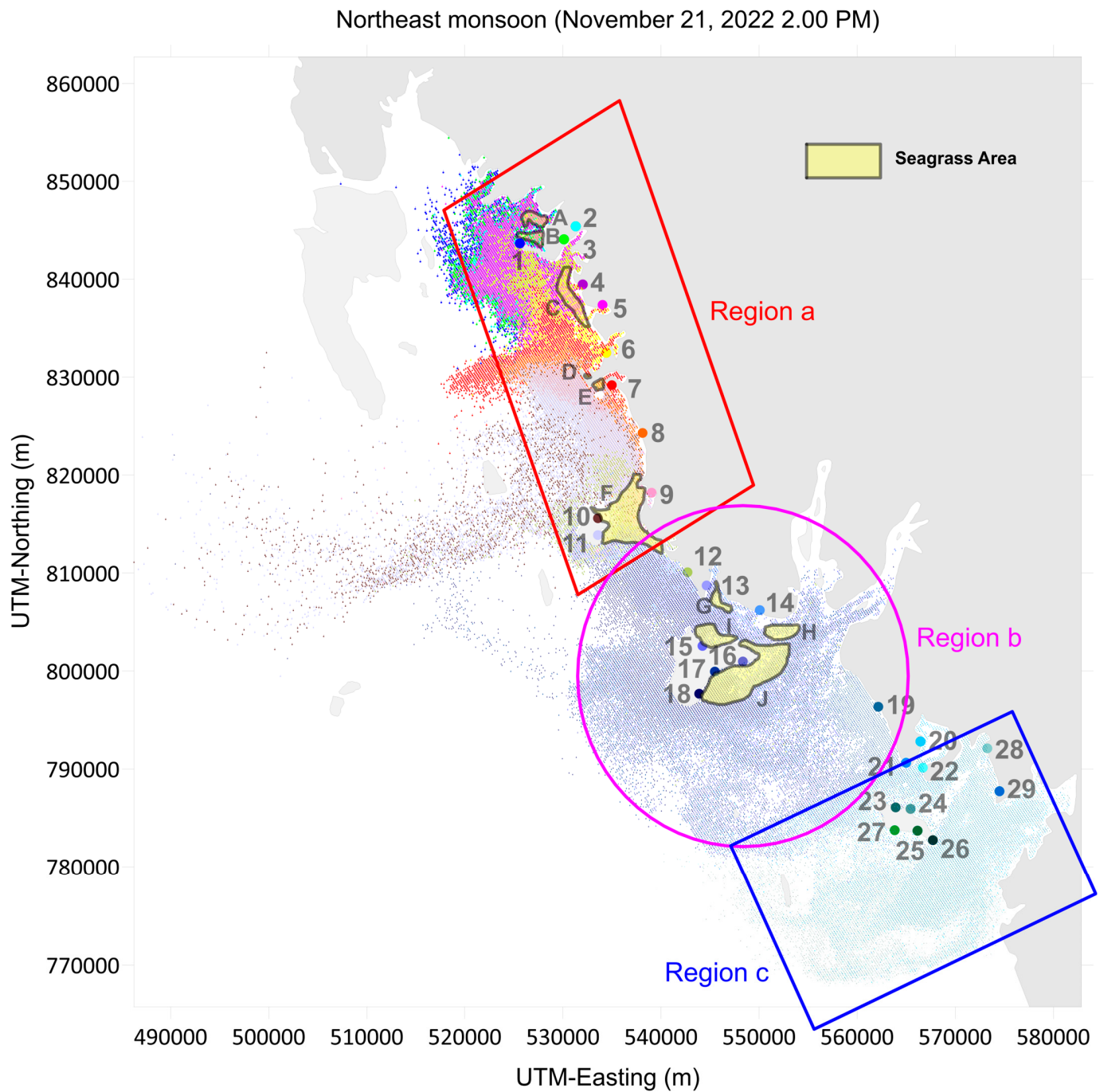


Figure 6. The modelled simulation reflects the dispersal patterns of virtual crab larvae released for 14 days (10,000 individuals per released point). These releases took place at 29 stations, originating from the crab bank coordinates, on 8 November 2022, during the spring tide at 3:00 p.m. The coloured dots represent the positions of the virtual crab larvae on 21 November 2022 at 2:00 p.m. after release from the crab banks. The different colours of the dots indicate the sources (release station) of the virtual larvae.

Table 2. The percentages of virtual crab larvae that were localised inshore, offshore, and in river mouths or near-shore tributaries after 14 days of release from crab banks.

Source of Crab Bank	Inter-Monsoon Megalopa (%)			Southwest Monsoon Megalopa (%)			Northeast Monsoon Megalopa (%)		
	Offshore (Depth > 20 m)	Inshore (Depth < 20 m)	River Mouths and Near-Shore Tributaries	Offshore (Depth > 20 m)	Inshore (Depth < 20 m)	River Mouths and Near-Shore Tributaries	Offshore (Depth > 20 m)	Inshore (Depth < 20 m)	River Mouths and Near-Shore Tributaries
1	0.00	96.50	3.50	0.00	83.65	16.35	0.00	91.18	8.82
2	0.00	70.25	29.75	0.00	42.60	57.40	0.00	78.00	22.00
3	0.00	74.76	25.24	0.00	45.10	54.90	0.00	78.25	21.75
4	0.00	77.25	22.75	0.00	70.95	29.05	0.00	81.02	18.98
5	0.10	89.50	10.40	0.00	79.75	20.25	0.00	89.14	10.86
6	0.50	87.50	12.00	0.00	81.43	18.57	0.00	89.44	10.56
7	5.00	82.50	12.50	0.00	81.43	18.57	0.00	89.42	10.58
8	1.70	93.30	5.00	0.00	82.00	18.00	0.00	98.95	1.05
9	5.00	90.00	5.00	0.00	84.72	15.28	0.00	98.15	1.85
10	21.52	75.48	3.00	16.62	71.38	12.00	14.14	84.84	1.02
11	18.00	80.50	1.50	24.14	70.62	5.24	16.18	82.96	0.86
12	6.48	83.52	10.00	0.00	78.72	21.28	1.28	90.18	8.54
13	0.00	72.25	27.75	0.00	67.21	32.79	0.00	89.11	10.89
14	0.00	79.81	20.19	0.00	57.85	42.15	0.00	89.29	10.71
15	0.00	82.33	17.67	0.00	78.66	21.34	0.00	90.44	9.56
16	0.00	87.49	12.51	0.00	78.25	21.75	0.00	94.69	5.31
17	1.46	86.57	11.97	0.00	74.60	25.40	0.00	96.73	3.27
18	7.22	84.05	8.73	0.00	81.96	18.04	1.53	95.88	2.59
19	0.00	98.02	1.98	0.00	86.00	14.00	0.00	97.93	2.07
20	8.32	85.73	5.95	0.00	82.44	17.56	0.00	92.91	7.09
21	8.20	82.40	9.40	0.00	81.93	18.07	0.00	91.54	8.46
22	4.96	73.64	21.40	0.00	67.55	32.45	0.00	87.11	12.89
23	0.64	87.11	12.25	0.00	75.44	24.56	0.00	92.02	7.98
24	8.82	84.28	6.90	0.00	85.42	14.58	0.00	96.73	3.27
25	13.12	75.43	11.45	0.00	80.93	19.07	5.43	87.41	7.16
26	13.88	76.12	10.00	0.00	80.88	19.12	7.05	88.75	4.20
27	8.66	78.80	12.54	0.00	78.69	21.31	5.42	89.89	4.69
28	13.95	69.75	16.30	0.00	75.95	24.05	7.59	81.83	10.58
29	7.00	76.00	17.00	0.00	72.95	27.05	5.04	81.99	12.97
Mean	5.33	82.10	12.57	1.41	75.14	23.45	2.20	89.51	8.30

3.2. Larval Settlement Patterns in Seagrass Meadows

The results from our particle tracking model can demonstrate the connectivity between released stations (sources) and larval settlement areas (sinks) within seagrass meadows along the coast of the Trang province (Table 3). The percentage of crab larval settlements varied following seagrass locations and periods of monsoon. During the inter-monsoon period, our simulated models indicated that the highest percentage of crab larval settlements was found in Ao Thung Chin, followed by Koh Mook and Ban Pak Klong-Koh Phi in descending order (Table 3). In seagrass areas of Ao Thung Chin, the settled megalopae were transported from Stations 12, 13, 14, 15, 17, and 18 (Region b). The total number of virtual larvae that were released from those stations was 60,000. Only 3271 larval individuals settled on the Ao Thung Chin seagrass bed, which was 5.45% of the total number of released virtual larvae. In Koh Mook, the settled crab larvae originated from both Region a and b, including Stations 8, 9, 10, 11, 12, 13, 14, 15, and 18. Only 4239 larvae from 90,000 individuals of the total larvae released from

those stations reached the Koh Mook seagrass meadow. These settled larvae were 4.71% of the total number of released virtual larvae. Only 2.61% of the crab larvae reached a seagrass meadow in Ban Pak Klong-Koh Phi; they originated from stations 2, 3, 4, 5, 6, 7, 8, 10, and 11 (Region a).

Table 3. The distribution and settlement patterns of virtual crab larvae released from crab banks across seagrass meadows along the Trang coastline. The Arabic numbers located in a column of sources of crab banks connected to seagrass beds represent the crab bank stations following Figure 1.

	Seagrass bed Size * (km ³)	Percentage Coverage * (%)	Status *	Sources of Crab Banks Inter-Monsoon (1)	Connected to Southwest Monsoon (2)	Seagrass Beds Northeast Monsoon (3)	Settlement of Megalopae (%)
A. Pak Klong Kalasae	0.91	51	good	1,2,3,4,5,6,7	1,2,3,4,5,6	1,2,3,4,5	(1) 2.59 (2) 3.64 (3) 1.23
B. Ban Laem Sai	0.88	50	intermediate	1,2,3,4,5,6,7	1,2,3,4,5,6	1,2,3,4,5	(1) 2.00 (2) 2.56 (3) 0.74
C. Ban Pak Klong-Koh Phi	2.43	15	threatened	2,3,4,5,6,7,8,10,11	2,3,4,5,6,7	1,2,3,4,5,6	(1) 2.61 (2) 3.35 (3) 2.72
D. Ao Boon Kong	0.14	42	intermediate	6,7,10,11	6,7	6,7	(1) 0.05 (2) 0.36 (3) 0.26
E. Ao Kham	0.59	21	threatened	7,8,9,10,11,12	7,8,9	7,8,10,11	(1) 0.20 (2) 0.63 (3) 1.83
F. Koh Mook	15.83	40	intermediate	8,9,10,11,12,13,14,15,18	8,9,10,11,12,13,14,15	8,9,10,11,12,13,14,15,18	(1) 4.71 (2) 5.57 (3) 7.59
G. Pak Klong Chao Mai	1.91	51	good	12,13,14,15,17,18	12,13,14,15,18	12,13,14,15,18	(1) 1.13 (2) 1.70 (3) 1.56
H. Koh Nok	3.06	36	intermediate	12,14,15,16,17,18	12,13,14,15,18	12,13,14,15,16,17,18	(1) 1.31 (2) 1.49 (3) 0.26
I. North Koh Libong	5.27	36	intermediate	12,13,14,15,17,18	13,14,15,18	12,13,14,15,17,18	(1) 0.63 (2) 0.90 (3) 1.23
J. Ao Thung Chin	20.89	36	intermediate	12,13,14,15,17,18	12,14,15,16,17,18	12,13,14,15,16,17,18	(1) 5.45 (2) 5.49 (3) 4.75

Note: The asterisk (*) indicates information reported by the Department of Coastal and Marine Resources of Thailand (2022). The percent seagrass coverage of <25% represents seagrass status is threatened by human activities; 25% is under a natural status; 25–50% is intermediate; 51–75% is good; >75% is very good.

During the southwest monsoon period, Koh Mook and Ao Thung Chin exhibited the highest percentage of larval settlements, followed by Pak Klong Kalasae (Table 3). Approximately 4452 larvae (5.57%) of the total number of 80,000 released virtual larvae successfully reached the Koh Mook seagrass area; they were derived from the same stations as observed during an inter-monsoon period, except for Station 18. In Ao Thung Chin, 5.49% of the released virtual larvae from Stations 12, 14, 15, 16, 17, and 18 were transported to this seagrass area. Only 3.64% of the released virtual larvae from Stations 1, 2, 3, 4, 5, and 6 (Region a) arrived at the Pak Klong Kalasae seagrass meadow.

During the northeast monsoon period, the highest percentage of settled larvae was found at Koh Mook, followed by Ao Thung Chin and Ban Pak Klong-Koh Phi in descending order (Table 3). During this period, the Koh Mook seagrass area was a sink for 7.59% of the released virtual larvae, derived from Stations 8, 9, 10, 11, 12, 13, 14, 15, and 18. Only 4.57% of the virtual larvae which originated from Stations 12, 13, 14, 15, 16, 17, and 18 reached the seagrass in Ao Thung Chin. The released virtual larvae of 2.72% derived from Stations 1, 2, 3, 4, 5, and 6 reached the seagrass bed at Ban Pak Klong-Koh Phi. Overall, seagrass areas at Koh Mook and Ao Thung Chin were the dominant areas that the released virtual larvae were transported to in all monsoon periods. Ban Pak Klong-Koh Phi was considered the

third highest larval settlement during an inter-monsoon and the northeast monsoon period while Koh Mook and Ao Thung Chin had the greatest percentage of larval settlements, followed by Pak Klong Kalasae, during the southwest monsoon period.

3.3. Validation of the Modelled Simulation of Larvae Dispersal

The result from our buoy tracking experiment showed that the observed buoy's trajectory was consistent with the particle's trajectory obtained by our Delft3D-PART model (Figure 7). The buoy travelled away from the coastline during the low tide period due to the ebb currents while the flood currents exerted it to return to the coast during the high tide period.

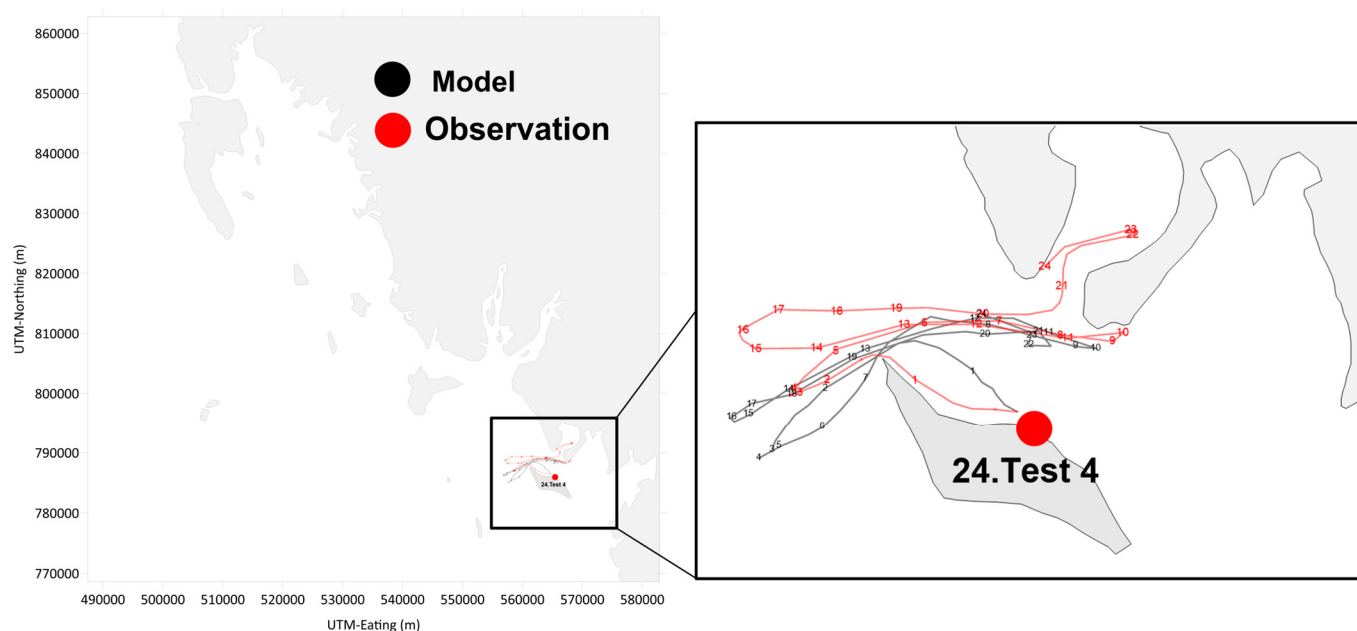


Figure 7. The simulated tracking of surface water currents was conducted concurrently with the release of 4 million crab larvae from representative release points at the crab bank near Sukorn Island's pier. This observation occurred between 16 May 2022 at 2:00 p.m. and 17 May 2022 at 3:00 p.m., spanning approximately 24 h. The red line represents the direction and movement based on the model tracking prediction. The dark line demonstrates the direction and movement of the buoy based on the field observation. The numbers above the red and dark lines represent the time (hour) after release from Sukorn Island.

After releasing the buoy, *P. pelagicus* zoeae were sampled following the trajectory of the buoy. The *P. pelagicus* zoeae were detected at several sampling times at either a surface depth or sub-surface depth. The density of zoeae found at each depth and sampling time interval are shown in Figure 8. The highest abundance of zoeae was found at a 0.5 m water depth at 1 a.m. and 2 m water depth at 2 a.m.

3.4. The Larval Settlement Pattern Based on the Modelled Simulation and Its Validation

After 14 days of virtual-larval releasing, our modelled simulation suggested that 31.95% of the virtual megalopae arrived at offshore areas. The virtual larvae that retained their dispersion in inshore areas made up 46.75% while 21.3% of the virtual larvae were transported into the Sikao brackish water river.

After the release of laboratory-reared larvae for 14 days, a total of 217 crab megalopae were found across all collecting sites, affirming their presence in accordance with the model-predicted coastal location near the Rajamangala CBLC (see Figure 9).

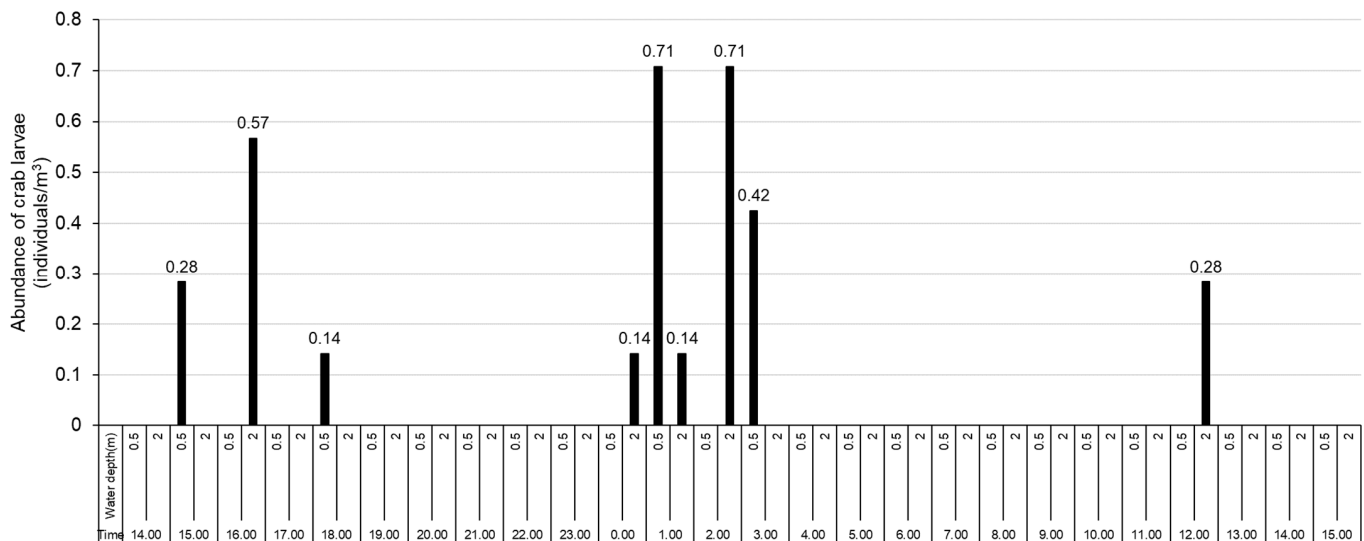


Figure 8. The abundance of crab-zoeal larvae *P. pelagicus* (individuals per m³) after the release from Sukorn Island at the depths of 0.5 and 2 m below the water surface. The crab larvae were sampled every hour following the trajectory of the buoy after the release from Sukorn Island.

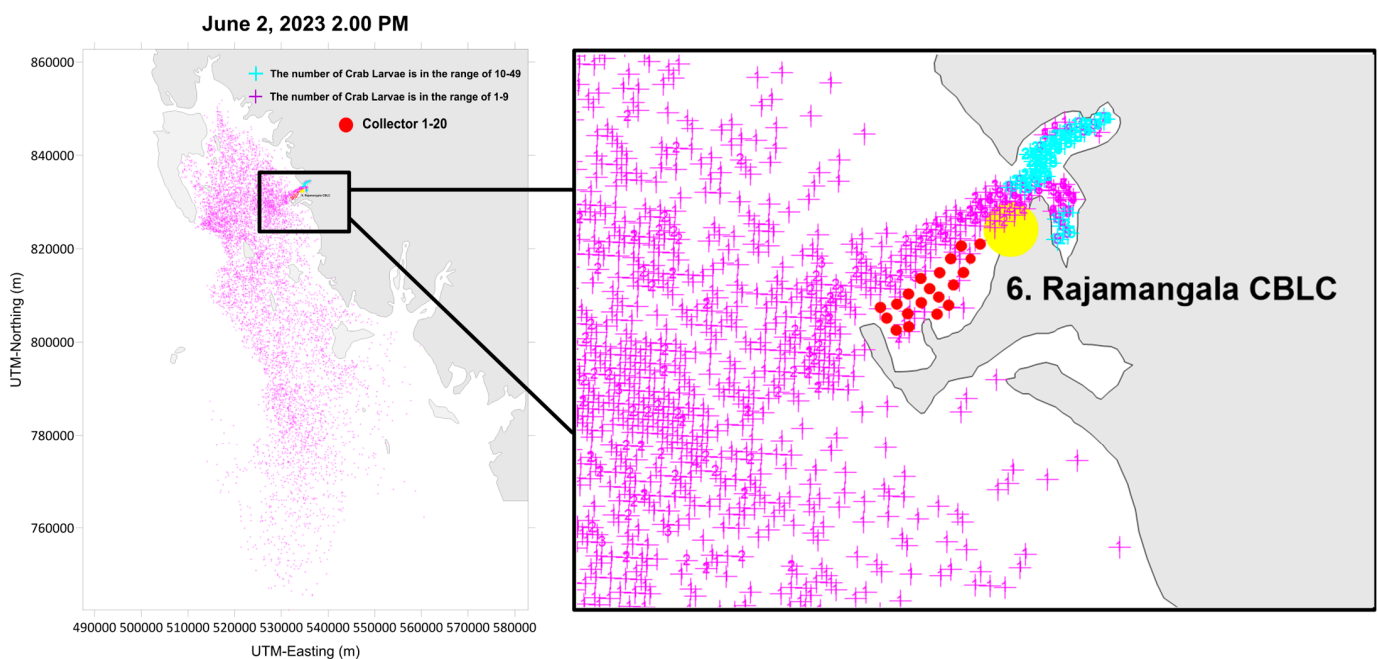


Figure 9. The modelled simulation of the settlement locations of crab megalopae after the release from the Rajamangala CBL (yellow point). The colours indicate an abundance of virtual crab larvae. The plus signs (+) are the locations of virtual crab larvae and the numbers located on the plus signs represent the numbers of individuals of virtual crab megalopae based on the simulation.

4. Discussion

Our study demonstrates the larval dispersal and settlement patterns of *P. pelagicus* released from crab banks along the Trang coastline using the Lagrangian particle tracking model coupled with local 3D-hydrodynamics. The results showed that the majority of virtual crab larvae were retained within inshore areas near their released stations (sources) rather than offshore waters across three monsoon periods. The crab larvae *P. pelagicus* lack swimming abilities against the horizontal water current [28]; they still retained their dispersal within inshore areas. This result suggests that their dispersal patterns are likely regulated by local hydrodynamic factors, particularly tidal-driven currents and monsoonal-

wind-induced currents. The larvae *P. pelagicus*, including zoeal to megalopa stages, can distribute throughout the water column; however, the majority of them are predominantly detected at the sub-surface depth (1–3 m below the water surface) [13,14]. In a previous study, zoeae *P. pelagicus* did not exhibit tidal vertical migration based on field observation [13]. This vertical retention of the larvae allows them to be horizontally dispersed, relying on the surface currents driven by tidal rhythms and winds. Due to semi-diurnal tides on the Trang coast, the larvae were shortly transported away from the coastline by the ebb current during the low tide period; meanwhile, they moved back toward the coastline again by the flood currents during the high tide period. For the crabs *P. pelagicus*, this larval dispersal pattern is concurrent with their short pelagic life, within which they transit from a pelagic to a benthic life within 11–19 days, approximately [5,15]. A brief pelagic larval duration (PLD) coupled with the coastal retention of *P. pelagicus* may enhance its settlement success, ensuring that most larvae can settle in their preferred habitats near the coastline, particularly in seagrass meadows. This agrees with a previous study that stated *P. pelagicus* exhibited high rates of self-recruitment within the same coastal region [33]. This phenomenon could be attributed to a short PLD and larval dispersal near their sources, controlled by tidal-driven currents and local oceanographic conditions. Hence, our modelled simulations imply that the larvae released from all crab banks along the coastline could dominantly disperse and complete their development within inshore areas.

Our results also showed that the virtual larvae had differences in larval dispersal patterns across monsoon periods. For instance, during the northeast monsoon period, the majority of the virtual larvae were retained within inshore areas higher than the inter-monsoon and southwest monsoon periods in descending order. This result indicates that monsoonal-wind-induced currents participate in regulating the larval dispersal associated with tidal-driven currents and local oceanographic conditions. Our findings are in agreement with a previous study that found monsoonal-driven water currents have been postulated to control the movement of larvae *P. pelagicus*, retaining within mid-shore areas close to the shoreline [14]. The dispersal pattern during the northeast monsoon period is probably maintained by the northeast monsoonal-wind-induced currents' cooperation with daily tidal-driven currents. The northeast monsoonal-wind-induced currents, which are directed from northeast to southwest direction, could transport the larvae away from the coastline, accompanied by the ebb currents during the low-tide period (Figure 6). The influences of the flood currents and the net current velocity (Figure 10c) toward the coastline likely play significant roles in retaining larvae within inshore areas, preventing transport out into offshore areas. During the inter-monsoon period, the coastline was influenced by wind-induced currents that were directed from both the southwest to the northeast and the northeast to the southwest (Figure 2). This phenomenon may cause more variability of wind directions compared to the southwest and northeast monsoon periods. The wind patterns may disperse the crab larvae to be transported out to offshore areas higher than the southwest and northeast monsoonal effects. Moreover, the transport of the larvae into estuaries was also greater than the northeast monsoonal effects. Therefore, the larval-releasing activities during the inter-monsoon period should be a concern following the southwest monsoon as some larvae may be transported into estuaries. During the southwest monsoon period, most virtual larvae still dispersed in inshore areas toward the coastline while some of them (23.45% of total released virtual larvae) were transported into river mouths and tributaries, greater than in other monsoon periods (Figure 5). This dispersal pattern likely relies on the southwest monsoonal-wind-driven surface currents, which are directed from southwest to northeast toward the shoreline. The wind direction could make some larvae released from the crab banks more susceptible to salinity challenges due to being transported into estuaries with dilute salinity.

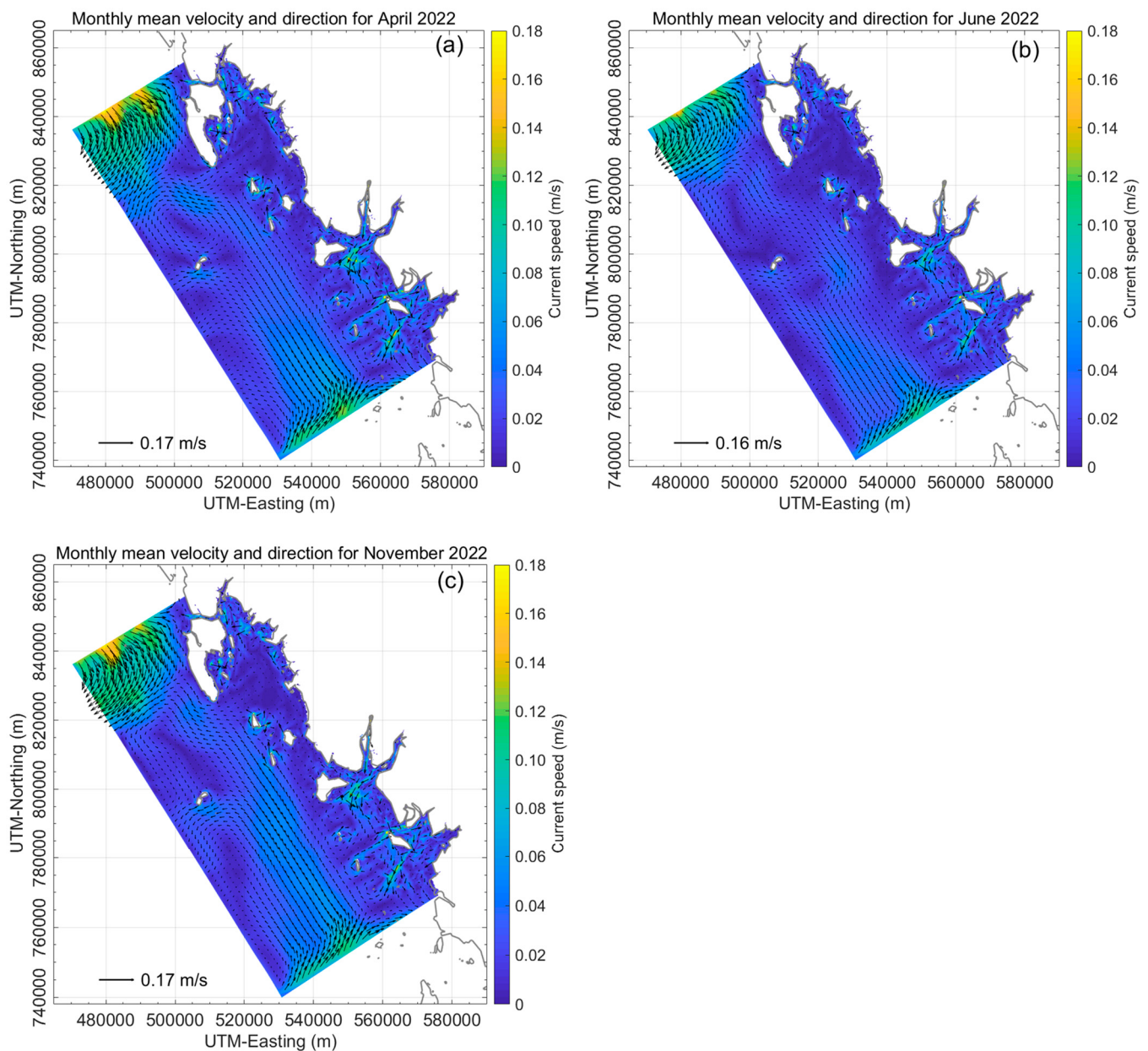


Figure 10. The monthly mean current velocities and directions based on Delft3D-FLOW during the inter-monsoon in April (a), the southwest monsoon in June 2022 (b), and the northeast monsoon in November (c).

Regarding our results of larval dispersal patterns, we recommend releasing the crab larvae during the inter-monsoon from the following 17 stations: Stations 1, 5, 6, 7, 8, 9, 11, 12, 15, 16, 17, 18, 19, 20, 21, 23, and 24. This strategy may result in high survival and settlement rates as more than 80% of the released larvae were retained within inshore areas. For the southwest monsoon period, we suggest releasing larvae from the following 12 stations: Stations 1, 6, 7, 8, 9, 18, 19, 20, 21, 24, 25, and 26. Similarly, during the northeast monsoon, 27 release stations, excluding Stations 2 and 3, are recommended for enhancing the success of larval settlements due to coastal retention. These recommendations are based on high percentages of larvae being retained in inshore areas rather than being transported to offshore or estuarine areas.

The transport of crab larvae into estuaries, such as river mouths and brackish water tributaries, is very critical and can potentially affect their fitness due to lower salinity compared to inshore seawater. Salinity is one of the key abiotic factors which

can influence the survival rates and development of larvae in swimming crabs [34,35]. In a previous study, zoeae *P. pelagicus* had good survival rates at a salinity of 30 PSU, while mass mortality was observed at salinities of 20 PSU and 10 PSU [35]. Similarly, crab larvae in Portunidae, including *P. pelagicus*, require high salinity to complete their developmental stages [36,37]. These findings suggest that the crab larvae transported into estuaries are highly susceptible to salinity stress, leading to decreased survival rates and incomplete larval development. Referring to our larval dispersal simulation, it was observed that the crab larvae released from Stations 2, 3, and 14 were transported into estuaries with higher proportions compared to other stations (see Table 2). To ensure high survival rates of released crab larvae during the southwest monsoon, the crab larvae obtained from those stations should be transferred for release at other stations, avoiding the transport of crab larvae into areas with low salinity conditions.

In addition to monsoonal-wind-induced currents and tidal-driven currents, coastal topography and local oceanographic conditions also play crucial roles in determining the dispersal patterns of marine larvae [38,39]. This phenomenon was exemplified by events in our study site where the virtual larvae in our simulations exhibited dispersal routes and movements associated with coastal topography. In Region c, several eddies were detected at the southern part of Libong Island and the western side of Sukorn Island (Figure 10). The presence of near-shore eddies may contribute to the coastal retention of virtual larvae in Region c (Figures 4–6). Eddies are capable of maintaining high productivity, which has the potential to sustain the high abundance of marine larvae [40,41]. This could explain the dispersal of virtual larvae released from Region c, mainly retained in inshore zones near their released stations (sources). In Region a, the released virtual larvae travelled along the coast toward the northern and northeast parts; however, they were still retained within inshore areas (Figures 4–6). This movement of virtual larvae is consistent with the presence of longshore currents, flowing from Ban Khuan Tung Ku (Station 9) to Ban Laem Sai (Station 1) (Figure 10). It could suggest that the longshore currents may aid in the virtual larval retention along the coastline within Region a.

After 14 days of releasing the virtual larvae, our simulations were able to identify the settlement areas of the larvae *P. pelagicus* released from the crab banks along the Trang coastline. On day 14, the virtual larvae arrived at numerous seagrass meadows located along the Trang coastline (Figures 4–6 and Table 3). During the 14 days following the release from the crab banks, the larvae underwent development from the zoeal stages to a megalopa stage, transiting from a pelagic to a benthic lifestyle [5,15]. In shallow-coastal waters, seagrass meadows are primarily considered suitable settlement areas, nursery grounds, and sheltered areas for various swimming crabs, including *P. pelagicus* [42,43]. Hence, our results suggest that the larvae released from the crab banks may successfully settle and grow within those seagrass areas. In our model simulation results, seagrass beds at Ao Thung Chin, Koh Mook, Ban Pak Klong-Koh Phi, and Pak Klong Kalasae exhibited high settlement rates of crab larvae released from crab banks in comparison to other seagrass areas. Similarly, these seagrass areas also received the larvae from various crab banks, suggesting that they serve as effective sinks for *P. pelagicus* larvae after being released from crab banks. Our findings can emphasize the importance of protecting and conserving these seagrass beds as major settlement sites for crab larvae, as indicated by our simulation. Moreover, the crab larvae released from Ban Laem, Ban Laem Makhm, Ban Thung Thong, Ban Pak Klong, Ban Chang Lang, Ban Khan Thung Ku, Rajamangala CBLC, Koh Mook, Ban Ao Kung, and Ban Koh Sathon can disperse to numerous seagrass meadows. These findings highlight the significant role of these release stations in distributing crab larvae to various seagrass areas along the coast. Therefore, releasing the crab larvae after hatching from those stations is highly recommended to enhance their survival and settlement rates.

In the current study, we validated the simulated tracking of particles at the surface water based on our modelling through field-based observation. Our result demonstrated that the buoy's direction and movement were consistent with the trajectory simulated by the particle tracking model. This outcome indicates the accuracy and reliability of

our modelled simulation of larval dispersal and settlement location, reflecting possible trajectories of the crab larvae after release from the crab banks. Following the tracking buoy's release, zoeae *P. pelagicus* were found at both 0.5 m and 2 m water depths at several sampling time periods. This result aligns with previous studies that claim zoeae *P. pelagicus* predominantly dispersed in sub-surface depths without significant tidal vertical migration [13,14]. Moreover, we also confirm the settlement sites for the crab larvae released from the Rajamangala CBLC station. The megalopae *P. pelagicus* were collected at the settlement location suggested by our modelled simulations. To further strengthen our modelled simulation, additional studies using genetic approaches are required to clarify the source/sink of zoeae and megalopae after release from crab banks.

5. Conclusions

In our study, we investigated the dispersal and settlement patterns of larvae *P. pelagicus* released from the crab banks along the Trang coastline using a comprehensive approach, combining the 3D hydrodynamic model and field observations. Our modelled simulation of larval dispersal revealed that tidal-driven currents and monsoonal-wind-induced currents significantly influenced the dispersal patterns of virtual crab larvae, resulting in the near-shore retention of larvae after release from crab banks. The southwest monsoonal-wind-induced currents were capable of transporting some larvae into estuaries, potentially exposing them to low salinity and causing mass mortality due to salinity stress. The release of crab larvae during the southwest monsoon should be carefully considered to prevent their transport into estuaries. Our results demonstrated that the crab larvae released from crab banks arrived at numerous seagrass meadows along the coastline for their settlement during a megalopa stage. Seagrass areas in Koh Mook, Ao Thung Chin, Ban Pak Klong-Koh Phi, and Pak Klong Kalasae, possibly, were identified as potential sinks for megalopa larvae *P. pelagicus* released from crab banks. Overall, these insights provide valuable guidance for decision making regarding the conservation and sustainable management of *P. pelagicus*, especially within the context of the Crab Bank Project in the Trang coastal areas.

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