

Aus dem Institut für Polarökologie
der Christian-Albrechts-Universität zu Kiel

THE ROLE OF HYDRODYNAMIC REGIMES AND WATER
PROPERTIES ON TRANSPORTS, RETENTIONS, AND SETTLEMENTS
OF MOLLUSC LARVAE AT A LAGOON AND ITS ADJACENT OPEN
SHORE IN KAI ISLANDS, INDONESIA

Dissertation

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Der Dekan

**‘Without turbulence there would be no life on earth’
H.J. Lugt (1983)**

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SUMMARY/ZUSAMMENFASSUNG

SUMMARY

The study was carried out in the Hoat Lagoon and its adjacent open shore near Ohoililir Village at the West Coast of Kai Kecil Island, Kai islands, Indonesia, at 15 sampling dates between 25 August 2001 and 22 May 2002. The area is located between 5° 37' 38.3" to 5° 39' 17.4" S and 132° 38' 16.1" to 132° 38' 25.4" E. The main objective of this study is to increase our understanding of the effects of hydrodynamic regimes and water properties on larval transport, retention, and settlement in a tropical lagoon. The following questions were addressed: How do the currents transport mollusc larvae to the lagoon? How many mollusc larvae are retained in the lagoon? How do water properties and turbulence intensity control the larval settlement? The investigations were guided by two main hypotheses: (1) *The greater the larval supply and the longer the retention time of the larvae, the higher the settlement densities in the lagoon are.* (2) *The higher the turbulence intensity and the higher the seawater density, the smaller the settlement densities are.* This study consisted of field investigations at the three sites (two inside the lagoon and one outside the lagoon), laboratory analyses, and the collection of environmental background data. The Hoat Lagoon is relatively small (0.56 km², 1200 m long at maximum 450 m broad) and shallow (4.7 m on average). Its total volume (referred to mean sea level) is about 2.6 million m³. It is connected with the open sea through a narrow (42 m) and shallow (3.8 m on average) entrance. The climate of the study area is determined by the recurrent change between the dry southeast monsoon (July to October) and the wet northwest monsoon (December to March). Surface water temperature ranged from 27°C in September/October to 33°C in November, but were relatively homogenous among the study sites. Salinity ranged from 27 (in November) to 36 (in April).

Seawater densities (as a function of the temperature and salinity) ranged from 1022.74 kg m⁻³ (in September) to 1015.71 kg m⁻³ (in November). Both salinities and densities increased from the lagoon to the adjacent shore. The effects of the climatic factors (rainfalls, numbers of rainy days, air temperature, wind speed and direction) on the water properties were also examined. The tide in the study area is a 'mixed predominantly semi diurnal tide', featuring two tidal cycles per day with different tidal ranges. The average inflow and outflow current speeds through the lagoon's entrance were 0.3 and 0.28 m s⁻¹, respectively. The mean speed of the main current in the lagoon was a magnitude smaller (0.03 ms⁻¹). Turbulence intensities (inferred from the dissolution rates of gypsum slabs) at the adjacent shore were in both rough and calm sea states 5 to 6.5 times higher than in the lagoon.

During flood tide, larvae were mostly transported in a shore-perpendicular current from the open sea through the lagoon's entrance to the eastern shore of the lagoon before they were separated into two branches flowing northward and southward along the eastern lagoon shore. During ebb tide,

the waters leaving the lagoon were mostly transported along the coast in north and northwest directions after passing through the entrance.

Maximum inflow speeds in January to May 2002 coincided with maximum wind speeds. Although inflow and outflow current speeds were not significantly different, larval influxes were identified to be significantly higher than larval outfluxes. The larval influxes were also significantly influenced by wind speeds (i.e., in October, November, December 2001, as well as March 2002).

Most larvae in the lagoon were supposed to come from the outside, only small portions were regarded to originate from local reproduction at the study sites.

There were no significant correlations between the larval influxes and the larval densities at the open shore. This suggests that most larvae introduced into the lagoon were advected from the Banda Sea (65 to 70 nm away from the study sites) ('teleplanic larvae) by wind-driven currents during the northwest monsoon or by upwelling during the southeast monsoon. The upwelling was probably responsible for the decreased water temperature at the study sites in September and early October 2001.

An average of about 38% of the water inflow and about 78 % of the imported larvae were retained in the lagoon after one tidal cycle. Most larvae that were retained in the lagoon settled and utilized the lagoon as a nursery ground. Due to the relatively short turnover time of the total water volume of the lagoon (about 19 hours), it is regarded as a well-flushed lagoon. About 29% of the total water volume is exported during a single outflow, i.e. it took approximately 3 ebb tides to exchange the water mass of the lagoon. This finding does not support the hypothesis that *the greater the larval supply and the longer the retention time of the larvae, the higher the settlement densities in the lagoon are.*

The settlement densities in the lagoon were significantly higher than those at the adjacent open shore. The settlement was not an uniformly continuous process but took place in distinct peaks. The settlement events, however, occurred during both southeast and northwest monsoons. This suggests that recruitment occurs the whole year round.

Seawater densities increased from the lagoon toward the open shore. They were negatively correlated with the settlement densities, supporting the hypothesis that *the higher the seawater density, the smaller the settlement densities are.* The turbulence intensities in the lagoon and at the open shore were significantly different. The turbulence regime ranged from almost laminar conditions in the lagoon to fully turbulent conditions at the open shore. Turbulence intensities were significantly negatively correlated with settlement densities, supporting the hypothesis that *the higher the turbulence intensity the smaller the settlement densities are.*

A total of 18 taxa of larvae and 38 taxa of settled post larvae (settlers) from 4 mollusc classes were found at the study sites. Bivalves (*Saccostrea* sp., *Perna viridis*), gastropods (*Nerita* sp., *Cerithium* sp.), and cephalopods (*Nautilus* sp.) and Polyplacophora (*Chiton trocophore*) were most common.

The larval assemblages recorded in the inflowing and outflowing waters were most similar in taxonomic composition, whereas those in the inflow and at the innermost site in the lagoon were least similar. The compositions of settler assemblages at the lagoon sites were clearly different from that outside the lagoon, reflecting the two different turbulence regimes.

The highest larval diversity (Shannon index) was found in the inflow, the lowest diversity at site-2 where *Saccostrea* sp. clearly dominated the larval assemblage. This difference was probably due to the effect of the species-specific retention of larval species. Species numbers and diversity of settlers were highest in the innermost lagoon and lowest at the adjacent open shore. This difference is thought to be attributed to the higher turbulence intensity and lower environmental stability at the adjacent shore.

ZUSAMMENFASSUNG

Die Studie wurde in der Hoat-Lagune und den angrenzenden offenen Küstengewässern in der Nähe des Dorfes Ohoilir an der Westküste von Kai Kecil, die zu den indonesischen Kai Inseln gehört, vom 25. August 2001 bis zum 22. Mai 2002 durchgeführt. Das Untersuchungsgebiet liegt zwischen $5^{\circ} 37' 38.3''$ bis $5^{\circ} 39' 17.4''$ S und $132^{\circ} 38' 16.1''$ bis $132^{\circ} 38' 25.4''$ O. Das Hauptziel dieser Studie ist es, das Verständnis der Wirkungen von Strömungsmustern und Wassereigenschaften auf Transport, Retention, und Ansiedlung von Mollusken-Larven in einer tropischen Lagune zu verbessern.

Die folgenden Fragestellungen wurden untersucht: Wie werden die Mollusken-Larven in die Lagune transportiert? Wie viele eingeströmte Mollusken-Larven bleiben in der Lagune? Wie beeinflussen die Wassereigenschaften (im besonderen die Seewasserdichte) und die Turbulenz-Intensität die Larvenansiedlung?

Die Untersuchungen basierten auf zwei Haupthypothesen: (1) Ein zunehmendes Larven-Angebot und eine längere Aufenthaltsdauer der Larven führen zu höheren Ansiedlungsdichten in der Lagune. (2) Je höher die Turbulenz-Intensität und Seewasserdichte, desto kleiner die Ansiedlungsdichten. Diese Studie bestand aus Felduntersuchungen, Laboranalysen und der Messung von Umweltdaten.

Die Hoat-Lagune ist relativ klein (0.56 km^2 , 1200 m lang und maximal 450 m breit) und flach (durchschnittlich 4,7 m). Ihr Wasservolumen (bezogen auf den mittleren Wasserstand) beträgt etwa 2,6 Millionen m^3 . Die Lagune ist mit dem Meer durch eine enge (42 m) und flache (durchschnittlich 3,8 m) Öffnung verbunden. Das Klima des Untersuchungsgebiets wird durch den halbjährlichen Wechsel zwischen dem trockenen Südost- (Juli bis Oktober) und dem feuchten Nordwest-Monsun (Dezember bis März) geprägt. Die Oberflächenwasser-Temperaturen bewegten sich zwischen 27° C im September/Oktober und 33° C im November. Es gab aber keine ausgeprägten räumlichen Unterschiede innerhalb des Untersuchungsgebiets. Die Salinitäten reichten von 27 (im November) in der teilweise brackigen Lagune bis 36 (im April) an der offenen Küste. Die Tide im Untersuchungsgebiet ist eine sogenannte „gemischte halbtägige Gezeit“ mit zwei Gezeitenzyklen unterschiedlicher Tidenhöhe pro Tag. Die durchschnittlichen Ein- und Ausströmgeschwindigkeiten in der Lagunenöffnung betragen 0,3 bzw. $0,28 \text{ m s}^{-1}$. Die Tidenströme in der Lagune waren um eine Größenordnung langsamer und betragen durchschnittlich nur $0,03 \text{ m s}^{-1}$. Die Turbulenz-Intensität war in der offenen See 5-6,5 mal höher als in der Lagune.

Bei auflaufendem Wasser transportierte ein senkrecht zur Küste setzender Hauptstrom die Mollusken-Larven durch den Eingang der Lagune. An der Ostseite der Lagune teilte sich die Strömung in Richtung Norden und Süden. Bei ablaufendem Wasser wurden die Larven zunächst aus der Lagune heraus und dann in der offenen See größtenteils in nördlicher Richtung transportiert. Die maximalen Windgeschwindigkeiten im Januar bis Mai 2002 fielen mit den maximalen Einstromgeschwindigkeiten

zusammen, d.h. die Windgeschwindigkeiten waren signifikant positiv mit den Einstromgeschwindigkeiten korreliert. Die Ein- und Ausstromgeschwindigkeiten waren nicht signifikant verschieden. Der LarvenEinstrom war jedoch signifikant höher als der Larvenabfluss und stieg signifikant mit zunehmenden Windgeschwindigkeiten (im Oktober, November, Dezember 2001, sowie März 2002).

Die meisten Larven in der Lagune wurden von außen eingeströmt, und nur eine Minderheit stammt aus autochthoner Reproduktion. Es gab keine signifikante Korrelation zwischen dem LarvenEinstrom und der Larvendichte in den angrenzenden Küstengewässern. Dies führt zu der Annahme, dass ein Großteil der importierten Larven aus Regionen außerhalb des Untersuchungsgebietes kam. Diese wurden wahrscheinlich durch windgetriebene Strömungen (während des NW-Monsuns) und durch Auftrieb (während des SO-Monsuns) aus dem Banda-Meer (~65 bis 70 Seemeilen entfernt) in das Untersuchungsgebiet transportiert. Das Auftriebsereignis hat auch zu den relativ niedrigen Temperaturen im September und Anfang Oktober 2001 im Untersuchungsgebiet geführt.

Durchschnittlich 38% des während einer Flut eingeströmten Wassers und 78% der eingeströmten Larven verblieben nach einem Gezeitenzyklus in der Lagune. Das heißt, ein Großteil der eingetragenen Larven hat sich wahrscheinlich dort angesiedelt und nutzte die Lagune als Aufwuchsgebiet. Die Austauschzeit des Wasservolumens der Lagune war nur sehr kurz (insgesamt etwa 19 h), d.h. die Lagune war gut durchmischt. Durchschnittlich etwa 29 % des Wasservolumens der Lagune wurden während eines Tidenzyklus ausgetauscht, d.h. ein kompletter Wasseraustausch benötigte etwas mehr als drei Tidenzyklen. Die Ansiedlungsdichten stiegen mit steigenden Dichten der pelagischen Larven, aber diese Beziehung war nicht signifikant. Diese Befunde unterstützen nicht die Hypothese, dass ein hohes Larvenangebot und eine lange Verweildauer der Larven zu hohen Ansiedlungsdichten in der Lagune führen.

Die Ansiedlungsdichten waren in der Lagune signifikant höher als in den angrenzenden Küstengewässern. Die Ansiedlung der Larven verlief nicht gleichmäßig, sondern in einzelnen Schüben. Diese Ansiedlungsereignisse wurden aber während des gesamten Untersuchungszeitraums (sowohl während des Südost- als auch während des Nordwestmonsuns) registriert, was dafür spricht, dass eine Rekrutierung das ganze Jahr über erfolgen kann.

Die Dichte des Seewassers (als Funktion von Temperatur und Salzgehalt) nahm von der Lagune zur offenen See hin zu. Sie war signifikant negativ mit den Ansiedlungsdichten korreliert. Dieser Befund stützt die Hypothese, dass höhere Seewasserdichten zu niedrigeren Ansiedlungsdichten führen.

Insgesamt 18 Taxa pelagischer Larven und 38 Taxa angesiedelter Post-Larven (Kolonisten) aus vier Molluskenklassen wurden während des Untersuchungszeitraums registriert. Larven der Muscheln

Saccostrea sp. und *Perna viridis*, der Schnecken *Nerita* sp. und *Cerithium* sp. sowie des Cephalopoden *Nautilus* sp. und Polyplacophora (Chiton trocophore) waren am häufigsten. Die Larvengemeinschaften des Ein- und Ausstroms durch die Lagunenmündung waren sich hinsichtlich ihrer taxonomischen Zusammensetzung am ähnlichsten, diejenigen des Einstroms und der innersten Lagune am unähnlichsten. Hinsichtlich der Zusammensetzung der Kolonistenassoziationen unterschieden sich die Lagune und die angrenzenden Küstengewässer deutlich, was auf die sehr unterschiedlichen Turbulenzbedingungen zurückgeführt werden kann.

Die höchste Diversität (gemessen mit dem Shannon-Index) wurde für die Larvengemeinschaften des Einstroms festgestellt. Die niedrigsten Diversitätswerte wurden in der inneren Lagune gefunden, wo eine Art (*Saccostrea* sp.) stark dominierte. Dieses Muster ist wahrscheinlich ein Ausdruck der art-spezifisch unterschiedlichen Retention der Larven in der Lagune. Artenzahlen und -diversitäten der Kolonistenassoziationen waren am höchsten in der inneren Lagune, nahmen zur Mündung hin ab und waren in den angrenzenden Küstengewässern am niedrigsten. Dieses Muster spiegelt die Unterschiede in den Turbulenz-Intensitäten und der allgemeinen Umweltstabilität wider.

LIST OF ABBREVIATIONS & SYMBOLS

A	= Cross sectional area of the lagoon's entrance (139 m ²)
ANOVA	= Analysis of Variance
C	= Number of organisms counted
D	= Density of the larvae (ind m ⁻³)
DF	= Dissolution/diffusion index factors
DGPS	= Differential global positioning system
EHWS	= Extremely high water of spring tides
ELWS	= Extremely low water of spring tides
fw	= Filter weight (mg)
π	= 3.14
GPS	= Global positioning system
HAT	= Highest astronomical tide
HP	= Horse power
HSD	= Honestly significant difference
Kn	= Knot (Nm ⁻¹ h ⁻¹)
LAT	= Lowest astronomical tide
LFi	= Inflow larval transport (ind s ⁻¹)
LFo	= Outflow larval transport (ind s ⁻¹)
M ₀	= The initial weight
M ₁	= Weight after exposure and drying
MDS	= Multidimensional scaling
MHWS	= Mean high water of spring tides
MHWN	= Mean high water of neap tides
MLWN	= Mean low water of neap tides
MLWS	= Mean low water of spring tides
mw	= Mass weight (mg)
MSL	= Mean sea level
μ	= Micron
Nm	= Nautical mile (= 1.852 meters)
n _i	= The number of individuals of a particular group taxon or species
O	= Outflow
p _i	= n _i / N
PVC	= Polyvinylchlorid
R	= Percent larval retention (%)
RMS	= Root mean square
SD	= Standard deviation
SPSS	= Statistical Package for Social Sciences
T _f	= TSS flux
TSS	= Total suspended solid
τ	= Turnover time (days)
V	= Flow speed (ms ⁻¹)
v	= Water volume transport of outflow through the entrance (m ⁻³ s ⁻¹)
V'	= Volume of the concentrated samples = 450 mL
V''	= Volume counted = 15 mL
V'''	= Volume of water filtered by plankton net (m ³)
v	= Water volume transport through the entrance (m ⁻³ s ⁻¹)
ϖ	= Water volume of the lagoon (m ³) with reference to mean sea level (MSL)
X	= Distance travel of currents (m)

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1. INTRODUCTION

1.1. Motivation

Investigations of the link between nearshore hydrodynamics and the larval supply and settlement are fundamental for understanding the variability in the recruitment of marine benthic populations (Bertness *et al.* 1996, Miller and Emlet 1997), which in turn greatly affect succession patterns, population densities, and community structures (Olafsson *et al.* 1994, Wildish and Kristmanson 1997, Crimaldi *et al.* 2002).

Variation in recruitment has been attributed to numerous physical processes that influence larval supply (Gaines & Roughgarden 1985b, Roughgarden *et al.* 1988, Shanks 1995). In particular, the influence of nearshore currents has been the focus of numerous studies (Banse 1955, 1956, 1986, Scheltema 1986, Farrell *et al.* 1991, Roughgarden *et al.* 1991, Wing *et al.* 1995a, b). Variation in larval supply to marine populations can directly influence the distribution and abundance of marine organisms (Sutherland 1974, Gaines & Roughgarden 1985a, b, Gaines & Bertness 1992) and population and community interactions (Sale 1977, Underwood & Denley 1984, Roughgarden *et al.* 1988, Warner & Hughes 1988, Menge 1991, Sanford *et al.* 1994).

Mechanisms responsible for generating variation in recruitment can operate on a range of spatial scales. In the size range of most sessile marine invertebrates (millimetres to tens of centimetres), larval settlement preferences and hydrodynamics are important. Small-scale hydrodynamic forces, however, can also influence larval settlement rates (Butman 1987, Eckman 1990, Pawlik *et al.* 1991, Snelgrove *et al.* 1993). At slightly larger spatial scales (meters to tens of meters), factors that influence larval concentrations and the rate of larval delivery to potential habitats are critical (Bertness *et al.* 1996), i.e. processes that dictate larval fluxes such as surface waves, currents, internal waves, and tidal bores, play a major role (Bousfield 1955, Hawkins & Hartnoll 1982, Shanks 1983, 1986, Bertness *et al.* 1991, Pawlik *et al.* 1991, Pineda 1991, 1994, Gaines & Bertness 1993). Finally, at large geographic spatial scales (tens to hundreds of kilometres) transport of larvae can also be important in generating spatial and temporal variation in settlement. For example, variation in the intensity of upwelling can influence shoreline larval settlement by affecting the spatial distribution of larvae in an onshore-offshore axis (Bailey 1981, Parrish *et al.* 1981, Roughgarden *et al.*, 1987, Farrell *et al.* 1991, Botsford *et al.* 1994). Similarly, estuarine flushing can influence the settlement by dictating the retention and export of passively dispersed larvae from estuaries (Ketchum 1954, Gaines & Bertness 1992, 1993). Moreover,

large-scale oceanographic currents also appear to play a major role in influencing the dispersal and biogeographic distribution of marine organisms with pelagic development (Parrish *et al.* 1981, Cowen *et al.* 1993, Hare & Cowen 1993). An understanding of the importance of settlement in regulating the abundance and distribution of marine populations will ultimately require integrating processes that affect recruitment across all of these spatial scales (Bertness *et al.*, 1996).

The issues are important to study since they are critical for understanding issues from population dynamics to species geographical ranges, from fisheries-management to design of marine reserves (Pineda, 1991; Bertness *et al.*, 1996). They also have been receiving growing attention, because of the increasing awareness of the importance of coastal water circulation dynamics for the short and long term sustainability of coastal marine ecosystems. However, most of the relevant studies have been done in high latitudes whilst only few investigations addressed these issues in tropical waters.

1.2. Objectives

The main objective of this study is to increase our understanding of the effects of hydrodynamic regimes and water properties on larval transports, retention, and settlement in a tropical lagoon and its adjacent shore. The following sequential questions were addressed:

- How do the currents transport mollusc larvae into the lagoon?
- How many mollusc larvae are retained in the lagoon?
- How do water properties and turbulence intensity control the larval settlement?

This investigation was guided by two main hypotheses:

- (1) The greater the larval supply and the longer the retention time of the larvae, the higher the settlement densities in the lagoon are.
- (2) The higher the turbulence intensity and the higher the seawater density, the smaller the settlement densities are.

The following aspects were investigated concomitantly:

- The hydrodynamic regime, i.e. the surface current pattern drifter study, and the turbulence intensity inferred from the measurement of the dissolution rates of gypsum slabs
- The seawater density (as a function of temperature and salinity) as a relevant water property to be studied with regard to its effect on the passive settling of mollusc larvae.
- The distribution and abundance of planktonic mollusc larvae and newly post larvae (settlers) by plankton catches and exposition of artificial substrates, respectively.

2. AN OVERVIEW OF THE KAI ISLANDS AND THE STUDY SITES

2.1. Geographical features of the Kai Islands

The archipelago Kai Islands, called 'Nuhu Evav' by the islanders, consists of about 100 small coral islands, lying between 5° 08' S to 6° 02' S and 131° 56' E to 133° 10' E (Figure 1). They are located between the deep Banda Sea with the deepest point called Weber Deep of 7400 m and the shallow Arafura Sea. The archipelago may be divided into four groups, namely: Kur Islands, Tayandu Islands, Nuhu Roa or Kai Kecil Island (Little Kai), and Nuhu Yut or Kai Besar Island (Great Kai). Nuhu Roa, including its northeastern portion Kai Dullah has many deep indentations, and several islands lie close to its coast. The island is generally low, though there are few hills of moderate height, with Gelanit Hill (Masbait) attaining an elevation of 111 m being the highest. There are some sandbanks located of the western and northern coast.

2.2. Climate

The main variable of Indonesia's climate, including the Kai Islands, is not temperature or pressure, but rainfall. The extreme variation of rainfall is linked to the monsoon wind system. There is a dry season (July to October) during the Northwest monsoon and a rainy season (December to March) during the Southeast monsoon. Local wind patterns, however, can greatly modify this general pattern. During the transitional periods, from April to June and in November, winds are unsteady (Tomczak and Godfrey, 1994; Wirtky, 1961). During the dry season in 2001 (the study period), rainfalls ranged from 6 to 111 mm, average air temperatures from 26.2 to 28 °C, and insolation from 72 to 88%, and air humidity from 81 to 84%. Average wind speeds were very weak and ranged from 3 to 10 knots. October was the warmest month, as each year, and was characterized by very weak winds a relatively calm sea state. During the wet season 2001/2002, the rainfalls ranged from 204 to 547 mm, average air temperatures from 26.8 to 27.6 °C, insolation from 32 to 70%, and air humidity from 87 to 90%. Average wind speeds ranged from 2 to 6 knots, with a maximum of 27 knots in February.

2.3. Sea bottom condition

The seabed around the Kai Islands consist of nearshore sand bottoms and mud bottoms in deeper waters. Dredge samples conducted by the Dana expedition (1922) off the northern

Kai Islands showed that the bottom at depths of 25 to 100 m consist of fine sand and corals and associated fauna and flora, such as lithothamnion, bryozoans, and molluscs dominated by the bivalve *Pecten* sp. and the gastropod *Murex* sp. At depths of 180 to 220 m sands dominate, from 250 to 275 m sand, corals, and Gastropods, and from 300 to 370 sandy mud, sands, shells, and corals. Corals had been even found at a depth of more than 385 m that are generally characterized by muddy bottom (Mortensen, 1923).

2.4. Study sites

The study was carried out at Hoat Lagoon and its adjacent open shore, nearby Ohoililir Village, at the West Coast of Kai Kecil Island ($5^{\circ} 37' 38.3''$ to $5^{\circ} 39' 17.4''$ S and $132^{\circ} 38' 16.1''$ to $132^{\circ} 38' 25.4''$ E) (Figure 1). This study area was selected to represent typical physical and biological conditions of the Kai Island's coastal areas.

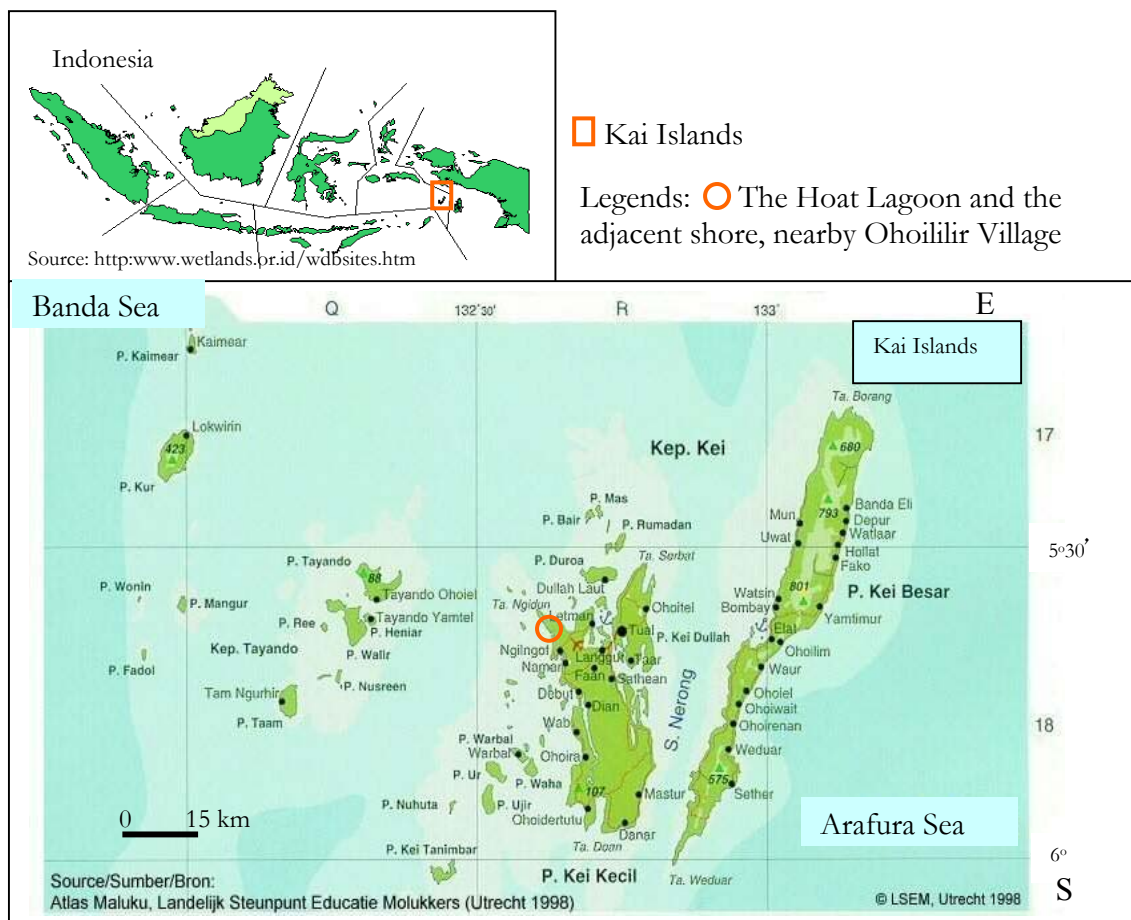


Figure 1. Map of Kai Islands and the study sites (scale: 1: 1,500,000) with an inset country map of Indonesia (not to scale).

Three sites were selected for placements of settlement collectors of mollusc larvae: one outside the lagoon at the adjacent shore (Figure 2a) (Site-3) and two located inside the Hoat Lagoon (Figure 2b) (site-1, site-2). The sites were selected to represent different physical and biological characteristics, especially with regard to hydrodynamic regimes and water properties. The lagoon is a current-dominated area, whilst the adjacent shore is a wave-dominated area. In addition, the lagoon coast is characterised by a mangrove community and sand-mud substrates, whilst the adjacent shore is dominated by a coral reef with sand-gravel substrates.

Site-1 and site-2 are about 700 m and 100 m away from the entrance of the Hoat Lagoon (Figure 2b), respectively. Both sites are 600 m apart from each other. Site-3 is situated about 2 km south of the entrance of the lagoon at the adjacent shore outside the lagoon, nearby the reef margin and about 300 meters from the shoreline of Ohoililir Village (Figure 2a).

The tides in the study area belong to the type ‘mixed prevailing semi-diurnal tide’, characterised by two daily high waters and two daily low waters, which differ significantly in water level heights (Wirtky, 1961).

The lagoon is not completely drained at extreme low water of spring tide. It does not receive significant fresh water inflows, except some brackish ground waters (seepages), which were found along the bottom of the eastern side of the lagoon, where mean salinity of seepage water was 25 (measured incidentally in this study).

The bottoms at the sites inside the lagoon are dominated by fine sand, whilst the seabed at site-3 outside the lagoon consists of sand to gravel. The water depths (referred to mean tide sea level; sea chapter 3.7.2) at site-1, site-2 and site-3 were 3.42 m, 3.27, and 3.20 m, respectively. The maximum depth in the lagoon was 9 m relative to the Extreme Low Water at Spring Tide (ELWS). The water depths at the entrance of the lagoon varied from 1.46 meter to 6.6 meters (referred to MSL). The total width of the entrance is 42 meters.

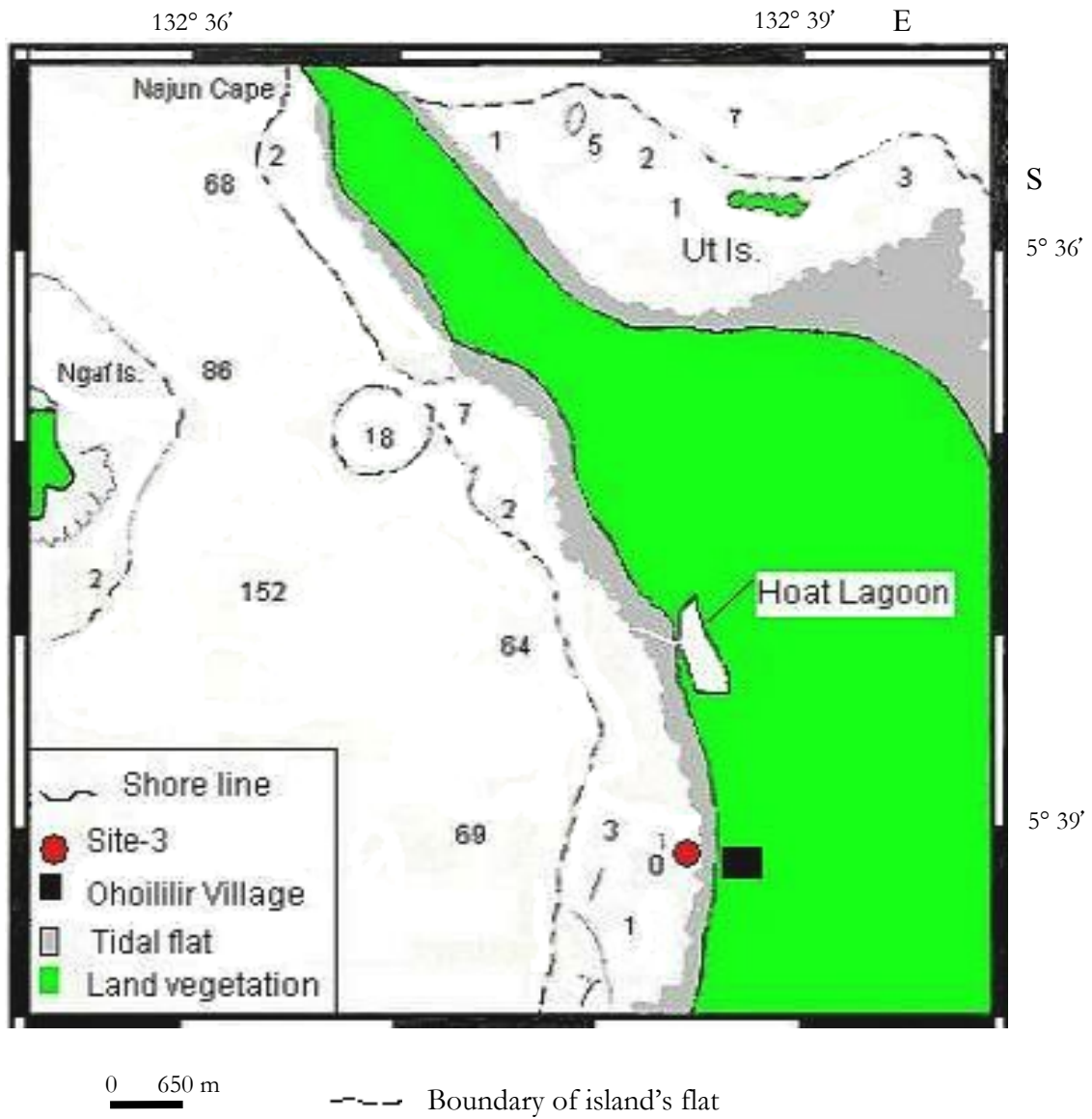


Figure 2a. Map of the adjacent shore and the lagoon, including location of site-3 and depth distributions (m) in LAT condition. Scale of the map: 1: 65000.

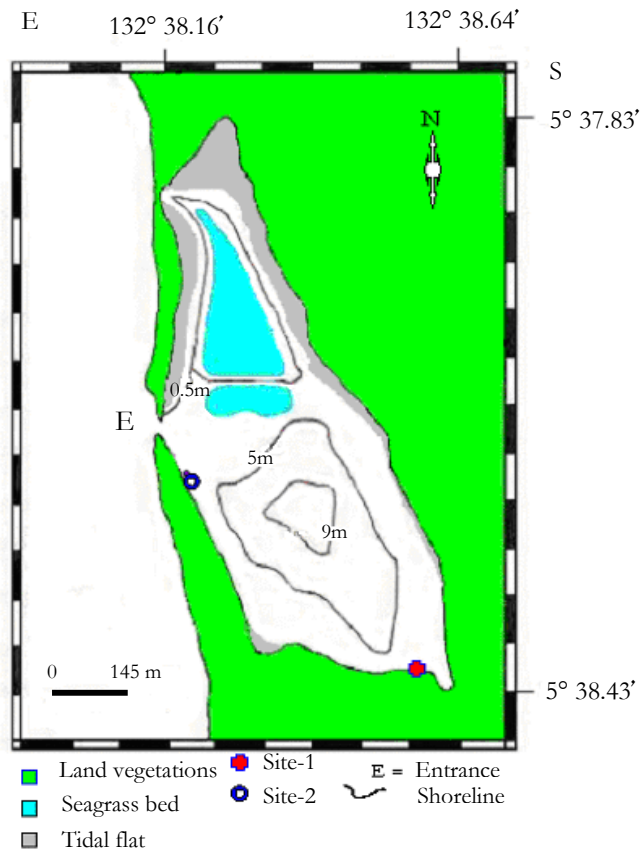


Figure 2b. Map of the Hoat Lagoon with depth and seagrass bed distributions, as well as locations of site-1 and site-2. Scale of the map 1:14500

3. MATERIAL AND METHODS

3.1. General approach

This study consisted of field investigations, laboratory analyses and the collection of environmental background data (Figure 3). The field study on the patterns and speeds of surface currents in the lagoon, using the drift method, were done in August 2001.

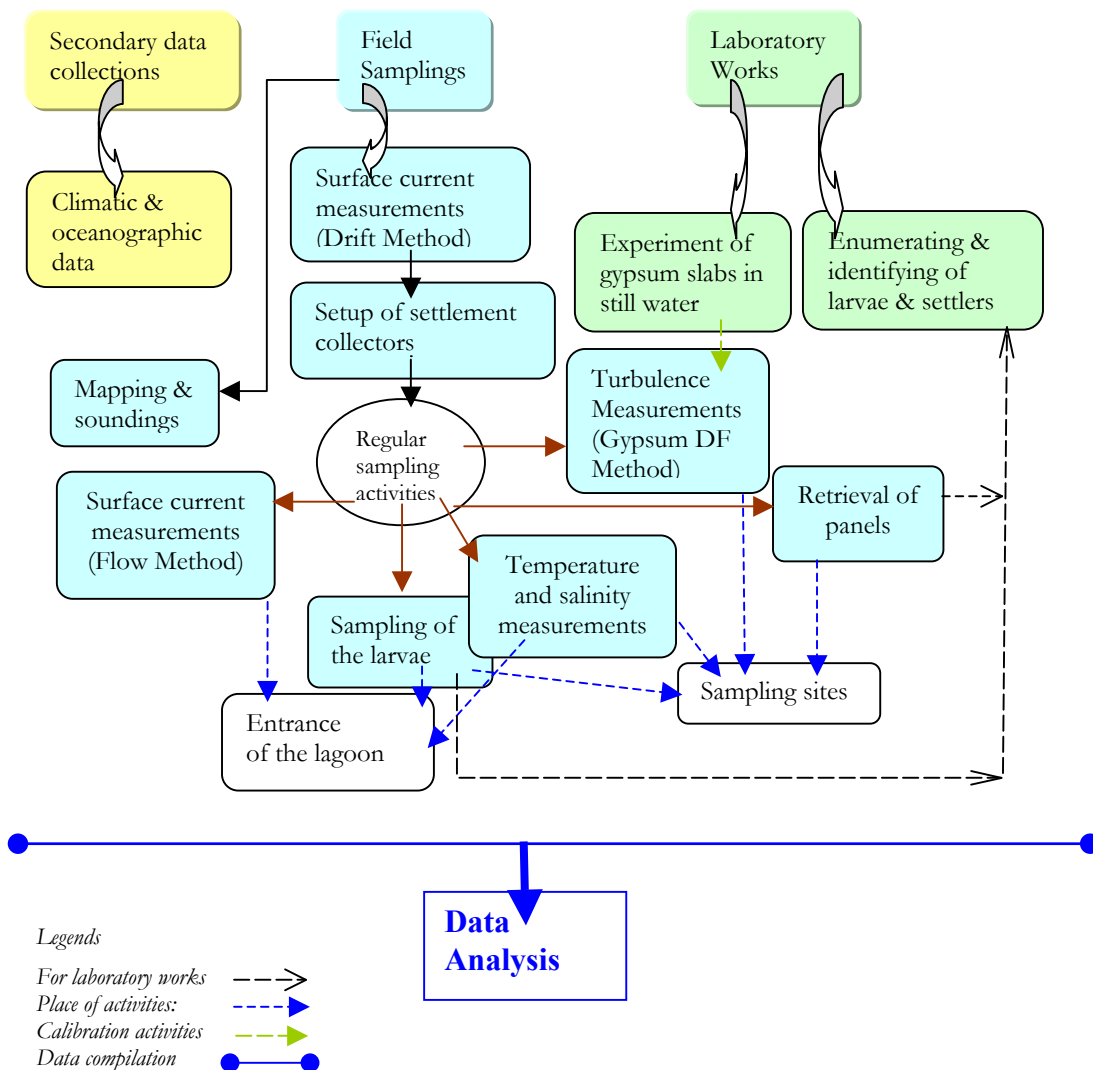


Figure 3. Summary of the research activities during 25 August 2001 to 22 May 2002

Samplings of mollusc larvae and settled post larvae (settlers) at the three study sites were done simultaneously with the measurements of salinities, temperatures, and surface currents using the flow method at 15 dates from 18 September 2001 until 22 May 2002. Intervals between sampling dates ranged from one week to one month. Each sampling

was carried out within 2 hours per tidal phase in order to minimise the effect of natural variability due to water level differences.

The laboratory work consisted of the identification and quantification of pelagic larvae collected with the plankton net and the settlers on the settlement collectors. Besides, a microcosm experiment was conducted to measure the diffusive dissolution rates of gypsum slabs in still water during 4 days.

Mapping and depth soundings of the lagoon and the adjacent shore, as well as collections of the climatic and oceanographic data, was done independently from the regular sampling schedule.

3.2. Assessment of surface current patterns using the Drift Method (Lagrangian approach)

The patterns and speeds of the surface currents at the study sites were investigated on 25 August 2001 by means of two mini drogues. The design of the drogues was a mimic of the well-known holey sock drogue but their size was smaller (Figure 4). The drogues consisted of a 1 meter PVC tube, the upper part of which was connected by three stainless wires of 20 cm length to a swivel, which in turn was connected by three other stainless wires of 20 cm length to a red plastic ball which was 20 cm in diameter. The bottom part of the PVC tube was also connected with three stainless wires of 20 cm length to a swivel, which was linked to a sinker by a 5 cm stainless wire. Two drogues were released both inside the lagoon and outside the lagoon and both during ebb and flood tides, respectively. The drifting paths of the drogues were used to assess the patterns and velocities of surface currents. The paths were determined by following (tracking) the route of the drogues using an outboard motor boat. The exact positions of the drogues were acquired every 30 minutes using GPS (Garmin GPS-48 with a spatial resolution of 1-5 meters (for DGPS correction) and 15 meters (for RMS correction)). The boat used for the tracking was fitted with a 15 Horse Power (HP) outboard. It did not disturb the relative disposition of the drifters. Nevertheless, a preliminary study showed that it was necessary to deploy the drifters at least 10 m apart from the boat to minimize the risk of convergence and collision.

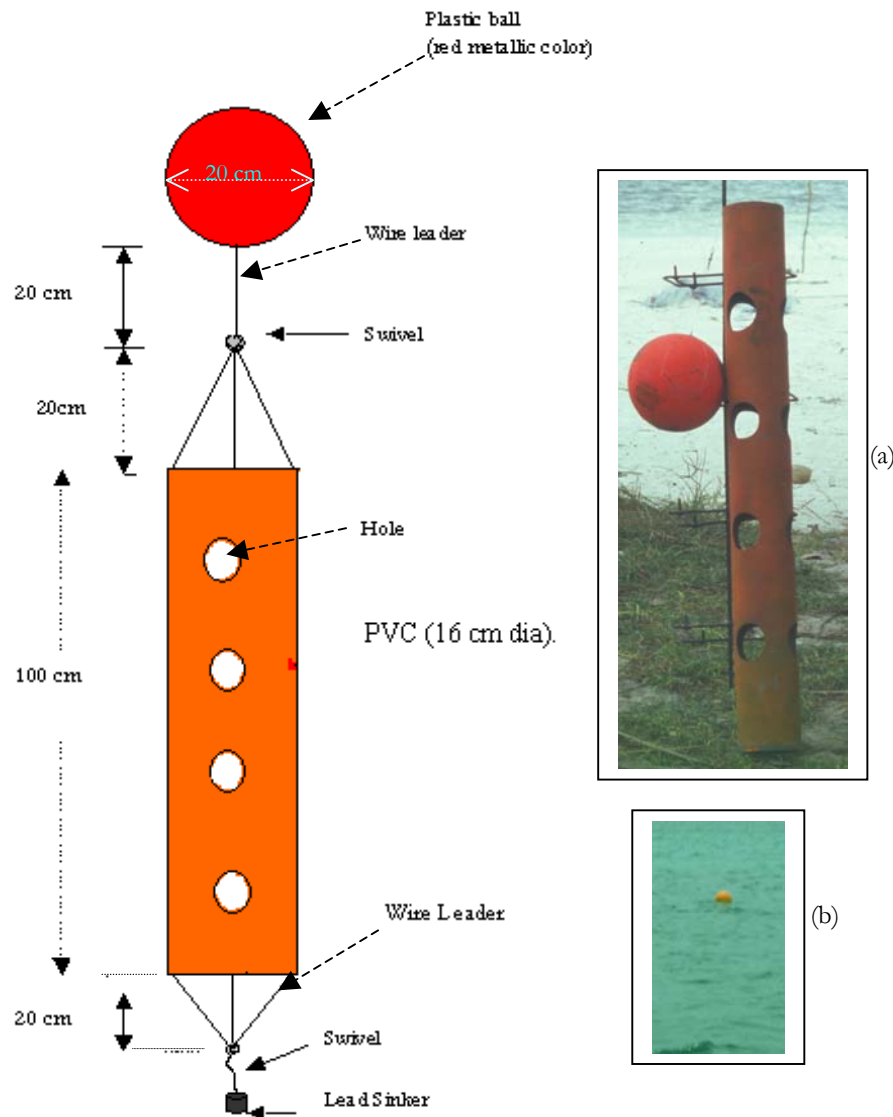


Figure 4. Design of the holey sock model drogue (drifter) with insets original pictures of the drifter used in the field sites (a & b).

3.3. Measurement of Surface Currents using the flow method (Eulerian approach)

The flow method was applied to measure the current speeds at the three study sites and at the entrance of the lagoon by means of a mechanical flow meter. The meter used featured a high-resolution rotor for low speeds (model 2030R2), i.e. velocities ranging from approximately 2 cm s^{-1} ($1/25 \text{ kn}$) to 100 cm s^{-1} (2 kn). The flow meter was placed about 30 cm under the sea surface and measurements were carried out during 30 seconds with five replications.

3.4. Application of the gypsum slab technique for measuring turbulence intensity

3.4.1. Preparation of the gypsum slabs

The measurement of the dissolution rate of gypsum (CaSO_4) slabs was used as an inexpensive comparative survey technique to estimate mean turbulence intensities. The use of gypsum slabs (clod cards) was first described by Dotty (1971) and has since been adopted as a standard method recommended by the Fifth International Marine Biological Symposium. The gypsum slabs used in this study for measurements over periods of 24-48 h were made as moulds in standard plastic ice-cube trays. About 45 ml of water was used for each 50 g of CaSO_4 . When mixing gypsum powder and water, care had been taken to avoid introducing large air bubbles that may remain after the mixture hardened, since such voids are a major source of error in the data obtained. When the slabs had set, the nearly dry slabs were removed from the ice cube compartments and air dried, then weighed until the stable weights were recorded (initial weights). Each individual slab was coded and kept in a small plastic bag, before deployment.

3.4.2. Calibration of gypsum slab dissolution in still water

The application of the gypsum slabs technique consisted of two stages, the first carried out in laboratory to get the diffusive dissolution rates of the gypsum slabs in a still-water condition (as a control), and the second conducted in the field. In the laboratory, ten pre-weighed gypsum slabs were submersed for four days in a chamber containing 250 liter of seawater from field study. The seawater was changed every day at the same time. The salinity of the seawater was regularly monitored using a refractometer. The temperature was maintained by placing a 100 Watt-bulb lamp 1 m above the chamber in daytime to mimic the temperature in the field. After the fourth day, the slabs were retrieved, rinsed with cleaned freshwater, air dried, and weighed until stable weights were reached to get the diffusive dissolution factor in no movement condition.

3.4.3. Application of the gypsum slab technique in the field

In the field, gypsum dissolution measurements were done 2 times: (1) from 17 to 18 February during rough sea state (high waves, strong winds), and (2) from 10 to 11 March during calm sea state (no waves, very weak winds). A pair of the pre-weighed gypsum slabs

was deployed at a given heights above the sea bottom (i.e., 0, 0.25, 0.5, 0.75 and 1.0 m (Figure 5).

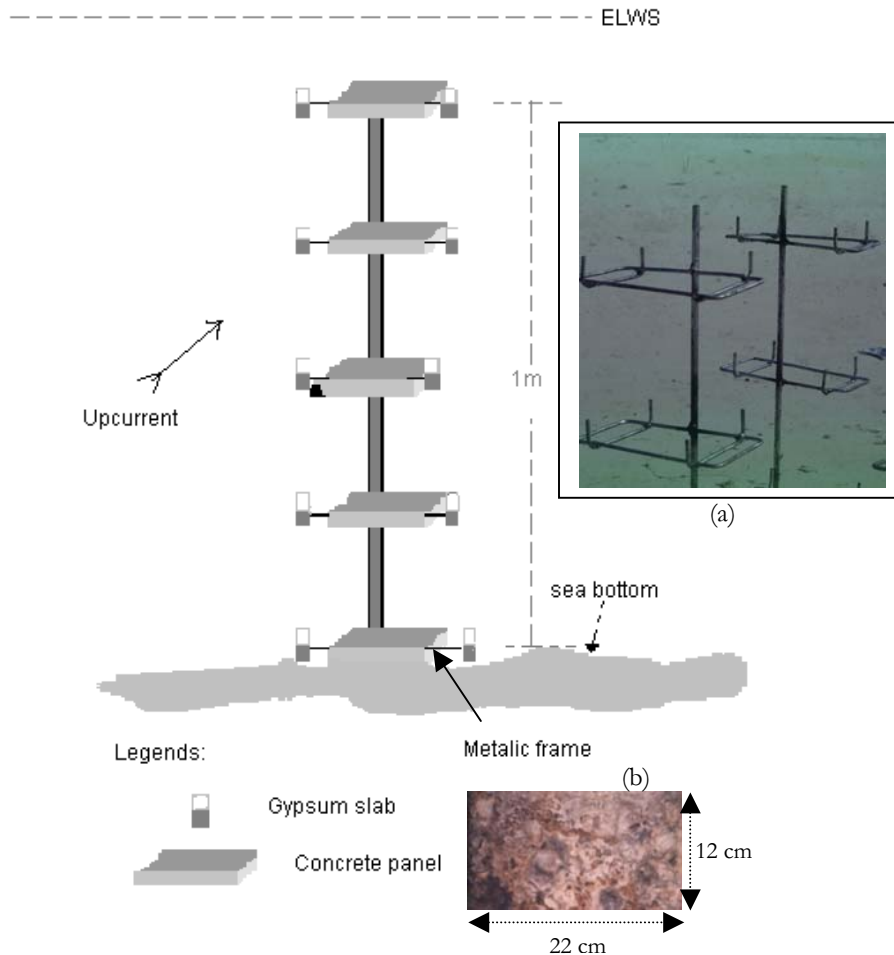


Figure 5. Design, dimensions, and set-up of a unit settlement collector placed at the three study sites with insets of original picture of the metallic frame (a) and the panel (b)

Upon retrieval of the slabs after 24 hour deployments, they were rinsed with freshwater, air-dried and weighed to get their weight losses, in order to calculate the advective dissolution rates of the gypsum in relation to the diffusive dissolution rates determined at still water condition.

3.5. Measurement of water properties

The basic water properties, such as temperature, salinity and seawater density, were determined on regular basis. The temperature was measured by means of a protected thermometer with an accuracy of $\pm 0.01^\circ$. The thermometer was lowered down to mid

water and was left there for 10 minutes before reading. For salinity measurements, water samples were taken from sea bottom to sea surface shortly after the larval samplings using the receiver of the plankton net. Salinities were measured using a refractometer. Each measurement consisted of five replications, values are expressed as total salts in g per kg.

3.6. Sampling of mollusc larvae and settlers

3.6.1. Mollusc larval samplings

The plankton net used for larval sampling had an opening of 0.4 m, a length of 1 m and a mesh size of 100 μ . At the centre of net mouth ring, a mechanical flow meter with a standard rotor (model 2030R) was attached with two monofilament wires, measuring current speeds ranging from approximately 10 cm s^{-1} (1/5 knots) to 7.9 m s^{-1} (15 knots). The plankton net was lowered vertically to the bottom. Therefore, a certain technique was applied to stop the rotor during the lowering toward the bottom to avoid reading errors. The net was vertically hauled to the surface after it touched the bottom. The haul time was recorded using a stopwatch.

At each of the 15 sampling dates between 18 September 2001 and 22 May 2002, samples were taken at each study site (Figure 2a and b) and at the entrance of the lagoon (Figure 6). Samples of the larvae were put into labelled bottles and preserved with 4 percent formaldehyde solution.

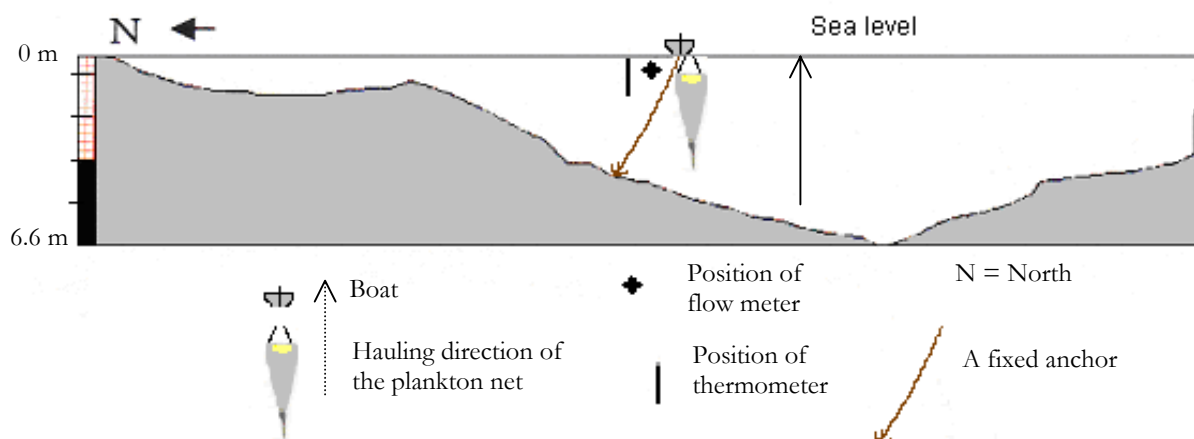


Figure 6. Sampling activities at a fixed anchor in the middle of the lagoon's entrance

3.6.2. Set-up of settlement collectors and samplings of the settlers

Sixty-six settlement collectors with a total of 330 cement panels were used to collect settlers. Each collector consisted of five panel. The panels were positioned on the metal rack at five different heights above the sea bottom (0 m, 0.25 m, 0.5 m, 0.75, 1.0 m). The length, width and depth of a panel were 22 x 12 x 1 cm, respectively. The panels were placed oriented parallel to the dominant direction of the sea current (Figure 5). Twenty-two settlement collectors (110 panels) were placed at each of the three study sites on 11 and 12 September 2001. Concomitantly to the plankton hauls (see chapter 3.6.1), five collector panels (one from each height above the sea floor) were randomly retrieved at each study site at 15 dates between 18 September 2001 to 22 May 2002. The time intervals between the sampling dates ranged from 6 to 48 days, the duration of exposition of the collector panels ranged from 6 to 253 days (Appendix 1). Most panels were sampled in a 14-days interval, but such a regular sampling schedule could not be kept up throughout the entire study period because of constraints due to logistic problems and weather condition. Upon retrieval, the panels were put into labelled plastic bags and preserved with 4 percent formaldehyde solution for laboratory analyses.

Unsystematic samplings (free collection) of benthic molluscs were also done at the study sites in September 2001 to verify the results of larvae and settler samples identified.

3.7. Other measurements and data collections

3.7.1. Measurement of the Total Suspended Sediment (TSS)

The upper sides of the collector panels were mostly covered by sediments after some exposition time. These sediment coatings were assumed to control the numbers of settlers on the upper sides of the panels and, therefore, the sediment fluxes (TSS) at the three sites were measured using three sediment trap units. Each unit consisted of two PVC tubes of 24 cm length and an inner diameter of 8 cm (i.e., an opening of 0.05 m²). One tube was placed directly at the sea bottom, the other one was deployed in the water column with its opening 1 m above the sea floor. Each unit was submersed at each study site for two weeks in November 2001. Upon retrieval, the content of the sediment traps were gravity filtered through a 0.5 µm cartridge membrane filter (Millipore), air dried and weighed, using a digital balance, to assess the sediment flux (mg m⁻²d⁻¹) in the vicinity of settlement collectors.

3.7.2. Mappings and Depth soundings

Mapping and depth soundings were conducted in the lagoon and off the adjacent shore (including the measurement of the cross sectional area of the lagoon's entrance) on 6 October 2001. The mapping of the shoreline was carried out by means of GPS. The depth soundings were done during extreme low water of spring tide (ELWS) from aboard a motor boat using plumb line (20 m) at GPS-determined positions which were distributed at 50 m intervals along the zigzag tracks. Simultaneously, data on the local tidal characteristics (timing, sea level heights, ranges) were collected using a labelled tidal pole during 24 hours with an hour interval sampling to check previous tide reports (e.g. Wirtky, 1961).

The mean high water of spring tides (MHWS), mean high water of neap tides (MHWN), mean sea level (MSL), mean low water of neap tides (MLWN), and mean low water of spring tides (MLWS) were identified based on data of tidal measurement done by Navy station-Tual (Appendix 2). While the extremely high water of spring tides (EHWS), the extremely low water of spring tide (ELWS) were identified by levelling the tidal mark in beach wall, also was confirmed by knowledge of indigenous people. The lowest astronomical tide (LAT) and highest astronomical tide (HAT) in this study were referred to the MHWS and the LHWS, respectively.

3.7.3. Collecting of climatic and hydrological data

Climatic data were obtained from the Meteorology and Geophysics Agency in Langgur, Kai Islands. The data include rainfall, number of rainy days, air temperatures, wind components (speed and direction), as well as air humidity from September 2001 to May 2002. Oceanographic data (daily tide levels and time) were taken from the Admiralty Tide Tables 2001-2002 (Tual, Kai Islands), produced by the Indonesian Naval Hydro-Oceanographic office, Jakarta.

3.8. Data Treatment and Analysis

3.8.1. Enumeration of the mollusc larvae

The replicate samples of planktonic mollusc larvae taken at each site were pooled and then treated using sedimentation techniques to concentrate the organisms prior to further analyses. Before examining them, they were filtered through filter papers (Whatman no 40). The filtered larvae were then put into a measuring cylinder holding 450 ml of water (V). The water in the cylinder was gently stirred until completely mixed and a sub sample

of 15 ml (V'') was poured into an open Counting Chamber (a modified Bogorov Chamber) of 12 cm length, 5 cm width, and 0.5 cm depth. The organism in the samples were identified using keys published by Newell and Newell (1967), Wickstead (1965), and Yamaji (1969). The larvae in the concentrated sub sample were counted under a dissecting microscope with a magnification of 20x to 40x or a compound microscope with a magnification of 100x when the identification was questionable. A mild detergent solution was placed in the chamber before enumeration to reduce movements of the larvae. The densities (D) of the larvae were calculated using the following formula (Anonymous, 1992a):

$$D = \frac{C * V'}{V'' * V'''} \quad (\text{ind m}^{-3})$$

Where
 C = number of organisms counted
 V' = volume of the concentrated samples = 450 mL
 V'' = volume counted = 15 mL
 V''' = volume of water filtered by plankton net (m^3)

The volume of water filtered by the plankton net (V''') was calculated using the following step formulas (Anonymous, 1992b);

$$A. \quad X \text{ (m)} = \frac{\text{Rotor Revolutions} * \text{Rotor Constant}}{999,999}$$

Where, the rotor constant of the mechanical flow meter (model 2030R) was 26,873.

X = distance travel of current (m)

$$B. \quad V''' \text{ (m}^3\text{)} = \pi * (\text{Net radius})^2 * X \text{ (m)}$$

3.8.2. Enumeration of the mollusc settlers

Post-larval settlers were enumerated on both the upper and under surfaces of each collector panel. The panel margins (4 cm of the upstream side, 2 cm of both long sides and 2 cm of the downstream side) were excluded to avoid edge effects (Mullineaux and Butman, 1990). The rectangular sample areas of 128 cm^2 on each panel side (16 x 8 cm)

were divided into 32 squares (2 x 2 cm grids) to cease enumeration of settlers. The numbers of organisms counted at both surfaces were added. The settlers were identified to the lowest taxonomic level possible according to Abbot (1974). In case of high abundance, a sub-sample (8 of 32 grids) was analysed and raised to the entire sample. *Petalonchus erectus* (a gastropod) was excluded in this study, since it only occurred on the panels but not in the larval samples

3.8.3. Analysis of the surface currents from the drift method

The surface current pattern was described based on the GPS-acquired drift paths of the drogues, plotted on the map using the Surfer mapping Package version 8.0 (Golden Software Inc.). Current speeds were computed from the drift distances of the drogues divided by the time intervals between the GPS position fixes.

3.8.4. Analysis of the mollusc larval fluxes at the entrance of the lagoon

The larval fluxes with the inflowing and outflowing water through entrance of the lagoon were calculated using the following formula:

$$LF \text{ (ind. s}^{-1}\text{)} = D * v$$

$$v = V * A$$

where,

- D = density of the larvae (ind.m⁻³)
- v = water volume transport through the entrance (m³s⁻¹)
- V = flow speed (ms⁻¹)
- A = cross sectional area of the lagoon's entrance (139 m²)

The cross-sectional area (A) of the entrance of the lagoon was estimated using a grid system method. The depths of the entrance were obtained from soundings at 5 m distance intervals across the entrance. The depth profile of the entrance (Figure 6) was plotted on graphic paper with scale of 1:100. The plotted area was divided into rectangular areas of 1 x 1 cm² (grid). The area of the plotted entrance cross-section in cm² is equivalent the cross-sectional area A of the entrance in m². The flow speed through the entrance was assessed with the mechanical flow meter, equipped with the high-resolution rotor (model 2030R2; rotor constant = 51,020).

3.8.5. Analysis of the turnover time of the watermass of the lagoon and percent of larval retention in the Lagoon

The turnover time of the water body of the lagoon is presumed to control the settlement rates of post larvae in the lagoon. The turnover time is defined as the ratio of volume of the lagoon to the volume flux entering or leaving the lagoon (Gallagher et al., 1971). Thus,

$$\tau = \frac{\varpi}{v} * 86400$$

where, τ = turnover time (days)
 ϖ = water volume of the lagoon (m³) with reference to mean sea level (MSL)
 v = water volume transport of outflow through the entrance (m³ s⁻¹)

In this calculation, evaporation, precipitation, and river runoff are assumed to not significantly affect the water volume of the lagoon during the study. Thus, they were neglected.

The net of larval transport was examined to find out how many percent of the larvae were retained in the lagoon after a tidal cycle, using following formula:

$$R (\%) = \frac{L_{Fi} - L_{Fo}}{L_{Fi}} * 100$$

Where, R = percent larval retention (%)
 L_{Fi} = inflow larval transport (ind s⁻¹)
 L_{Fo} = outflow larval transport (ind s⁻¹)

3.8.6. Analysis of water properties

Seawater density (as a function of temperature and salinity) was calculated using the online computer package Seawater Library version 1.2e by Phillip P. Morgan CSIRO 2003 (<http://kot.ucsd.edu/mathlab/oc1.htm>).

3.8.7. Analysis of turbulence intensities

The relative weight loss of the gypsum slabs deployed in the field over a full tidal cycle, the so-called dissolution factor (DF) was used to determine the turbulence intensities within the study area. The DF provides a reasonable index to compare results among the slabs deployed at different heights above the sea bottom. It is determined by dividing the weight loss of gypsum exposed in the field by the weight loss of gypsum in still water of the same temperature and salinity (Doty, 1971):

$$DF = \frac{[M_o - M_1] \text{ field}}{[M_o - M_1] \text{ still}}$$

Where, M_o = initial weight
 M_1 = Weight after exposure and drying

DF values can range from about 1 (still water) to 12 or 13 at extreme turbulences (Culliney, 1994). In this study, the means of the weight losses of a pair of deployed slabs at a given height above the sea bottom were used.

3.8.8. Analysis of the particulate mass fluxes of the Total Suspended Sediment (TSS)

The TSS flux (Tf) is calculated using following formula (Baker *et al.* 1988):

$$Tf = (mw - fw) / (d * A) (\text{mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1})$$

Where, mw = mass weight (mg)
 fw = filter weight (mg)
 d = days deployed
 A = cross-sectional area of the trap

3.8.9. Diversity of the mollusc larvae and settlers

The diversity indicates the degree of complexity of the community structure. It is a concise expression of how many species occur and how individuals are distributed among the species (Omori and Ikeda, 1985). It was calculated using the Shannon-Weaver diversity index (H'), using logarithms to the base e in the calculations (Shannon & Weaver, 1947):

$$H' = - \sum_{i=1}^n p_i (\ln p_i),$$

Where,

$$p_i = n_i / N$$

n_i = the number of individuals of a particular group taxon or species

$$N = \text{total number of individuals} = \sum_{i=1}^s n_i$$

3.8.10. Statistical and Multivariate Analyses

Prior to statistical tests, homocedasticity (homogeneity of variances) tests were applied to determine whether parametric or nonparametric statistics should be used. If the observed F value was smaller than F table at $P = 0.05$, the variances were assumed to be homogenous (homocedastic), and a parametric test was used (Bakus, 1990).

t- Test

The t-test was applied to test the significance of the differences between mean inflow and outflow speeds, and mean larval influxes and outfluxes.

ANOVA

One-way ANOVA was applied to compare the means of each of the following factors among the three study sites: temperatures, salinities, seawater densities, turbulence intensities (at rough and calm states), and densities of mollusc larvae. Post-hoc Tukey (HSD) tests were applied for multiple comparisons of pairs of means with equal sample size.

Pearson's correlation Test

Pearson's correlation coefficient was used to assess whether there is a significant relationship between two or more variables:

- It was applied to determine whether rainfall (mm), frequency of rain (days), air temperature (°C), insolation (%), air humidity (%), wind speed (kn), wind direction (degree), air pressure (mb) as local climatic factors affected the salinity and temperatures at the three study sites.

-
- It was applied to determine whether larval density, net larval transport, and seawater density affect the settlement density inside the lagoon and at the adjacent shore.
 - It was applied to assess the significance of the relationship between larval influx and larval outflux, net larval transport, seawater density and larval densities and settlement density in the lagoon.
 - It was applied to determine whether the larval influx was significantly associated with the larval density in the water column off the adjacent shore
 - Finally, it was applied to determine whether the turbulence intensities and the positions of panels above the sea bottom (0, 25, 50, 75, and 100 cm) at each study site and among the three study sites had an effect on the number of settlers on the collector panels.

Spearman's Rank Correlation Test

The Spearman's rank correlation test was used to assess whether there were significant relationships:

- Between inflow and outflow volume transports, inflow and outflow larval transports and the larval retention in the lagoon
- Between the durations of tidal phases, minimum and maximum water levels, tidal asymmetry, wind speed and wind directions and the inflow and outflow larval transports
- Between inflow current speeds and maximum wind speeds
- Between the submersion times of the panels under the water and the numbers of settlers.

Kendall's tau correlation Test

Kendall's tau correlation test is used to assess whether there were significant relationship:

- Between the maximum wind speeds and density of larvae at adjacent shore

Multivariate analyses

Multidimensional Scaling (MDS) ordination and cluster analysis were applied to assess the degree to which the sites differ in the composition of species of mollusc larvae. MDS (Kruskal & Wish, 1978) is a non-parametric method, which use the rank order of similarities between samples rather than their absolute values. The ordination procedure results in a scatter plot in which a point represents each sample. The distances between the points follow as good as possible the same rank order as the pair-wise dissimilarities in species composition between samples. The extent to which this is realised in the plot is indicated by a 'stress' coefficient. The cluster analysis depicts the resemblance pattern in a dendrogram. The clustering method used in this study was the 'space conserving' or group average linkage and used to assess the degree to which the sites differ in species composition of settlers. Both MDS and cluster analyses are based on a matrix of similarities between each pair of samples calculated using the Bray-Curtis similarity coefficient (Bray-Curtis, 1957; Anderson and Underwood, 1994).

All multivariate analyses were done using the PRIMER program package (courtesy of M.R. Carr and K.R. Clarke, Plymouth Marine Laboratory, UK). Other statistical analyses were carried out using SPSS 11.

4. RESULTS

4.1. Environmental setting

4.1.1. Dimensions of the Hoat Lagoon

The length of the Hoat lagoon is ~1200 m, and its maximum width is ~450 meters. The length of the lagoon's shoreline is approximately 3 km, resulting in an area of 0.56 km². Water depths of the lagoon (referred to the lowest astronomical tide) ranged from 0.5 to 9 meters. The average depth was 4.76 m. The deepest point was located in the middle of the southern part of the lagoon (Figure 2a). In contrast, most of the northern part of the lagoon is drained during the lowest water of spring tide.

The width of the lagoon's entrance is 42 m, its depth varied from 1.5 to 6.6 m and was on average 3.79 m, resulting a cross-section area of 139 m², referred to MSL (Figure 7). Total volume of the lagoon's water mass (referred to the MSL) was approximately about 2.6 million m³.

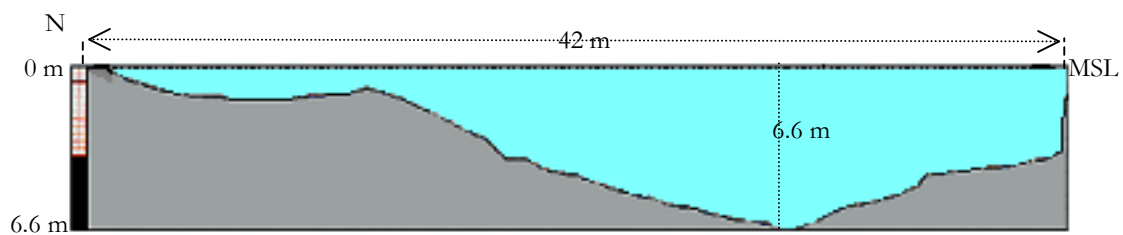


Figure 7. Cross section of the entrance of the Hoat Lagoon (Landward view)
MSL = Mean sea level; N = North direction; = cross section area (139m²)

4.1.2 Water properties

4.1.2.1. Temperatures

The sea surface temperatures at the three sites (Figure 8a) and at entrance of the lagoon (Figure 8b), obtained at 15 sampling dates from 18 September 2001 to 22 May 2002, ranged from 27°C to 33°C. The lowest temperatures were recorded at site-3 on 18 September and 14 October at site-1 on 01 October 2001. The highest temperature was recorded at adjacent shore on 25 November 2001. The mean temperatures at site-1, site-2, and site-3 were 29.4°C, 29.5°C, and 29.4°C, respectively. The largest variation in temperatures (mean = 29.42±1.39) was recorded at the adjacent shore, and ranged from 27°C to 33°C. The lowest variation (mean=29.45±1.06) was recorded at site-1 and ranged

from 27°C to 31°C. While, the temperatures variation at site-2 was intermediate (mean = 29.48 ± 1.06) and ranged from 28°C to 31°C.

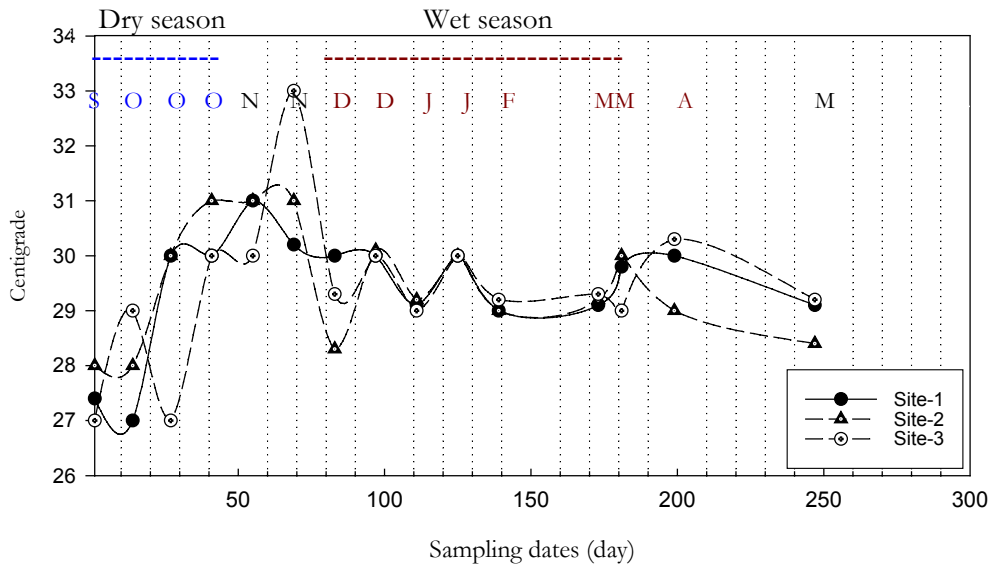


Figure 8a. Temperatures (centigrade) in Hoat Lagoon (site-1 and 2) and its adjacent shore (site-3), obtained at 15 sampling dates from 18 September 2001 (the 1st day) to 22 May 2002 (the 247th day) over the dry and wet seasons.

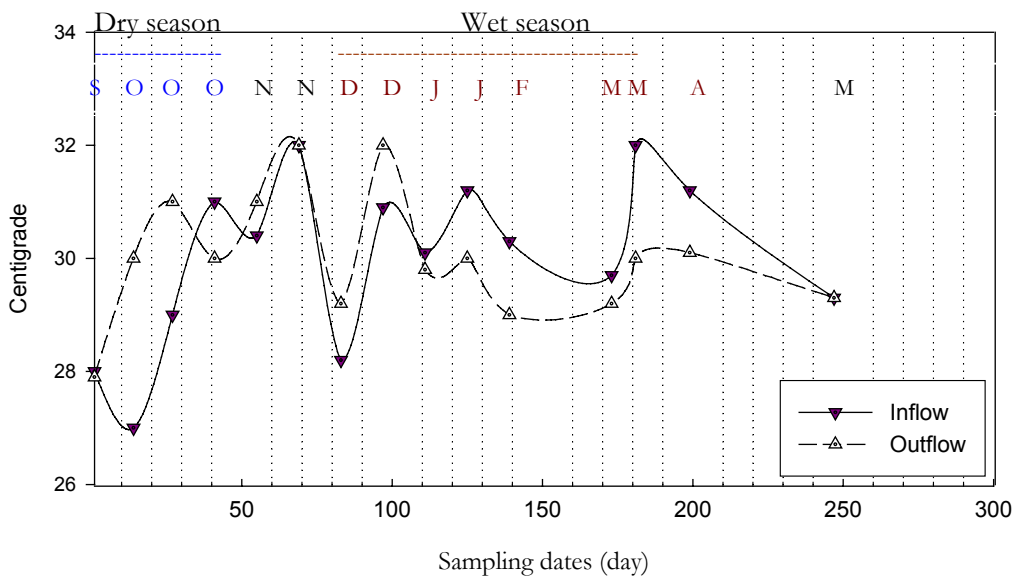


Figure 8b. Inflow and outflow temperatures (centigrade) at the entrance of the Hoat Lagoon, obtained at 15 sampling dates from 18 September 2001 (the 1st day) to 22 May 2002 (the 247th day) over the dry and wet seasons.

The largest variation in temperature at the entrance of the lagoon (mean = $30.02 \pm 1.48^\circ\text{C}$) occurred during the inflow and ranged from 27°C to 32°C . The inflow temperatures were relatively higher than outflow temperature (mean = $30.03 \pm 1.11^\circ\text{C}$) and ranged from 27.9°C to 32°C .

ANOVA indicated that the mean temperatures among the three sites were not significantly different ($F = 0.991$; $df = 4, 70$; $p > 0.05$).

Moreover, the Pearson correlation coefficient indicated that the fluctuations in the seawater temperatures were significantly inversely correlated with fluctuation in wind speed ($r = -0.741$; $p < 0.05$; $n = 9$), i.e. an increased wind speed leads to a decreased sea surface temperature. Rainfall, number of rainy days, air humidity, insolation as well as air pressure were not significantly correlated with seawater temperature. Thus, the lower temperatures at the study sites on 18 September to 14 October 2001 in the dry season (Figure 8a and 8b) must be associated with the well-documented up-welling in the nearby Banda Sea that always brings colder water (Table 1) from greater depths to the surface during southeast monsoon.

Table 1. Monthly climatic data from September 2001 to May 2002, collected at the station of Meteorology and Geophysics Agency in Langgur, Kai Islands, which is ~ 15 km east of the study area

Month	Rainfall (mm)	No. rainy (days)	Air Temperature ($^\circ\text{C}$)	Insolation (%)	Air humidity (%)	Mean wind velocity (knot)	Max. wind velocity (knot)	Wind directions
September 2001	111	8	27.4	76	81	7	16	130
October 2001	87	6	28	75	84	3	16	150
November 2001	305	22	27.5	39	89	2	21	150
December 2001	547	27	26.9	28	88	5	18	290
January 2002	30.3	24	27.1	40	89	4	19	310
February 2002	204	23	27.6	70	87	7	27	310
March 2002	316	25	26.9	43	96	2	20	310
April 2002	372	20	27	56	87	3	16	130
May 2002	137	13	27.4	67	85	6	15	130

The relatively higher temperature on 28 October, 11 and 25 November 2001 coincided with the relatively higher air temperatures, high insolation, low rainfall, and very weak wind. Whereas, the decreased of temperature on 09 December 2001 until 17 March

2002 (wet season) and May (transitional period) coincided with the relatively stronger wind, and higher rainfall.

4.1.2.2. Salinities

Salinities measured at the three study sites (Figure 9a) and at the entrance of the lagoon (Figure 9b) at 15 sampling dates during the study ranged from 27 (at site-1 on 25 November 2001) to 36 (at site-3 on 4 April 2002). Mean salinities at site-1, site-2 and sites-3 were 30, 30.5, and 36, respectively. Variations in salinities were highest at site-1, ranging from 27 to 34 (29.9 ± 1.82), intermediate at site-2, ranging from 29 to 34 (30.5 ± 1.45), and lowest at site-3, ranging from 31 to 36 (33.4 ± 1.40). Salinities in the lagoon (both at site-1 and 2) fluctuated concomitantly, and were relatively lower than that at the adjacent shore (site-3).

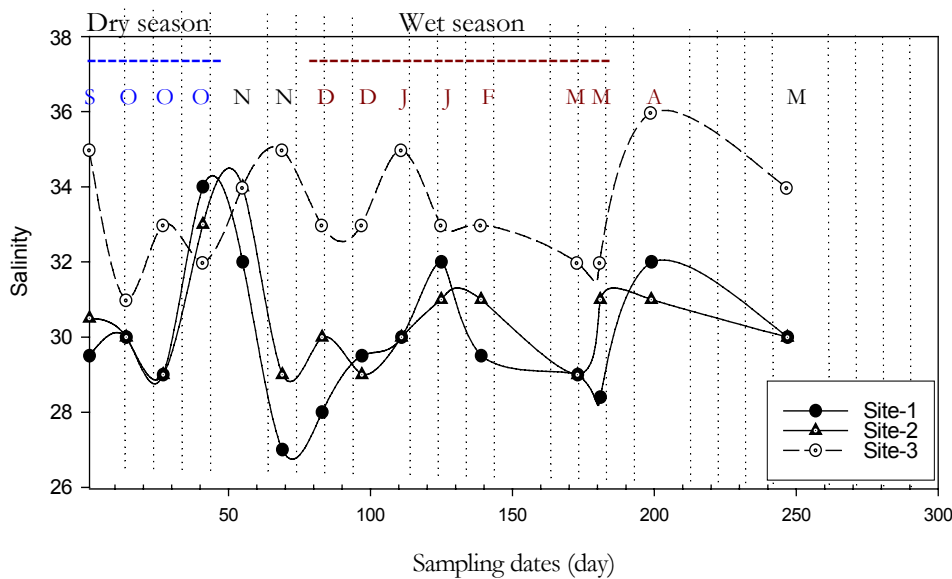


Figure 9a. Salinities in Hoat Lagoon (site-1 and 2) and at its adjacent shore (site-3), obtained at 15 sampling dates from 18 September 2001 (the 1st day) to 22 May 2002 (the 247th day) over the dry and wet seasons.

Inflow salinity at the entrance of the lagoon ranged from 30 (on October and 23 December 2001) to 34 (on 6 January 2002). Variations in outflow salinities (31.47 ± 1.24) were higher than in inflow salinities (32.84 ± 0.92). Inflow and outflow salinities ranged from 31 to 34 and 30 to 33, respectively.

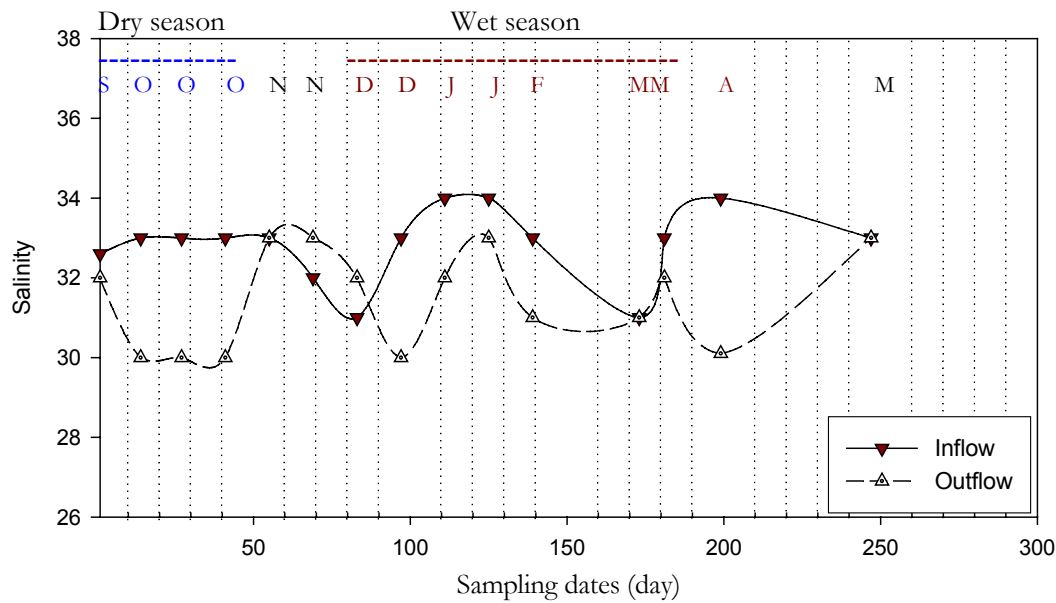


Figure 9b. Inflow and outflow salinities at the entrance of the Hoat Lagoon, obtained at 15 sampling dates during 18 September 2001 (the 1st day) to 22 May 2002 (the 247th day) over the dry and wet seasons.

ANOVA indicated that the mean salinities among the study sites were significantly different ($F = 16.477$; $df = 4, 70$; $p < 0.05$). Post hoc tests (Tukey tests) indicated that there were four site groups with regard to salinity: site-1 and site-2 (group-1), site-2 and outflow (group-2), outflow and inflow (group-3), inflow and site-3 (group-4).

The salinities were not significantly correlated with any of the climatic factors (Table 1). However low salinity values at the three study sites and in the inflow and outflow waters on 03 February, 09 and 17 March 2002 coincided with higher rainfall. Besides, the fluctuations of the salinities in the lagoon were probably also influenced by brackish ground waters, seeping out of the bottom of the lagoon, especially during ebb tides (e.g., 01 and 14 October 2001).

4.1.2.3. Densities

The seawater densities at the three study sites ranged from $1022.74 \text{ kg m}^{-3}$ at site-3 on September 2001 to $1015.71 \text{ kg m}^{-3}$ at site-1 on November 2001 (Figure 10a). The densities decreased from the adjacent shore towards the innermost side of the lagoon (site-1) followed the salinity pattern. The largest fluctuations in the densities occurred at site-1 (1018.89 ± 1.34), ranging from 1015.71 to 1021 kg m^{-3} , intermediate at site-3 (1020.74 ± 1.06),

ranging from $1019.09 \text{ kg m}^{-3}$ to $1022.74 \text{ kg m}^{-3}$ and lowest at site-2 (1018.55 ± 1.01), ranging from 1016.92 to $1020.65 \text{ kg m}^{-3}$.

Fluctuations in outflow seawater densities (1019.09 ± 1.03) were higher than in inflow seawater densities (1020.12 ± 0.72). Outflow seawater densities ranged from $1017.32 \text{ kg m}^{-3}$ to $1020.49 \text{ kg m}^{-3}$, inflow seawater densities from 1018.81 to $1021.24 \text{ kg m}^{-3}$ (Figure 10b).

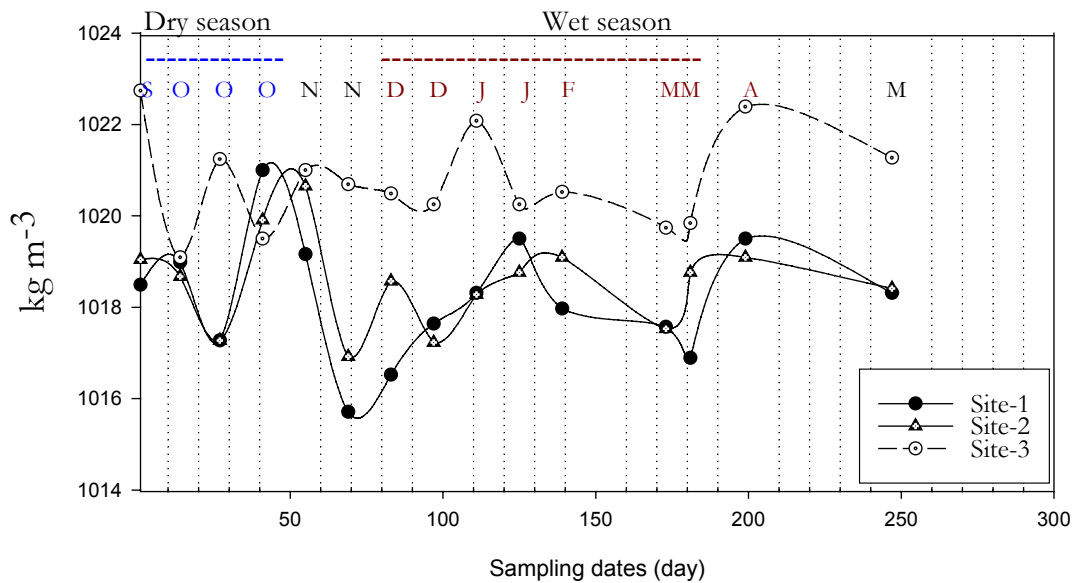


Figure 10a. Seawater densities (kg m^{-3}) in Hoat Lagoon (site-1 and 2) and at its adjacent shore (site-3), obtained at 15 sampling dates from 18 September 2001 (the 1st day) to 22 May 2002 (the 247th day) over the dry and wet seasons.

The mean seawater densities among the sites were significantly different (ANOVA, $F=15.502$; $df= 4, 70$; $p< 0.05$). Post hoc tests (Tukey tests) indicated that there were three groups with regards to seawater density: site-1, site-2 and outflow as group-1, outflow and inflow as group-2, and inflow and site-3 as group-3. Seawater densities were primarily controlled by salinity.

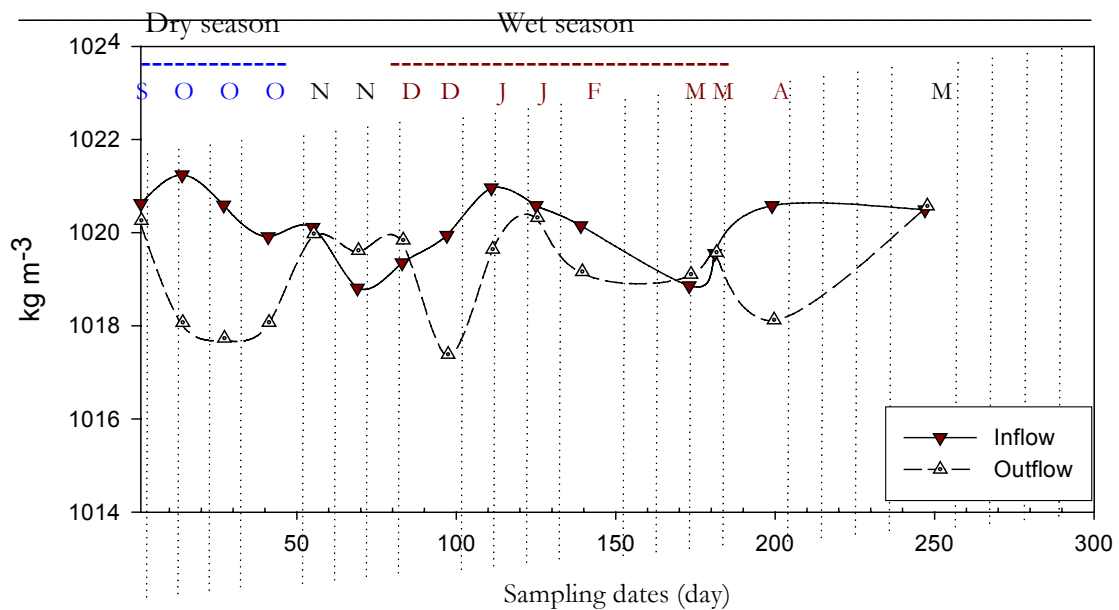


Figure 10b. Inflow and outflow water densities (kg m^{-3}) at the entrance of Hoat Lagoon, obtained at 15 sampling dates during 18 September 2001 (the 1st day) to 22 May 2002 (the 247th day) over the dry and wet seasons.

4.1.3. Tides

The tide in this study area is a ‘mixed predominantly semi-diurnal tide’, which is characterised by the occurrence of two high and two low waters in a day with unequal amplitudes. The tidal range between the highest astronomical tide (\sim MHWS) and the lowest astronomical tide (\sim LHWS) was 260.56 cm, and the range between the MHWN and MLWN was 130.28 cm. One-hour-interval measurements of tidal levels during 24 hours on 6 October 2002 (Figure 11) indicated that the maximum tidal range in the lagoon was 160 cm.

The range between EHWS and ELWS was 300 cm. It usually occurs at full and new moon periods in April and October and coincides with the spawning of the seaworm (*Eunice* sp.). Therefore it is called by local people ‘*metruat su*’, meaning ‘the tide of the worm’.

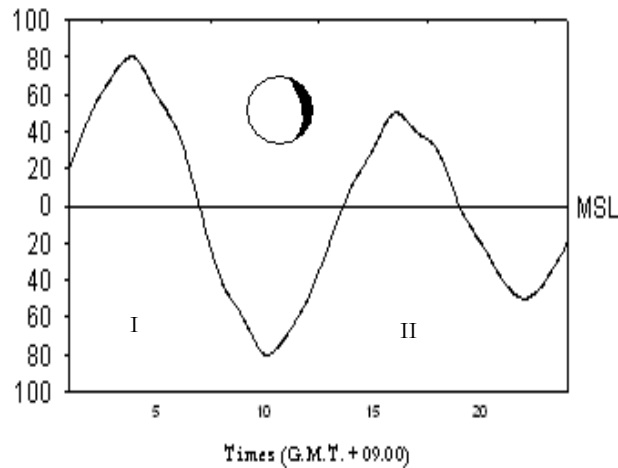


Figure 11. Curve of the tide levels and patterns at the study sites, measured during 24 hours with an hour interval of observation at the last quarter of lunar phase (6 October 2001), using a tide pole. MSL = Mean tide level; I = First tide; II = Second tide; \circ = the last quarter of lunar phase.

4.1.4. Surface current patterns in the Hoat Lagoon

The drift studies indicated that tide drive the surface currents in the Hoat Lagoon, since the changes of current directions and speed coincided with the tidal rhythms.

Once the main inflow current entered the lagoon during flood tide, two reverse marginal currents at both sides of the entrance flowed shoreward but were turned around after a certain distance to follow the main flow inwards. The main inflow current moved eastwards into the lagoon until it separates into a southward and a northward branch flowing along the eastern shore of the lagoon (Figure 12a).

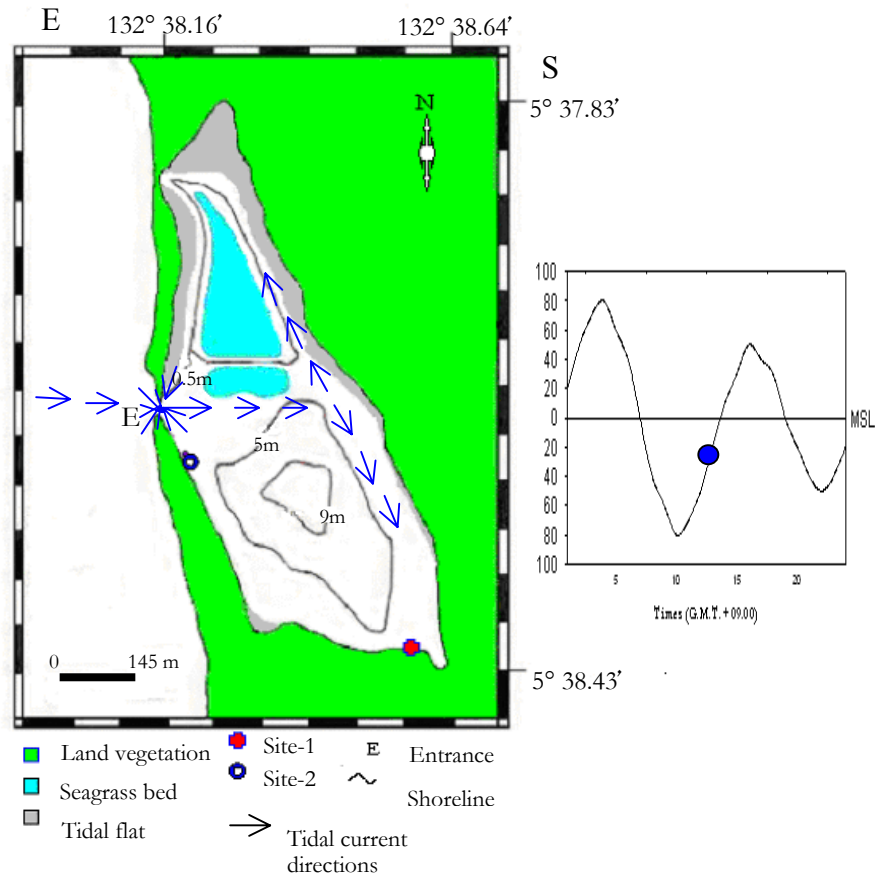


Figure 12a. Schematic sketch of the main surface flood current patterns through the entrance of the lagoon. Sea level data is plotted in graph in lower right corner of the map with the time of the current vector (\rightarrow) field estimate, denoted by the dot. Dimensions of the arrows are not to scale.

During ebb tide, the main outflow current (shortly after slack water) moved outward to the northwest along the shore line of the adjacent shore. However two reverse currents flowed at the edge of the entrance inwards until they were turned around after a certain distance to follow the main current outwards. These reverse currents disappeared after a certain state of the tide (Figure 12b).

In general, the surface currents in the lagoon were very weak. The mean speed was only 0.03 ms^{-1} .

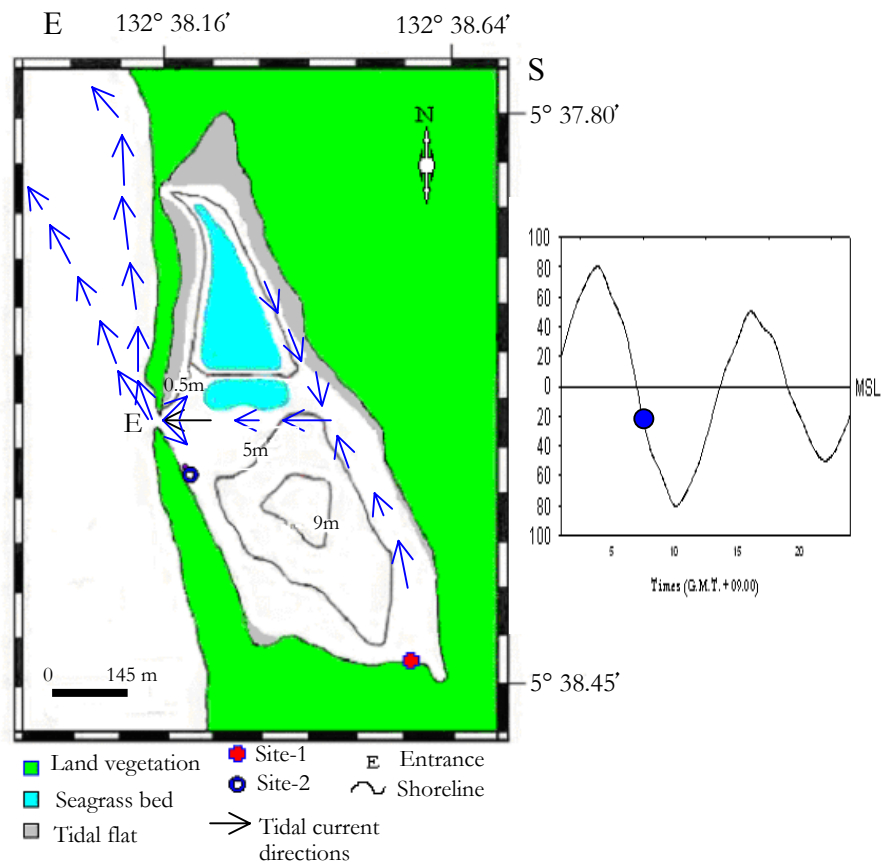


Figure 12b. Schematic sketch of the main ebb current patterns through the entrance of the lagoon. Sea level data is plotted in graph in lower right corner of the map with the time of the current vector (\rightarrow) field estimate, denoted by the dot. Dimensions of the arrows are not to scale.

4.1.5. Current speeds through the entrance of the Hoat Lagoon

Mean inflow and outflow current speeds through entrance of the Hoat Lagoon were 0.30 ms^{-1} and 0.28 ms^{-1} , respectively. The lowest inflow and outflow speeds were 0.06 ms^{-1} and 0.12 ms^{-1} (Figure 13), recorded on 23 December 2001 and on 6 January 2002, respectively. The highest inflow and outflow speeds of 0.68 and 0.45 ms^{-1} , respectively, both recorded on 09 March 2002. The inflow and outflow speeds were not significantly different ($t = 0.648$; $p > 0.05$; $n = 15$).

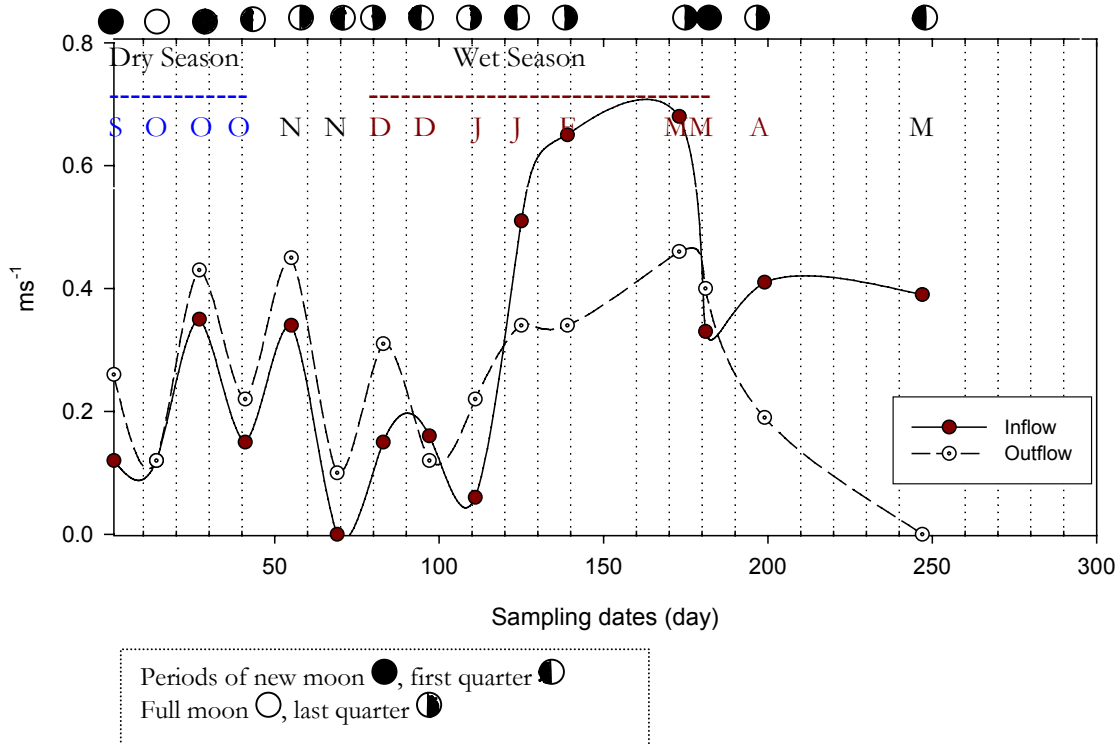


Figure 13. Curves of inflow and outflow speeds (ms^{-1}) at the entrance of the Hoat Lagoon, obtained at 15 sampling dates (days) during 18 September 2001 (the 1st day) to 22 May 2002 (the 247th day) in different lunar phases and over the dry and wet seasons.

The inflow and outflow current speeds increased significantly from January to reach a peak on 17 March 2002. The relatively high-speed inflow currents on 20 January, 03 February, and 09 March 2002 coincided with strong westerly winds in the wet season with maximum wind speeds of 19 to 27 knots (Table 1). The Spearman correlation coefficient indicated that maximum wind speeds during 20 January to 22 May 2002 have significantly affected the maximum inflow current speeds at the same period ($r = 0.9$; $p < 0.05$; $n = 5$).

4.1.6. Water mass transport through the entrance of the Hoat Lagoon

Inflow volume transport via entrance of the lagoon ranged from $8.2 \text{ m}^{-3} \text{ s}^{-1}$ on November 2001 to $93.1 \text{ m}^{-3} \text{ s}^{-1}$ on March 2002. Outflow volume transport ranged from $13.7 \text{ m}^{-3} \text{ s}^{-1}$ on November 2001 to $58.9 \text{ m}^{-3} \text{ s}^{-1}$ on October 2001 (Table 2). The mean inflow volume transport ($40.3 \text{ m}^{-3} \text{ s}^{-1}$) was greater than the mean outflow volume transport ($38.7 \text{ m}^{-3} \text{ s}^{-1}$).

Table 2. Inflow-outflow speeds (ms^{-1}), and inflow-outflow volume transports (m^3s^{-1}), obtained at 15 sampling dates (days) from 18 September 2001 to 22 May 2002. ST = speed under the threshold of current meter ($<0.02 \text{ ms}^{-1}$); N/A = not available; N/S = no sampling; A/L = accidentally lost

Date of samplings	Inflow speeds (m s^{-1})	Outflow speeds (m s^{-1})	Inflow volume transports ($\text{m}^3 \text{s}^{-1}$)	Outflow volume transports (m^3s^{-1})
18 September 2001	0.12	0.26	16.4	35.6
01 October 2001	0.12	0.12	16.4	16.4
14 October 2001	0.35	0.43	47.9	58.9
28 October 2001	0.15	0.22	20.5	30.1
11 November 2001	0.34	0.45	46.5	61.6
25 November 2001	ST	0.10	N/A	13.7
09 December 2001	0.15	0.31	20.5	42.4
23 December 2001	0.16	0.12	21.9	16.4
06 January 2002	0.06	0.22	8.2	30.1
20 January 2002	0.51	0.34	69.8	46.5
03 February 2002	0.65	0.34	89.0	46.5
09 March 2002	0.68	0.46	93.1	63.0
17 March 2002	0.33	0.40	45.2	54.8
04 April 2002	0.41	0.19	56.1	26.0
22 May 2002	0.39	N/S	53.4	N/A
Mean	0.3	0.28	40.3	38.7

Fluctuations of the water masses that were transported via the entrance of the lagoon were obviously controlled by the tidal inflow and outflow speeds. For inflow volume transports, the fluctuations also due to the westerly wind during northwest monsoon, since Spearman rank correlation coefficient ($r = 0.9$; $p < 0.05$; $n=5$), indicated that the maximum inflow speeds were significantly correlated with the maximum westerly wind.

The inflow speeds that were measured on 24 November 2001 was written as ST, since the speeds were less than 0.02 ms^{-1} , which is under the threshold of the flow meter used, and therefore calculation on the inflow volume transport could not be done due to unavailable data (N/A). Sampling was not done (NS) on 22 May 2002, since schedule of sampling in ebb tide coincided with the nighttimes, whereas the research samplings were planned to be performed only during the daytime.

4.1.7. Retention and turn over time of water mass in the Hoat Lagoon

On the average $0.97 \times 10^6 \text{ m}^3$ ($\text{SD}=0.69 \times 10^6\text{m}^3$; $n =15$) of water volumes were transported from outside the lagoon into the lagoon. While, $0.88 \times 10^6\text{m}^3$ ($\text{SD}=0.46 \times 10^3\text{m}^6$; $n=14$) of the water volumes were transported from the lagoon toward the adjacent shore, resulting in an inflow surplus of the water volumes.

Although in most sampling dates showed more frequently outflow surplus (negative values) however, with lesser water volumes, compared to the inflow volume

transports. On the average, about 38 % of inflow water mass (surplus water mass) were retained in the lagoon after a tidal cycle (Table 3).

Table 3. Inflow, outflow and net volume transports ($\text{m}^3 \cdot 10^6/6\text{hr}$), percent retention of volume water mass in the Hoat Lagoon, obtained at 15 sampling dates (day) from 18 September 2001 to 22 May 2002. N/A = not available; (+) = calculated only from positive numbers.

Date	Inflow volume transport ($\text{m}^3 \cdot 10^6/6 \text{ hr}$)	Outflow volume transport ($\text{m}^3 \cdot 10^6/6 \text{ hr}$)	Net volume transport ($\text{m}^3 \cdot 10^6/6 \text{ hr}$)	% volume retention
18 Sep. 2001	0.4	0.8	-0.4	-100
01 Oct. 2001	0.4	0.4	0.0	0
14 Oct. 2001	1.0	1.3	-0.2	-20
28 Oct. 2001	0.4	0.7	-0.2	-50
11 Nov. 2001	1.0	1.3	-0.3	-30
25 Nov. 2001	N/A	0.3	N/A	N/A
09 Des. 2001	0.4	0.9	-0.5	-125
23 Des. 2001	0.5	0.4	0.1	20
06 Jan. 2002	0.2	0.7	-0.5	-250
20 Jan. 2002	1.5	1.0	0.5	33.33
03 Feb. 2002	1.9	1.0	0.9	47.36
09 Mar. 2002	2.7	1.8	0.9	33.33
17 Mar. 2002	1.0	1.2	-0.2	-20
04 Apr. 2002	1.2	0.6	0.7	58.33
22 May. 2002	1.0	N/A	N/A	N/A
Mean	0.97	0.88		+38.47
SD	0.72	0.46		+14.7
N	15	14		+5

The turnover time in water mass of the lagoon is approximately about 19 hours. Since estimation of the total volume of the lagoon was referred to MSL, the turnover time must be regarded as the lower bound of the turnover time. Due to duration of the outflow is ~ 6 hours, thus only about 29 percent ($6 \text{ hrs}/19 \text{ hrs} * 100\%$) of the lagoon's water mass can be exported during an ebb tide. Since there are two ebb tides in a day according to the type of the tide in this area, therefore the water mass of the lagoon can be totally replenished in ~ 3 times ebb tides ($19 \text{ hrs}/6 \text{ hrs}$) or about one and half day, and therefore the lagoon is considered to be a well-flushed lagoon.

Spearman rank correlation coefficient indicated that the outflow volume transport was significantly correlated with the inflow volume transport ($r = 0.546$; $p < 0.05$; $n = 15$). This suggests due to amounts of water volumes that exported shoreward from the lagoon were replaced by inflow water volumes from outside the lagoon after a tidal cycle.

4.1.8. Turbulence intensities

4.1.8.1. The diffusive dissolution rate in still water

Diffusive dissolution rates of gypsum slabs in still water were obtained from the 4-day laboratory experiments. The dissolution rate (weight loss) of the gypsum slabs, ranged from, 0.525 to 1.225 gram per slab per day with an initial weight per slab ranged from 13.1 to 16.6 gram with a mean of 0.79 gram or 5.26 percent of the weight loss per slab per day (Table 4). The differences in the initial weights of the slabs were known due to the difference in compactness of the slabs, where the compactness depends on the amount of air bubbles in the slabs, something that is difficult to avoid during the preparation of the slabs. The mean of the diffusive dissolution rate per day was used as a calibration coefficient, in order to separate the effect of the diffusion process from the effect of the advection process on the dissolution rate of gypsum slabs used in the field study.

Table 4. Initial weights and weight losses of gypsum slabs in the laboratory experiment

No	Initial weight (gram)	Weight after 4 exposure days (gram)	Weight losses per 4 days (gram)	Weight losses per day (gram)	Percentage of the dissolution rates (%)
1	13.1	10.2	2.9	0.725	5.53
2	19.9	10.9	3.0	0.75	3.77
3	14.3	11.6	2.7	0.675	4.72
4	14.6	11.4	3.2	0.8	5.48
5	14.6	10.6	4.0	1	6.85
6	14.0	10.6	3.4	0.85	6.07
7	14.1	11.8	2.3	0.575	4.08
8	14.7	12.6	2.1	0.525	3.57
9	14.9	11.8	3.1	0.775	3.20
10	16.6	11.7	4.9	1.225	7.38
		Mean	3.16	0.79	5.26

4.1.8.2. Turbulence intensities in different sea states

Average turbulence intensities at 0 m, 0.25 m, 0.50 m, 0.75 m, and 1.0 m above bottoms at the three study sites (Figure 14) indicated that the intensities increased from 1.95 at the innermost side of the lagoon (site-1) to 2.55 nearby the entrance of the lagoon (site-2), and even much higher (12.5) at the adjacent shore (site-3). On the average, the intensity at site-3 was almost 5 times higher than that at site-2 and about 6.5 times higher than that at site-1, and the mean intensity at site-2 was 1.3 times higher than that at site-1

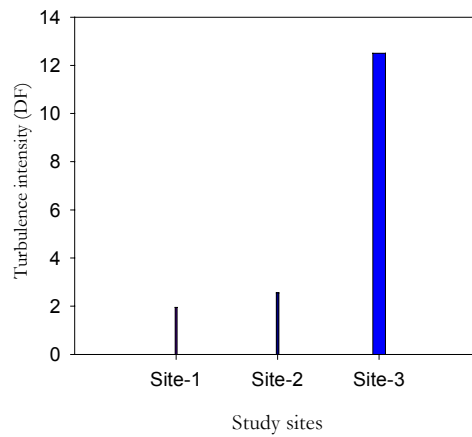


Figure 14. Mean turbulence intensities in the Hoat Lagoon (site-1 and 2) and at the adjacent shore (site-3), derived from dissolution factor (DF) of gypsum slabs, deployed in rough (17 to 18 February 2002) and calm (11 to 12 March 2002) sea states.

The turbulence intensities at the five different heights in both the rough sea (Figure 15a and b) and the calm (Figure 16a, and b) sea states in the lagoon (site-1 and site-2) were less than 5 (DF), and were categorised as laminar flows. While the intensities at the adjacent shore ranged from greater than 5 to 19 both in rough (Figure 15c) and calm (Figure 16c) sea states, which were categorised as intermediate to fully turbulence.

In the calm sea state, about 50.89% of the mean turbulence intensities were reduced at site-3, 45.45% at site-2, and only 29.63% at site-1.

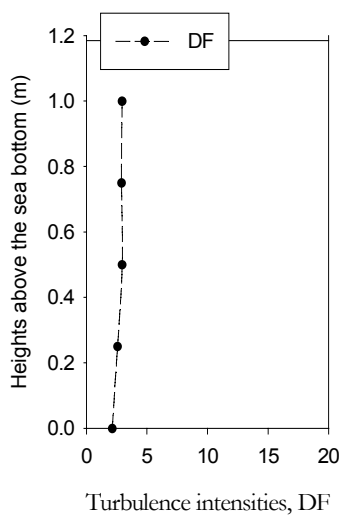


Figure 15a. Turbulence intensities throughout water column between 1 m above the sea bottom at site-1 in rough sea state

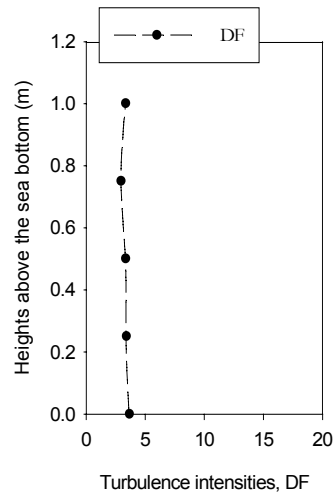


Figure 15b. Turbulence intensities throughout water column between 1 m above the sea bottom at site-2 in rough sea state

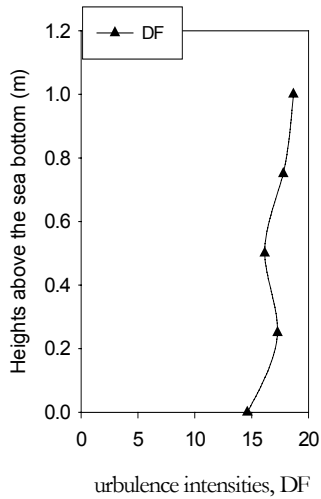


Figure 15c. Turbulence intensities throughout water column between 1 m above the sea bottom at site-3 in rough sea state

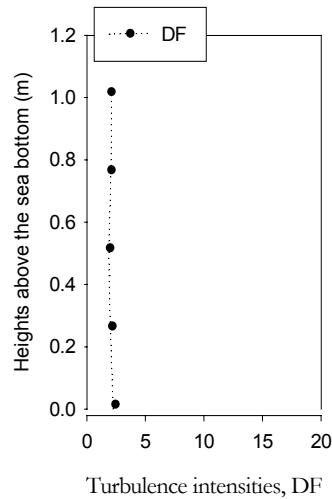


Figure 16a. Turbulence intensities throughout water column between 1 m above the sea bottom at site-1 in calm sea state

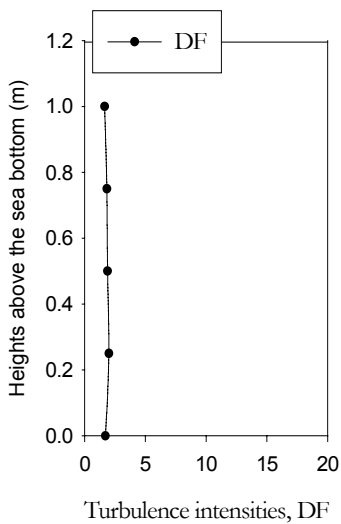


Figure 16b. Turbulence intensities throughout water column between 1 m above the sea bottom at site-2 in calm sea state

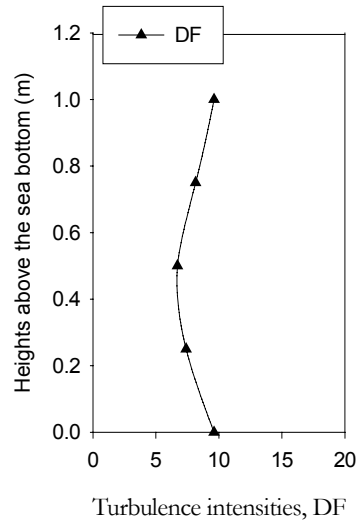


Figure 16c. Turbulence intensities throughout water column between 1 m above the sea bottom at site-3 in calm sea state

Results of the ANOVA indicated that the turbulence intensities among the three study sites in both rough ($F=491.19$; $df = 2, 12$; $p < 0.05$) and the calm ($F=273.84$; $df = 2, 12$; $p < 0.05$) sea states were significantly different.

Eventually, post hoc Tukey tests indicated that two homogeneous site groups in mean turbulence intensities occurred in both the rough and calm sea states, i.e., the first group consist of site-1 and site-2, while site-3 was alone as the second group.

Briefly, one can be proposed that both in the calm and rough sea states, there were occurred two different turbulence regimes at the lagoon and the adjacent shore, where the intensity at the adjacent shore ranged from intermediate to fully turbulence ($DF = 8.3$ to 16.9), while the intensity was laminar and ranged 1.8 to 3.3 .

4.1.9. Fluxes of Total Suspended Sediment (TSS) in the Hoat Lagoon

Fluxes of the Total Suspended Sediments (TSS) in water columns near the panels can indicate the amount of settled sediment dynamics at the upper side of the panels. Besides,

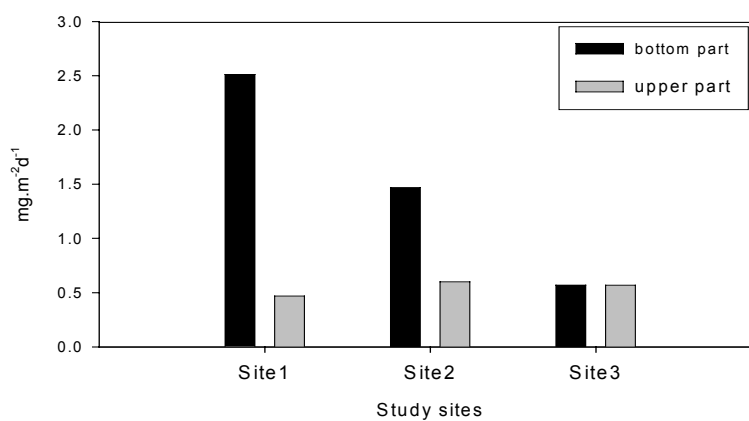


Figure 17. The fluxes of Total Suspended Sediment ($\text{mg.m}^{-2}\text{d}^{-1}$) at 1 m above the sea bottom (upper part) and at 0.24 m above the bottom (bottom part) in the three experimental sites

the settled sediment were supposed to control the density of mollusc settlers on the panels, where the higher the amounts of settled sediments on panel surfaces, lead to a decreased in settlement densities on the panels. Results of the TSS measurements using sediment traps (Figure 17) indicated that the greatest TSS flux was $2.5 \text{ mg.m}^{-2}\text{d}^{-1}$, recorded at 0.24 m above the sea bottom (the bottom part) of site-1, and the smallest TSS flux was $0.47 \text{ mg.m}^{-2}\text{d}^{-1}$ was recorded at 1 meter above the bottom (upper part) also at site-1. At site-2, the TSS flux was higher at the bottom part of the water column with $1.47 \text{ mg.m}^{-2}\text{d}^{-1}$ than in the upper part (0.6 gram/liter), whereas TSS flux of $0.57 \text{ mg.m}^{-2}\text{d}^{-1}$ was found in similar concentration throughout the depths of site-3.

Types of bottom substrates and local hydrodynamic regimes determined amounts of the settled sediment on the surface of panels. The substrates at site-1 were finer (very fine sand) than site-2 (sand). This must be related to relatively lower turbulence intensity at site-1 compared to the two other sites, because site-1 also located nearby mangrove colonies, which is naturally associated with a lower turbulence intensity and finer sediment.

The TSS was also suspected transported by ground water, seeping out from nearby sea bottom. The TSS at site-2 was smaller than site-1 since substrate at site-2 was coarser than site-1. This substrate type may be related to relatively higher turbulence intensities at site-2 than site-1 (see Figure 14). The TSS at adjacent shore was smaller than in the lagoon, and was distributed homogeneously throughout the water depths due to higher turbulence intensity and coarser bottom substrate at the adjacent shore.

4.2. Mollusc larvae and post larvae (settlers)

4.2.1. Taxonomic composition, diversity and species distribution patterns

4.2.1.1. Planktonic larvae passing through the entrance of the Hoat Lagoon

Taxonomic compositions of the mollusc larvae, transported by inflow and outflow through entrance of the Hoat Lagoon (Table 5) during this study consisted of a total 11 taxa of mollusc larvae from class gastropoda, pelecypoda, and cephalopoda. *Saccostrea* sp., *Perna viridis*, *Nautilus* sp., *Nerita* sp., *Cerithium* sp. were found as common species both in inflow and in outflow waters. Eight taxa of them were found in inflow, while nine of them were found in outflow. *Charonia tritonis* and *Argonauta nodosa* were only found in inflow, whilst *Patella* sp., *Oliva* sp., and a veliger1 (gastropod) were only found in outflow. Off the three classes, gastropod larvae were the most common both in the inflow and in outflow during this study.

Table 5. Taxonomic composition of larval densities (%) in inflow and outflow via entrance of the Hoat Lagoon, obtained at 15 sampling dates (days) from 18 September 2001 until 22 May 2002.
* only in inflow; ** only in outflow

NO	CLASS	Familly	Larvae in inflow	Larval density (%)	Larvae in outflow	Larval density (%)
1	Pelecypoda	Ostreidae	<i>Saccostrea</i> sp.	20.1	<i>Saccostrea</i> sp.	28.6
2		Mytilidae	<i>Perna viridis</i>	6.1	<i>Perna viridis</i>	2.1
3	Cephalopoda	Nautilidae	<i>Nautilus</i> sp.	3.5	<i>Nautilus</i> sp.	1.4
4			<i>Argonauta nodosa</i> *	0.8		
5	Gastropoda	Neritidae	<i>Nerita</i> sp.	8.4	<i>Nerita</i> sp.	5.9
6		Cerithidae	<i>Cerithium</i> sp.	1.5	<i>Cerithium</i> sp.	1.5
7			<i>Charonia tritonis</i> *	8.7		
8			Gastropoda1	2.2	Gastropoda1	4.0
9		Pattelidae			<i>Patella</i> sp.**	0.9
10		Olividae			<i>Oliva</i> sp.**	2.0
11					Veliger1**	2.3
Total				51.3		48.7

4.2.1.2. Taxonomic composition and diversity of mollusc larvae at the three study sites

- Taxonomic composition

A total of four classes of mollusc larvae (Gastropoda, Pelecypoda, Cephalopoda, and Polyplacophora), comprising 18 taxa were collected during 18 September 2001 and 22 May 2002 (Table 6). Total numbers of taxa collected from site-1, site-2, and site-3 were 11, 10, and 13 taxa, respectively.

Oliva sp., *Nerita* sp., *Saccostrea* sp., *Perna viridis*, and *Nautilus pompilius* were found as common species at each study site. *Saccostrea* sp. was the most abundant species. *Charonia tritonis* and *Nautilus* sp. were only found at the adjacent shore. *Patella* sp., *Melo imbricatus*, and *Veliger1* were only found in the lagoon. The gastropod *Charonia tritonis* was found in the inflow and at the adjacent shore. *Patella* sp. and *Veliger1* (gastropoda) were collected inside the lagoon (site-2) and in the outflow.

Table 6. Mean density per taxon of mollusc larvae (ind. m⁻³), obtained at 15 sampling dates from 18 September 2001 to 22 May 2002 at the three study sites.

Class/Genus	Family	Site-1	Site-2	Site-3
Gastropoda				
<i>Charonia tritonis</i>	Charoniidae	N/A	N/A	4.3
<i>Cerithium</i> sp.	Cerithiidae	6.1	N/A	3.1
Gastropoda1		1.2	N/A	1.0
Gastropoda2		N/A	0.4	0.4
Gastropoda3		N/A	1.4	1.4
<i>Melo imbricatus</i>	Volutidae	N/A	5.4	N/A
<i>Nerita</i> sp.	Neritidae	0.9	0.7	6.3
<i>Oliva</i> sp.	Olividae	6.3	8.4	2.1
<i>Polinices</i> sp.	Naticidae	12.1	N/A	72.5
<i>Patella</i> sp.	Pattelidae	N/A	1.9	N/A
Veliger 1 (gastropoda)			2.3	N/A
Bivalvia				
<i>Anadara</i> sp.	Arcidae	0.8	NA	N/A
<i>Perna viridis</i>	Mytilidae	2.3	1.4	0.9
<i>Saccostrea</i> sp.	Ostreidae	27.2	19.6	35.1
<i>Tellina</i> sp.	Tellinidae	13	NA	N/A
Cephalopoda				
<i>Nautilus</i> sp.	Nautilidae	N/A	N/A	3.5
<i>Nautilus pompilus</i>	Nautilidae	1.6	0.5	1.3
Polyplacophora				
<i>Chiton trocophore</i>	Chitonidae	8.1	N/A	8.1
Mean		4.2	2.2	7.4

• **Diversity the mollusc larvae**

The highest diversity of mollusc larvae was found in inflow waters ($H' = 1.2318$) (Figure 18). The lowest diversity was recorded at site-2 with a diversity index H' of 0.76133.

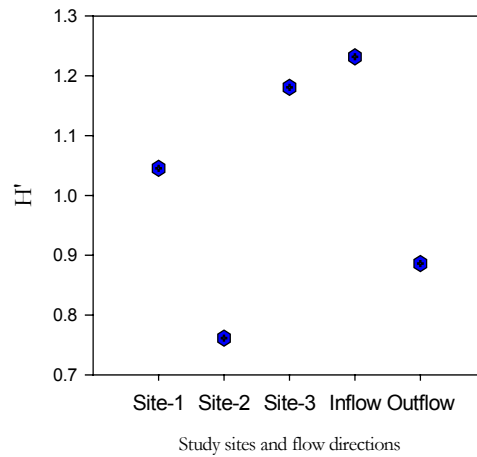


Figure 18. Bubble plots of the Shannon diversity index (H') of mollusc larvae at three study sites and in inflow and outflow waters at the entrance of the Hoat lagoon, collected from 18 September 2001 to 22 May 2002 at 15 sampling dates.

• **Associations among the mollusc larvae**

The two dimensional map of the Multi Dimensional Scaling (MDS) (Figure 19), based on Bray Curtis similarities (Table 7), visualizes the pattern of taxonomic similarity among the study sites. Inflow and outflow assemblages resembled most, while site-2 and the inflow were most dissimilar.

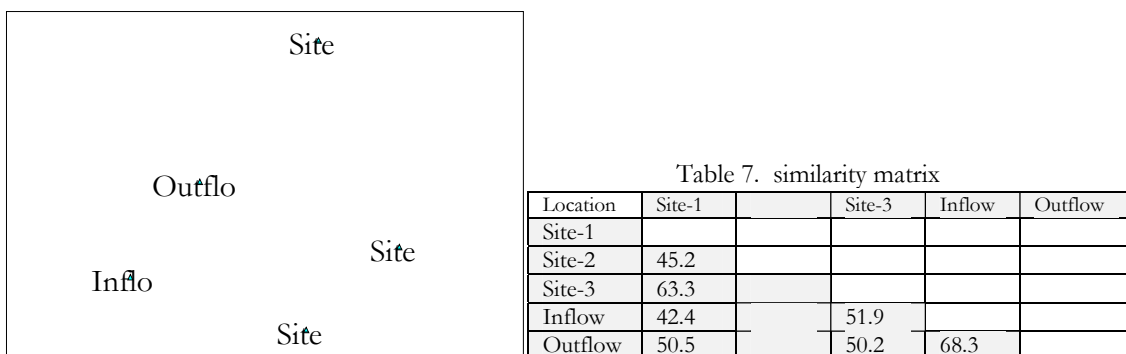


Figure 19. The two dimensional map of the MDS ordination of taxonomic site groups of mollusc larvae at the three study sites, and in inflow and outflow, based on \sqrt{V} -transformed and Bray-Curtis similarity coefficients with a stress coefficient of 0.00.

4.2.1.3. Taxonomic composition and diversity of mollusc settlers

A total of 38 taxa of mollusc settlers from the classes Gastropoda, Pelecypoda, and Cephalopoda (Table 8) were collected at the three study sites.

Melo imbilicatus, *Murex* sp., *Saccostrea* sp., *Perna viridis*, *Tellina* sp., *Spondylus* sp., and *Nautilus* sp. were found at each study site. *Saccostrea* sp., *Perna viridis*, *Spondylus* sp., and *Tellina* sp. were most abundant.

- **Diversity of mollusc settlers**

The mollusc settler assemblage at site-1 was most diverse ($H' = 1.4564$). The lowest diversity was found at the adjacent shore (site-3) ($H' = 0.97284$) (Figure 20).

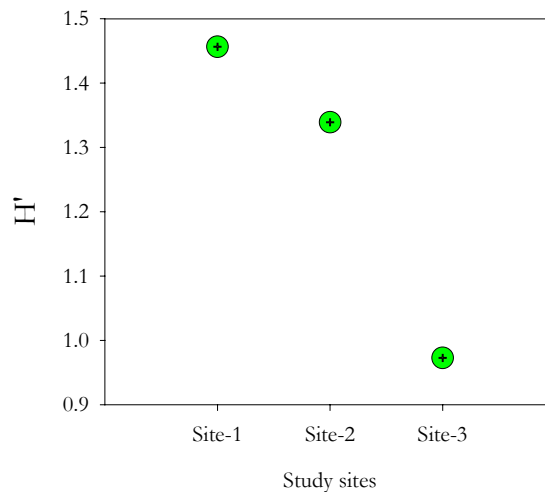


Figure 20. Bubble plots of Shannon diversity index (H') of mollusc settlers at the three study sites with \log_e transformation, collected at 15 sampling dates from 18 September 2001 to 22 May 2002.

The diversity of settlers decreased from the innermost side of the lagoon towards the adjacent shore.

Table 8. Mollusc settlers on the panels at the three study sites, obtained at 15 sampling dates from 18 September 2001 to 22 May 2002. N/A= not available.

Class/Species	Family	Site-1	Site-2	Site-3
Gastropoda				
Gastropoda1		1	N/A	N/A
Gastropoda2		5	12	N/A
Gastropoda3		24	N/A	N/A
Gastropoda4		6	N/A	N/A
Gastropoda5		6	N/A	N/A
<i>Polinices</i> sp.	Naticidae	5	N/A	N/A
<i>Patella</i> sp.	Patellidae	N/A	10	N/A
<i>Oliva</i> sp.	Olividae	141	45	N/A
<i>Oliva</i> sp.2	Olividae	15	N/A	N/A
<i>Nerita</i> sp.	Neritidae	84	1174	N/A
<i>Rhinoclavis</i> sp.	Cerithiidae	24	N/A	N/A
<i>Cerithium</i> sp.	Cerithiidae	N/A	80	10
<i>Melo imbilicatus</i>	Volutidae	534	495	1
<i>Nasarius</i> sp.	Nassariidae	N/A	45	39
<i>Conus</i> sp.	Conidae	10	N/A	N/A
<i>Turritella</i> sp.	Turritellidae	N/A	10	1
<i>Murex</i> sp.	Muricidae	50	29	72
<i>Murex machyntip</i>	Muricidae	N/A	5	N/A
<i>Lambis</i> sp.	Strombidae	N/A	N/A	24
<i>Terebralia</i> sp.	Potamididae	N/A	24	N/A
<i>Coralliophila</i> sp.	Coralliophilidae	N/A	24	N/A
<i>Cypraea</i> sp.	Cypraeidae	N/A	5	N/A
Pelecypoda				
Bivalvia1		N/A	1	N/A
Bivalvia2		N/A	2	N/A
Bivalvia3		N/A	N/A	3
Bivalvia4		N/A	N/A	12
Bivalvia5		N/A	N/A	12
<i>Saccostrea</i> sp.	Ostreidae	6225	10386	4123
<i>Perna viridis</i>	Mytilidae	3691	3839	828
<i>Tellina</i> sp.	Tellinidae	528	494	109
<i>Tridacna</i> sp.	Tridacnidae	N/A	N/A	24
<i>Pinctada margaritifera</i>	Pteriidae	N/A	N/A	10
<i>Spondylus</i> sp.	Spondylidae	1375	1206	147
<i>Pinctada maxima</i>	Pteriidae	20	N/A	N/A
<i>Malus malus</i>	Malleidae	N/A	24	5
<i>Anadara</i> sp.	Arcidae	11	20	N/A
Cephalopoda				
<i>Nautilus</i> sp.	Nautilidae	247	54	41
<i>Argonauta nodosa</i>	Argonautidae	5	N/A	74
Total		13007	17984	5535

- **Associations among the mollusc settlers**

Results of the clustering analysis according to the space conserving (group average) of the mollusc settlers (Figure 21), based on Bray Curtis similarity (Table 9) indicates that there were two site group of settler assemblages in the study area namely site-1 and site-2), based on an arbitrary cut-off point of similarity at level of 76.725 percents. The site

group of (1-2) was only a small distance apart (i.e., high degree of association between one another or a very high level of similarity). Site-3 was alone and some distance apart from the group 1-2.

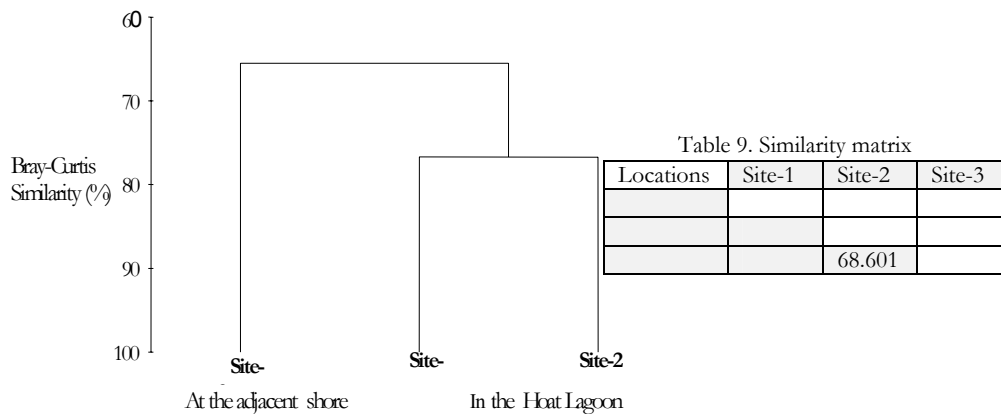


Figure 21. Cluster dendrogram for comparison of the settlers in the Hoat Lagoon and its adjacent shore, during 18 September 2001 until 22 May 2002, based on Bray Curtis similarity coefficients.

The two site groups were also presumed regulated by the difference turbulence intensities and water properties, especially seawater salinity and density.

4.2.2. Larval density

4.2.2.1. Larval densities in inflow and outflow waters at the entrance of the Hoat Lagoon

Densities of mollusc larvae in inflows ranged from 3 ind.m⁻³ on 20 January 2002 to 178 ind. m⁻³ on 04 April 2002. Densities of larvae transported by outflows ranged from 1 ind.m⁻³ on 03 February 2002 to 64 ind. m⁻³ on 04 April 2002. The mean inflow larval density (42.3 ind. m⁻³) was significantly higher than the mean outflow larval density (13.2 ind. m⁻³) (Figure 22). Two peaks of inflow larval densities appeared in two different seasons.

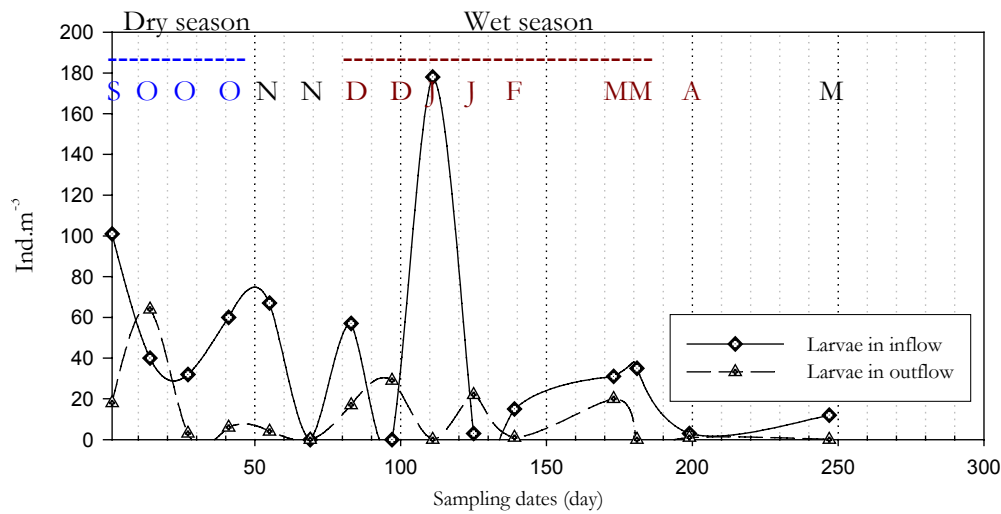


Figure 22. Inflow and outflow larval densities (ind. m⁻³) at the entrance of the Hoat Lagoon, obtained at 15 sampling dates during 18 September 2001 (the 1st day) until 22 May 2002 (the 247th day) over the dry and wet seasons

The first peak occurred on 18 September 2001 (in the dry season), and the second on 6 January 2002 (in the wet season). The first peak was presumably affected by the up-welling during the dry season in the nearby Banda Sea, while the second peak coincided with relatively high rainfalls.

4.2.2.2. Larval densities at the three study sites

Larval densities at the three study sites ranged from 7 ind. m⁻³ at site-1 and at site-3 on 04 April 2002 and 22 May 2002, respectively to 537 ind. m⁻³ on 18 September 2002 at site-1 (Figure 23).

Fluctuation in larval densities at site-2 (19302.8 ± 311.8 ind. m⁻³) were higher than at site-1 (196 ± 311.9 ind. m⁻³) and much higher than site-3 (66 ± 107.7 ind. m⁻³). In general, the larval densities were higher inside the lagoon than at its adjacent shore.

ANOVA indicated that the densities among the three study sites were significantly different ($F = 10.54$; $p < 0.01$; $df = 44$; $n = 45$). Post hoc tests indicated that there were two different groups, i.e., group-1 (site-1 and site-3) and group-2 (site-2).

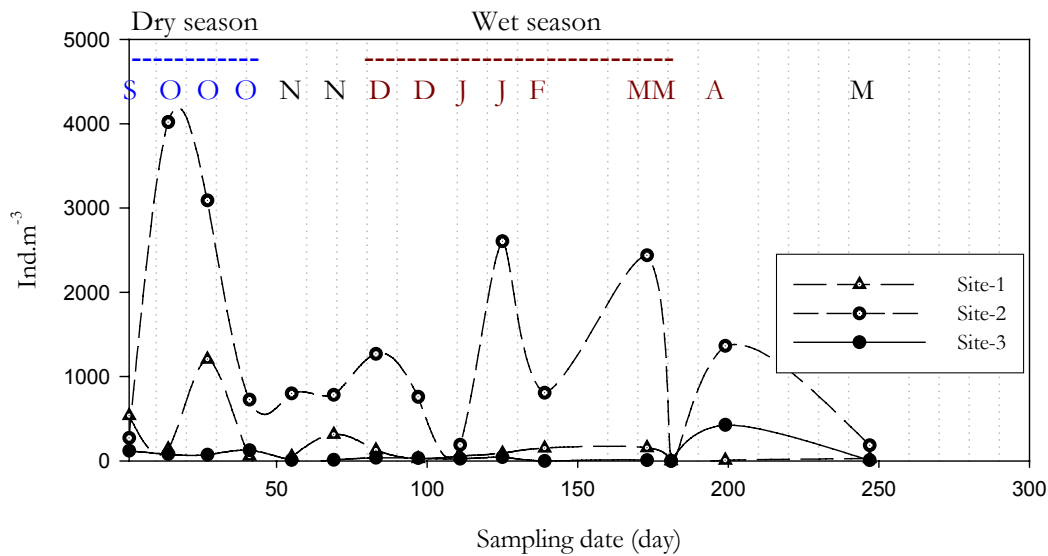


Figure 23. Mollusc larval densities (ind. m⁻³) at the study sites, obtained at 15 sampling dates from 18 September 2001 (the 1st day) to 22 May 2002 (247th day) over the dry and wet seasons

Since all of the larval samplings at the three study sites during this study were carried out in ebb tide condition, thus, effects of other factors were considered to be more dominant than the tidal effects. Kendall's correlation coefficient indicated that the fluctuation of maximum larval density at the adjacent shore (site-3) in September 2001 to March 2002 were significantly influenced by the maximum wind speeds (Table 1), where decreased in wind speeds, lead to increased in larval density ($r = -0.9$; $p < 0.05$; $n = 8$), and vice versa.

4.2.3. Larval fluxes at the entrance of the Hoat lagoon

Occurrence of mollusc larvae and settlers in the lagoon were assumed, partly controlled by a succession of changes (fluxes) of the mollusc larvae at the entrance of the lagoon. The larval fluxes were assumed depend on larval density at the entrance, flow speeds and directions. During ebb tide the current from the lagoon mostly flowed toward the North (along the shore) and northwest directions, while in flood tide, current mostly flowed from the West (cross shore direction) in to the entrance of the lagoon (Figure 24).

The peaks of mollusc larval influxes (Figure 25) at the entrance of the Hoat Lagoon appeared on 11 November 2001 and 09 March 2002 with 22.78 and 21.08 ind.s⁻¹ respectively. The peaks of the larval influxes were dominated by *Saccostrea* sp. and *Nerita* sp. (see, Table 5). In contrast, there was no any distinct peak of larval out-fluxes during this period of study. The larval out-fluxes were dominated by *Saccostrea* sp., *Nerita* sp. and

Polinices sp. In addition, fluctuation of the larval influxes ($1176.7 \pm 948.8 \text{ ind.s}^{-1}$; $n = 15$), were relatively higher than the larval out-fluxes ($417.8 \pm 445.4 \text{ ind.s}^{-1}$; $n = 14$).

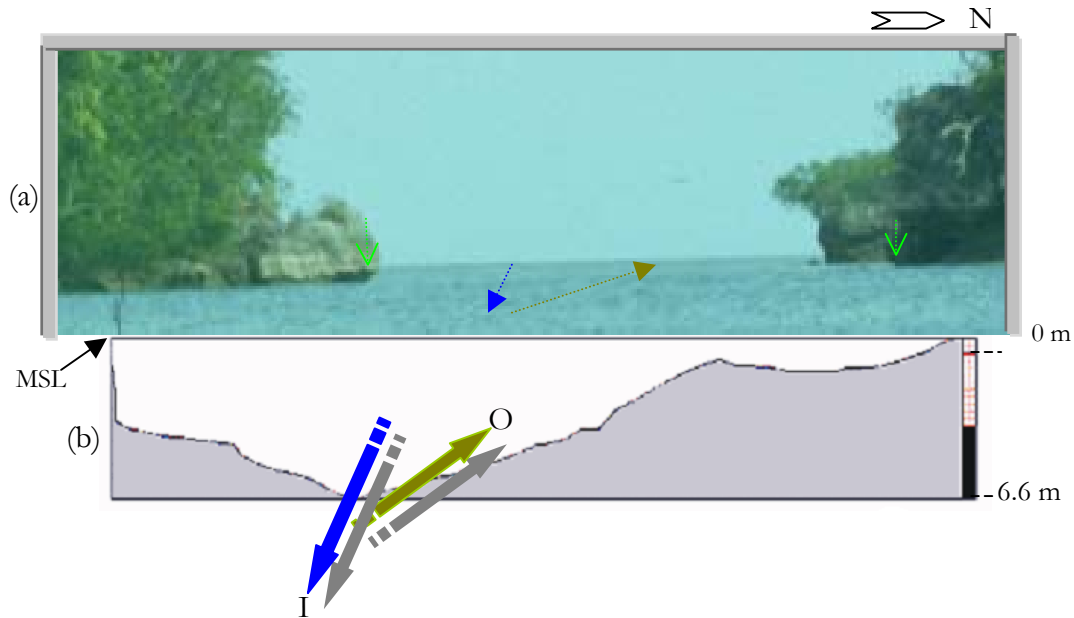


Figure 24. Seaward view of Hoat Lagoon's entrance above sea level (a) and cross section of the entrance below the sea level (b). I = inflow; O = outflow; N = the North direction; \downarrow southern and northern ends of the entrance; \rightarrow inflow and \rightarrow outflow current directions; MSL = Mean sea level. The arrows are not to scale.

Results of the t-test indicated that the numbers of the larval influxes and out-fluxes were significantly different ($t=3.302$; $p<0.05$; $n = 15$). Besides, Pearson correlation coefficient indicated that the larval influxes were not significantly correlated with the larval density of site-3 at the adjacent shore, ($r = -0.305$; $p>0.05$; $n=15$). This could be interpreted that most of the larvae in the lagoon were not always come from its adjacent shore but may come from a long distance far from the lagoon and presumably transported by wave and tidal currents or other advection process (e.g. upwelling). Factor that generated peaks of the inflow larval flux during this study, was presumed to be controlled by the inflow current speeds. Pearson correlation coefficient indicated that the larval influxes in October, 11 November, and 09 December 2001, as well as 09 and 17 March 2002 were significantly influenced by inflow current speeds ($r = 0.779$; $P<0.05$; $n = 7$). This suggests that the increased of the inflow speeds, lead to the increased of the larval influxes.

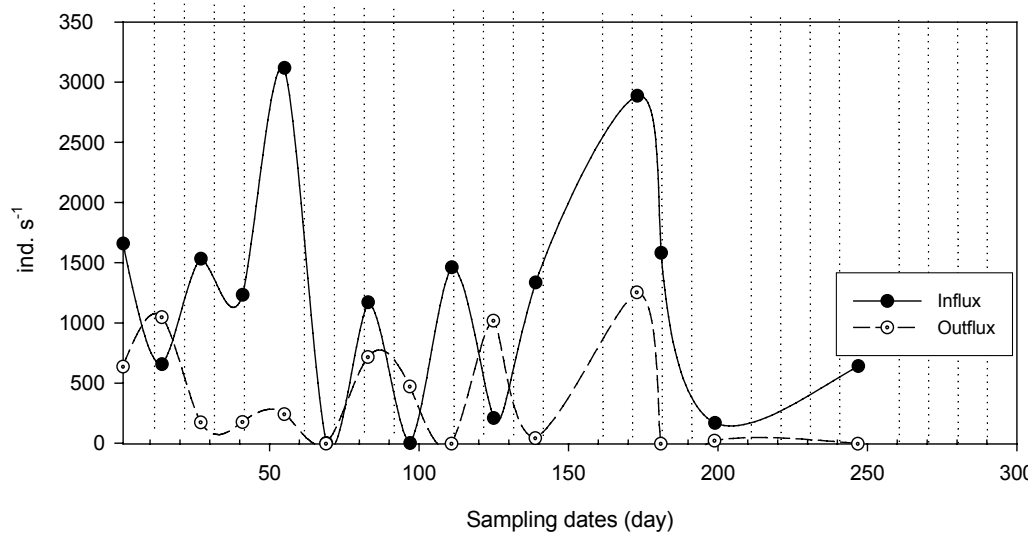


Figure 25. Larval influx and outflux (ind. s^{-1}) through the entrance of the Hoat Lagoon, obtained at 15 sampling dates from 18 September 2001 (1st day) to 22 May 2002 (247th day) over the dry and wet seasons.

4.2.4. Larval retention in the Hoat Lagoon

Portion mollusc larvae that can be retained in the Hoat lagoon after a tidal cycle were quantified based on the 6 hours inflow or outflow (Table 10).

Table 10. Inflow, outflow and net larval transports ($\text{ind. } 10^6/6 \text{ hours}$), as well as percent retention of larvae in the lagoon (only positive numbers) obtained at 15 sampling dates (days) from 18 September 2001 to 22 May 2002. N/S = no sampling; A/L = accidentally lost; N/C = not calculated; N/A = not available; (+) = calculated only from positive values

Date	Inflow larval transport	Outflow larval transport	Net larval transport	% Larval retention
18 Sep. 2001	35.8	13.8	22.0	61.4
01 Oct. 2001	16.6	26.5	-9.9	-60.0
14 Oct. 2001	33.1	3.8	29.3	88.5
28 Oct. 2001	26.6	3.9	22.7	85.3
11 Nov. 2001	67.4	5.3	62.0	92.1
25 Nov. 2001	N/A	N/A	N/C	N/C
09 Dec. 2001	25.3	15.6	9.7	38.4
23 Dec. 2001	N/A	10.3	-10.3	0.0
06 Jan. 2002	31.6	A/L	N/C	N/C
20 Jan. 2002	4.5	22.1	-17.6	-388.9
03 Feb. 2002	28.8	1.0	27.8	96.5
09 Mar. 2002	83.1	36.3	46.8	56.4
17 Mar. 2002	34.2	N/A	34.2	100.0
04 Apr. 2002	3.6	0.6	3.1	84.6
22 May. 2002	13.8	N/S	N/C	N/C
Mean	26.9	9.4	28.62	(+)78.13
SD	23.5	11.5	17.9	(+) 21.0

Numbers of the mollusc larvae that transported by the inflow were higher than the outflow in this study, where on the average 26.9×10^6 ind. (SD= 23.5×10^6 ind.; n=15) of the larvae were transported by an inflow into the lagoon. In contrast, 9.4×10^6 ind. (SD = 11.5×10^6 ind; n=14) of the larvae, transported by the outflow toward the adjacent shore, resulting in an inflow surplus of the mollusc larvae. The surplus indicates the number of larvae that are retained in the lagoon after a tidal cycle. Whereas percent average of larval retention in the lagoon was 78 %, which imply that about 78% of mollusc larvae that transported from outside the lagoon into the lagoon were retained in the lagoon after a tidal cycle.

Spearman rank correlation coefficient indicated that the outflow volume transports was significantly correlated with the inflow larval transport ($r = 0.776$; $p < 0.05$; $n = 15$), also correlated with percent larval retention in the lagoon ($r = 0.568$; $p < 0.05$; $n=15$). Furthermore, inflow larval transport was significantly correlated with the percent larval retention in the lagoon ($r = 0.581$; $p < 0.05$; $n = 15$). This means that increased inflow larval transports lead to increased of larval retention in the lagoon.

The local oceanographic and climatic factors (Table 11) are also suspected to influence the transports mechanisms of larvae and the larval retention in the lagoon and therefore they were examined.

Table 11. Duration of inflow and outflow currents, tidal asymmetry (duration of flood-ebb tides), maximum and minimum water levels from Admiralty tide table (referred to MSL), monthly mean wind speed (knot) and directions, as well as lunar phases (1=new moon; 2 = first quarter; 3= full moon; 4 last quarter) at the study area from 18 September 2001 to 22 May 2002. SE = Southeast; W= west; NW= northwest.

Date	Duration of inflow and outflow (hr)	Tidal asymmetry (min.)	Max. water level (cm)	Min. water level (cm)	Lunar phase (category)	Monthly mean wind speed (knot)	Wind direction (degree)
18.09.01	6	0	180	50	1	7	130 (SE)
01.10.01	7	0	160	70	3	3	150(SE)
14.10.01	6	0	160	70	1	3	150(SE)
18.10.01	6	0	190	40	1	3	150(SE)
11.11.01	6	0	150	90	4	2	150(SE)
25.11.01	6.5	-60	140	100	2	2	150(SE)
09.12.01	6	0	160	80	4	5	290(W)
23.12.01	6	0	160	90	2	5	290(W)
06.01.02	6	0	170	70	4	4	310(NW)
20.01.02	6	0	170	70	2	4	310(NW)
03.02.02	6	0	190	60	4	7	310(NW)
09.03.02	8	0	160	70	4	2	310(NW)
17.03.02	6	0	190	50	1	2	310(NW)
04.04.02	5.5	60	190	50	4	3	130(SE)
22.05.02	5.5	60	160	90	2	6	130(SE)

Duration of inflow and outflow ranged from 5.5 (ebb or flood) to 8 hours with a mean duration of 6 hours. Most of the tidal phases during the sampling dates were symmetries. The mean monthly wind speeds ranged from 2 to 7 knots and mostly being South-easterly and North-westerly winds. The minimum and the maximum water levels during the sampling dates ranged from 40 cm on the first quarter of lunar period until 190 cm on the new moon period which is referred to the MSL, in fact the sampling activities, mostly carried out on the last quarter of the lunar period.

Spearman rank correlation coefficient (one tailed) indicated that the duration of the inflow and outflow was correlated significantly with the outflow larval transports ($r = 0.786$; $p < 0.01$; $n = 11$) but not with the inflow larval transport and the other oceanographic and climatic factors also were not significantly correlated with both inflow and outflow larval transports.

4.2.5. Effect of the larval flux and retention on density of larvae and settlers

A large amount of mollusc larvae (78%) was retained in the lagoon after a tidal cycle. Thus, it is reasonable to predict that there should be more larvae available in the water column of the lagoon after a tidal cycle, which should have promoted settlement events in the lagoon, since settler densities were predicted to be dictated by larval fluxes at the entrance of the lagoon and the larval retention in the lagoon. However, Pearson rank correlation indicated that only the larval out-fluxes were significantly correlated with the density of larvae inside the lagoon ($r = 0.372$; $p < 0.05$; $n = 30$), suggesting that increased larval densities in the lagoon lead to an increased exported of larvae. The larval influx was significantly correlated with the net larval transports ($r = 0.924$; $p < 0.01$; $n = 30$), suggesting that increased larval influx lead to an increased larval retention in the lagoon. In contrast, there were no significant effects of both larval influx ($r=0.017$; $p > 0.05$; $n= 30$) and larval retention ($r = 0.125$; $p > 0.05$; $n = 30$) on the density of settlers. These the results did not support the **hypothesis** that *the greater the larval supply and the longer the retention time of the larvae, the higher the settlement densities in the lagoon are.*

4.2.6. Effects of seawater density on densities of larvae and settlers

Seawater density is also presumed as a determinant factor that controls settlement rates with respect to the passive larval gravity settling. In order to test this hypothesis, the relationships among the larval and settler densities and the seawater density were examined. The mean densities of larvae increased along with settler densities from the adjacent shore

to the lagoon, while seawater densities decreased from the adjacent shore towards the lagoon (Figure 26).

Pearson correlation tests indicated that larval densities were not significantly correlated with the densities of settlers. In contrast, seawater densities at the three study sites were significantly correlated with the densities of settlers ($r = -0.446$; $p > 0.01$; $n = 14$). These results supported the **hypothesis** that *the higher the seawater density, the smaller the settlement densities are*.

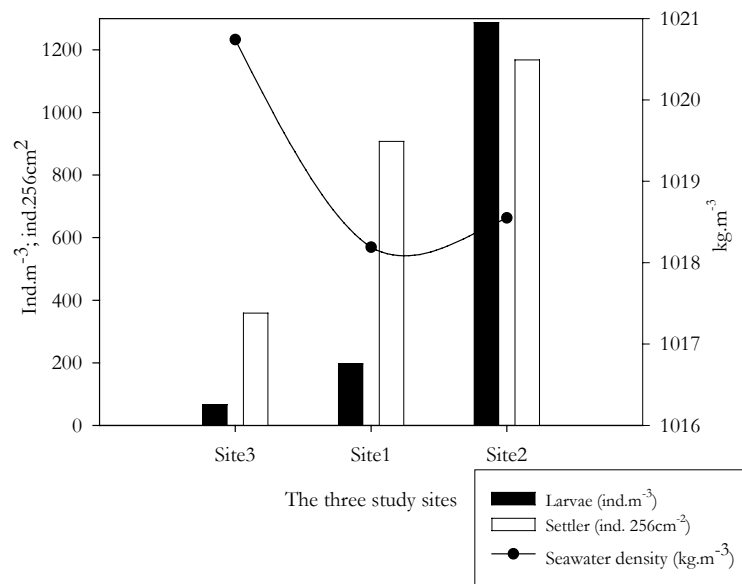


Figure 26. Distributional charts of mean densities of mollusc larvae (ind.m^{-3}), settlers (ind.256cm^{-2}), and seawater (kg.m^{-3}) at the three study sites, obtained at 15 sampling dates from 18 September 2001 to 22 May 2002.

4.2.7. Effects of the turbulence intensities on the densities of settlers

Turbulence intensities near the surface of the panel substrates were supposed to dictate the settlement process on the substrates. In order to test this hypothesis, the relationship between the turbulence intensities near the panels and numbers of settlers on each panels at five different heights above the sea bottom were examined.

The mean turbulence intensities at site-1 (Figure 27a) and site-2 (Figure 27b) were less than 4 DF. At site-1, the intensities increased slowly upward the surface, while the densities of settlers increased downward the sea bottom. At site-2, the densities of settlers increased downward along with turbulence intensities.

The mean turbulence intensities at site-3 (Figure 27c) above 11 DF. There was an inverse relationship between turbulence intensities and densities of settlers. At all three

sites, the densities of settlers were always drastically decreased at the bottom, probably due to the effect the sedimentation.

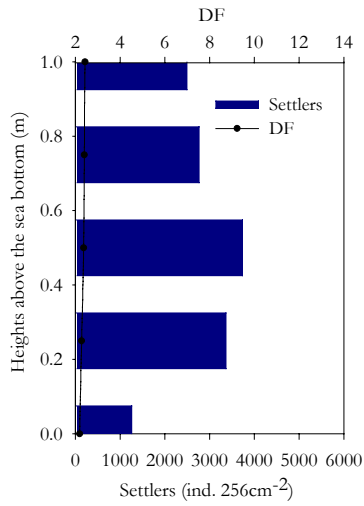


Figure 27a. Turbulence intensities (DF), and densities of settlers (ind. 256 cm⁻²) on panels at five different heights (m) above the sea bottom of site-1

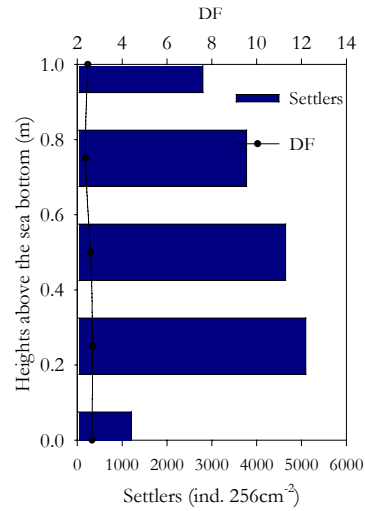


Figure 27b. Turbulence intensities (DF), and densities of settlers (ind. 256 cm⁻²) on panels at five different heights (m) above the sea bottom of site-2

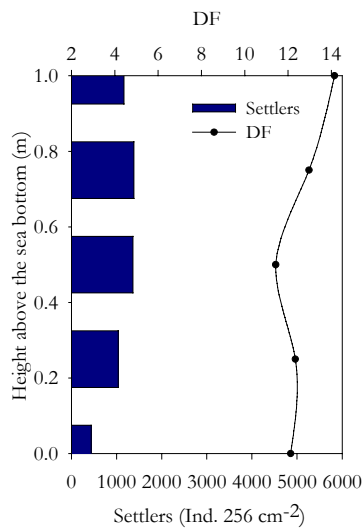


Figure 27c. Turbulence intensities (DF), and densities of settlers (ind. 256 cm⁻²) on panels at five different heights (m) above the sea bottom of site-3

Pearson correlation coefficient indicated that the turbulence intensities in the lagoon had a significant correlation with the differences of heights above the sea bottom (positions of panels above the bottom) at site-1 ($r = 0.967$; $p < 0.01$; $n = 15$), where increased of the distances above the bottom lead to increased of the turbulence intensity. In contrast, there were no significant correlation between the turbulence and the distances above the bottom at site-2 and site-3. Furthermore, Pearson correlation indicated that the turbulence intensities significantly negatively correlated with the settlement densities ($r = -0.674$; $p < 0.01$; $n = 15$). Therefore this result is consistent with the *hypothesis that the higher the turbulence intensities, the smaller the settlement densities are.*

4.2.8. Post-larval settlement

Settlement in this case, is defined as the successful and semi-permanent attachment of the larvae to the substratum (Keough and Downes, 1982).

There were 37 taxa of mollusc settlers, found on the panels during 18 September 2001 to 22 May 2002, with 7 common taxa, i.e., *Saccostrea* sp, *Perna viridis* sp, *Tellina* sp, *Spondyllus* sp, *Melo imbricatus* sp, *Murex* sp., and *Nautilus* sp.

4.2.8.1. Settlement density at Site-1

No mollusc settlers occurred at site-1 after 6 days (18 September 2001) of submersion of the settlement collector (panels). At least 3 peaks of settlement events occurred at site-1 during this study (Figure 28a). The first peak occurred on substrate panels at 1 m above the sea bottom on 14 October 2001 (or after 33 days of submersion) with a settlement density of 740 settlers/256 cm². The second peak occurred on 11 November 2001 (after 61 days of submersion) on panel at 0.50 m above the sea bottom, with a settlement density of 755 settlers/256 cm², and the third peak occurred on 23 December 2001 (after 103 days) at 0.75 m above the sea bottom, with a settlement density of 845 settlers/256cm².

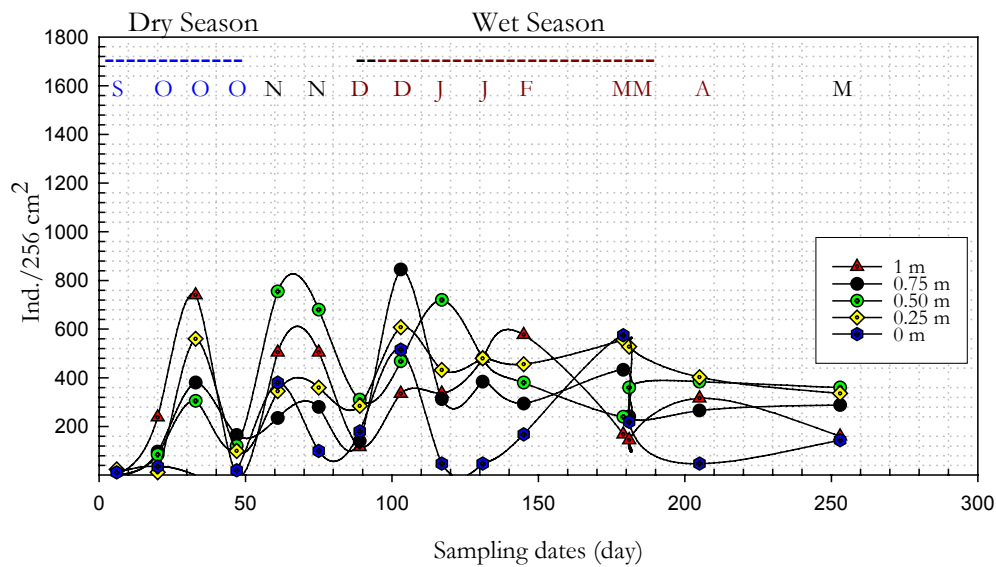


Figure 28a. Distributional curves of densities of mollusc settlers (ind. 256/cm²) on substrate panels at five different heights above sea bottom of site-1, obtained at 15 sampling dates (day) after 6 days (18 September 2001) to 253 days (22 May 2002) of submerssion.

Spearman rank correlation coefficient indicated that only the density of settlers at the sea bottom (0 m) were correlated significantly with the length of the submersion ($r=0.523$; $p < 0.05$; $n = 15$), where the longer the length of the submersion, the higher the settlement density.

4.2.8.2. Settlement density at Site-2

At least two settlement peaks occurred at site-2. The first peak (Figure 28b) occurred on 28 October 2001 (after 47 days submersion) on panel 0.50 m above the sea bottom with a settlement density of 1280 settlers/256 cm². The second peak occurred on 23 December 2001 (after 103 days of submersion) on panel 0.25 m above the bottom with a settlement density of 1704 settlers/256 cm².

Spearman rank correlation coefficient indicated that none of the settlement densities at the five different heights above the bottom was significantly correlated with the length of submersion.

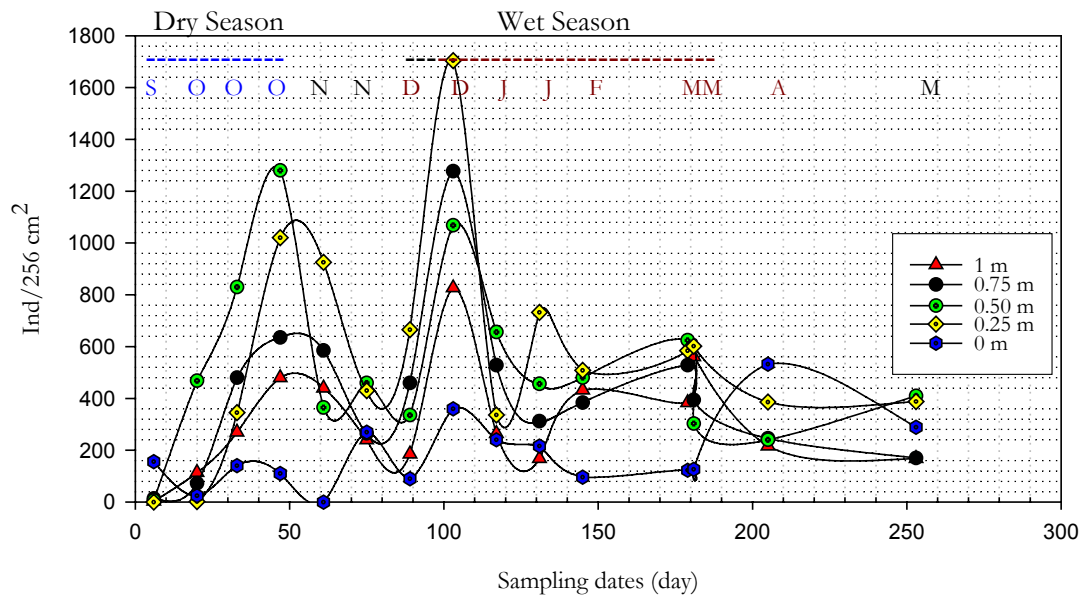


Figure 28b. Distributional curves of density of mollusc settlers (ind./256cm²) on substrate panels at five different heights above sea bottom of site-2, obtained at 15 sampling dates (day) after 6 days (18 September 2001) to 253 days (22 May 2002) of submersion

4.2.8.3. Settlement density at Site-3

At least one peak of settlement event of the mollusc settlers occurred at site-3 (Figure 28c). The peak occurred on 3 February 2002 (after 145 days of submersion) on panels at the sea bottom with a settlement density of 720 settlers/256 cm².

Spearman rank correlation coefficient indicated that only the density of the settlers on panels at 0.5 and 0.75 m above the sea bottom were correlated significantly with the submersion ($r = 0.550$; $p < 0.05$; $n = 15$) and ($r = 0.611$; $p < 0.05$; $n = 15$). This suggests that the longer the length of the submersion of panels at 0.5 and 0.75 m above the bottom, the higher the settlement densities.

In general, peaks of the settlement events during this study occurred earlier inside the lagoon (especially site-2) than the adjacent shore.

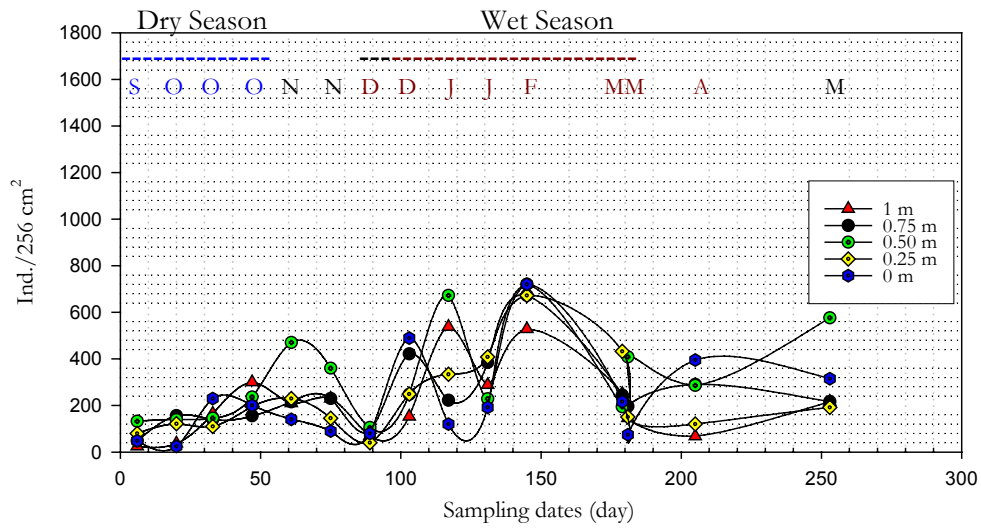


Figure 28c. Distributional curves of density of mollusc settlers (ind/256 cm²) on substrate panels at five different heights above sea bottom of site-3, obtained at 15 sampling dates (day) after 6 days (18 September 2001) to 253 days (22 May 2002) of submersion

5. DISCUSSION

5.1. Salinity and temperature

The temperatures at the study sites were relatively homogenous with only 6°C differences between the maximum and minimum. The relatively small seasonal variation of temperature is typical of a tropical area (Tait and Dipper, 1998). In general, the circulation of the oceans and their enormous heat capacity ensure that the extent of temperature variation in the sea is small great geographical and seasonal differences in absorption and radiation of heat.

Among the climatic factors (air temperature, insolation, rainfall, number of rainy days, air humidity and pressure, and wind the latter was identified to significantly affect the seawater temperatures during this study. Increased wind speeds lead to decreased sea temperatures (Mann and Lazier, 1991) due to the enhanced loss of heat at the surface. Laevastu (1995) pointed out that surface temperature is not a conservative water property, but is a function of surface winds (advection & mixing) and local heat exchange. The reason why the other climatic factors have not significantly affected the seawater temperature could be explained according to Laevastu (1995) that the ocean is an integrator atmospheric effect. Therefore, the changes in the ocean are usually slower and the anomalies are more persistent than in the atmosphere. In addition, spatial scales of the anomalies in the ocean are usually smaller than the scales of atmospheric features, and they are modified by ocean boundaries (e.g. coastal and frontal zone). The well-documented upwelling in the Banda Sea probably caused the lower temperatures in the study area in September and early October 2001.

The Kai islands, located between the deep Banda Sea (> 4000 m) and the shallow Arafura Sea (< 100 m) are under monsoonal influence. The southeast monsoon prevails between April and November and causes mainly westerly ocean currents. The northwest monsoon occurs between December and March and leads to mainly easterly currents (Zijlstra and Baars, 1990). According to Laevastu (1995), the change of the wind system also leads to the occurrence of upwelling, which brings colder waters from greater depths to the surface and causes local temporary rainfalls. This agrees with Wirtky (1958, 1961) who postulated the presence of an alternating monsoon-related system of up- and downwelling for the eastern Banda Sea and the nearby northwestern coast of Australia. He postulated upwelling during the southeast monsoon, indicated on a decline in sea surface temperatures and sea level in that period. The upwelling results in a relatively high nutrient

concentration, which was also observed in the southern part of the Arafura Sea during the southeast monsoon (Rochford, 1962, 1966). The upwelling can also lead to an onshore transports of planktonic invertebrate larvae (Pineda, 1991, Leichter et al., 1998). This would support the assumption, that the larvae that entered the Hoat Lagoon area are 'long distance larvae' (Thorson, 1961) or 'teleplanic larvae' (Scheltema, 1971b) transported from the Banda Sea about 65 to 70 nm away from the study site. Studies of long distance larvae transported by surface currents have been reported by Thorson (1950), Shuto (1974), Scheltema (1977), and Jablonski and Lutz (1980). The dispersal of bivalve and gastropod veligers has been most extensively studied (Pineda, 1991). Veliger larvae of the bivalve *Perna perna*, for instance, were reported to be dispersed in 15 to 20 days over 250 km (Hicks and Tunnell, 1995). Whether such teleplanic larvae have been transported by upwelling advection in September and early October 2001 to the study area is still an open question.

The pronounced spatial and temporal salinity differences at the study sites (Figure 9a) were not significantly correlated to climatic factors. This suggests that they were mainly caused by brackish waters with salinities of 25, seeping out from the bottom of the lagoon. Salinity is a conservative seawater property and is determined by physical processes, such as advection or loss of freshwater (Parsons et al., 1977). The salinity gradient at the study sites was also assumed to indicate the current regime that was characterized by a flow from the adjacent shore towards the inner lagoon. Pickard and Emery (1990) pointed out that the salinity of surface waters can be used as "passive tracers" indicating the flow directions of water masses by their salinity signatures.

Temperature and salinity also affect the vertical distribution of many invertebrate larvae (e.g. Crisp 1984, Stancyk & Feller 1986, Pearce *et al.* 1996), as they vary over various spatio-temporal scales (e.g. diurnal rhythms, tidal cycles, seasons) and drive vertical migration of larvae. Their influence changes in relation to larval stage (Cragg 1980). For instance, pediveligers of the giant scallop *Plactopecten magellanicus* have been shown in mesocosm experiments to leave discontinuity layers (e.g. a thermocline) after reaching competency in favour of the surface layer (Gallagher et al. 1996).

The temperature also may influence (enlarge, narrow, or shift) the salinity range of a species and alter to a certain extent the biological effects of salinity, the salinity, in turn, may influence the effects of the temperature (Kinne, 1958). Both temperature and salinity are well known affecting the metabolic rate, growth, osmoregulation, and other physiological processes. In tropical regimes, the seawater density is mainly controlled by

the salinity, temperature is of minor importance. The seawater density (as a function of the salinity and temperature) is regarded in this study as a major determinant of larval transport and settlements. It increased from the lagoon to the adjacent shore. The density gradient was more pronounced during ebb tide due to the effect of the ground seepage in the lagoon.

5.2. Surface currents and larval transport

Most of meroplanktonic larvae are regarded to be passively drifted by surface currents, except for only few larger decapod larvae that can swim faster than ocean currents and, thus, can control their horizontal distribution (Mileikovsky, 1973). Most larvae of shallow-water invertebrates are small (< 1 mm) and cannot swim long distances. The swimming speed of the mollusc larvae may be on the scale of mm/second, while the current velocities are commonly on the scale of m/second (Vogel, 1981). Therefore, they depend on external transport mechanisms (currents and eddies) to reach adult habitats, which are often far from the favorable habitat of their parents and from their spawning areas (Thorson, 1950, Jackson, 1986).

Tidal current have been identified to determine larval transports in the Hoat lagoon, since changing of speeds and directions of surface currents occurred simultaneously with the tidal rhythm. The study sites is a 'mixed prevailing semi-diurnal tide' (Figure 11), which is characterized by two daily high waters and two daily low waters with different heights (Wirtky, 1961). The semi-diurnal tides cause water to flow inwards twice (flood tide) and seawards twice (ebb tide) within a period of approximately 24 and 48 minutes (Bernshtein et al, 1997).

With the ebb currents, most of the larvae from the lagoon were transported northward along the shore once they left the lagoon. Cross-shore larval transports during the ebb tides were not pronounced, because the coastal currents are stronger parallel to the shore than perpendicular to the shore (Winan (1976, Winan & Bratkovich, 1981). In contrast, the cross-shore larval transports with the flood current seemed to be more pronounced. These transports might be generated by two types of mechanisms that have been proposed for explaining the onshore transports of invertebrate larvae off the Pacific Coast of North America: internal waves (Norris, 1963, Shanks, 1983) and bores (Pineda, 1991), as well as the relaxation of wind-driven upwelling (Ebert, 1983, Farrell et al., 1991). This may imply that both shore-parallel currents along the adjacent shore and shore-perpendicular currents over long distances from open sea transport larvae into the lagoon.

It is well known that planktonic larvae can be transported over long distances by ocean currents (Mileikovsky, 1966, 1968, Robertson, 1964; Scheltema, 1964, 1968, 1971a). This knowledge has been acquired through direct observations of planktonic larvae in the epipelagic waters of the open ocean, including larvae of bivalves (Allen and Scheltema, 1972, Scheltema 1971c, Simroth, 1896, Thiede, 1974) and gastropoda (Laursen, 1981; Lebour, 1934; Scheltema, 1971b, 1977, 1978, 1979, Simroth, 1895, and Thorson, 1961). The drifter study suggests that, once the drifting larvae entered the lagoon, the main tidal current first transported them eastwards in to the lagoon before being separated by southward and northward branches flowing along the eastern lagoon shore (Figure 12a; 12b).

The mean speed of the main current in the lagoon was only 0.03 ms^{-1} (Figure 13). However, because the lagoon is relatively small, larvae that were transported through the entrance can reach the two study sites in the lagoon (100 m and 600 m from the entrance, respectively) during a single inflow period of 6 hours and 12 minutes. Current speed can affect the ability of species with distinct habitat preferences to reach their preferred habitats (Butman et al, 1988, Gross et al, 1992). Hatcher et al (1987) pointed out that planktonic larvae distribution also depends on the relevant hydrodynamic time scale. The question arises when the larvae were supposed to settle in the lagoon and the adjacent shore.

Meroplanktonic larvae can only settle during a certain phase of competence. Jackson (1986) pointed out that after the larvae developed from a pre-competent to a competent stage, water currents determine where they actually settle. If larvae during their competent phase encounter an unsuitable hydrodynamic regime or unsuitable substrate, they can prolong their larval stage and delay the metamorphosis if they do not encounter positive cues, and this delay can last from a few days up to months (Peckenik 1985, 1990). Strathmann (1985) hypothesized that long-lived larvae have a higher probability of finding a suitable site for metamorphosis. However, some larvae with a long pre-competent period have only short competent periods similar to that of short-lived larvae. Moreover, a long pre-competent period can make larvae drift far from good settlement sites.

5.3. The larval fluxes at the entrance of the Hoat Lagoon

In the study area larval influxes were found to be significantly higher than larval outflow fluxes, although the inflow and outflow current speeds were not significantly different. Larval influxes on 01 October, 14 October, 28 October, 11 November, and 09 December 2001, as well as on 09 and 17 March 2002, were significantly influenced by the inflow

current speeds, i.e. increased inflow speeds lead to increased larval influxes. This implies that most of the larvae in the lagoon were transported from the outside the lagoon and did not originate from local reproduction. There was no significant correlation between the larval influxes and larval density at site-3 at the adjacent shore. This might be because site-3 was located south of the main current transporting larvae mostly from western and northwestern directions to the lagoon's entrance (Figure 2a). This finding also supports the assumption that the larvae in the lagoon have been transported from a long distance by advection-processes such as wind-driven currents, internal waves and bore coupled with tidal current or the relaxation of a recurrent wind-driven upwelling event in the Banda Sea during the southeast monsoon.

5.4. Turnover time and percent retention of water masses and larvae in the lagoon

The dynamics of the larval outfluxes depend on the hydrodynamic regime and, in particular, on the rate at which the lagoon water masses are renewed. Therefore an estimation of the turnover time of the lagoon's water mass is crucial.

The inflow water transports and inflow larval transports were greater than the outflow transports. The surplus inflows were considered as the amounts of the inflow water mass and or the inflow larvae that are retained in the lagoon after a tidal cycle. On the average, about 38 of the water mass and 78 percents of inflow drifting larvae, were retained in the lagoon after a tidal cycle.

Duration for the larvae to be retained in the lagoon is dependent on the turnover time of the lagoon's water body. The turnover time is obtained by averaging the residence time over the volume of the lagoon (Tartinville et al, 1997) or, by estimating the ratio of the volume of the lagoon to the volume of the flux entering or leaving the lagoon (Gallagher et al, 1971). The magnitude of the exchange of the lagoon water depends upon several factors, such as bathymetry, tidal amplitude, and freshwater discharge (Sankarankutty and Medeiros, 1986). The turnover time is also a parameter of crucial importance for the biological processes taking place in a lagoon (Tartinville et al, 1997).

The lagoon is relatively small ($\sim 0.56 \text{ km}^2$) and shallow (average depth of $\sim 4.76 \text{ m}$), and the maximum tidal range (MHWS minus MLWS) is greater than 2.60 m (Appendix 2). This features lead to a relatively short turnover time of the lagoon's water mass. It is approximately ~ 19 hours. This value must be regarded as the minimum estimate since the total volume of the lagoon used in the computation was referred to the MSL. About 29 percent of the lagoon's water volumes were exported during a single ebb tide. Thus, the

water mass of the lagoon can be totally replenished in about 3 ebb tides or about one and half day. The relatively short turnover time that it is a well-flushed lagoon. The retention time was also determined by duration of inflow and outflow (tidal phases). Only the flow duration among other climatic and oceanographic factors (tidal asymmetry, water level, lunar phase, wind components) was identified to affect the outflow larval transport. The longer the outflow duration, the more larvae were exported from the lagoon and the shorter was the larval retention time in the lagoon. This seems to suggest larval retention does not significantly affect the larval and settler densities in the lagoon (section 4.2.4) and that the hypothesis '*the greater the larval supply and the longer the retention time of the larvae, the higher the settlement densities in the lagoon are*' was not consistent with the results of the study.

However, the retention of larvae in the lagoon does not only depend on hydrodynamic process but also on their behavioral adaptations which have been developed to exploit specific transporting or concentrating mechanisms (Scheltema, 1986, Rothlisberg et al, 1995). Even larvae that are larvae unable to swim against currents can still control their horizontal movements by changing their vertical position in a water column to reach a current which move in a different direction. This principle is best illustration of the larvae in estuaries, which possess a net seaward flow. Thus may be a passive phenomenon akin to the retention of fine sediments (Korringa, 1952; De Wolff, 1974), but it is more likely that biological adaptation increase the probability of retention. For example, the larvae of some decapod species which are highly dependent on estuarine conditions were found only in the land-ward moving lower water strata while larvae of species not restricted to estuaries were found throughout the water column (Sandifer, 1975).

In conclusion both the larval input into the lagoon and the turnover time are important for the ecological function of the lagoon, i.e. whether the lagoon can act as spawning area (source), nursery area, or a settlement area (sink). My results suggest that most of larvae retained in the lagoon are more likely to utilize it as a nursery area.

5.5. Taxonomic composition, diversity, and patterns of species distribution

5.5.1. Mollusc larvae passing through the entrance of the lagoon

Saccostrea sp., *Perna viridis*, *Nautilus* sp., *Nerita* sp., *Ceritium* sp., were common in both inflow and outflow. *Charonia tritonis* and *Argonauta nodosa* were only found in the inflow, while *Patella* sp., *Oliva* sp., and *Veliger*1 only occurred in outflow. The phenomenology associated with larval transport, is affected by both larval behavior and physical transport mechanisms (Pineda, 1999). The identity of the larvae transported in a current might indicate the

location of the area where they came from. Renjaan and Pattisamallo (1999) who studied mollusc larval transports through the entrance of an estuary (lagoon) nearby (~ 15 km from the study sites) of the lagoon reported that all taxa except one *Nerita* sp., consisted of holoplankton, and only two species *Diacria* sp. and *Creseis* sp., were found only in a specific flow direction (outflow).

5.5.2. Mollusc larvae and settlers in the lagoon

A total of 19 taxa of pelagic larvae and 38 taxa of settled post larvae (settlers) were found at the study sites during 18 September 2001 to 22 May 2002. The highest diversity was recorded in the inflow into the lagoon. It was higher than that recorded at the adjacent shore (site-3), suggesting that the larvae inhabiting the Hoat Lagoon not only originated from the adjacent shore but also from more distant source areas. The lowest diversity was recorded at site-2 in the lagoon, where composition of the larval assemblage was dominated by few species (e.g. *Saccostrea* sp.).

Various factors influence diversity such as time (Fischer, 1960; Simpson, 1964), climatic stability (Klopfer, 1959; Fischer 1960, Dunbar, 1960), spatial heterogeneity (Simpson, 1964), competition (Dobzhansky, 1950), predation (Paine, 1966), and disturbance (Connel, 1978; Gutt and Piepenburg, 2003). According to Omori and Ikeda (1985) diversity is often related to certain environmental characteristics and the degree of complexity of the energy flow within the community. They also suggested that higher diversity tends to be seen in areas of greater environmental stability (or predictability), especially if associated with higher levels of productivity.

Spatial heterogeneity due to the difference in turbulence intensities between the lagoon and the adjacent shore was the regarded as most probable determinant of larval diversity at the study sites. The lowest larval diversity in the outflow may be caused by the larval retention i.e. by the fact that some species are retained from being exported from the lagoon. The highest diversity of settlers was found at site-1 in the lagoon, while the lowest was found at the adjacent shore (site-3). This suggests that many larvae imported by the inflow settled in the lagoon. The higher turbulence intensity at the adjacent shore reduced the numbers of successful settlers (section 4.1.8.2). This finding agrees with Connell's (1980) hypothesis that in very harsh condition population densities decrease below levels, at which they compete, by physical elimination and in benign conditions by predation. In intermediate, moderately harsh environments, where mortality from direct physical stresses

and from natural enemies should decline, populations are more likely to reach levels, at which they compete, and so competition becomes the dominant organizing force.

In conclusion, the diversity of settlers is assumed to be primarily controlled by the fact that the environmental conditions in the lagoon were relatively more stable than at the adjacent shore and that according to Giller (1984) the number of species should increase with environmental stability.

The larval assemblages in the inflow and outflow and the settler community at site-1 and site-1 in the lagoon were most similar in taxonomic composition. This similarity pattern reflects the difference in environmental factors (e.g. hydrodynamic regimes). If species are found to be grouped according to their habitat distribution, this grouping may be related to similarities in morphology or behavior (Digby and Kempton, 1987).

5.6. Effect of seawater density on larval settlement

Larval settlement besides depends on the numbers of propagules, hydrodynamic conditions, and behavioural factors (Connel, 1985). In the Hoat Lagoon the settlement was presumed to be primarily controlled by the influence of seawater density on the passive sinking of the larvae.

The larval supplies to the three study sites were not homogenous, indicated by the significant differences of larval densities among sites. The larval densities were not significantly correlated with the settlement densities, although both larval and settlement densities increased from the innermost lagoon toward the adjacent shore (Figure 26). However, the seawater densities were inversely correlated with settlement densities, supporting the hypothesis that *the higher the seawater density, the smaller the settlement densities are*. The explanation for this is that the settlement density depends on the ratio between the specific gravity of seawater (seawater density) and the specific gravity of the larvae. A larva with a specific gravity of less than the specific gravity of seawater will float, while a larva with a specific gravity of more than the specific gravity of the seawater will sink. Seawater with a salinity of 35 has an average specific gravity of 1.028. Numerous authors (e.g., Thorson (1964), Crisp (1984), Sulkin (1984), Young & Chia (1987) have demonstrated that environmental stimuli, both biological (e.g., food, predator, prey) and or/physical (e.g., gravity, light, pressure, salinity, temperature, and tide), influence larval vertical movements. In addition, a large number of studies have shown that physical factors such as salinity and temperature (i.e., haloclines and thermoclines, respectively) can influence the movement of planktonic invertebrates (Pearce, et al 1996). Species from a wide variety of taxonomic

groups, including gastropods and bivalves, produce larvae whose vertical position in the water column is influenced by vertical discontinuities in salinity and/or temperature and, hence, seawater density (e.g. Harder 1968; Oshurkov et al. 1982; Scope-Howe & Jones 1986; Boudreau et al. 1991, 1992; Thiebaut et al. 1992; Raby et al. 1994; Gallagher et al. 1996, and Manuel et al, 1996b). This suggests that the density also controls larval settling to the panels installed in the Hoat Lagoon.

Several mechanisms of larval settling through the water column were proposed by Pires and Woollacott (1983) responses to the gravitational forces of the earth, generally referred to as geotaxis, are a commonly reported behavior among planktonic marine invertebrate larvae. The larvae of some marine invertebrates possess statocytes that are thought to function in the perception of gravity. An apparent geotaxis has been observed in both larvae that are known to have gravity receptors and those that do not, but there is no evidence that the movement is accomplished through an active, direct response to gravity. Yet, some larvae exhibit apparent negative geotaxis prior to settlement. Several explanations for this behavior have been proposed:

- (i) orientation to the magnetic field;
- (ii) response to a partial pressure gradient of dissolved gases;
- (iii) positive buoyancy, a passive direct effect of gravity;
- (iv) high barokinesis, an active indirect effect of gravity; and
- (v) orientation to gravitational forces, an active direct response to gravity.

Young (1986) reported that larvae of some species increase their concentration near the seabed, others favor near-surface water while still others may respond to pressure and density changes by many factors including larval behavior.

Besides the passive direct effect of gravity, positive buoyancy is also accounted in relation to the effect of the seawater density. Buoyancy is known to be a contributing factor in determining the vertical orientation and distribution of certain aquatic organisms. Many larvae have also the ability to keep their position in the water column by producing mucus or lipid. Holland (1974) reported that the main storage products of invertebrate larvae are lipids, which are lighter than seawater. Aleyev (1976) noticed parachute structures, for example, setae, long spines, long arms and feathery appendages, which increase the surface area of aquatic organisms and, therefore, reduce their sinking rates, and Sigurdsson et al (1976) pointed out that the dispersal of post larval bivalve molluscs was aided by the secretion of byssus threads. Bhaud and Casaux (1990) found that many

plankton species that have no ability to move horizontally but can adjust their vertical position by mucus secretion, the function of which is primarily the provision of buoyancy.

5.7. Effects of turbulence intensity on the larval settlement

5.7.1. Dissolution rate of gypsum slab and turbulence intensity

Turbulence is a term loosely applied to various complex and irregular movements of water by which different water layers become mixed (Tait and Dipper, 1998). The turbulence intensities were determined qualitatively in this study from the dissolution rates (DF) of gypsum slabs, which were deployed at five different depths at the three study sites. The concept of using the dissolution rate of a solid as an index of 'water motion' was introduced by McConnell & Siegler (1959), who showed that the weight loss in tablets of sodium chloride during a defined immersion period was a useful index of current speeds in streams. This method has been accepted as a measure of the degree to which the diffusion or dissolution was enhanced by the water movement to which the clod-card (= gypsum slab) was exposed (Muus, 1968; Doty, 1971). Thus, the DF is an integrated measure of the degree to which water characteristics and water movements of all kinds enhance diffusion of material into and out of benthic organisms (Doty, 1971). Nixon *et al* (1980) speculated that turbulence might have contributed to dissolution rates in their studies. Santchi *et al.* (1983), calling the gypsum-dissolution technique "a poor man's turbulence sensor," used it for the determination of the diffusive boundary-layer thickness. The mass transfer of gypsum to the water is controlled by the thickness of the diffusive boundary layer around the gypsum objects and the concentration gradient across the diffusive boundary layer (Barton and Wilde 1971; Liu and Nancollas 1971; James and Lupton 1978; Opdyke *et al.*, 1987). The diffusive boundary layer is a bottleneck for the transfer of solutes and gases because the transfer is controlled by molecular diffusion in the diffusive boundary layer. If it is assumed that the Ca^{2+} concentration is saturated at the gypsum sphere and near zero in the surrounding environment and that Ca^{2+} is transported away from the sphere, then the thickness of the diffusive boundary layer is the only controlling factor for gypsum dissolution, i.e., for mass transfer. A thinner boundary layer leads to an increased rate of gypsum loss to the surrounding water, and thus to enhanced dissolution rates (Porter, *et al.*, 2000).

The turbulence intensities in the lagoon and at the open shore were significantly different. They ranged from an almost laminar situation in the lagoon to a fully turbulent regime at the adjacent open shore.

Currents in the lagoon were dominantly controlled by the tides, whereas the turbulence regime at the open shore is controlled by wind and waves. The slightly higher turbulence at site-2 than at site-1 is assumed to be due to its proximity to the entrance of the lagoon, which is characterized by the intensive mixing of water masses.

5.7.2. Effect of turbulence regime on the settlement density

Only at site-1, the turbulence intensities were significantly correlated to the distances above sea bottom i.e. they increased with height above the seabed (Figure 27 a, b, c). There was a significant negative correlation between turbulence intensities and settlement densities, supporting the hypothesis that *'the higher the turbulence intensity, the smaller the settlement densities are'*.

This is because meroplantonic larvae settling from the water column to the ground, to begin their adult life, they will face problems in approaching the substrate if the turbulence intensity (current velocity) exceeds their swimming speeds.

Densities and species numbers of settlers at the adjacent shore were relatively smaller than that in the lagoon due to the greater shear stress near the panel substrates. The larval settlement at the shore is supposed to occur both during slack water (lull period) and at a rough sea state. Settling larvae in a turbulent flow experience numerous hydrodynamic forces associated with the fluid motion. These forces fluctuate in time, and the character of the fluctuation is governed by the structure of the turbulence. The hydrodynamical forces include lift, form drag, skin friction, fluid acceleration reaction forces, and forces due to, viscous and turbulent shear stresses. The relative strength of the various forces depends on the larval morphology, the character of the seabed, and the flow states (Allen, 1985; Denny, 1988). Only certain species are able to cope with the turbulent condition, leading to reduced species diversities. Predicting actual forces acting on a larva is complex. At the scale of a larva, the temporal variation of all the hydrodynamics forces depends only on the temporal variation of the local velocity field, i.e., the turbulence structure (Allen, 1985; Denny, 1988). The transport of larvae to the seabed is governed by a combination of active swimming, passive sinking, and turbulent advection (Crimaldi *et al.* 2002).

Crimaldi *et al.* (2002) stated larval behaviour can affect settling only during a lull period, especially when the larval swimming speed is less than the transport rate. Because most larvae are not able to swim against currents or turbulence in a natural tidal system, except during slack tide, the process of being transported to the seabed is likely to be

passive most of the time. If there was insufficient time between turbulent resuspension events (i.e., during the lull periods), a larva is likely to be resuspended in a manner similar to a passive particle. However, if the lull duration is sufficient for the larva to react, behaviour can influence the probability of successful settlement. Larva behaviour in these cases can include either an attachment to the substrate or a burrowing in the sediment due to favourable chemical, tactile, or hydrodynamic cue. Most larvae will settle during relatively calm and low-velocity periods, when instantaneous shear stresses are smallest and lull periods are longest (Gross *et al.*, 1992; Eckman, 1990). This hypothesis is used to explain the pronounced recruitment patchiness that is prevalent in many benthic communities (Crimaldi *et al.* 2002).

Among the cues that may induce behaviour resulting in actual settlement of meroplanktonic larvae are, according to Abelson and Denny (1997), flow characteristics and other factors that are mediated by flow characteristics (e.g., delivery of chemical attractants and suspended sediment). Most flow characteristics that are relevant to settling larvae, including flow direction, shear stress, pressure gradients, turbulence intensity, boundary-layer or viscous sub-layer thickness, and flow acceleration (Abelson and Denny, 1997) are affected by reduced velocities.

The decreasing settler densities at the panels located at the sea bottom (0 m) of the two study sites in the lagoon were due to the effect of higher sedimentation rates (Figure 17). They may cause that larvae are buried after settling and probably die (Wilson, 1956). In general, sediments can have attractive or a repellent effects on the larvae. Metamorphosing larvae ready to settle are able to distinguish between favorable and unfavorable sediments. When the larvae settle, they appear to first explore the settling ground. If the substrate is unfavorable, they leave it, swim away, settle again, and repeat their exploration. This behavior can continue over a period of several days, with metamorphosis delayed until a suitable substrate is found (Tait and Dipper, 1998).

5.8. Settlement patterns

The settlement densities in the lagoon peaked in October (dry season), November (transitional) period and December 2001 (wet season) at 1 m, 0.50 m, and 0.75 m above the sea bottom, respectively. At site-2, the settlement density peaked in October and December 2001 at 0.5 m and 0.25 m above the bottom, respectively. However only settlement density at the bottom panels (0 m) at site-1 were significantly correlated with the length of submersion. In contrast, the settlement densities at site-3 peaked in February

2002 (wet season) at panels 0.5 and 0.75 m above the bottom and were significantly correlated with the length of submersions. This suggests that in the lagoon most of the settlement peaks occurred in earlier periods of the submersion whereas at the adjacent shore larvae settled more or less continuously. This might imply that recruitments took place the whole year round, and that the peaks were dominantly influenced by larval supply from other places, site-specific oceanographic and hydrodynamic conditions (including the turnover time of the lagoon) and behavioural factors. Osman (1978) estimates that at least 90% of the colonists of artificial substrates have immigrate as larvae, even for species who as adults are capable of mobility. Immigration occurs during the early pelagic phase in the life cycle of species characterized by sessile adulthood. The settlement patterns of panels can be explained by concept of island colonization (MacArthur and Wilson, 1963) if the panels are assumed to represent uninhabited islands. Initial colonization is essentially a noninteractive process primarily influenced by the dispersal capacities and extinction potentials of the colonizing organisms. With the establishment of an equilibrium species pool, interactive processes such as competition and predation take precedence in determining the island's species composition (Cairns and Ruthven, 1970). The islands assemblage soon manifests the characteristic of an autonomous community capable of maintaining its integrity in the face of environmental change (Cairns et al, 1976). During the noninteractive phase of colonization, artificial substrates act as sampling devices that passively collect organism from the natural community. With the acquisition of an equilibrium, the substrate ceases to function primarily as a sampling device, and the associated species assemblage begins to evolve its own characteristic composition. The appropriate immersion time is varying under different environmental conditions, making the choice of comparable sampling days difficult (Cairns, 1982).

5.9. Conclusions and Outlook

The conclusions that could be drawn from this study are as follows:

1. *How can the current regimes transport mollusc larvae to the lagoon and its adjacent shore?*
 - Mollusc larvae were transported during flood tide by mostly shore-perpendicular currents through the lagoon's entrance. After passing the entrance, they were transported toward the eastern side of the lagoon before then were turned partly northward and southward. During ebb tide, the larvae transported through the entrance and mostly northward and north-westward by shore-parallel coastal current.

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- The inflow and outflow current speeds through the entrance were similar, while larval influxes were significantly higher than larval outfluxes.
 - The larval influxes in October, November, December 2001 and March 2002 were significantly correlated with wind speeds, i.e. the higher the wind speed, the lower the larval influxes.
 - There was no correlation between the larval densities at the adjacent open shore (site-3) and larval influxes, suggesting that most larvae that entered the lagoon might have come from remote areas as ‘teleplanic larvae’ (Scheltema, 1982). The larvae were regarded to be transported from the Banda Sea (~65 to 70 nm apart from the lagoon) by advection due to a well-documented upwelling caused by wind relaxation during the southeast monsoon, which also caused the distinctly lower temperatures at the study sites in September and October 2001.
 - Larvae that were transported into the lagoon with a flood tide could reach whole areas of the lagoon.
 - Larval settlements in the lagoon were supposed to originate from the outside, only small portions were regarded to come from local reproduction.

2. How many mollusc larvae are retained in the lagoon?

- The lagoon is well flushed because turnover time of its water volume was only approximately 19 hours. During an ebb tide (6 hr and 12 minutes), an average of 29% of the lagoon’s water volume were exported. This means that it took three ebb tides to totally replenish the lagoon water’s mass.
- The relatively short turnover time did not support the hypothesis that *the greater the larval supply and the longer the retention time of the larvae, the higher the settlement densities in the lagoon are.*
- This suggests that the larval settlement is controlled by seawater density and other factors (turbulence intensity and biological factors).
- An average of 38% of the water volume and 78% of the larvae entering the lagoon during a flood tide were retained in the lagoon after a tidal cycle.
- The larvae that were retained in the lagoon are supposed to settle and utilize the lagoon as a nursery ground.

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2. *How do water properties (in this case, seawater density) and turbulence intensity control the larval settlement?*
- Seawater densities decreased from the adjacent open shore toward the inner most lagoon. They were significantly negatively correlated with settlement densities, supporting the hypothesis that *the higher the seawater density, the smaller the settlement densities are*. Larval densities increased with settlement densities but this correlation was not significantly.
 - Turbulence intensities in the lagoon and at the adjacent open shore different significantly. The turbulence regime ranged from almost laminar condition in the lagoon to fully turbulent condition at the adjacent open shore. The turbulence intensities were significantly negatively correlated with settlement densities, supporting the hypothesis that *the higher the turbulence intensity, the smaller the settlement densities are*.
 - Settlement densities were higher and peaked earlier in the lagoon than at the adjacent open shore. Settlement events occurred over a wide range of seasons (southeast and northwest monsoons), suggesting that recruitment occurred the whole year round.

Some open questions should be addressed in the future. For instance, Are the larval species entering the lagoon during the southeast monsoon consist of teleplanic larvae? Are the larvae found only in the outflow (*Patella sp.*, *Oliva sp.*, and a veliger1) products of autochthonous reproduction in the lagoon? What is the fate of those larvae (e.g. *Charonia tritonis*) that were found in the inflow but not on the settlement panels?

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APPENDIX 1. Schedules of sampling dates from 25 August 2001 to 22 May 2002

Earlier activities	Date		
<ul style="list-style-type: none"> • Measurement of surface current using drougths (drifters) • Free collections of benthic mollusc 	25 August 2001		
Set-up of settlement collectors in the field sites	13 September 2001		
Measurements of the tide and depth soundings	06.10.2001		
Samplings	Date	Samplings Intervals (Day)	Durations of the submersion times (day)
The first (I)	18.09.2001	6	6
The second (II)	01.10.2001	14	20
The third (III)	14.10.2001	13	33
The fourth (IV)	28.10.2001	14	47
The fifth (V)	11.11.2001	14	61
The sixth (IV)	25.11.2001	14	75
The seventh (VII)	09.12.2001	14	89
The eighth (VIII)	23.12.2001	14	103
The ninth (IX)	06.01.2002	14	117
The tenth (X)	20.01.2002	14	131
The eleventh (XI)	03.02.2002	14	145
The twelfth (XII)	09.03.2002	34	179
The thirteen (XIII)	17.03.2002	8	187
The fourteen (XIV)	04.04.2002	18	205
The fifteen (XV)	22.05.2002	48	253

CURRICULUM VITAE

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Qualifications and Education

1969-1974 : Elementary School in Langgur
1975-1977 : Secondary School in Langgur
1978-1981 : High School in Langgur
BSc (1987) *in Aquatic Resource Management* from Faculty of Fisheries, Pattimura University-Ambon, **Indonesia**. (Thesis: *Application of Swept Area Methods in Drift Gill Net using different shortening values in Oboidertutu waters, Kai Islands Indonesia*).
MSc (1996) *in Marine Sciences* from International Marine Sciences Programme, Faculty of Science, Aarhus University, **Denmark**. (Thesis: *Effect of surface current and roughness densities of eelgrass and mussel beds on the flux of particles in the benthic boundary layer*)
1994 : Course in Advance Marine Biology at Tjarno Marine Biological Station, Goteborg University, **Sweden**.
1994 : Course in Experimental Marine Biology at Ronbjerg, Marine Station, Aarhus University, **Denmark**
1997 : Course in Integrated Coastal Zone Planning and Management (equivalent to 1/3 of MSc degree course) at Departments of Tropical Environmental Science and Geography (TESAG), James Cook University, Townsville, **Australia**.
2000-2003 : PhD Student at Institut für Polarökologie- Faculty of Mathematic and Natural Science-Christian-Albrechts-Universität zu Kiel.

Professional Experience

1988-present: Academic Staff at Faculty of Fisheries and Marine Science, Pattimura University, Ambon
1997-2000 : Secretary of the Department of Aquatic Living Resource Management, Faculty of Fisheries, Pattimura University, Ambon.

Erklärung

Hiermit erkläre ich, dass die vorliegende Dissertation - abgesehen von der Beratung durch meine akademischen Lehrer - nach Inhalt und Form meine eigene Arbeit ist. Sie wurde keiner anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegt. Dies ist mein erster Promotionsversuch.

Kiel, den 03 November 2003

(Eugenius Alfred Renjaan)