ECOLOGY OF HERMIT CRABS (FAMILY DIOGENIDAE) IN MATANG MANGROVE ESTUARY AND ADJACENT COASTAL WATERS

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ABSTRACT

Ecological aspects of diogenid hermit crabs were studied in Matang mangrove estuary and adjacent coastal waters to determine their abundance and distribution in relation to abiotic and biotic factors, population dynamics, shell use patterns, reproduction and trophodynamics. Samplings of hermit crabs and environmental parameters were carried out at mid-estuary, river mouth, coastal mudflat and offshore shoal waters, using a small otter trawl from August 2009 to March 2011. The major hermit crab species were *D. lopochir* Morgan, 1989, *Diogenes moosai* Rahayu & Forest, 1995, and *Clibanarius infraspinatus* Hilgendorf, 1869 which dominated the shoal area, mudflat and mid-estuary, respectively. The growth (K) and total mortality (Z) rates of *D. moosai* and *D. lopochir*, as fitted by the von Bertalanffy growth function were 1.4, 7.06 and 1.3, 3.54, respectively. Both *Diogenes* species reproduced mainly in January/February and July which resulted in one major and one minor recruitment pulse in a year. The two sympatric species of *Diogenes* adopted different reproduction strategies. *D. moosai*, at higher risk of exposure to extreme physical conditions in the mudflat, generally spreads its reproduction over the year (continuous reproduction), while *D. lopochir*, at greater risk of predation in the subtidal shoal area reproduces at the most favourable period (discontinuous reproduction). The availability of gastropod shells is an important biotic factor modulating the distribution and abundance of hermit crabs, since empty shells were few and broken shells were occupied. Shells of 14 gastropod species were used by both *Diogenes* species, but >85% comprised shells of mainly four species, *Cerithidea cingulata*, *Nassarius cf. olivaceus*, *N. jacksonianus* and *Thais malayensis*. Extreme bias in shell use pattern by male and female of both *Diogenes* species suggests that size compatibility between hermit crab and shell determines the shell use pattern and explains ecological partitioning between species and sex of hermit crabs. Where their distribution overlaps in offshore waters, interspecific competition between *D. moosai* and *D. lopochir* is hypothesized to be modulated by predation thus allowing coexistence. Stable isotope analysis revealed the dependency of *Diogenes* hermit crabs on microphytobenthos (49.9%±14.6%) as their major primary source of nutrition, followed by phytoplankton (27.6%±9.3%) and mangrove (22.5%±7.7%). Hermit crabs serve as prey organisms to predatory fishes indicating the intermediary role played by hermit crabs (2nd and 3rd trophic level) in the food web of the Matang ecosystem.

ABSTRAK

Penyelidikan tentang aspek ekologi umang-umang diogenid telah dijalankan di kawasan muara paya bakau di Matang dan kawasan perairan di sekitarnya untuk menentukan kelimpahan dan taburan umang-umang dibawah pengaruh faktor-faktor biotik dan abiotik, dinamik populasi, corak penggunaan cangkerang gastropod, pola pembiakan dan trofodinamik. Persampelan umang-umang dijalankan di hulu sungai, muara sungai, lapangan lumpur dan kawasan pesisiran pantai dengan menggunakan pukat tunda kecil bermula dari Ogos 2009 hingga Mac 2011. Spesis-spesis utama yang di rekodkan di kawasan tersebut adalah *D. lopochir* Morgan, 1989, *Diogenes moosai* Rahayu & Forest, 1995, dan *Clibanarius infraspinatus* Hilgendorf, 1869 yang masing-masing mendominasi kawasan pesisiran pantai, lapangan lumpur dan hulu sungai. Kadar pertumbuhan (K) dan kadar mortaliti (Z) untuk *D. moosai* dan *D. lopochir* yang ditentukan melalui penyesuaian fungsi pertumbuhan Von Bertalanffy (VBGF) adalah masing-masing 1.4, 7.06 dan 1.3, 3.54. Kedua-dua spesis *Diogenes* membiak secara khususnya pada bulan Januari/Februari dan Julai yang menyebabkan satu tempoh pengrekruitan utama dan satu tempoh pengrekruitan kecil dalam setahun. Kedua-dua spesis *Diogenes* yang simpatrik mempunyai strategi pembiakan yang berbeza. *D. moosai* yang terdedah kepada keadaan fizikal yang ekstrem di lapangan lumpur, secara umumnya mempunyai corak pembiakan yang berterusan, manakala *D. lopochir* yang terdedah kepada risiko tinggi pemangsaan membiak secara bertempoh dan pada masa yang sesuai. Keberadaan cangkerang gastropod merupakan faktor biotik yang penting dalam mempengaruhi taburan dan kelimpahan umang-umang, memandangkan cangkerang kosong adalah terhad malahan cangkerang rosak turut digunakan. Sejumlah 14 spesis cangkerang gastropod digunakan oleh kedua-dua spesis *Diogenes*, tetapi >85% spesis cangkerang yang digunakan terdiri daripada *Cerithidea cingulata*, *Nassarius cf. olivaceus*, *N. jacksonianus* dan *Thais malayensis*. Corak penggunaan cangkerang yang berbeza oleh jantan dan betina kedua-dua spesis menunjukkan bahawa keserasian saiz di antara umang-umang dan cangkerangnya adalah penting dalam menentukan corak penggunaan cangkerang dan memperjelaskan pemetakan ekologikal di antara spesis dan seks umang-umang. Di mana ada pertindihan taburan di kawasan luar pantai, persaingan antara spesis yang melibatkan *D. moosai* dan *D lopochir* dihipotesiskan dipengaruhi oleh pemangsaan, justeru membenarkan kewujudan bersama spesis-spesis tersebut. Hasil analisis isotop stabil mendedahkan kebergantungan umang-umang *Diogenes* terhadap mikrofitobentos (49.9%±14.6%) sebagai sumber primer utama, diikuti oleh fitoplankton (27.6%±9.3%) dan bakau (22.5%±7.7%). Umang-umang juga merupakan mangsa pemakanan oleh ikan-ikan pemangsa. Ini membuktikan peranan umang-umang sebagai pengantara rantaian makanan (tahap trofik 2 dan 3) dalam ekosistem di kawasan perairan Matang. .

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CHAPTER 1

INTRODUCTION

1.1 An overview of hermit crabs and their environment

Hermit crabs are decapod crustaceans of the infraorder Anomura and Superfamily Paguroidea. This superfamily represents an approximately 2,002 described species worldwide (Appeltons et al. (eds), 2012) distributed throughout the tropical, subtropical and cold seas and occupying a semiterrestrial to abyssal habitats (Rahayu & Wahyudi, 2008). Hermit crabs are common inhabitants of mainly intertidal areas such as rocky shores, mangroves and mudflat areas where they can occur in high abundance. They are well adapted to living in empty gastropod shells that protect them from predators and minimize the risk of desiccation, making this crustacean successfully adapted to live on land and seas (Reese, 1969).

The understanding of hermit crabs especially in the aspects of ecology of principally their physiological responses and population dynamics, in relation to environmental changes such as tides, freshwater inundation, pollution, competition and predation are still scarce. There are relatively few publications related to the ecology of hermit crabs in western Indo-Pacific region despite their ecological importance to the intertidal and sublittoral communities. For this reason and in consideration of the characteristic behavior of the hermit crabs such as changing the shell as they grow, competition to acquire optimum shell fit and shell selection pattern, hermit crabs have been an attractive subject for research for ecologist (Hazlett, 1996).

Mangrove fringed estuary is one of the most productive coastal habitats being sustained by energy inputs from microphytobenthos, phytoplankton and mangrove detritus and supports a diversity of invertebrates and young fishes (Chong, 2005). Like other invertebrates within the mangrove ecosystem, hermit crabs are subjected to environmental disparity regulating their population distribution and abundance. Animals must tolerate different forms of stress caused by extreme fluctuation in temperatures, salinity (freshwater influence), dissolved oxygen and periodic emersion and submersion caused by tides in the case of intertidal zone. Traditionally, environmental dynamics such as temperature, sediment type, intensity of currents and topography has been largely considered to be determinant of zonations in benthic marine communities (Haedrich et al., 1975) at soft bottom marine habitats (Hecker, 1990) reflecting the different adaptability and specific roles of these fauna in the ecosystems.

McNaughton & Wolf (1970) hypothesized that dominant species of invertebrates may play an important role in structuring the distributions of other benthic marine fauna by the fact that dominant species are able to adapt to wide range of environmental changes (Fransozo et al., 2008). Hermit crabs are known to be able to tolerate environmental extremities and are ubiquitous in coastal shore inhabiting diverse type of marine habitat; mangrove forest, mudflats, sandy shore, rocky shore and coral reefs. Nevertheless, habitat partition or segregation may at times be distinct within various tropical hermit crab assemblages as macro and microhabitat preferences is in advantage of alleviating competition of resources (Abrams, 1980; Leite et al., 1998).

It is generally accepted that abiotic factors (e.g. depth, temperature, sediment texture, organic content of sediment and salinity) exert more influence than biotic factors (e.g. intra and interspecific competition and crowding) in limiting the distribution and abundance of benthic marine fauna (Abele, 1974; Meireles et al., 2006). Therefore, it is uncommon for a species to have a homogenous distribution as presence of a species in an area is constantly regulated by these environmental conditions according to different demands during the life stages of the animals (Mantellato et al., 1995). Amongst the abiotic factors, sediment texture invokes a relatively more important factor in the distribution and maintenance of anomuran crustacean populations (Fransozo et al., 1998) as sediment is utilized by these animals as shelter and food source (Abele, 1974). The influence of environmental factors varies among seasons and habitats, leading to variations in the seasonal and spatial distributions of organisms and such information serve as an essential knowledge in elucidating the life cycle of the animal's populations (Santos et al, 1994).

1.2 Previous studies on population distribution of hermit crabs

Imazu & Asakura (1994) described the spatial distribution, reproduction and shell utilization patterns of three species of common intertidal hermit crabs *Pagurus geminus*, *Pagurus lanuginosus* and *Clibanarius virescens* on a rocky shore at Kominato, Boso Peninsula, Japan. The distribution of the three species greatly overlapped with *P. geminus* generally more widespread along the intertidal zone whereas *C. virescens* and *P. lanuginosus* occupy the lower zone. This pattern of distribution was maintained over a one year period despite a few minor changes. Generally, female *P. geminus* and *C. virescens* inhabit farther out at lower zone than males whereas for *P. lanuginosus*, such a distinct difference in distribution between sexes was not seen. In a study of three common hermit crab species in a Panama rocky shore, Bertness (1981a) observed spatial separation among these species with *Calcinus obscurus* generally inhabit the middle to low intertidal zone, *Calcinus albidigitus* from the middle to high intertidal zone and *Pagurus* species confined at the lower intertidal zone.

A study on the clustering behaviour of the hermit crab, *Clibanarius laevimanus* in a mangrove swamp was carried out by Gherardi & Vannini (1991) during the semi-lunar tide cycle in Kenya. They noted that *C. laevimanus* tend to form clusters around the mangrove prop roots and in the open within four metres from the mangrove fringe during every low tide and each of the cluster may consist of quiescent hundreds of individuals. The clusters of *C. laevimanus* would disband during flood tide and when the water recedes, crowded groups of *C. laevimanus* would form back the clusters, occupying the same position as well as maintaining their number, size and shape of the clusters. Gherardi & Vannini (1991) concluded that there are two main components of space utilization by *C. laevimanus*; firstly, is the adoption of “isospatial” strategy by the hermit crabs as they remained within a narrow belt along the sea-land axis of periodic submergence and emergence and secondly, is the “isophasic” strategy in which the clustering and the distribution of the hermit crabs are dependent on the oscillation of the water medium. The energy expenditure of locomotion for “isospatial” strategy is more reduced as compared to “isophasic” animals.

Most of the ‘social’ activities of the hermit crabs are carried out during the incoming flood tide whereby hermit crabs move around, grazing on the vegetable debris and performing shell cleaning by grazing on the shell of the conspecific hermit crabs. During this phase also, the hermit crabs perform rapping motions, mating and even shell exchange with each other or occupying new shells which are available (Snyder-Conn, 1981).

1.3 Diel activity of hermit crabs

Diel movements of hermit crabs are invariably impacted by tidal periodicity and are related to their feeding behaviour, avoidance of predators, reproduction and social activities such as aggregation for shell exchange (Turra & Leite, 2000a). These activities may compensate each other on the basis of cost and benefit derived through such movements. Typically, hermit crab activity is triggered by immersion at high tide where crabs move towards foraging areas (Gherardi & Vannini, 1993). However, when they forage, hermit crabs are exposed to higher risk of predation (Borjesson & Szelistowski, 1989). Deposits of food sources such as carrion, algae and plant propagules may be more during spring tide and hence, greater movements during this time may yield greater energy returns (Barnes, 2003).

Studies have shown the association between circatidal/circadian rhythms and distributional/activity patterns of hermit crabs (eg. Bertness, 1981a; Gherardi & Vannini, 1989, 1993, 1994; Barnes, 2001, 2003; Turra & Denadai, 2003; De Grave & Barnes, 2001). For a species, variation in migration patterns is largely related to ontogenetic stages with different habitat requirements and the increase in locomotive capabilities as the animals grow (Gibson, 2003). Large hermit crabs have been known to move faster than their smaller conspecifics which is probably a result of biomechanical consequence of muscle development and lever length (Barnes, 2003). Barnes (2003) studied short range migration of the terrestrial hermit crab, *Coenobita* sp. and found positive relationship between tidal range and number of active hermit crabs, and between migration distance and hermit crab size at night. Animals make use of either the ebb or flood tide current as passive transport to get from one location to the other (Tankersley et al., 2002).

1.4 Reproduction aspects of hermit crabs

Studies on hermit crab reproduction biology are scarce especially in the western Indo-Pacific region while information on population dynamics and growth of hermit crabs are limited to a few studies (see Branco et al., 2002; Turra & Leite, 2002; Manjon-Cabeza & Garcia-Raso, 1998). Studies on the population dynamics and reproduction of hermit crabs, often occurring in large populations, will contribute to greater understanding of their ecological significance in tropical estuaries.

A study done by Imazu & Asakura (1994) on the three species of hermit crab, *Pagurus geminus, Pagurus lanuginosus* and *Clibanarius virescens,* in a rocky shore at the Boso Peninsular, Japan, revealed that the reproductive season for *P. geminus* was 11 months. This period of reproduction was longer than the recorded reproduction period for any other intertidal decapod crustaceans either in the temperate or warm water regions of Japan and adjacent waters. The reproductive season of the *P. geminus* is not a rare case compared to the species on the east Pacific and Atlantic coast as year round reproductive seasons have been reported in tropical hermit crab species such as *C. zebra*, *Calcinus laevimanus* and *Calcinus latens* (Reese, 1968), *Clibanarius chapini* and *Clibanarius senegalensis* (Ameyaw-Akumfi, 1975) and *Clibanarius clibanarius* (Varadarajan & Subramoniam, 1982). Lancaster (1990) suggested a year-round reproductive season for the European species of hermit crab, *Pagurus bernhardus*.

Seasonal changes in abundance of hermit crabs are often reflected by the reproductive intensity over a period of time (e.g. Vandarajan & Subramoniam, 1982; Mura et al., 2006; Mantellato et al., 2007; Garcia & Mantellato, 2001; Squire et al., 2001) and density (e.g. Turra et al., 2002; Branco et al., 2002) related to environmental parameters (e.g. Meireles et al., 2006; Ayres-Peres & Mantellato, 2008). Complex interactions between abiotic and biotic factors provide a condition within a definite space that is well adapted by the animals and thus, sustaining the animal's populations (Pulliam, 2000). Reproduction phenology or seasonal reproductive periods may vary among species and even for sympatric species under similar environmental conditions. Wada et al. (2000) showed variations in the spawning season, hatch out season, annual spawning times, maturity size and incubation period among four sympatric species of *Pagurus* on a Japanese shore. Segregation in reproductive traits among sympatric species has been hypothesized to reduce interspecific larval competition for important resources such as food and empty shells (Reese, 1968).

1.5 Sexual dimorphism and sex ratio of hermit crabs

There are three hypotheses to interpret the difference in sexual size of hermit crabs; first, the competitive displacement hypothesis in which a size difference would reduce the competition for shells; second, the energy hypothesis in which the male's testes require less energy to develop than the female's ovaries, thus the smaller size of females and third; the sexual selection hypothesis in which the larger size of the male would be advantageous in acquiring females for reproduction through male to male competition (Abrams, 1988). In a study carried out by Imazu & Asakura (1994), it was reported that the sex ratio of each size class of the three species of hermit crabs studied (*P. geminus, P. lanuginosus* and *C. virescens*) showed a tendency to an even sex ratio in smaller size class, male-bias in the largest size class and a female-bias in the intermediate size class. Their findings thus, show that the sex ratio were more even in the smaller classes where the growth rate of male and female is expected to be similar and the high mortality of male occurred in the intermediate size.

1.6 Shell-hermit crab relationships

1.6.1 Shell use pattern and its effects on hermit crabs

The dependence of hermit crabs on gastropod shells as shelter is fundamental to their survival. Optimum shell selection by hermit crabs is vital as it directly affects growth, reproduction, protection from predators (Fotheringham, 1976; Bertness, 1981a; Elwood et al., 1995) and reducing risk of desiccation (Bertness 1981b; Bertness & Cunnigham 1981). A hermit crab constantly moves to a larger gastropod shell as it grows in order to maintain an optimum shelter that adequately protects it from predator. For the female, the shell must provide a sufficient gap for its brood (Childress, 1972). Crabs occupying smaller than optimum fit of a shell are more vuInerable to predation than crabs with optimum fit since a higher percentage of their body is exposed or they are unable to retreat further inward (Hazlett, 1981). On the other hand, crabs occupying larger and heavy shells may experience slow growth and their reproduction is affected (Bertness, 1981a; Hazlett & Baron, 1989; Elwood et al., 1995; Osorno et al., 1998) since heavier shells incur higher energy cost for locomotion (Dominciano et al., 2009). Shell selection patterns have been known to be influenced by shell resources and availability in an ecosystem (Orians & King, 1964; Turra & Leite, 2001; Sant' Anna et al., 2006). Empty shells are usually scarce in a habitat (Scully, 1979) and thus, it is an important limiting factor for hermit crab population. Increased abundance of shell resources has been shown to increase hermit crab population size (Vance, 1972). Locating shell supplying sites in a vast habitat may pose a challenge; however, hermit crabs are known to be able to detect chemicals released by tissues of dead gastropods (Rittschof et al., 1990; Kratt & Rittschof, 1991; Rittschof & Cohen, 2004). Hermit crabs often search for new shells by tracing odor from sites where gastropod are being non-destructively predated leaving behind shells with little or no damage; these sites are collectively known as 'gastropod predation sites' (McLean, 1974; Tricarico & Gherardi, 2006). In an environment where empty shells are limiting, intraspecific and interspecific competitions may occur between conspecific or sympatric species (Hazlett, 1966; Dowds & Elwood, 1983) and between sexes (Briffa & Dallaway, 2007). Shell partitioning between hermit crabs is possible in the presence of different shell species (Kellogg, 1977; Gherardi & Nardone, 1997; Leite et al., 1998; Turra & Leite, 2001, 2002). Sexual dimorphism and size differences between species could be developed to minimize intraspecific competition and to guarantee shell fitness in the population in response to the limiting resources (Garcia & Matellato, 2001).

Hermit crabs are a successful taxon and unique as they choose shelters that they cannot produce themselves (Fotheringham, 1976). Shell selection by hermit crabs is not a random process as suggested by multiple evidences (Grant & Ulmer, 1974). In the selection of appropriate shell types, hermit crabs seem to have the ability to distinguish between different species of shells based on relative weight of shell as well as shell morphology rather than actual species recognition (Scully, 1983). Shells that belong to the same genus may have morphological overlaps or similarity in terms of size, weight and texture (Bertness, 1982) and as well as shape and structures (Shih & Mok, 2000). The ability to secure shell occupancy compatible to the morphology of both hermit crabs and gastropod shells is an outcome shaped by a long evolutionary process (Cunningham et al., 1991, Schram, 2001).

Hermit crabs choose shells on the basis of how they benefit from them (Garcia & Mantellato 2001) such as minimal energy cost for locomotion, sufficient protection from predators and water retention (Fotheringham, 1976; Bertness, 1981b; Elwood et al., 1995). However, any advantage in shell use may be compromised by ill-fitting shells that are incompatible with the crab’s biometrics (Blackstone 1985, Turra & Leite

2003) rendering the animal vulnerable to predators (Hazlett, 1981), reduced reproductive potential (Hazlett & Baron, 1989; Elwood et al., 1995; Osorno et al., 1998) and retarded growth (Fotheringham, 1976, Osorno et al, 2005).

The shell selection process includes gathering of information, assessing shell quality and lastly, making decision accordingly. In an experiment by Imafuku (1984), approximately 80% of hermit crabs changed to new shells that were experimentally provided and abandoned their original shells occupied from the environment. Knowledge acquired about a shell resource has a profound effect on the motivational state of hermit crab. Tricarico & Gherardi, (2007a) studied the motivation and behaviour of the hermit crab *Pagurus longicarpus* in deciding whether to retain its original shell or move to a newly found shell following information gathering via investigation. The study revealed that the motivation of *P. longicarpus* to occupy a new shell is exclusively affected by the worth of the original shell rather than the value or quality of shell resource offered.

The morphometrics of gastropod shells have a direct influence on shell selection patterns of hermit crabs particularly in the context of shell size, weight and shape. These features apparently affect hermit crab reproduction, protection and growth (Fotheringham, 1976; Bertness, 1981c; Elwood et al., 1995). Morphometric data from both hermit crabs and their gastropod shells have been commonly used to quantify shell utilization patterns (Blackstone, 1985; McClintock, 1985; Shih & Mok, 2000; Turra & Leite, 2004; Barnes & Kuklinski, 2007; Nakin & Somers, 2007; Caruso & Chemello, 2009) and in addition, in-situ and laboratory experiments that were carried out to elucidate the behavioural aspect of shell use (Wilber, 1989; Garcia & Mantellato, 2001;

Turra & Denadai, 2002; Gherardi, 2004; Tricarico & Gherardi, 2007a; Dominciano et al, 2009; Bach & Hazlett, 2009; Pereira & Goncalves, 2000; Tricarico et al., 2009).

Turra & Leite (2004) carried out a study on crab-shell size relationship of three species of tropical intertidal hermit crabs; *Clibanarius antillensis*, *Clibanarius sclopetarius* and *Clibanarius vittatus*. They found that crab size and weight were significantly related to all morphometric parameters of shells measured. There is also frequent negative allometry between crab and shell variables suggesting that larger crabs utilize lighter shells rather than smaller crabs. In addition, the relationship between crab size and shell length or shell weight is not dependent on species of both crab and shell. The results indicate the role of crab size and crab weight in determining the shell size preference of hermit crabs and that crab-shell size relationship are not species specific.

Caruso & Chemello (2009) employed multivariate analysis to quantify the relative role of shape and size of shells on shell use by hermit crab, *Clibanarius erythropus*. The result indicated that shell size was more important than shell shape based on the patterns of shell use whereby larger crabs used larger shells. Although shell shape expressed in terms of degree of elongation varied in both males and females, these variations are accounted only towards males as shell shape features have been correlated with male biometrics but not with female biometrics. Caruso & Chemello (2009) further hypothesized that the larger male may have access to larger, heavier and more available shells such as *Osilinus turbinatus* which cannot be occupied by averaged-sized males or ovigerous females. However, once males reach an adequate size, they are free to choose shells of the desired shape from relatively larger resource of heavy shells.

Blackstone (1985) investigated experimentally the effects of variations in shell size and shape on growth and cheliped form in the hermit crab, *Pagurus longicarpus* from two geographic locations on the north and south Atlantic coast. Results showed that crabs occupying small, high-spired shells attained smaller sizes but produced relatively longer claws and greater asymmetry between two claws, while crabs occupying large, low-spired shells, attained larger sizes but produced relatively shorter claws. These results are compatible with the results from field observations made on *P. longicarpus* from the two geographic locations whereby the southern crabs occupying small, high-spired shells are smaller and have longer claws compared to the larger and shorter claws of northern crabs that occupy large, low-spired shells. Thus, Blackstone (1985) concluded that size and shape differences between *P. longicarpus* of these two geographic locations are due to differences in shell occupation.

The energetic cost of carrying a shell as ‘mobile home’ has been demonstrated; nevertheless the benefit of increase feeding rate and food quality may overpower it (Osorno et al., 2005). When carrying a shell, the terrestrial hermit crab, *Coenobita compressus* consumes 50% more oxygen than when is ‘naked’ (Herreid & Full, 1986). Likewise for marine hermit crabs which are fully submerged, they require a lesser effort to carry shells (Briffa & Elwood, 2005). The energy cost could also be expressed in term of increased lactate which causes potential fatigue and consequently affecting general activities of the crabs (Doake et al., 2010). The trade-off between growth and protection can be shown by crabs occupying lighter shells that permit growth due to larger internal volume. As lighter shells are also thinner walled, therefore, the lighter shells which are more brittle may offer less protection from predators and would expose the hermit crabs to higher risk of desiccation. Hermit crabs can compensate higher energy expenditure due to carrying heavier shell by increasing food intake (Osorno et al., 2005).

Empty gastropod shells usually are masked by thick epiphytic algae that encrust the shell surface (Reese, 1969) and other symbiotic associates of hermit crabs such as polychaetes, arthropods, bryozoans and cnidarians. There are a total of 550 species of invertebrates found to be associated with 180 species of hermit crabs. These epibionts particularly cnidarians and bryozoans may benefit hermit crabs by reinforcing the extension of shell aperture lip hence lessen the need to change shell and protection (Williams & McDermott, 2004) by enhancing crypsis along with stinging tentacles of cnidarians to deter predators. However, an encrusted shell means additional weight that is likely to impose energetic cost of carrying it particularly shells that are heavily encrusted with barnacles and tubicolous polychaetes (Briffa & Elwood, 2005).

Briffa & Elwood (2005) investigated the effects and preference of hermit crabs towards both encrusted and non-encrusted shells. The results showed that hermit crabs have clear preference towards shells free of epibionts. This outcome is elucidated by the fact that encrusted shells are heavier and have lower internal volume to weight ratio compared to non-encrusted shells and consequently, elevated the haemolymph lactate levels due to increase drag. Effects of increased lactate include potential fatigue impinging on the general activities of the hermit crabs (Doake et al., 2010).

Bertness (1982) carried out an experiment to examine shell selection patterns of two common hermit crabs, *Clibanarius antillensis* Stimpson and *Calcinus tibicen* which inhabit hard bottom reef flats on the Carribean coast of Panama in relation to predation pressure and physical stresses. The study revealed that *C. antillensis* has distinct preference towards high-spired shells which would provide protection from thermal stress due to the high water retaining capability of the shells and thus, reducing the risk of desiccation, while *C. tibicen* has a preference towards low-spired shells which would enhance resistance to predators.

1.6.2 Shell availability in the environment

In nature, hermit crabs do not predate on gastropods to acquire their shells (Scully, 1983) and therefore, they would have to depend on natural mortality of gastropods (Scully, 1979). For this reason, the availability of gastropod shells is a limiting factor for the hermit crab populations and their distribution (Shih & Mok, 2000). Generally, shell resources in a given habitat are thought to be scarce (Reese, 1969; Vance, 1972) and have a direct effect on hermit crab populations (Vance, 1972; Kellogg, 1976). The abundance of shell resources available for hermit crabs is not constant as they can be removed from the habitat by wave action, buried in soft sediment, broken (Bertness, 1980) or occupied by other faunas. In contrast, empty shell resources are added following mortality of gastropods.

Turra & Leite (2002) investigated the relationship between shell availability and patterns of shell use by three sympatric species of *Clibanarius*. They revealed that the influence of shell resource availability is dependent on hermit crab species as the preference of certain shell species is distinct among the hermit crabs; *C. antillensis* used exclusively shells of *Cerithium atratum* which is the most abundant shells while, *C. sclopetarius* and *C. vittatus* occupied shell species that were less available in the field. In contrast, the compatibility of size between shell and hermit crab is not dependent on species.

Shih & Mok (2000) analysed the shell utilization by two common species of hermit crabs, *Calcinus latens* and *Calcinus gaimardii* in intertidal and subtidal zones at Kenting, Southern Taiwan, by comparing field data and laboratory results from shell-selection test. The results of the study showed that intertidal *C. latens* did not use the most abundant shell type in the field. This pattern of shell preference is caused by the small size of the most abundant shell type in the field. However, both species showed strong preference for the most abundant shell type in the shell-selection tests. Also, the result showed that most hermit crabs lived in shells that fitted adequately at least in term of internal volume. The shell-selection test proved that larger crabs (carapace length > 5mm) were more shell limited than the smaller ones. Shih & Mok (2000) also found that the common shell types used by *C. latens* collected from intertidal are different from the common shell types used at subtidal zone. They related this to the variability in the distribution of empty shells between and within the intertidal and subtidal zone.

When empty shells are in short supply, a portion of the hermit crab population would inhabit damaged shells. The inhabitants of the damaged shells are often very small crabs (Shih & Mok, 2000). In intertidal reef flat of Guam, Asakura (1987) reported use of highly damaged shells by *C. latens*. Imafuku (1984) reported two individuals of hermit crab, *Pagurus geminus* occupying a single empty shell together whereas other smaller individuals occupy large holes on the wall of rocks. These conditions indicate that high quality empty shells are in shortage in those areas.

Mortality of gastropod and hermit crabs resulted from predation, increase the shell resource available for hermit crabs (Carikker, 1981; Mather, 1991; Tirelli et al., 2000). McClintock (1985) noted that hermit crabs tend to be attracted to sites where there is high predation of gastropods. Although empty shells are abundant at these sites, there is also high proportion of damaged shells due to predation that the hermit crabs have to occupy. Through laboratory tests on hermit crabs, *Pagurus pollicaris*, McClintock (1985) reported that the use of damaged shells with lip damage, hydroid colonies and pits formed by boring organisms, increased the rates of shell exchange.

Communities of hermit crabs from both Diogenidae and Paguridae in variety of habitats have been widely known to form clusters. In a shell limited environment, it has been theorized that the formation of clusters facilitates shell exchange activities by serving as a ‘meeting place’ for hermit crabs to explore and investigate potential shell resources in order to acquire better fitting shells (Gherardi & Vannini, 1993) through competitive exchange or bargaining (Hazlett, 1978, 1980). Gherardi et al. (1994) suggested that clustering is a form of social phenomenon assisting in aggregations of similarly sized, conspecific crabs with intricate forms of communication system whereby mutual benefits are gained from the chain process in shell exchange.

1.6.3 Shell resource partitioning and competitive behaviour in acquiring shell

Contests for shells is common in nature and at times may result in injury and even death of hermit crabs (Osorno et al., 1998). Coexisting hermit crabs may encounter competitive interactions for empty shells (Bach et al., 1976; Gherardi, 1990; Turra & Denadai, 2001). Empty shells are often in short supply and when occupying a shell of sub-optimal quality, hermit crabs rely on aggression to obtain better shell from another individual through ‘shell fights’ (Briffa & Elwood, 2005). However, the outcome of the conflict depends on the resource-holding potential (RHP) of the hermit crab which is the ability of an individual to win a fight against its opponent to retain possessed resources; dominant individuals with higher RHP are likely to retain their resource or possess resources from others (Parker, 1974).

Shell partitioning and competition are considered as important mechanisms resulting in the ecological separation of hermit crabs in an evolutionary time frame (Bach et al, 1976; Bertness, 1981c). Size variation among coexisting crab species is common (Kellogg, 1977). Therefore, the size, amount, type and quality of shells are common criterion influencing population size (Vance, 1972), growth (Fotheringham, 1976; Turra & Leite, 2003), morphology (Blackstone, 1985; Turra & Leite, 2003), fecundity (Childress, 1972; Fotheringham, 1976; Bertness, 1981a) and survivorship (Vance, 1972; Reese, 1969; Bertness, 1981b; Taylor, 1981; Lively, 1988; Angel, 2000).

Turra & Denadai (2004) suggested two ways in which shells are acquired by hermit crabs; firstly, attraction of hermit crabs via chemical cues towards site where a new shell resource is available. However, due to difference in competitive abilities, certain species or individual may have an advantage in acquiring resources more rapidly and thus, reducing the available shell resources to other coexisting species or individuals (Busato et al, 1998). Secondly, the agonistic display of shell fight behaviour between species or individuals of the same species. Both modes of competition are used to explain intraspecific and interspecific resource partitioning of the hermit crab community (Bach et al., 1976; Busato et al., 1998).

Agonistic behavior induced by the need to acquire optimum shells and other factors influencing the outcomes of shell fights have been the focus of most hermit crab studies (Gherardi, 2006). The relative fighting ability or RHP (Parker, 1974) of individual crabs, which depends on body size and weaponry (Caldwell & Dingle, 1979; Sneddon et al., 1997), has been generally considered to be the key determinant of the outcome of shell fight (Gherardi, 2006). There are different forms of shell competition ranging from non-contact display to injurious lethal combat. The worth of a shell fight is prompted by the motivational state of hermit crabs based on assessment of the shell resource value (Arnott & Elwood, 2008). The shell resource value is assessed by the hermit crab to determine the worth of both shells, i.e. originally occupied by crabs and shell from external source (Tricarico & Gherardi, 2007a). Hermit crabs with lower quality shell have the tendency to instigate fights and their attacks were independent of the opponent’s shell quality (Gherardi, 2006). An experiment was carried out by Tricarico & Gherardi (2007b) to test the influence of past experience (shell ownership) towards agonistic behavior of the hermit crab, *Pagurus longicarpus*. They revealed that hermit crabs subjected to worsening shell quality exhibited more aggression compared to hermit crabs subjected to improving shell quality. The study concluded that agonistic behaviour of hermit crabs at least in *P. longicarpus* is dependent on previously occupied shell.

Aggressiveness of individual crabs is also influenced by their physiological condition such as reproductive and hunger states which consequently, influence the duration, intensity and outcome of shell contest (Briffa et al., 1998; Briffa & Elwood, 2000). Agonistic display such as shell-rapping which is a signal of fight may incur physiological costs in the form of increase lactate level, influences subsequent outcomes of crab fights (Briffa & Elwood, 2002). Briffa & Elwood (2002) examined the relationship between crab agonistic signals from shell rapping and consequent lactate and glucose levels. They revealed that defender crabs that successfully resist eviction have higher glucose content while those that disallowed to fight contained lower glucose level. Most of defending crabs would give up their shells early if power of initial shell rapping measured by sound intensity is high while attacker crabs would give up if their lactate levels soared high. They concluded that initial intensity of agonistic signals played a pivotal role in determining success for attackers despite its energetic cost.

RHP of hermit crabs is influenced by contestant size, with larger individuals having advantage over smaller opponents (Yoshino & Goshima, 2002). Sexual dominance and effects of asymmetries in size toward aggressiveness and outcome of shell fights have been assessed experimentally by Yoshino & Goshima (2002). They revealed that intruder crabs tended to win in both intersexual and intrasexual contest more often as their size increase, overcoming the ownership advantage of opponent crabs. Male intruders required shorter time to deprive female owners of their shells than to deprive male owners from their shells. The experiment concluded that males are more dominant as both intruders and owners since they can afford to expend energy for fighting.

From the literature, it can be summarised that shell use in hermit crabs is determined by at least three factors, shell shape (or species), size, and availability. However, only very few studies (e.g. Mantellato and de Meireles, 2004) have examined all three factors in a single study. Therefore, the present study will examine the role of all three factors in shell selection of diogenid hermit crabs to to answer the research question (see 1.8).

1.7 Hermit crab trophodynamics

Hermit crabs are known to employ various feeding modes including deposit feeding, suspension feeding, predation and scavenging depending on the food availability (Schembri, 1982). Generally, hermit crabs feed during high tide when water inundates their habitats. In the mangrove area, there is no risk of the hermit crabs being washed away during high tide, however, when they forage, the hermit crabs are exposed to a higher predation. For example, the portunid crab, *Thalamita crenata* adopts a sit-and –wait strategy to prey on *C. laevimanus* (Gherardi & Vannini, 1991). In Costa Rica, predation on *C. panamensis* by puffer fishes, portunid, xanthid and grapsid crabs was similarly high in the mangrove estuaries during the foraging period of the hermit crabs (Borjesson & Szelistowski, 1989). For *C. laevimanus,* the time spent in foraging and the quality of the food ingested is a critical factor in its energy balance. Therefore, although hermit crabs may expose to high predation when they forage during high tide, the advantage of having a longer feeding time outweigh the disadvantages of higher predation risk (Gherardi & Vannini, 1991).

In mangroves, hermit crabs are scavengers feeding on carion, detritus, fallen leaves and other mangrove derived organic materials. The ability of hermit crabs in deposit and filter feeding and their role as scavengers (Schembri, 1982) may be important in nutrient recycling within the mangrove ecosystems. In addition, hermit crabs through their larval dispersals contribute appreciably to the planktonic mass which serves as important food source for many commercially important species of fish and invertebrates in nearshore waters (Squires et al., 2001).

Stable isotope technique has been used to trace carbon flow from primary producer to animals of higher trophic levels. This approach determines the ratio value of the dual isotopes of carbon and nitrogen of consumers. The $^{13}C/^{12}C$ or $\delta^{13}C$ value of the sample consumer's tissue determines the primary energy source (Haines & Montague. 1979; Chong et al., 2001), while its $^{15}N/^{14}N$ ratio ($\delta^{15}N$) estimates the trophic position of the organism (McCutchan et al., 2003). The technique has the advantage over stomach content examination since it provides a time-integrated signature of the consumer’s diet, whereas the latter provides only a snapshot view of the consumed food after ingestion.

Carbon from various primary sources would have different dual isotope signatures/ratio values. By tracing these values, the carbon dynamics/cycling in mangrove ecosystems could be elucidated (see Bouillon et al., 2008). Okamura et al. (2010) estimated the contribution of mangrove derived organic matter and phytoplankton in the surface sediment in creek and coastal areas of Matang waters. Hayase et al. (1999) suggested that particulate organic matter (POM) at the river mouth and mudflat areas in Matang estuary consist primarily of phytoplankton-derived detritus from the sea based on the carbon isotope ratio. Using the same principle, the relative contribution of mangroves and phytoplankton to carbon source for the commercially important penaeid prawns in Matang waters was determined (Chong et al., 2001). Carbon source and/or trophic position of various other organisms such as bivalves, squids, shrimps, decapods and zooplankton were estimated using δ^{13}C (energy source) and δ^{15}N (trophic position) values (see Rodelli et al., 1984; Hayase et al., 1999; Chew et al., 2012; Niiyama et al., 2012). Lately, such technique was also used to reveal the ontogenetic migration and importance of mangrove as feeding grounds for John’s snapper, *Lutjanus johnii* based on the variation in the dual isotopic values (Tanaka et al., 2011). Further, stable isotope analysis using R-programme (SIAR) based on mathematical mixing model (with δ^{13}C and δ^{15}N of primary producers and consumers as input data) has the ability to estimate the proportional contribution of each primary source on the diet of the consumers (see Phillips, 2012). Due to the growing interest and the effectiveness of stable isotope technique in elucidating the energy flow in an ecosystem, this technique would be used in this study to examine the trophic role of hermit crabs in the coastal food web.

Several studies have been done in Matang Mangrove Forest Reserve (Chew, 2012; Okamura et al., 2010; Chong et al., 2001; Hayase, 1999) and isotope carbon readings for primary producers are available in literature. Therefore, this offers a good opportunity to compare the isotopic signals of the potential primary producers to that of hermit crabs in order to trace the source of carbon hermit crabs depend on and hence, to elucidate the trophic contribution of hermit crabs. Rather than looking at the specific food items consumed by hermit crabs, the present study will look at the overall trophic energy contribution by three major producers in the study area, namely, mangrove, phytoplankton and benthic diatom, via hermit crabs to higher trophic levels. Preliminary observations revealed that hermit crabs constituted substantial proportion of food items consumed by some of these fishes in Matang waters. Therefore, quantitative data are needed to elucidate the contribution of hermit crabs as food organism to coastal fishes.

1.8 Research questions

In view of the absence of literature pertaining to the ecology of hermit crabs in Malaysian waters, this study was further motivated by the abundance and wide distribution of hermit crabs in Matang waters. It is also well known that molluscs particularly gastropods are also abundant in the mangrove and mudflat environment (Muhammad Ali, 2004; Broom. 1982). Research questions that motivated the present study are as follows:

1. Are the different species of hermit crab spatially and temporally distributed along the environmental gradients of their habitats?
2. What are the growth, mortality and recruitment parameters of the hermit crabs?
3. How do the sympatric species of hermit crabs share or compete for similar shell resources inter- and intraspecifically?

4. Do reproductive traits and strategies differ among sympatric hermit crab species?
5. What is the trophic role of hermit crabs in the coastal food web?

1.9 Significance of study

This PhD study was carried out with the overall aim to contribute to new knowledge and understanding of the ecology of these often neglected organisms. Despite the ubiquitous presence of diogenids on Malaysian shores, detailed ecological studies on hermit crabs in Indo-west Pacific and adjacent regions are scarce. Also, little attention has been given to the ecology and behaviour of hermit crabs from the genus *Diogenes* which totalled 85 recorded species (Appeltans et al. (eds) 2012). The Matang Mangrove Forest Reserve (MMFR) is among the best managed production mangrove forests in the world on a sustainable basis (Gan, 1995). This site provides an ideal place to study its marine biodiversity due to the complex ecological features of the mangrove forest and adjacent habitats (Chew, 2012). The exemplary management of MMFR which covers a total area of 41,000 ha since more than a century ago without loss of a single hectare, is believed to sustain the highest fishery catch in the country, attributable to mangrove ecosystem functions and services (Chong, 2007). Hermit crabs, common creatures of mangrove and other intertidal systems, may play some significant role in nutrient recycling and trophic dynamics. In general, coastal environments are very dynamic, being subjected to atmospheric and oceanic influences that regulate the abundance and distribution of the benthic community including hermit crabs. Therefore, a detailed study and monitoring of the dynamics of a small area (such as a bay) pertaining to particular species like hermit crabs may provide a greater understanding of the complex mechanisms that shape the distributional patterns of benthic animals (Santos & Pires-Vanin, 2004). This study pertains to fundamental science research. It explores further the basic ecological concepts of competition among sympatric hermit crab species, ecological partitioning and the modulating effect of predation on competition. The extent and intensity of predation on hermit crabs by predators in the food web may illuminate their contribution to the nursery ground function of mangrove and coastal mudflat linked to fishery production.

1.10 Objectives of study

The aims of this study are:

(1) to determine the abundance and distribution of hermit crabs in relation to the abiotic factors,

(2) to study the population dynamics of hermit crabs,

(3) to determine the shell use pattern of hermit crabs and the factors affecting shell selection,

(4) to determine the spatial and temporal reproductive pattern of hermit crabs, and

(5) to elucidate the trophodynamics of hermit crabs.

Four hypotheses will be tested in this study:

(1) Spatial and temporal distribution and abundance of hermit crabs are regulated by abiotic factors (water parameters, sediment characteristics and tidal conditions),

(2) Shell use by hermit crabs is modulated by shell size, shell shape and shell availability,

(3) Sympatric species of diogenid hermit crabs adopt different reproductive strategies to avoid/reduce competition for similar resources by their young,

(4) Small diogenid hermit crabs serve as prey organisms to large predators.

1.11 Addressing the study objectives

The following investigations were carried out to address the above objectives and hypotheses:

1. Distribution and abundance of hermit crab community at Matang mangrove estuary, including spatial and temporal distribution patterns in relation to environmental parameters (water and sediment characteristics) and effects of tides and lunar phases on short term variability in abundance of hermit crabs (Section 3.1 and 3.2).
2. Population features of hermit crabs community in Matang mangrove estuary including size distribution and population dynamics (growth rate, asymptotic length, recruitment pattern and total mortality) of hermit crabs estimated using length frequency data (Section 3.3).
3. Shell-hermit crab relationships based on shell size, shape and availability (Section 3.4).
4. Reproduction pattern based on temporal presence of ovigerous females of diogenid hermit crabs (Section 3.5).
5. Hermit crab trophodynamics based on stable isotope results of primary producers (microphytobenthos, phytoplankton and mangroves), hermit crabs (juveniles and adults from mudflat and shoal areas) and predatory fishes (ariid and sciaenid fishes), and fish stomach content analyses (ariid and sciaenid fishes) (Section 3.6).

CHAPTER 2

MATERIALS AND METHODS

2.1 Study area

The Matang Mangrove Forest Reserve (MMFR) is situated on the west coast of Peninsular Malaysia with forest area of 40,711 hectares. Not included in the forest area, are six major water channels namely Sungai Sepetang, Sungai Selinsing, Sungai Sangga Besar, Sungai Sangga Kecil, Sungai Larut and Sungai Jaha which are interconnected and with the extensive mudflat, forming a total area of 55, 306 ha. The mudflats are dominant coastal biotopes in the west coast of Malaysia representing about one third of the mangrove area (MPP-EAS, 1999). The coastal mudflat serves as an important feeding site for diverse species of fishes and invertebrates during high tide (Sasekumar et al., 1994). MMFR experiences semidiurnal tides with a mean water depth at the highest spring tide of 2.5m and the lowest of 0.5m above chart datum. The climate of this area is influenced by southwest monsoon which usually prevails from May to September and the northeast monsoon from November to March. The influx of freshwater influenced the salinity of the Matang estuaries which varies between 19-30 ppt.

Four sampling stations (station A, B, C and D) were established from mid-estuary of Sungai Sangga Besar to the coastal mudflat (Fig. 2.1). Station A was located about 7 km upriver from the river mouth of Sungai Sangga Besar and about 3km from Kuala Sepetang fishing village. This station is greatly influenced by inflow of freshwater with the lowest mean salinity compared to other stations due to its upper most location. Station B was established at the river mouth of Sungai Sangga Besar. It was located about 0.5km from the small fishing village of Bagan Sungai Besar. This station is bordered by coastal mudflats that are open up by the river mouth. Station C was established at coastal mudflat which extends farther out to the sea. This mudflat is extensive being exposed up to 2km from the shore during spring low tide. Station D was located about 4km from station C and about 5-6km from coastal mangrove fringe. It is located at the shoreface of a tongue like offshore shoal of sandy mud. This station was slightly deeper (2.9±0.5m) compared to the coastal mudflat station (2.2±1.0m) at high water. Samplings did not cover the upper estuary since preliminary survey revealed very low abundance of hermit crabs. This was also similarly reported by Muhammad Ali (2004) that there was very low density of macrobenthos including hermit crabs at the upper estuary.

Table 2.1. Coordinates, mean depth (m) and salinity (ppt) and approximate distance between sampling stations established for monthly sampling of hermit crabs in this study.

Station	Coordinate	Mean depth (m)	Mean salinity (ppt)	Distance from river mouth
A (Mid-estuary)	N04º50'39.71" E100º36'05.29"	3.1	23.38	-7km
B (River mouth)	N04º51'21.21" E100º33'05.17"	2.7	25.56	0km
C (Mudflat)	N04º51'10.31" E100º30'29.34"	2.2	26.95	3.5km
D (Shoal)	N04º50'03.51" E100º28'47.60"	2.9	28.28	5.5km

('-' indicates upstream of river mouth)

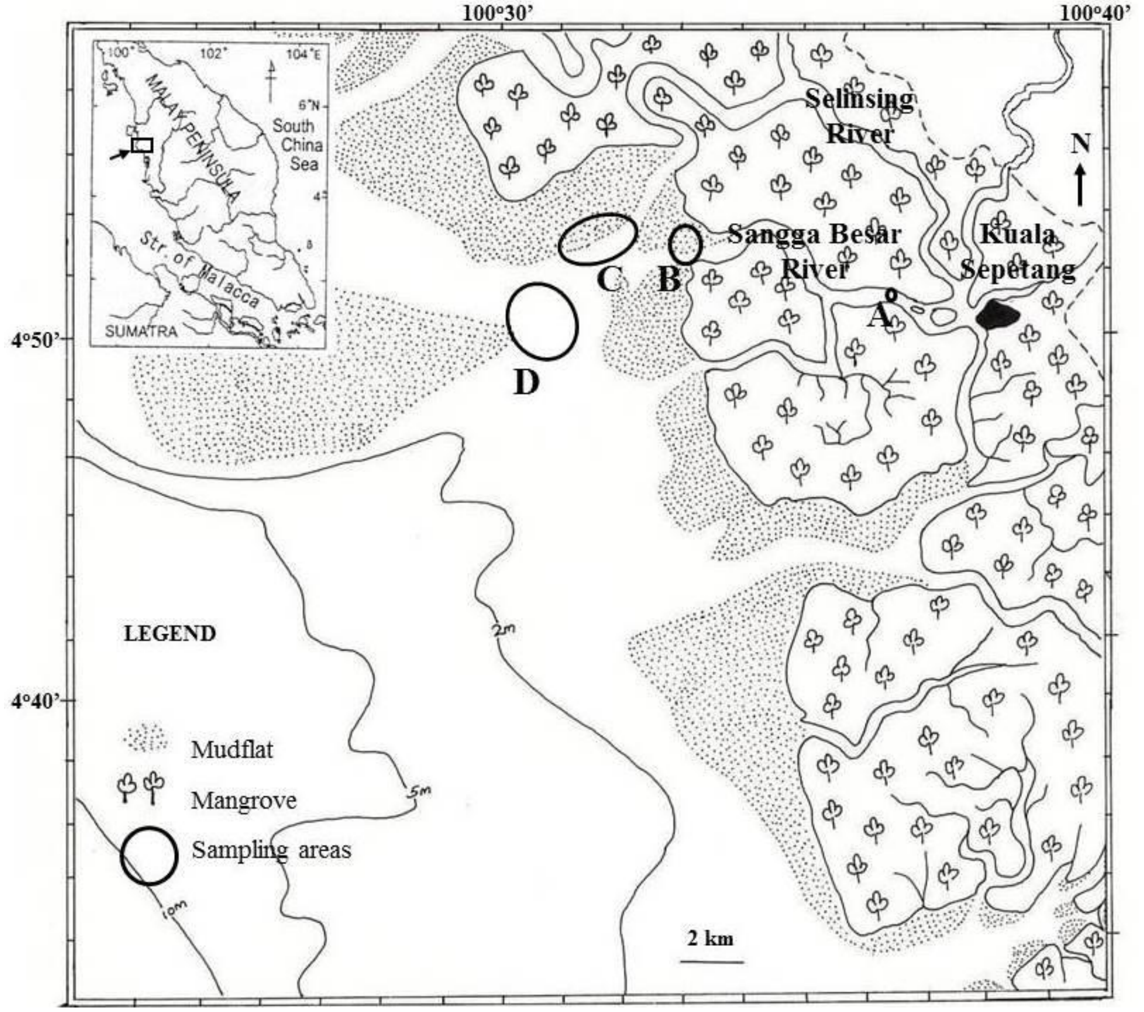


Fig. 2.1. Map of study area showing sampling sites (A=mid-estuary, B=river mouth, C=mudflat, D=shoal) of hermit crabs at Matang Mangrove Forest Reserve, Peninsular Malaysia.

2.2 Field sampling

2.2.1 Collection of hermit crabs

Monthly samplings were carried out from August 2009 to March 2011. Hermit crabs were sampled using a small otter trawl with mouth opening of approximately 6 m (width) by 2 m (height) and codend stretched mesh size of 2 cm. The generally sparse distribution of hermit crabs at subtidal mudflat zone made it necessary to use a trawl net to increase coverage of the surveyed area. The trawl net also served the purpose of capturing predatory fishes and crabs. All monthly samplings were carried out during flood tide about one to two hours before slack water except for October 2009 and end of June and September 2010 where samplings at station C (mudflat) and station D (shoal) were delayed and carried out during ebb tide due to rough weather. Duration of trawling for each replicate was fixed at 5 minutes so as to reduce bycatches. At mid-estuary and river mouth stations, two replicate trawls were done each at mid river and river bank while three replicate trawls were done randomly for both mudflat and shoal stations due to the homogeneity and extensiveness of these stations. At each replicate trawl, location was taken using GPS (Garmin Rino 130) before and after trawling. Ground speed of boat during trawling was noted using GPS at least three times within the 5 minutes trawling period. The average speed (v) of boat was then determined. All samples of hermit crabs, gastropods and fishes were temporarily stored in ice-filled box immediately after retrieval from net, transported back to laboratory and frozen at -20°C freezer for further analysis. For catches that are too abundant, subsamples of 1/2, 1/4 or 1/8 were taken.

2.2.2 Water parameters and sediment samples

Before trawl samplings were made, water characteristics such as temperature, salinity, pH, dissolved oxygen and total dissolved solids were measured using pre-calibrated YSI Multiprobe Sensors (Model 556 MPS). Water depth was measured using a hand-held Speedtech echo sounder (Model SM-5) at the start and end of each trawling. All water parameters were taken at no more than 0.3m above bottom as indicated by marked measurements on cables connected to the sensors. Sediment samples for organic content analysis were collected using Ekman grab sampler (Wildco, Canada). Surface sediment of not more than 1cm deep was scrapped using a pill box whereby the sample would be kept. Bottom water samples to determine the amount of suspended particulate matter were collected by a 4.2L Van Dorn water sampler at depth of about 0.5m above sediment bottom.

2.2.3 Collection of juvenile samples

Since the otter trawl net was not effective in capturing very small hermit crabs due to its cod end mesh size of 2cm, therefore, the collection of juvenile hermit crabs was done using a sledge net with a mouth opening of 0.5 m (Pullen et al., 1968) and an attached net of 500 µm mesh size. For each replicate, the sledge net was pulled over the mud bottom by slowly paying out a fixed 30 m length of the tow line while on a moving boat and pulling it into the deck after the boat has stopped. Juvenile crabs retained in the net were washed into a container and large organisms were first removed to avoid predation on the juvenile hermit crabs. Leaves and other large debris were dipped into the same container and shaken gently (before removal) to ensure that juveniles clinging on to these objects were completely dislodged.

2.2.4 Diel samplings

24-hour field samplings were separately performed at subtidal zone of mudflat station (>500m from nearest mangrove fringe) on two seasonal occasions; wet period in December 2009 during Northeast monsoon and dry period in July-August 2010 during Southwest monsoon. At each occasion, four separate samplings of one week interval were carried out to cover four lunar phases (new moon, first quarter, full moon and third quarter) representing two instances of neap tides (first and third quarter moon) and spring tides (full moon and new moon). To elucidate diel variability in abundance of hermit crabs in the mudflat, environmental differences between day and night, spring and neap, and ebb and flood. Three-hour interval samplings over 24 hour period were done comprising two replicates of each of the following factor levels were tested; day-ebb, day-flood, night-ebb and night-flood for spring and neap tides. For each replicate, 5 minutes trawling was done. Water parameters were taken using YSI Multiprobe Sensor (Model 556 MPS) before each trawl. All 24 hour samplings were carried out

2.3 Laboratory procedures

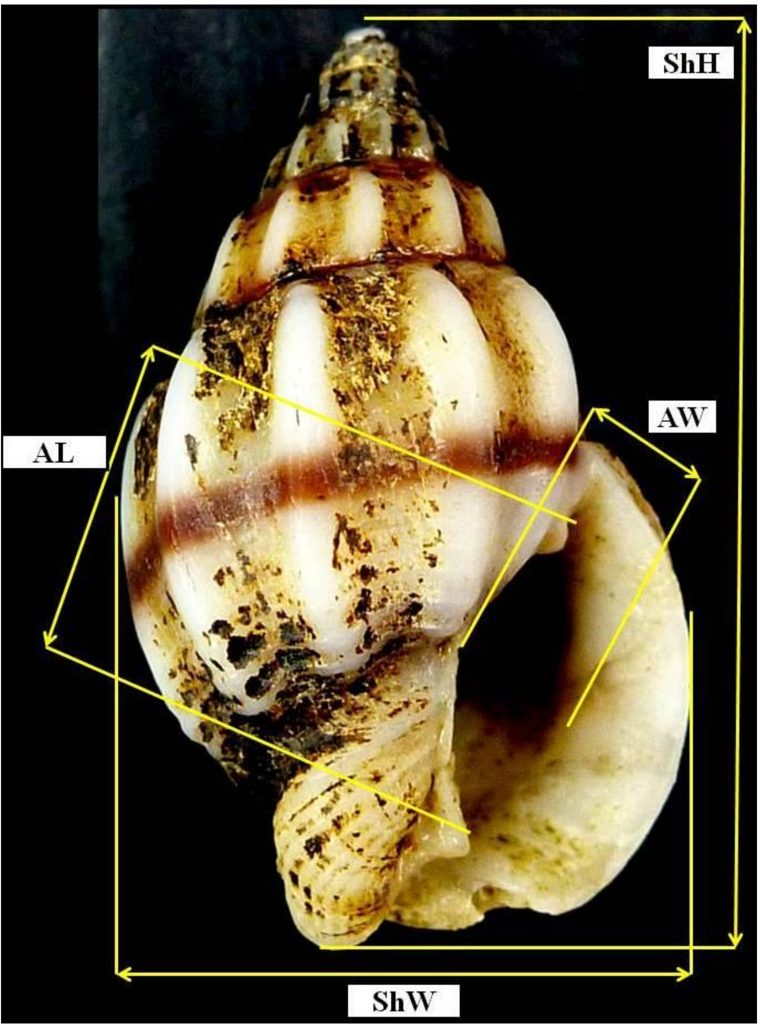
2.3.1 Morphometric measurements of hermit crabs and their occupied shells

Hermit crabs, gastropods and fishes samples were thawed and sorted out and identified to the lowest taxa. Hermit crabs were blotted dry using a piece of cloth. Shell length, shell width, aperture length and aperture width were measured to the nearest 0.01 mm using a pair of Mitutoyo digital vernier calipers. Shell height (ShH) refers to the length from the apex to the anterior of siphonal canal. Shell width (ShW) refers to the widest span of the shell whorl. Aperture length (AL) refers to the length from the inner end of the posterior canal to the inner notch of the siphonal canal. The aperture width (AW) refers to the widest span between both inner lips (Fig. 2.2a). The degree of shell elongation could be expressed by the ratio of the shell height to shell width (Edgell and Miyashita, 2009). Shell thickness was indicated by the ratio shell weight/L' where L' is the average shell size determined from (ShH+ShW)/2 (Blackstone, 1985). The condition of the shell was noted based on the description given in Table 2.2:

Table 2.2. Criteria of shell condition.

Shell Condition	**Descriptions**
Undamaged	No observable damage
Slightly Damaged	Apex and/or aperture slightly worn out, sometimes with small perforations
Damaged	Apex and/or aperture broken, with significant perforations on shell surface which modestly expose hermit crab within
Greatly Damaged	Half or less than half of the anterior or posterior part of shell broken off, greatly exposing body of hermit crab within; or shell greatly perforated to the point of easy breakage upon handling.

Each crab with its shells was weighed (g) together using a Mettler Toledo digital balance to three decimal points. The hermit crab was then pulled out gently from its shell by twisting the crab against direction of shell spiralisation to minimize friction between crab's uropod and inner shell surface. This would prevent uropod from being hooked within the spiral. In the event when crabs were unable to be retrieved from their shells due to clasping of uropod, light hammer was used to gently crack these shells before pulling out the crabs. Hermit crabs were blotted again using dry cloth to remove excess water and then weighed. Morphometric measurements; shield length (SL), shield width (SW), length of larger left cheliped (LCh), length (ChL) and width (ChW) of carpus were then taken. Shield length refers to the length from tip of the rostrum to the posterior margin of the hardened portion of the carapace. Shield width refers to the widest span of the carapace shield. Length of larger cheliped refers to the length from tip of the fixed finger of carpus to the proximal end of coxa of the larger left cheliped. Carpus length refers to length from tip of the fixed finger to proximal end of the palm of larger left cheliped. Carpus width refers to the widest span of the carpus measured from both lateral edges (Fig. 2.2b). Smaller individuals were measured with the aid of dissecting microscope Hermit crabs were then sexed; female and male crabs have gonopores on the coxae of the third and fifth pereopods respectively. For smaller individuals with inconspicuous gonopores, a drop of diluted methylene blue was applied on the coxa to stain the openings. Another method was to examine the pleopods; a female has biramous pleopods while a male has uniramous pleopods. Presence of eggs attached on pleopods of females was noted as pigmented or non-pigmented.



(a)

(b)

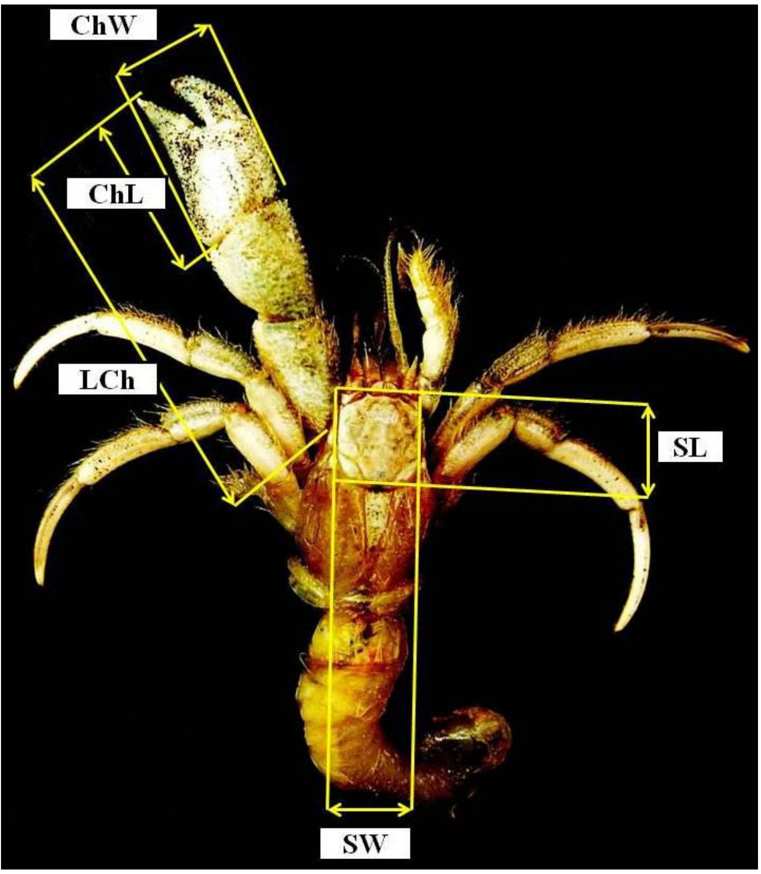


Fig. 2.2. Morphometric measurements of (a) shell (ShH=shell height; ShW=shell width; AL=aperture length; AW=aperture width) and (b) hermit crab (SL=shield length, SW=shield width; ChL=chelae length; ChW=chelae width; LCh=length of left cheliped).

2.3.2 Juvenile hermit crabs

Samples collected by the mud sledge were washed under running tap through a 500 µm Endecott sieve to remove mud. Samples were then spread thin onto a tray and hermit crabs were sorted out. Due to difficulty in identification of juvenile hermit crabs, all juveniles of *Diogenes* sp. were pooled for analysis. The number of juvenile individuals was then counted. Juvenile in this study refers to the individual smaller than the smallest ovigerous females.

2.3.3 Suspended particulate matter

Total suspended particulate matter was estimated as a relative measure of chalkiness of water replacing turbidity reading since turbidity sensor was faulty. Bottom water samples collected from field samplings were filtered through a pre-weighed GF/C filter (0.7-1.0 µm) and volume of water sample filtered is noted. The filter together with the particulate matter retained by the filter was oven dried at 60°C for 48 hours. Weight (g) of both filter and particulate matter was measured by a chemical balance Model GR-200 to four decimal points. Suspended particulate matter of the water sample was then estimated by deducting the weight of the GF/C filter from the total weight of both filter and particulate matter.

2.3.4 Sediment organic contents

Ash-free dry weight (AFDW) method was used to estimate the organic content of sediment. Approximately 1g of sediment sample was placed onto the pre-weighed aluminium foil. The sediment with aluminium foil was oven dried at 60°C for 5 days. The weight of both the aluminium foil and dried sediment was taken using a digital balance (GR-200) before combustion at 500°C for 24 hours in a muffle furnace (Model: JSMF-30T). Aluminium foil containing the combusted sediment was then, weighed again. Organic content of sediment is estimated based on the following equation.

$$\text{Percent composition of sediment organic matter} = \frac{(C-D) \times 100}{C-A}$$

Where, A= weight of aluminium foil

C = weight of aluminium foil + sediment (dried) before combustion

D = weight of aluminium foil + sediment after combustion

2.3.5 Particle size of sediment

Large particles such as pieces of broken shells and leaves were removed manually from the sediment samples. Sediment samples were then added with 10% hydrogen peroxide (H_2O_2) in a beaker, gently stirred, and left for 24 hours for the organic matter to dissolve. The resulting supernatant was poured out and distilled water was added and gently stirred to rinse off the hydrogen peroxide. This step was repeated four to five times and at each time the sediment samples were allowed to settle down for 24 hours before the resulting supernatant of distilled water was decanted out. All rinsed samples were placed inside an oven and dried at 60ºC. Clumped sediments were gently pounded with a light pestle to loosen the aggregation. Composition of particle by size categories of sediment samples (<5g needed) were then estimated using Beckman Coulter Particle Size Analyser (Model LS230). The categories of sediment based on particle size are described in Table 2.3:

Table 2.3. Categories of sediment based on particle size.

Particle size class (μm)	**Categories**
0-3.9	Clay
3.9-15.6	Fine silt
15.6-62	Coarse silt
62-125	Very fine sand
125-250	Fine sand
250-500	Medium sand
500-1000	Coarse sand
1000-2000	Very coarse sand

2.3.6 Analysis of stomach contents of fish predators

Stomach content analysis in this study was carried out for the purpose of quantifying contribution of hermit crabs as food for known hermit crab predators. Preliminary observation of stomach content of some common fishes at study area was done to select fish species that feed on hermit crabs. Two families of fishes were identified, they were Ariidae and Sciaenidae both of which were the most common fishes from trawl catches at Matang mangrove estuary (Then, 2008). Stomach content of 137 individuals of sciaenids comprising three species *Johnius belangerii*, *J. weberii* and *J. carouna* with standard length (SL) that ranged from 5.2 cm to 17.1 cm were analysed. However, ariid fishes occurred in very low abundance compared to sciaenids at the mudflat and shoal stations. Therefore, stomachs of only 14 individuals with SL that ranged from 9.5 cm to 17.5 cm were examined; two from mudflat and 12 from river mouth comprising five species; *Arius caelatus*, *A. sagor*, *A. truncatus*, *A. venosus* and *Osteogeneiosus militaris*.

Standard length (SL) of each fish was taken before its gut was dissected out. Fullness of stomach was subjectively estimated by eye on a scale of 0 to 5; 0 for empty, 1 for ¼ filled, 2 for ½ filled, 3 for ¾ filled, 4 for full and 5 for distended stomach. The stomach was then slit open and its contents were washed into either a petri dish if there were large amount of prey items, or a Sedgewick rafter cell if only a small amount of food was present. Stomach contents were sorted out and identified to the lowest possible taxa. The composition (%) of each sorted food item was estimated with the aid of a 10 x 10 grid cells on the Sedgewick rafter under a compound microscope. The number of grid cells covered by each prey item was noted. If a prey item did not cover fully a single cell, the area was estimated as part thereof (1/4, ½ and ¾). In the rafter cell, the height of small prey items was assumed equal and area cover was used. The area covered by each prey item was then converted into percent volume compositions before analysis. For stomach contents with large prey items, percent composition was estimated based on the weight of the items measured using a fine balance (GR-200) of four decimal points. The number of individuals or intact prey items was also noted. Prey items that were amorphous and difficult to identify was categorized as unidentified organic materials.

2.3.7 Stable isotope analysis

To determine the relative contribution and trophic position of hermit crabs, the stable isotopes technique was used to quantitatively determine the proportional contribution of primary food sources to both hermit crabs and their predators. This method could trace energy flow from primary producers to consumers. Ratio of $^{13}C/^{12}C$ could determine primary energy source while ratio of nitrogen isotopes could reveal trophic level of that particular organism. Therefore, stable isotopes data could also be used to support results of stomach content analysis. The standard length of selected fishes was measured. Sterilised dissecting blades were used to remove muscle tissue from the fishes. Tissue was then rinsed in a series of distilled water to remove extraneous sediment and debris.

Tissue samples were then oven dried at 60ºC for 4-5 days depending on the thickness of the sample. Dried samples were then sealed individually in zip lock bag and labeled accordingly. Samples of adult hermit crabs (1.80-3.40mm shield length) of both *D. moosai* and *D. lopochir* from mudflat and nearshore stations respectively were also oven dried at 60ºC for 4-5 days and the dried samples were pooled according to station and sealed in zip lock bag.

All samples were sent to Marine Biological Laboratory in Woods Hole, USA for stable carbon and nitrogen isotopes analyses. For hermit crab samples, acid treatment was done to remove any form of calcium carbonate. The stable isotope analyses were performed using an Europa 20-20 mass spectrometer. Results were expressed by the values of standard δ notation which were determined based on the following equations with standard reference materials for carbon and nitrogen being Peedee Belemnite (PDB) and N_2 in air (AIR) respectively:

$$\delta^{13}C,‰=[(^{13}C/^{12}C)_{sample}/[(^{13}C/^{12}C)_{standard,\ PDB}-1] \times 1000$$

$$\delta^{15}N,‰=[(^{15}N/^{14}N)_{sample}/[(^{15}N/^{14}N)_{standard,\ AIR}-1] \times 1000$$

2.3.8 Rainfall data

Daily rainfall data from August 2009 to March 2011 were obtained from Malaysia Meteorological Department. The standardized precipitation index (SPI) expressed as the difference of precipitation from the mean for a specified time period divided by the standard deviation determined from past rainfall records (McKee et al., 1993) was applied in this study to analyze the precipitation pattern in the study area.

SPI was calculated for all sampling months using mean and standard deviation computed from rainfall records from January 2000 to April 2012 based on the following equation:

$$\mathrm{SPI} = \frac{X_i - \bar{X}}{\mathrm{SD}}$$

Where $\boldsymbol{X_i}$ is the total rainfall in the *i*th month; $\bar{X}$ is the mean monthly rainfall calculated over 12 years time scale (2000-2012); **SD** is the standard deviation of monthly rainfall calculated from a 12-year time scale (2000-2012). The intensity of rainfall were categorised based on the SPI value (Table 2.4):

Table 2.4. Categories of rainfall based on SPI value.

SPI	Category
>2.0	Extremely wet
1.5 to 1.99	Very wet
1 to 1.49	Moderately wet
-0.99 to 0.99	Near normal
-1 to -1.49	Moderate drought
-1.5 to -1.99	Severe drought
<-2	Extreme drought

2.4 Data analyses

2.4.1 Estimate of density for trawl and sledge net sampling

The swept area (A) of otter trawling (perSparre and Venema, 1998) was calculated based on the following equation:

$$A = D*L, \text{ where } D = v*t$$

Where, A=swept area (m^2)
D= distance of trawling (m)
v= average speed of boat during trawling (m/s)
t= duration of trawling (s)
L=width of horizontal mouth opening of trawl net during trawling (m)

Therefore, the density of hermit crabs/gastropods (individual/hectare) caught with otter trawl net was estimated based on the following equation:

$$\text{Density of hermit crabs, ind/ha} = (N_i/A)*10000$$

Where, N_i = number of individual hermit crabs of *I* species

The proportion of hermit crabs/gastropods retained by the trawl net was assumed to be 1.0 (i.e. all retained) instead of 0.5, a proportion normally taken to estimate fish abundance.

The fixed swept area (a) for sledge net was estimated at 15 m^2 (tow distance x width of beam opening) since the tow distance was set at 30 m and width of beam was 0.5m. Juvenile individuals caught using sledge net were counted and their density (individual/hectare) was computed based on the following equation:

$$\text{Density of juvenile hermit crabs, ind/ha} = (N_i / a)*10000$$

Where, Ni = number of individual juvenile hermit crabs of *i* species

a = swept area of sledge of towed net (m^2)

2.4.2 Univariate significant tests

All numerical data by factors were tested at 5% significance level for homogeneity of variance using Levene's test and normality using Kolmogorov-Smirnov's test before analysis of variance (ANOVA) (Zar, 1998). If homogeneity of variance and normality requirements were not fulfilled, the data set were logarithmically transformed [log (x + 1)]. Composition (%) data were arcsine transformed. Factorial ANOVA test was used to investigate interactive effects of independent variables. Tukey HSD was performed as post hoc test to elucidate multiple comparisons of the means. Kruskal-Wallis test was used as non-parametric test if both raw and log transformed data did not fulfill the requirements of homogeneity of variance and normality. All statistical analysis was performed using Statistica Version 8 Software Package.

2.4.2.1 Data from monthly samplings

One-way ANOVA was used to examine the influence of spatiality (mid-estuary, river mouth, mudflat and shoal stations) and temporality (sampling months) on abundance of *Diogenes moosai*, *D. lopochir* and *Clibanarius infraspinatus*. Due to non-normality of data sets, non-parametric Kruskal-Wallis test was used to determine significant difference in density of ovigerous female *D. moosai*, *D. lopochir* and *C. infraspinatus*, juvenile *Diogenes* sp., and various water (temperature, salinity, total dissolved solids, oxygen saturation and concentration, pH) and sediment parameters (sediment particle size and organic content) between stations and sampling months. Mann-Whitney test was used to determine significant difference between northeast (NE) and southwest (SW) monsoons (intermonsoon, IN was omitted due to few replicates) in terms of density of hermit crabs by species, water parameters and sediment organic content. One-way ANOVA test was also performed to determine the significant difference in monthly total rainfall between seasons and daily rainfall between wet (December 2009) and dry (15th July to 15th August 2010) periods of 24-hour samplings.

2.4.2.2 Data from diel samplings

Interactions among factors could not be elucidated due to non-normality in data sets. Kruskal-Wallis was used to determine the differences in density by species (*D. moosai*, *D. lopochir* and *C. infraspinatus*) and sexes of *D. moosai* (male, non-ovigerous and ovigerous female) among factors; 1) sampling periods (dry and wet period); 2) lunar phases (new moon, first and third quarter moon, and full moon) and 3) tidal conditions (flood and ebb). Kruskal-Wallis was not performed for density of *D. lopochir* and *C. infraspinatus* by sex due to few samples.

2.4.2.3 Hermit crab size

Kruskal-Wallis test was used to determine the significant differences in size (shield length, mm) of hermit crabs by species (*D. moosai*, *D. lopochir* and *C. infraspinatus*) among stations (mid-estuary, river mouth, mudflat and shoal stations) and sex (male, non-ovigerous female and ovigerous female).

2.4.3 Correlation analysis

Spearman non-parametric rank correlation analysis (R tested at 5% significance level) was used to determine:

1) the relationship between abundance of hermit crabs with water or sediment parameters. For each species of hermit crabs, correlation analysis was performed between monthly crab density with corresponding temperature, salinity, DO, pH, total dissolved solids or sediment organic contents. The relationship between the two

variables is indicated by the r value of the analysis (either positively ‘+’ or negatively ‘-‘correlated).

2) the association between abundance of hermit crabs and living gastropods whose shells were commonly occupied. The correlation analysis was performed each for mudflat (between *D. moosai* and live gastropods) and shoal station (between *D. lopochir* and live gastropods).

Pearson correlation analysis was used to determine the relationship between abundance of hermit crabs and predatory fishes. For each species of hermit crabs, analysis was performed between monthly crab density with the abundance of their corresponding predators (sciaenids and ariids). The relationship between the two variables is indicated by the r value of the analysis (either positively ‘+’ or negatively ‘-‘correlated). The possibility of lag time between abundance of hermit crabs and predators were also tested using distributed lag analysis with predator density as dependent variable. Two lag lengths of one-month lag and two-month lag were tested. The correlation and lag time between the variables were tested at 5% level of significance. This analysis was performed using Statistica Version 8 Software Package.

2.4.4 Canonical correlation analysis

Canonical correlation analysis was carried out to determine the relationships between the two set of variables measured on the hermit crab (shield length, shield width, left carpus length, left carpus width, length of larger left cheliped and weight) and its gastropod shell (shell height, shell width, aperture length, aperture width and weight). Chi-square test was performed to reveal significance of correlation between the two sets of data (hermit crab and shell variables). The redundancy analysis result was used to indicate overall relationship between two sets of data based on the portion of variance accounted for by the opposing set of variables. Interpretation of the relative contribution of each variable in each data set was based on the magnitude of the canonical weights generated in root 1 which was the most significant root. This analysis was performed using Statistica Version 8 Software Package.

2.4.5 Redundancy analysis (RDA)

RDA was carried out to visualize the spatial distribution of hermit crabs in relation to bottom water characteristics and sediment characteristics. The species data comprised of the abundance of hermit crab species (*C. infraspinatus*, *D. moosai* and *D. lopochir*). The sample data set comprised of sampling stations (upstream, river mouth, mudflat and nearshore) whereas the environmental data set comprised of bottom water parameters (temperature, salinity, total dissolved solids, pH, dissolved oxygen concentration, oxygen saturation, suspended particulate matter and depth), sediment organic content and sediment texture (clay, fine silt, coarse silt, very fine sand, fine sand, medium sand, coarse sand and very coarse sand). RDA analysis was performed using CANOCO 4.5 software (Ter Braak and Smilauer, 2002).

2.4.6 Canonical correspondence analysis (CCA)

CCA was carried out to analyze the relationships between crab and shell parameters and visualize the main features of crab (species, sex and size) distribution according to the gastropod shell species and characteristics. CCA was performed using CANOCO 4.5 software (Ter Braak and Smilauer, 2002). The site or sample data set comprised of the species of gastropod shells occupied by the hermit crab. The species data set comprised of the hermit crab species by sex and size class (Table 6.5), while the environmental data set comprised of the shell characteristics (AL, ShW, AW, SWt, ShH).

2.4.7 Discriminant analysis

Discriminant analysis was performed to discriminate shell species groupings (*Nassarius jacksonianus*, *Nassarius cf. olivaceus*, *Cerithidea cingulata*, *Thais malayensis, Thais lacera*, *Nassarius bellulus* and *Natica tigrina*) based on the following variables: aperture length, aperture width, shell height, shell width and shell weight. Canonical weights generated from these data sets indicated the relative contribution of each variable to the groupings. The canonical scores were then visualized as scatterplots on the axes of the first two discriminant functions. Chi-square test was performed to find out whether the resulting roots generated were statistically significant. Classification matrix was performed to reveal the percent of cases that were correctly classified or misclassified. All the above statistical tests were performed using Statistica Version 8 Software Package.

2.4.8 Generalised Regression Model (GRM)

Regression analysis in this study was used to examine the relationship between two sets of variables by building a model equation. Scatterplots were firstly plotted to identify outliers which were removed so as improve accuracy of the generated equation. Slope or regression coefficient of the fitted lines corresponded to the correlation between dependent variable and categorical predictor of the hermit crabs. Significant correlation between the analysed variables was tested at 5% significant level. Regression analysis was applied to determine length-weight relationship of hermit crabs. The length parameter corresponded to the shield length (SL) of the hermit crabs. Log linear regression model based on the equation; Log W=b.Log L + Log a, was determined using scatterplots generated from log data of shield length and weight for each species and sex. The value of a (y-intercept) and b (regression coefficient or slope) were thus, used to determine the length-weight relationship of hermit crabs via the equation, $W=aL^b$. The significant difference between male and female regression coefficients or slopes (b) of each species was determined using Student's t-test. This analysis was performed using the generalised linear model module in Statistica Version 8 Software Package.

2.4.9 Wilcoxon matched pairs test

Wilcoxon matched pairs test of the monthly proportions of ovigerous female *Diogenes moosai* was used to test whether hermit crabs at both mudflat and shoal area belonged to the same spawning population. This analysis was performed using Statistica Version 8 Software Package.

2.4.10 Log linear model

Shell use of gastropod species by the two hermit crab species as possibly related to sex of crab and site was analyzed by log-linear analysis of frequency tables via crosstabulation. The goodness of fit for the observed cell frequency for each hermit crab species (*Diogenes moosai* and *D. lopochir*) model were tested with maximum likelihood chi- square for association between shell use (*Cerithidea cingulata*, *Nassarius jacksonianus*, *N. cf. olivaceus* and *Thais malayensis*) and sex (male and female), and between shell use and stations (mudflat and shoal stations). If $p>0.05$, it indicates that shell use is associated with sex or station and vice versa for $p<0.05$. This analysis was performed using Statistica Version 8 Software Package.

2.4.11 Analysis of length frequency data (ELEFAN I)

Von Bertalanffy growth function (VBGF) was used to estimate the growth rate and life span of hermit crabs by determining asymptote length, L_∞ (refers to length when growth becomes constant) and growth coefficient K. The estimation of these two values was guided by goodness of index (Rn) value which is an indicator of the reliability of the generated curve (Gayanilo et al., 1994). Estimation of life span, t_{max} of hermit crabs was done using K value yielded form VBGF with approximate relationship of $t_{max} \approx 3/K$ (Pauly, 1984). Formula of the VBGF is shown as follow:

$$L_t=L_\infty\{1 – e^{(-K[t-t0])}\}$$

Total mortality, Z was estimated from length frequency data using length converted catch curve with L_∞ and K values generated from VBGF as input parameters (Pauly 1984). This is with the assumption that growth rate oscillation between seasons (C) is equal to zero since in Malaysia, a tropical region, there is no true winter. The equation for this relationship is:

$$\ln(N/dt) = a + b \cdot t$$

Where ‘N’ is the number of hermit crab, ‘dt’ is the time to grow from one size class midpoint to the next, ‘t’ is the time required to grow from lower to upper size class interval, ‘a’ is Y-intercept and ‘b’ is the regression slope.

Natural mortality, M of hermit crabs was estimated using Pauly’s empirical formula (Pauly 1984) with L_∞, K and T (annual mean temperature, ºC) as input parameters. The equation of this formula as shown below is derived from 175 independent sets of M estimates and predictor variables for most tropical species (Gayanilo et al. 1994):

$$\text{Log } M = -0.0066-0.279 \log L_\infty + 0.6543 \log K + 0.463 \log T$$

Recruitment pattern is reconstructed from time series data of length-frequency to display number of recruitment pulses and relative strength of each pulse over one year period (Gayanilo et al. 1994). All analyses of length frequency data were performed using Fisat ii software.

2.4.12 Stable Isotope Analysis using R statistics (SIAR)

The proportional contribution of primary sources; mangroves, phytoplankton and microphytobenthos on hermit crabs using stable isotope results as input data is estimated using Stable Isotope Analysis in R (SIAR) package (Parnell et al., 2010). The $\delta^{15}N$ values of hermit crabs and predatory fishes were averaged to determine their trophic level in Matang mangrove food web based on the method described in Vander Zanden & Rasmussen (1999):

$$\text{Trophic position}_{\text{consumer}} = 2 + [(\delta^{15}N_{\text{consumer}} - \delta^{15}N_{\text{base}}) (\Delta\delta^{15}N)^{-1}]$$

Where,

$\delta^{15}N_{\text{consumer}}$ = $\delta^{15}N$ value for a given consumer

$\delta^{15}N_{\text{base}}$ = $\delta^{15}N$ value for a representative baseline for 2nd trophic level

$\Delta\delta^{15}N$ = trophic fractionation value

The value of $\delta^{15}N_{\text{base}}$ is based on mean $\delta^{15}N$ value obtained from herbivorous copepod *Pseudodiaptomus* which is 7.6‰ in Matang mangrove estuary (Chew et al., 2012). By knowing the trophic level of hermit crabs, the isotopic signatures ($\delta^{15}N$ and $\delta^{13}C$) of hermit crabs were adjusted based on the following equation prior to SIAR analysis (Chew et al., 2012):

$$\delta X_{\text{adjhermit}} = \delta X_{\text{hermit}} - (TL_{\text{hermit}} - 1)\Delta\, \delta X_{\text{hermit}}$$

Where,

$\delta X_{\text{adjhermit}}$ = adjusted δ^{15}N and δ^{13}C values of hermit crabs

δX_{hermit} = initial δ^{15}N and δ^{13}C values of hermit crabs

TL_{hermit} = assigned trophic level of hermit crabs

$\Delta\ \delta X_{\text{hermit}}$ = trophic fractionation value for hermit crabs

The trophic fractionation value was based on literatures whereby a value of 0.5‰ for all trophic levels was assigned for $\Delta\delta^{13}$C (Vander Zanden & Rasmussen, 2001). For $\Delta\delta^{15}$N, a value of 2‰ between first and second trophic levels (McCutchan et al., 2003) and of 3‰ between third and fourth trophic level (Chew et al., 2012) were adopted.

CHAPTER 3

RESULTS AND DISCUSSIONS

3.1 ENVIRONMENTAL CHARACTERISTICS OF MATANG MANGROVE ESTUARY AND ADJACENT COASTAL WATERS

3.1.1 Spatial and temporal variation of environmental parameters

3.1.1.1 Rainfall

Based on the wind data obtained from Malaysia Meteorological Department, the onset of southwest (SW) and northeast (NE) monsoon was between May-September and November-March respectively, whereas intermonsoon period occurred in April and October. The monthly total rainfall during the sampling period is shown in Fig. 3.1.1. Monthly total rainfall throughout the sampling period from August 2009 to March 2011 ranged from 176.1 mm to 614.8 mm. Highest total rainfall was recorded in October 2009 during the period of the intermonsoon, while the lowest total rainfall was recorded in July 2010 during the southwest monsoon. Overall, the mean monthly rainfall was 400.3±130.6 mm. Number of rainfall days during the period of sampling is shown in Fig. 3.1.2. High number of rainy days was observed in November (26 days) and December 2009 (27 days) coinciding with the NE monsoon, while the lowest number of rainfall days was 13 days recorded in October 2010. Overall mean number of rainfall day was 21.1±3.7days.

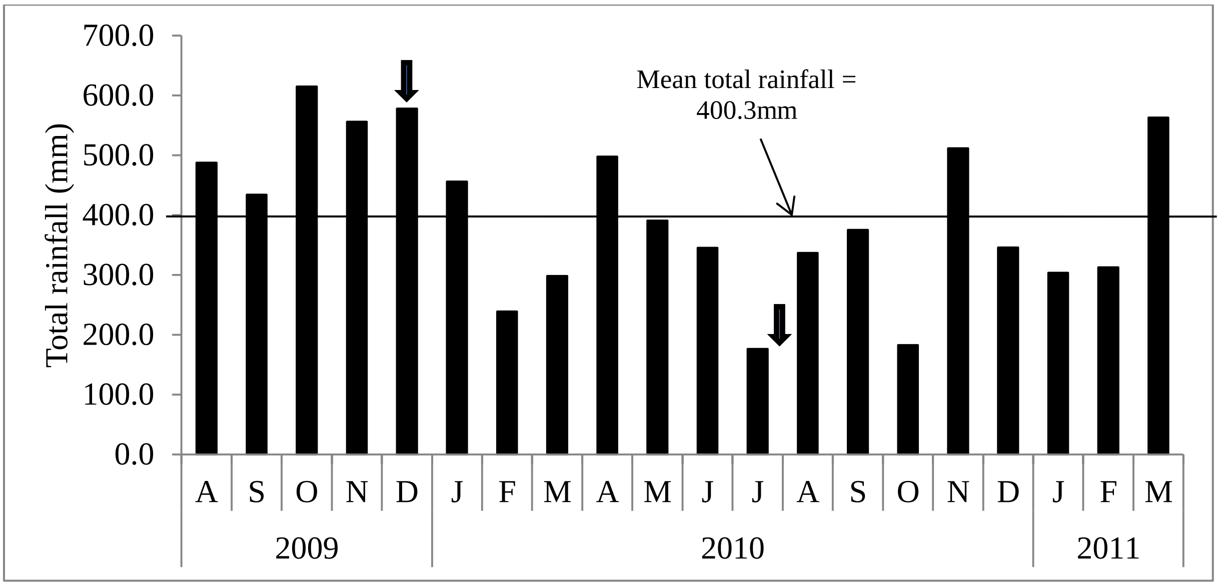


Fig. 3.1.1. Total rainfall (mm) in each month throughout sampling period from August 2009 to March 2011 (bold arrows show period of 24 hour samplings) in Taiping (Hospital Taiping station). (Data obtained from Meteorological Department Malaysia).

Table 3.1.1. Summary results of Mann-Whitney test (tested between NE and SW) (Appendix IIIa) of monthly total rainfall categorized into seasons in Taiping during sampling period (August 2009 to March 2011) (Taiping Hospital station) (NE=northeast monsoon; IN=intermonsoon period; SW=southwest monsoon). SD=standard deviations; Max=maximum; Min=minimum; n=number of sample and ns=no significant.

Monthly total rainfall (mm)	Season	Period	Season	Period	
	NE	IN (Apr)	SW	IN (Oct)	p-level
Mean	416.4	497.7	363.7	398.7	p<0.05
SD	129.9	-	97.9	305.6	
Max	578.2	-	487.6	614.8	
Min	238.8	-	176.1	182.6	
n	10	1	7	2	

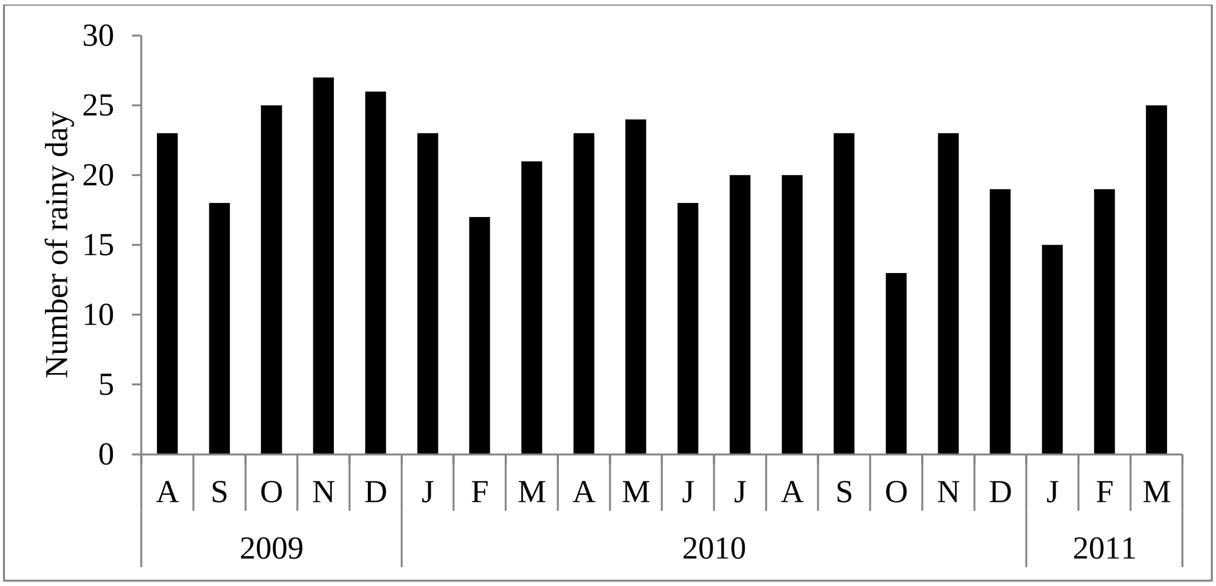


Fig. 3.1.2. Number of rainy day in each month throughout sampling period from August 2009 to March 2011 in Taiping (Hospital Taiping station). (Data obtained from Meteorological Department Malaysia).

SPI during sampling months are shown in Fig. 3.1.3. These values were computed from mean and standard deviation of total monthly rainfall over 12 years time scale (January 2000 to April 2012). Average SPI was 0.31 which is a near normal category of precipitation based on Table 2.4. There was no period of severe and extreme drought (SPI<-1.5) nor an extremely wet period (SPI>2.0). A period of moderate drought was recorded in July 2010 with SPI value of -1.01 during SW monsoon. Other months with lower than average SPI were February to March, May to October and December 2010 and January to February 2011. Category of ‘very wet’ period was observed in October 2009 with SPI of 1.57 which was then followed by period categorized as moderately wet in November (SPI=1.22) and December (SPI=1.35) 2009 coinciding with NE monsoon. Another month categorized as moderately wet was March 2011 with SPI of 1.26.

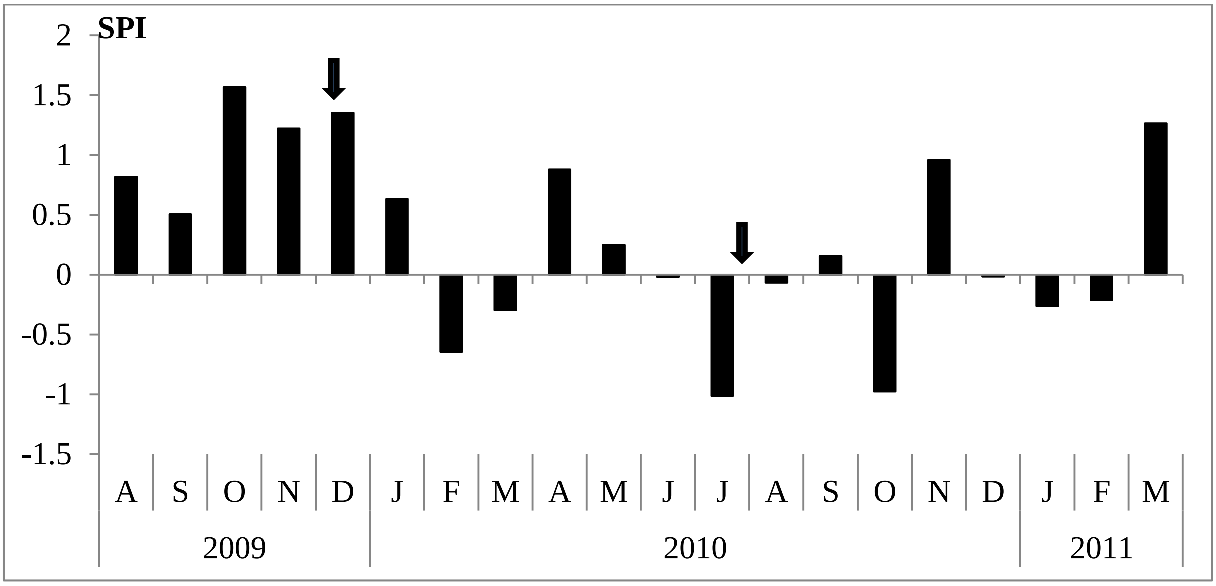


Fig. 3.1.3. Monthly standardised precipitation index (SPI) of Taiping (Hospital Taiping station) throughout sampling period from August 2009 to March 2011 computed from mean and standard deviation of monthly total rainfall from 2000 (January) to 2012 (April) at Taiping. (Data obtained from Meteorological Department Malaysia).

3.1.1.2 Water depth

Although the water depth at the study area was generally shallow (2.7±1.0 m), the depth range particularly at mid-estuary was high from 1.1 m to 5.9 m, while at river mouth, the depth ranged from 1.1 m to 4.1 m. With reference to mid-estuary and river mouth, it is also important to note the difference in depths especially between river bank and mid river since typical river would have a ‘U’ shaped cross section making mid water characteristically deeper. Water depth at the mudflat and offshore shoal was relatively more uniform with a depth that ranged from 0.5 m to 2.9 m and 1.7 m to 3.1 m, respectively. Mean water depth at mid-estuary, river mouth, mudflat and shoal was 3.03±0.95 m, 2.69±0.21 m, 2.12±0.68 m and 2.94±0.43 m respectively.

Table 3.1.2. Summary results of water depth (m) among sampling stations in Matang mangrove estuary from September 2009 to March 2011. n=number of samples; SD=standard deviation; Max=maximum, Min=minimum

Water depth (m)	Station			
	Mid-estuary	River mouth	Mudflat	Shoal
n	29	28	35	45
Mean	3.1	2.7	2.2	2.9
SD	1.4	1.1	1.0	0.5
Max	5.9	4.1	3.0	3.8
Min	1.1	1.1	0.5	1.7

3.1.1.3 Temperature

Temperatures recorded throughout sampling period were quite uniform in all the four stations ranging from 26.48 °C to 32.45 °C with a mean of 30.39±0.17 °C. Spatially, mean temperatures recorded for mid-estuary, river mouth, mudflat and shoal were 30.30±0.18 °C, 30.51±0.17 °C, 30.36±0.19 °C and 30.40±0.13 °C, respectively. Kruskal-Wallis test revealed that there was no significant difference ($H=2.17$, $p>0.05$) in temperature between these stations (Appendix IIIb). Overall, mean surface water (30.54±1.14 ºC) was significantly ($H=7.46$, $p<0.05$) warmer than bottom temperature (30.13±0.72 ºC). Highest mean temperature in mid-estuary (32.46±0.06 °C), river mouth (32.69±0.25 °C) and mudflat (31.95±0.09 °C) stations were recorded in March 2010. Lowest temperature at mid-estuary (27.17±0.23 °C), river mouth (26.48±0.04 °C) and mudflat (26.68±0.42 °C) stations were recorded in October 2009. Temperature at shoal area was quite uniform throughout sampling period with highest and lowest mean temperature observed in February 2010 (32.45±0.64 °C) and September 2010 (29.41±0.18 °C), respectively.

3.1.1.4 Salinity

Salinity at the study area gradually increased towards the sea, with mean salinity at mid-estuary, river mouth, mudflat and shoal stations being 23.38±0.49 ppt, 25.48±0.35 ppt, 26.78±0.55 ppt and 28.15±0.40 ppt, respectively. Overall salinity ranged from minimum of 10.79 ppt recorded at mid-estuary station to maximum of 31.61 ppt recorded at shoal station. Kruskal-Wallis test showed that salinity at mudflat station was significantly (H=57.41, p<0.05) higher than mid-estuary station while salinity at shoal station was significantly (H=57.41, p<0.05) higher than both mid-estuary and river mouth station (Appendix IIIc). There was however, no significant difference (H=1.53, p>0.05) in salinity between surface (26.82±2.79 ppt) and bottom water (27.23±2.64 ppt). Temporally, two salinity depressions were observed in November 2009 and 2010. These salinity depressions were more obvious in mid-estuary where the temporal changes in salinity were the most pronounced (10.79 ppt to 28.58 ppt). At the offshore shoal station, salinity was quite uniform throughout sampling period (Table 3.1.3; Fig. 3.1.4).

3.1.1.5 Total dissolved solids

Total dissolved solid (TDS) is a measure of the concentration of both organic and inorganic materials in water which is often expressed in g/L. TDS values are often similar but slightly higher than salinity values since salinity only measures the concentration of inorganic substance. Mean TDS at mid-estuary, river mouth, mudflat and shoal stations were 24.01±0.44 g/L, 25.99±0.32 g/L, 27.21±0.49 g/L and 28.28±0.66 g/L, respectively. Kruskal-Wallis test showed that TDS at mudflat station was significantly (H=53.00, p<0.05) higher than mid-estuary station, while TDS at shoal station was significantly (H=53.00, p<0.05) higher than river mouth and mid-estuary stations (Appendix IIId). There was however, no significant difference (H=1.89, p>0.05) between surface (27.29±2.57 g/L) and bottom TDS (27.66±2.43 g/L) as shown by Kruskal-Wallis test.

3.1.1.6 Dissolved oxygen concentration

Concentration of DO increased steadily towards the sea with mean concentrations at mid-estuary, river mouth, mudflat and shoal stations of 3.36±1.92 mg/L, 4.35±0.39 mg/L, 4.61±0.96 mg/L and 4.65±1.72 mg/L, respectively. Kruskal-Wallis test showed that dissolved oxygen concentration at river mouth, mudflat and shoal stations was significantly ($H=22.15$, $p<0.05$) higher than mid-estuary station (Appendix IIIe). Overall, mean surface DO concentration (5.38±1.59 mg/L) was significantly ($H=6.40$, $p<0.05$) higher than bottom DO concentration (4.93±1.37 mg/L) as revealed by Kruskal-Wallis test. There were two periods of low DO concentration observed in March 2010 and 2011 (Fig. 3.1.4).

3.1.1.7 Oxygen saturation

DO saturation increased gradually towards the sea with mean saturation at mid-estuary, river mouth, mudflat and shoal stations being 51.08±20.42%, 67.04±6.14%, 71.21±15.23% and 72.34±20.72%, respectively. DO saturation at river mouth, mudflat and shoal stations were significantly higher than mid-estuary station ($H=23.43$, $p<0.05$) (Appendix IIIf). Relative to other parameters, DO saturation exhibited a wide range of fluctuation in its temporal pattern. Two periods of low DO saturation were observed in February/March 2010 and March 2011 (Fig. 3.1.4).

3.1.1.8 pH

Kruskal-Wallis test showed that seawater at river mouth (7.67±0.39), mudflat (7.74±0.35) and shoal (7.70±0.36) stations were significantly ($H=23.40$, $p<0.05$) more alkaline than mid-estuary (7.36±0.33) station (Appendix IIIg). There was however, no significant difference ($H=0.42$, $p>0.05$) between surface (7.69±0.43) and bottom (7.62±0.38) pH as shown by Kruskal-Wallis test. There were two periods of lower pH which was distinct at mid-estuary observed in November/December 2009 (6.90±0.03) and November/December 2010 (6.85±0.31).

3.1.1.9 Suspended particulate matter (SPM)

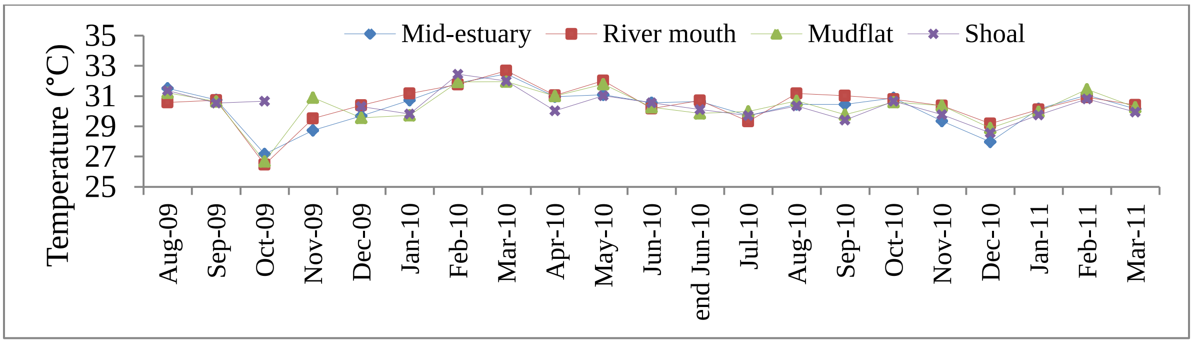
Since turbidity data were not available in this study due to faulty sensor, SPM expressed as g/L is thus, used as alternative indicator of turbidity. Amount of SPM at mid-estuary, river mouth, mudflat and shoal stations were 193.8±93.1 mg/L, 172.959.3 mg/L, 395.4±226.9 mg/L and 336.7±114.1 mg/L, respectively. Kruskal-Wallis test showed that the amount of SPM at shoal station was significantly ($H=12.90$, $p<0.05$) higher than mid-estuary station (Appendix IIIh). At mid-estuary station, highest amount of SPM was recorded in August 2010 (715.86±NA mg/L) while lowest in January 2010 (54.30±16.51 mg/L). Amount of SPM at river mouth ranged from 371.17±48.32 mg/L in March 2010 to 88.72±30.42 mg/L in July 2010. At mudflat station, there were two apparent peaks in the amount of SPM which occurred in April (933.48±63.07 mg/L) and September (1937.46±813.13 mg/L) 2010 while lowest SPM was recorded in January 2010 (102.11±9.08 mg/L). Highest and lowest SPM at shoal station were 1037.70±102.71 mg/L (April 2010) and 104.07±24.58 mg/L (January 2010) respectively.

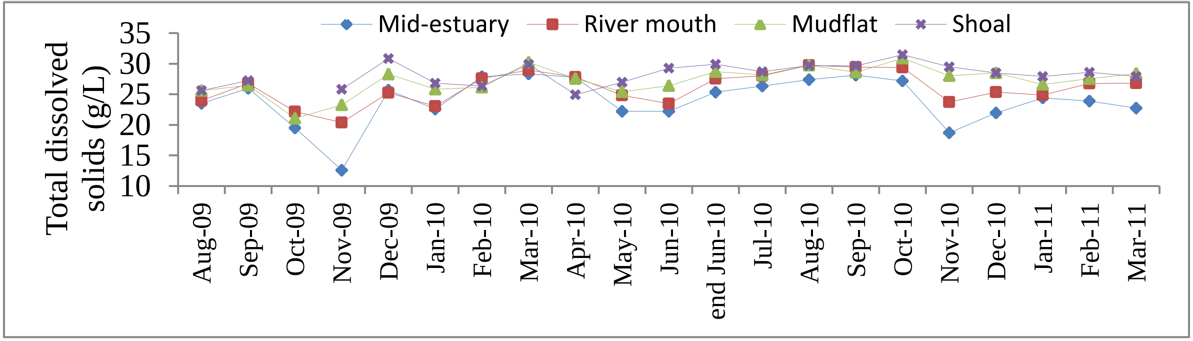
3.1.1.10 Sediment organic content (%)

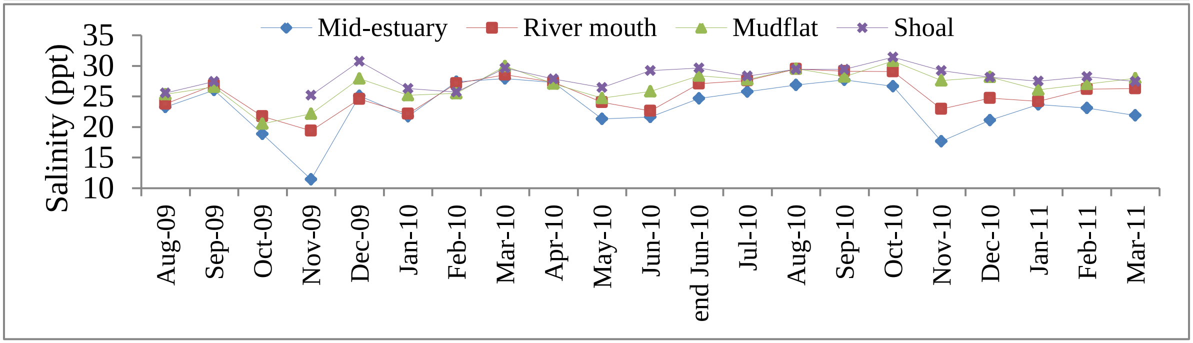
Sediment organic content was expressed as weight composition of organic matter relative to weight of dry sediment. Highest organic content was recorded at mid-estuary with mean of 11.61±2.39% and ranged from 6.90% to 18.37%, while lowest was recorded at shoal station with mean of 8.31±1.61%g. Both river mouth and mudflat recorded similar organic content with mean of 9.82±1.77% and 9.85±0.91% respectively. Kruskal-Wallis test revealed that sediment organic content at mid-estuary station was significantly higher (H=46.85, p<0.001) than all of the stations while no significant difference was detected between mudflat and shoal station (H=46.85, p<0.001) (Appendix IIIi). Temporally, there were some apparent peaks in organic content particularly in February, August and October 2010 at both mid-estuary and river mouth stations and October 2010 at both mudflat and shoal stations. Nevertheless, Kruskal-Wallis test showed no significant difference in sediment organic content between months in all the stations (p>0.05).

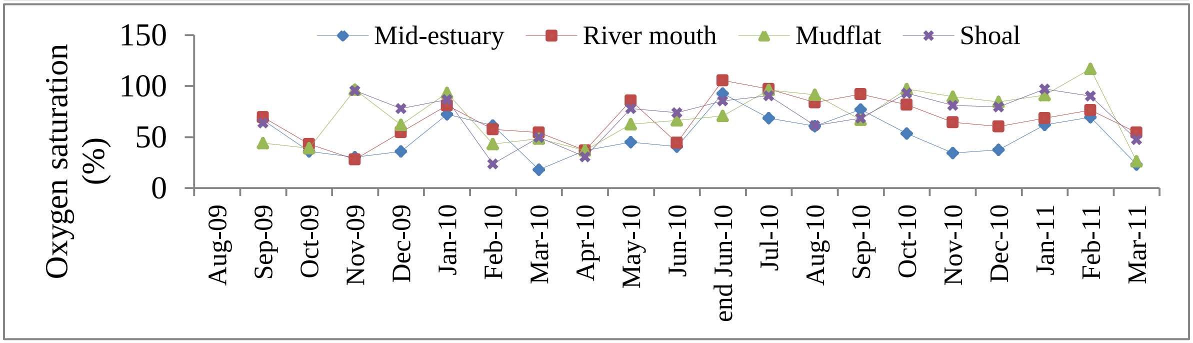
Table 3.1.3. Mean water parameters, standard deviations (SD) and summary of Kruskal-Wallis test results between four sampling stations in Matang mangrove estuary. Min=minimum, Max=maximum.

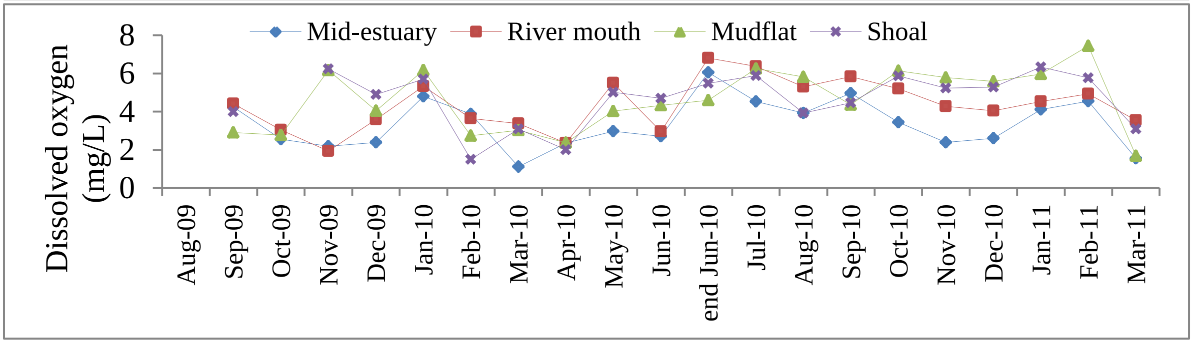
Water parameters		Station				
		Mid-estuary	River mouth	Mudflat	Shoal	p-level
Temperature (°C)	Mean	30.24	30.50	30.39	30.34	0.766
	SD	1.23	1.28	1.11	0.86	
	n	40	40	57	59	
	Min	27.01	26.45	26.38	28.54	
	Max	32.50	32.86	32.40	32.84	
Salinity (ppt)	Mean	23.38^{a}	$25.56^{a,b}$	$26.95^{b,c}$	28.28^{c}	<0.001
	SD	4.11	2.78	2.42	1.74	
	n	40	40	57	59	
	Min	10.79	19.38	20.52	23.69	
	Max	28.58	29.76	30.91	31.61	
DO (mg/L)	Mean	3.36^{a}	4.35^{b}	4.68^{b}	4.66^{b}	<0.001
	SD	1.28	1.35	1.65	1.50	
	n	40	40	57	59	
	Min	0.72	1.86	1.66	0.41	
	Max	6.48	7.11	8.21	6.91	
DO (%)	Mean	51.08^{a}	67.04^{b}	72.41^{b}	72.47^{b}	<0.001
	SD	20.16	21.47	25.81	23.23	
	n	40	40	57	59	
	Min	11.70	27.10	25.70	6.3	
	Max	99.60	110.60	129.20	106.20	
pH	Mean	7.38^{a}	7.67^{b}	7.74^{b}	7.70^{b}	<0.001
	SD	0.31	0.39	0.35	0.36	
	n	40	40	57	59	
	Min	6.63	7.01	7.00	7.00	
	Max	7.89	8.40	8.31	8.42	
TDS (g/L)	Mean	24.04^{a}	$26.10^{a,b}$	$27.39^{b,c}$	28.42^{c}	<0.001
	SD	3.91	2.60	2.25	2.09	
	n	40	40	57	59	
	Min	11.92	20.32	21.01	18.20	
	Max	28.97	30.00	31.02	31.63	
SPM (mg/L)	Mean	171.10^{a}	172.92^{a}	395.40^{a}	339.91^{b}	<0.05
	SD	157.83	105.31	562.12	287.32	
	n	23	24	36	36	
	Min	37.12	67.21	71.65	80.26	
	Max	715.86	437.00	2867.27	1097.48	
Sediment organic content (%)	Mean	11.61^{a}	9.82^{b}	9.85^{b}	8.31^{c}	<0.001
	SD	2.39	1.77	0.91	1.61	
	n	32	32	47	48	
	Min	6.91	7.11	8.25	6.06	
	Max	18.37	13.76	11.49	12.32	


Mid-estuary
River mouth
Mudflat
Shoal
Temperature (°C)
35
33
31
29
27
25
Aug-09
Sep-09
Oct-09
Nov-09
Dec-09
Jan-10
Feb-10
Mar-10
Apr-10
May-10
Jun-10
end Jun-10
Jul-10
Aug-10
Sep-10
Oct-10
Nov-10
Dec-10
Jan-11
Feb-11
Mar-11


Mid-estuary
River mouth
Mudflat
Shoal
Total dissolved solids (g/L)
35
30
25
20
15
10
Aug-09
Sep-09
Oct-09
Nov-09
Dec-09
Jan-10
Feb-10
Mar-10
Apr-10
May-10
Jun-10
end Jun-10
Jul-10
Aug-10
Sep-10
Oct-10
Nov-10
Dec-10
Jan-11
Feb-11
Mar-11


Mid-estuary
River mouth
Mudflat
Shoal
Salinity (ppt)
35
30
25
20
15
10
Aug-09
Sep-09
Oct-09
Nov-09
Dec-09
Jan-10
Feb-10
Mar-10
Apr-10
May-10
Jun-10
end Jun-10
Jul-10
Aug-10
Sep-10
Oct-10
Nov-10
Dec-10
Jan-11
Feb-11
Mar-11


Mid-estuary
River mouth
Mudflat
Shoal
Oxygen saturation (%)
150
100
50
0
Aug-09
Sep-09
Oct-09
Nov-09
Dec-09
Jan-10
Feb-10
Mar-10
Apr-10
May-10
Jun-10
end Jun-10
Jul-10
Aug-10
Sep-10
Oct-10
Nov-10
Dec-10
Jan-11
Feb-11
Mar-11


Mid-estuary
River mouth
Mudflat
Shoal
Dissolved oxygen (mg/L)
8
6
4
2
0
Aug-09
Sep-09
Oct-09
Nov-09
Dec-09
Jan-10
Feb-10
Mar-10
Apr-10
May-10
Jun-10
end Jun-10
Jul-10
Aug-10
Sep-10
Oct-10
Nov-10
Dec-10
Jan-11
Feb-11
Mar-11

(Figure 3.1.4, continued)

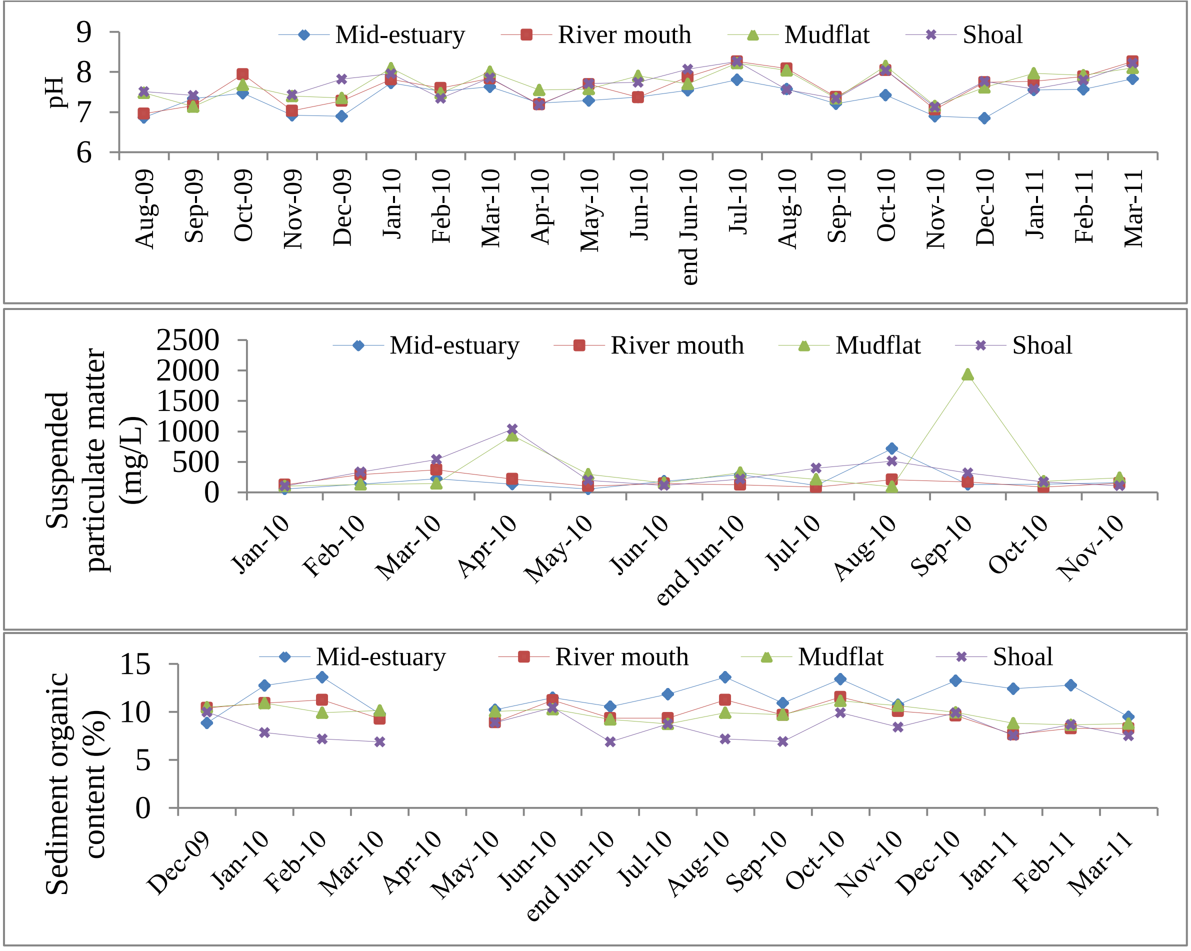
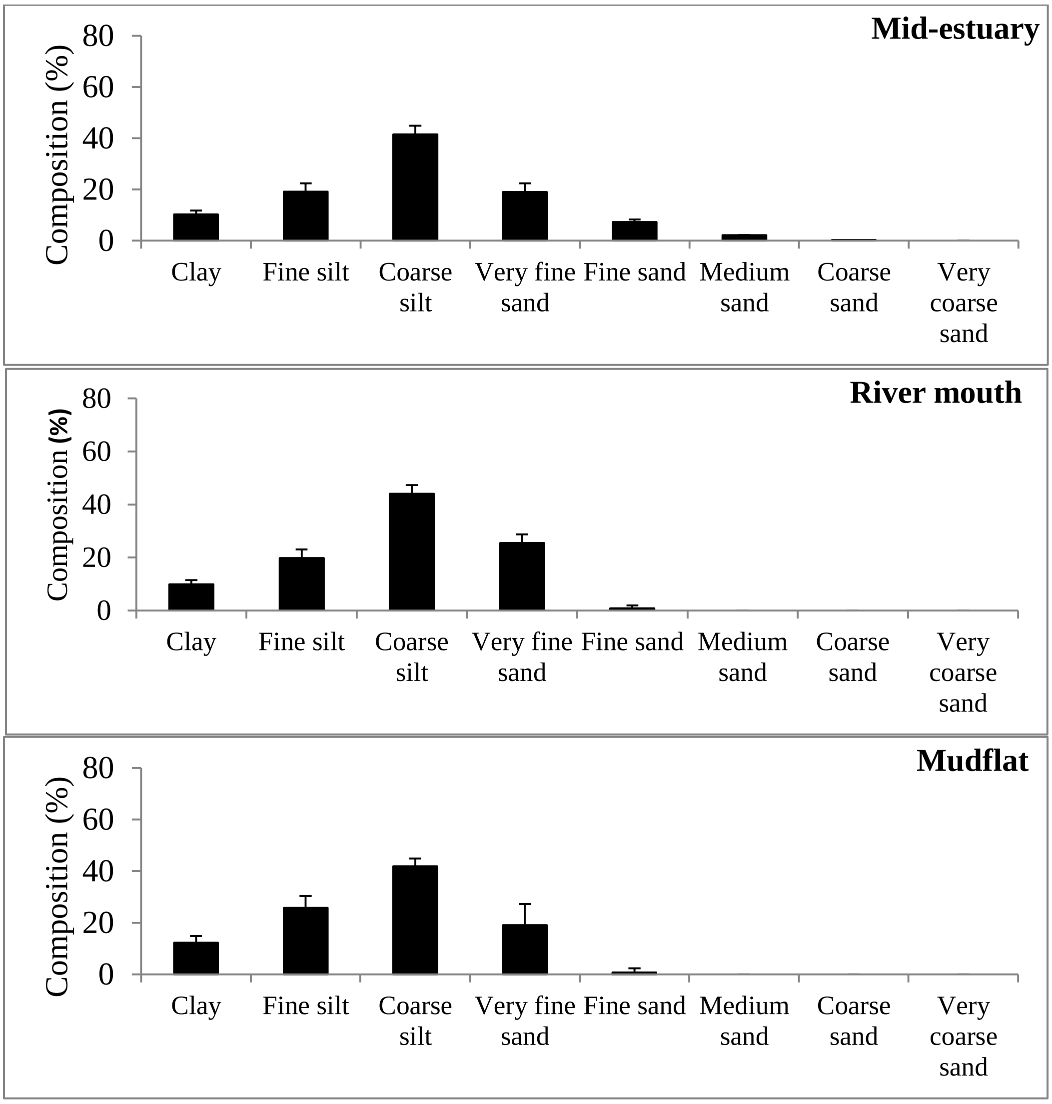


Fig. 3.1.4. Monthly mean values of water parameters and sediment organic contents at each sampling station in Matang mangrove estuary (note: difference in length of sampling period; standard deviation omitted for clarity).

3.1.1.11Sediment particle size

Fig. 3.1.5 shows the size composition of sediment particle at each sampling station. Sediment particles showed similar size compositions at all stations with coarse silt having the highest composition ranging from 41.58% at mid-estuary to 55.21% at nearshore. At mid-estuary station, compositions of fine silt and very fine sand were similar with 19.15% and 19.08% respectively. At the river mouth, very fine sand made up the second highest particle size category followed by fine silt with composition 25.43% and 19.76% respectively. Among all stations, sediment texture at mudflat was the finest with higher composition of fine silt (25.75%) and very fine sand (19.15%). At shoal station, very fine sand (25.85%) had much higher composition than fine silt

(10.19%). Fine sand was the largest particle size category for sediment at the river mouth, mudflat and shoal stations, whereas coarse sand occurred as the largest particles at mid-estuary station with very low composition (0.35%). Kruskal-Wallis test showed that composition of fine silt was significantly higher (H=9.75, p<0.05) at mudflat compared to shoal station while there was no significant difference for all other particle size categories among stations (p>0.05) (Appendix IV).



(Figure 3.1.5, continued)

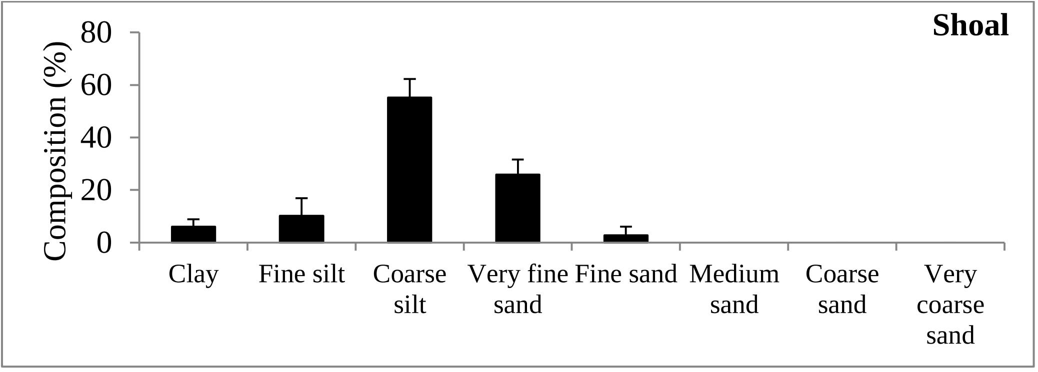


Fig. 3.1.5. Size compositions of sediment particle (based on Table 2.3) at mid-estuary, river mouth, mudflat and shoal stations in Matang mangrove estuary.

3.1.2 Seasonal variations of water parameters and sediment organic content

At mid-estuary station, salinity (24.65±2.40 ppt) was slightly higher ($p>0.05$) at SW monsoon compared with NE monsoon (22.09±4.70 ppt). Salinity fluctuated greatly in NE with range of 10.79-28.58ppt compared to SW which ranged from 20.03-28.10ppt. Percent organic content of sediment did not change significantly ($p>0.05$) throughout NE and SW at all stations; however, NE had highest range (6.91-18.37%). With exception of dissolved oxygen and suspended particulate matter, Mann-Whitney test revealed no significant difference in all water parameters between season ($p>0.05$) in all stations (Table 3.1.4-3.1.7). Both DO were significantly higher ($p<0.05$) during SW at mid-estuary and river mouth (Table 3.1.4 and 3.1.5). At mudflat, amount of suspended particulate matter was significantly higher ($p<0.05$) in SW denoting the turbid water during that period (Table 3.1.6) (Appendix V).

Table 3.1.4. Summary results of Mann-Whitney test (tested between NE and SW) and basic statistics on water parameters between seasons at mid-estuary station in Matang mangrove estuary from September 2009 to March 2011. SD=standard deviation; n=number of samples; Min=minimum; Max=maximum; ns=no significant.

Parameter		Season	Period	Season	p-level
		NE	IN	SW	
Temp (ºC)	Mean	30.22	29.67	30.65	p=0.2028
	SD	1.35	1.94	0.55	(ns)
	n	20	6	16	
	Min	27.83	27.01	29.66	
	Max	32.50	30.98	31.89	
Salinity (ppt)	Mean	22.09	24.26	24.65	p=0.0746
	SD	4.70	4.21	2.40	(ns)
	n	20	6	16	
	Min	10.79	18.58	20.03	
	Max	28.58	27.50	28.10	
TDS (g/L)	Mean	22.88	24.80	25.14	p=0.1079
	SD	4.49	4.14	2.26	(ns)
	n	20	6	16	
	Min	11.92	19.22	21.01	
	Max	28.97	27.95	28.48	
DO (%)	Mean	44.42	42.12	60.51	$p<0.05$
	SD	19.82	9.50	22.84	
	n	20	6	15	
	Min	11.70	34.40	5.60	
	Max	79.00	58.70	99.60	
DO (mg/L)	Mean	2.96	2.79	3.94	$p<0.05$
	SD	1.28	0.56	1.47	
	n	20	6	15	
	Min	0.72	2.32	0.36	
	Max	5.22	3.77	6.48	
pH	Mean	7.34	7.38	7.38	p=0.8484
	SD	0.40	0.12	0.30	(ns)
	n	20	6	16	
	Min	6.63	7.22	6.58	
	Max	7.89	7.50	7.84	
Organic content (%)	Mean	11.52	13.43	11.44	p=0.8323
	SD	2.96	1.73	1.26	(ns)
	n	18	2	12	
	Min	6.91	12.21	9.76	
	Max	18.37	14.65	14.16	
SPM (g/L)	Mean	0.1434	0.1330	0.2051	p=0.7341
	SD	0.0756	0.0557	0.2177	(ns)
	n	8	4	11	
	Min	0.0426	0.0637	0.0371	
	Max	0.2947	0.1987	0.7159	

Table 3.1.5. Summary results of Mann-Whitney test (tested between NE and SW) and basic statistics on water parameters between seasons at river mouth station in Matang mangrove estuary from September 2009 to March 2011. SD=standard deviation; n=number of samples; Min=minimum; Max=maximum; ns=no significant.

Parameter		Season	Period	Season	p-level
		NE	IN	SW	
Temp (ºC)	Mean	30.66	29.44	30.72	p=0.4640
	SD	1.04	2.30	0.76	(ns)
	n	20	6	16	
	Min	29.03	26.45	29.24	
	Max	32.86	31.18	32.07	
Salinity (ppt)	Mean	24.62	26.05	26.33	p=0.0648
	SD	2.60	3.43	2.48	(ns)
	n	20	6	16	
	Min	19.38	21.69	22.50	
	Max	28.57	29.32	29.76	
TDS (g/L)	Mean	25.28	26.44	26.71	p=0.0856
	SD	2.44	3.40	2.34	(ns)
	n	20	6	16	
	Min	20.32	22.09	23.32	
	Max	28.98	29.59	30.00	
DO (%)	Mean	60.07	53.87	82.66	p<0.01
	SD	15.80	21.69	20.49	
	n	20	6	14	
	Min	27.10	35.60	40.30	
	Max	96.10	82.10	110.60	
DO (mg/L)	Mean	3.92	3.53	5.31	p<0.01
	SD	1.02	1.33	1.31	
	n	20	6	14	
	Min	1.86	2.28	2.68	
	Max	6.26	5.23	7.11	
pH	Mean	7.63	7.73	7.60	p=0.8112
	SD	0.39	0.42	0.45	(ns)
	n	20	6	16	
	Min	7.01	7.18	6.91	
	Max	8.32	8.12	8.40	
Organic content (%)	Mean	9.54	11.55	9.97	p=0.5533
	SD	1.75	1.31	1.79	(ns)
	n	18	2	12	
	Min	7.11	10.62	7.61	
	Max	13.76	12.47	13.76	
SPM (g/L)	Mean	0.2346	0.1534	0.1383	p=0.1742
	SD	0.1364	0.1113	0.0614	(ns)
	n	8	4	12	
	Min	0.0833	0.0857	0.0672	
	Max	0.4370	0.3192	0.2867	

Table 3.1.6. Summary results of Mann-Whitney test (tested between NE and SW) and basic statistics on water parameters between seasons at mudflat station in Matang mangrove estuary from September 2009 to March 2011. SD=standard deviation; n=number of samples; Min=minimum; Max=maximum; ns=no significant; similar superscripts of a or b denotes homogenous group.

Parameter		Season	Period	Season	
		NE	IN	SW	p-level
Temp (°C)	Mean	30.53	29.78	30.49	p=0.9924
	SD	1.02	1.93	0.72	(ns)
	n	29	8	22	
	Min	28.80	26.38	29.51	
	Max	32.30	31.16	32.40	
Salinity (ppt)	Mean	26.72	26.84	27.14	p=0.3612
	SD	2.19	4.32	1.78	(ns)
	n	29	8	22	
	Min	22.02	20.52	23.35	
	Max	30.02	30.91	29.60	
TDS (g/L)	Mean	27.24	27.19	27.51	p=0.4640
	SD	1.96	4.16	1.67	(ns)
	n	29	8	22	
	Min	22.88	21.01	24.16	
	Max	30.25	31.02	29.85	
DO (%)	Mean	75.66	60.11	72.70	p=0.4977
	SD	28.62	32.10	16.80	(ns)
	n	29	8	21	
	Min	26.00	25.70	39.90	
	Max	129.20	100.10	104.90	
DO (mg/L)	Mean	4.89	3.88	4.70	p=0.3925
	SD	1.85	1.97	1.06	(ns)
	n	29	8	21	
	Min	1.68	1.66	2.56	
	Max	8.21	6.33	6.79	
pH	Mean	7.72	7.81	7.71	p=0.8716
	SD	0.36	0.30	0.35	(ns)
	n	29	8	22	
	Min	7.11	7.41	7.00	
	Max	8.30	8.20	8.31	
Organic content (%)	Mean	9.82^{a}	11.17^{b}	9.66^{a}	p=0.5308
	SD	0.92	0.44	0.77	
	n	27	3	17	
	Min	8.38	10.67	8.25	
	Max	11.30	11.49	10.69	
SPM (g/L)	Mean	0.1539	0.5566	0.5027	p<0.05
	SD	0.1007	0.4150	0.7286	
	n	12	6	18	
	Min	0.0955	0.1540	0.0717	
	Max	0.4688	0.9809	2.8673	

Table 3.1.7. Summary results of Mann-Whitney test (tested between NE and SW) and basic statistics on water parameters between seasons at shoal station in Matang mangrove estuary from September 2009 to March 2011. SD=standard deviation; n=number of samples; Min=minimum; Max=maximum; ns=no significant.

Parameter		Season	Period	Season	p-level
		NE	IN	SW	
Temp (ºC)	Mean	30.41	30.35	30.39	p=0.7082
	SD	1.12	0.35	0.63	(ns)
	n	30	6	24	
	Min	28.54	30.02	29.23	
	Max	32.84	30.70	31.53	
Salinity (ppt)	Mean	27.81	29.64	28.19	p=0.2542
	SD	1.72	1.95	1.80	(ns)
	n	30	6	24	
	Min	25.13	27.77	23.69	
	Max	31.61	31.44	30.58	
TDS (g/L)	Mean	28.21	28.19	28.38	p=0.4283
	SD	1.56	5.14	1.77	(ns)
	n	30	6	24	
	Min	25.77	18.20	23.91	
	Max	31.63	31.49	30.68	
DO (%)	Mean	72.90	61.90	72.36	p=0.5658
	SD	24.19	34.41	21.53	(ns)
	n	30	6	22	
	Min	12.10	28.30	6.30	
	Max	106.20	97.10	102.00	
DO (mg/L)	Mean	4.71	3.93	4.64	p=0.4815
	SD	1.59	2.13	1.38	(ns)
	n	30	6	0.41	
	Min	0.76	1.89	6.40	
	Max	6.91	6.11		
pH	Mean	7.69	7.61	7.70	p=0.9861
	SD	0.34	0.50	0.38	(ns)
	n	30	6	24	
	Min	7.10	7.06	7.00	
	Max	8.42	8.21	8.30	
Organic content (%)	Mean	8.22	9.94	8.18	p=0.7369
	SD	1.43	1.38	1.82	(ns)
	n	27	3	18	
	Min	6.06	9.03	6.13	
	Max	10.80	11.52	12.32	
SPM (g/L)	Mean	0.2708	0.6043	0.2979	p=0.0918
	SD	0.2331	0.4793	0.1932	(ns)
	n	12	6	18	
	Min	0.0803	0.1550	0.0813	
	Max	0.7535	1.0975	0.6540	

3.1.3 Diel variation in water parameters at mudflat

3.1.3.1 Rainfall during wet and dry periods of diel samplings at mudflat

Total rainfall during samplings in December 2009 (wet period) and between July and August 2010 (dry period) were 578.2 mm and 324.9 mm respectively. Mann-Whitney test did not detect any significant difference ($p>0.05$) in amount of rainfall between the two sampling periods (Appendix VIa) despite sampling period during NE monsoon having higher total monthly rainfall than sampling period during SW monsoon. Daily rainfall in both sampling periods ranged from 0.0 mm to 94.5 mm in NE and 54.7 mm in SW respectively. Mean and standard deviation used to compute SPI for both sampling periods were derived from past rainfall data over 12 year time scale (January 2000 to April 2012). Diel sampling during NE can be categorized as moderately wet with SPI of 1.35 while diel sampling during SW can be categorized as moderate drought with SPI of -0.14 (Table 3.1.8).

Table 3.1.8. Summary of rainfall information during diel sampling period at mudflat in northeast (NE) and southwest monsoon (SW) and results of Mann-Whitney test on mean daily rainfall between the two sampling periods. n=number of samples; Max=maximum; Min=minimum; SPI=standard precipitation index; ns=no significant.

Rainfall data (mm)	Diel sampling period		
	NE (Wet period)	SW (Dry period)	p-level
Period	Dec 2009	Between Jul-Aug 2010	
Total rainfall	578.2	324.9	
Mean daily rainfall	18.7	10.5	p=0.1551 (ns)
SD	23.5	15.0	
Max	94.5	54.7	
Min	0.0	0.0	
n	31	31	
Number of rainy day	26	23	
SPI	1.35	-0.14	
Category	Moderately wet	Moderate drought	

3.1.3.2 Water parameters

a) Temperature

Daily temperatures recorded throughout samplings (December 2009 and July/August 2010) ranged from 27.81 °C to 34.20 °C. Mean daily temperature during the wet and dry period were 30.36±0.98 °C and 29.73±0.57 °C, respectively. Although temperature recorded throughout the 24 hour sampling period were quite homogenous compared to other water parameters, Kruskal-Wallis test revealed significant difference ($H=19.89$, $p<0.001$) in temperature between wet and dry period for all lunar phases. Generally, temperatures dropped during night time and lowest temperature usually occurred during dawn and early morning (0500-0900 hour) while higher temperature usually occurred during afternoon and late morning (1100-1600 hour) (Fig. 3.1.6). Tidal conditions did not significantly affect temperatures ($p>0.05$) at both sampling periods (Appendix VIb).

b) Salinity

Salinity during 24 hour sampling ranged from 19.78 ppt to 42.8 ppt. Salinity during wet period (25.36±3.47 ppt) was significantly lower ($H=30.935$, $p<0.001$) than dry period (27.65±1.04 ppt). Variation in salinity was more pronounced during the wet period (range of 23 ppt) than dry period (range of 5 ppt). Salinity at flood tide was significantly lower ($p<0.05$) than ebb tide during spring tides (full moon and new moon) in both sampling periods. Overall, diel variation in salinity is shown in Fig. 3.1.7 whereby salinity increased gradually during period of flood tide and decrease during period of ebb tide ($p<0.05$). There was no significant difference ($p>0.05$) in salinity between flood and ebb tides during neap conditions (first quarter and third quarter moon) (Appendix VIc).

c) Total dissolved solids

Generally, diel variations in TDS followed patterns of salinity readings since this measurement takes into account content of inorganic salts. Mean TDS during wet period and dry period were 25.62±2.48 g/L and 27.65±0.95 g/L, respectively. Kruskal Wallis test showed significant difference ($H=36.289$, $p<0.001$) in TDS between wet and dry period. TDS during wet period ranged from 20.18 g/L to 31.00 g/L while during dry period TDS ranged from 26.43 g/L to 30.32 g/L. Significant difference in TDS between flood and ebb tides was detected during spring tides ($p<0.05$) but not during neap tides ($p>0.05$) (Appendix VId).

d) pH

Mean pH values during wet and dry period were 7.67±0.40 and 7.52±0.48, respectively which were typical of estuarine environment. Kruskal-Wallis showed no significant difference ($H=0.710$, $P>0.05$) in pH between wet and dry period. There was no significant difference ($p>0.05$) between flood and ebb tide (Appendix VIe).

e) Dissolved oxygen concentration

DO concentrations at both dry and wet sampling periods varied between 1.67mg/L to 11.3mg/L. Mean DO during wet and dry periods were 5.03±1.63 mg/L and 5.38±1.87 mg/L, respectively with no significant difference ($H=2.511$, $p>0.05$). In wet period, DO during both first quarter and new moon were significantly higher (Kruskal-Wallis, $H=34.773$, $p<0.001$) than both third quarter and full moon while in dry period, DO level during first and third quarter moon were significantly higher ($H=46.768$, $p<0.001$) than both full moon and new moon. DO level were occasionally lower during flood tide but were not significant ($p>0.05$) (Appendix VIf).

f) Dissolved oxygen saturation

Mean DO saturation in wet and dry period were 76.81±25.39% and 82.50±28.92%, respectively with no significant difference ($H=2.650$, $p>0.05$). Similar to DO concentration, oxygen saturation was significantly higher ($H=32.872$, $p<0.001$) during first quarter and new moon in wet period while in dry period, DO saturation was significantly higher ($H=46.768$, $p<0.001$) during first and third quarter moon. Tidal condition did not significantly affect DO saturation ($p>0.05$) (Appendix VIg).

g) Suspended particulate matter

In wet period, SPM ranged from 0.0284 g/L to 1.0880 g/L while in dry period SPM ranged from 0.0487 g/L to 2.1435 g/L. However, no significant difference was detected between the two sampling periods (Kruskal-Wallis, $H=2.503$, $p>0.05$). Also, both moon phase and tidal condition did not significantly ($p>0.05$) affect amount of SPM (Appendix VIh).

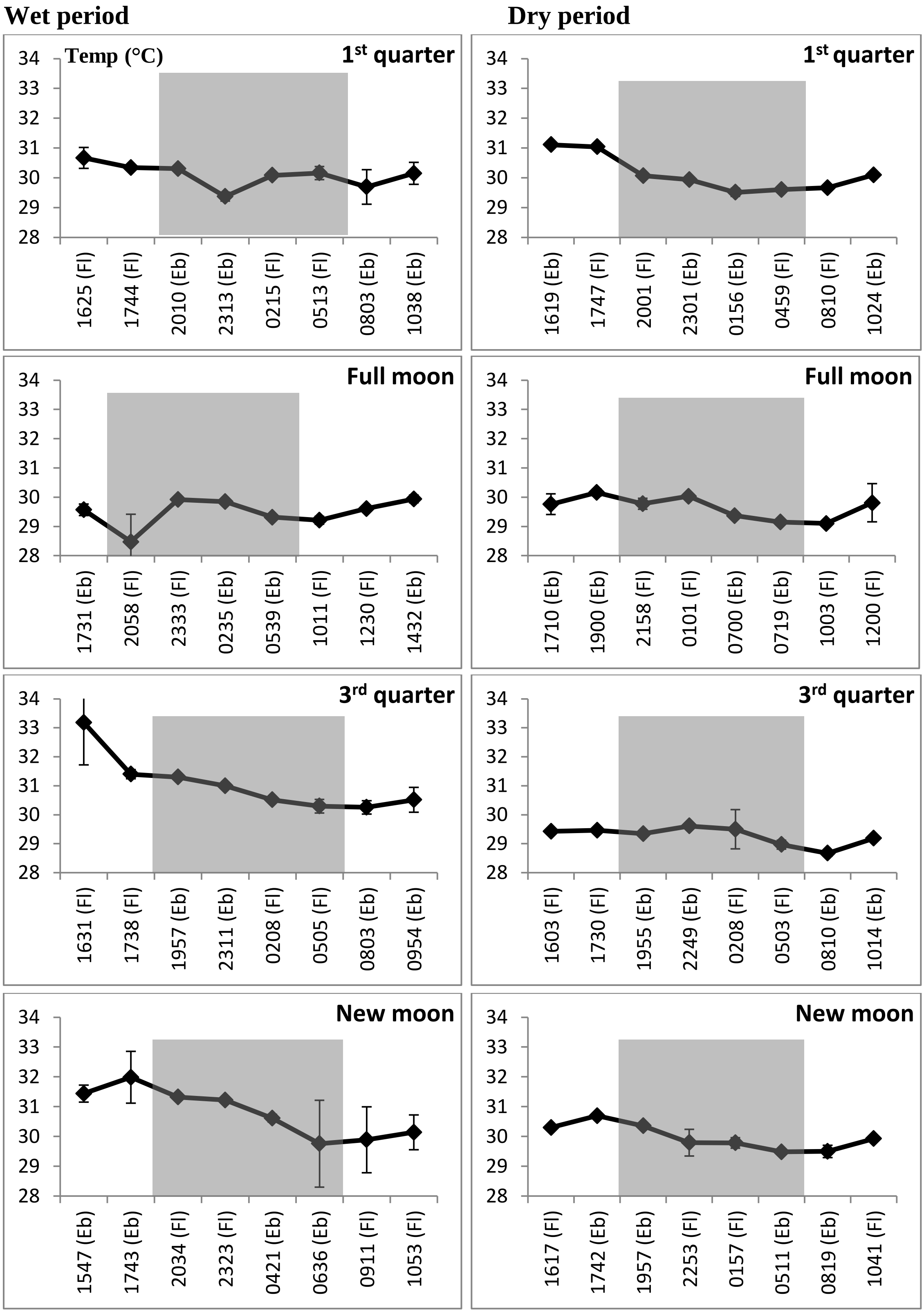


Fig. 3.1.6. Mean temperature (°C) of bottom water recorded over 24 hours for four consecutive lunar phases during wet (December 2009) and dry (July/August 2010) periods. ‘Eb’ denotes ebb tide while ‘Fl’ denotes flood tide. Shaded column denotes night time.

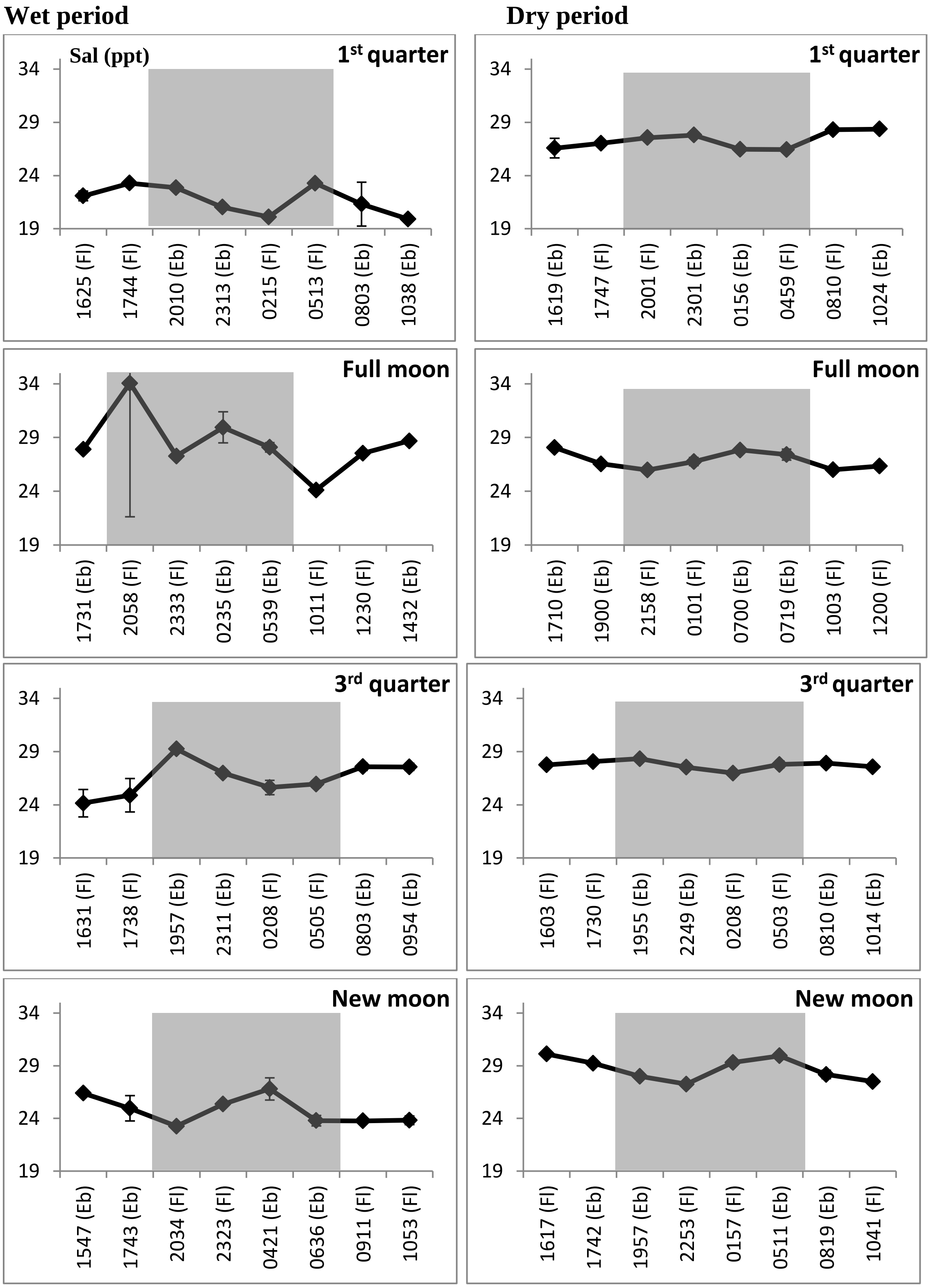


Fig. 3.1.7. Mean salinity (ppt) of bottom water recorded over 24 hours for four consecutive lunar phases during wet (December 2009) and dry (July/August 2010) periods. ‘Eb’ denotes ebb tide while ‘Fl’ denotes flood tide. Shaded column denotes night time.

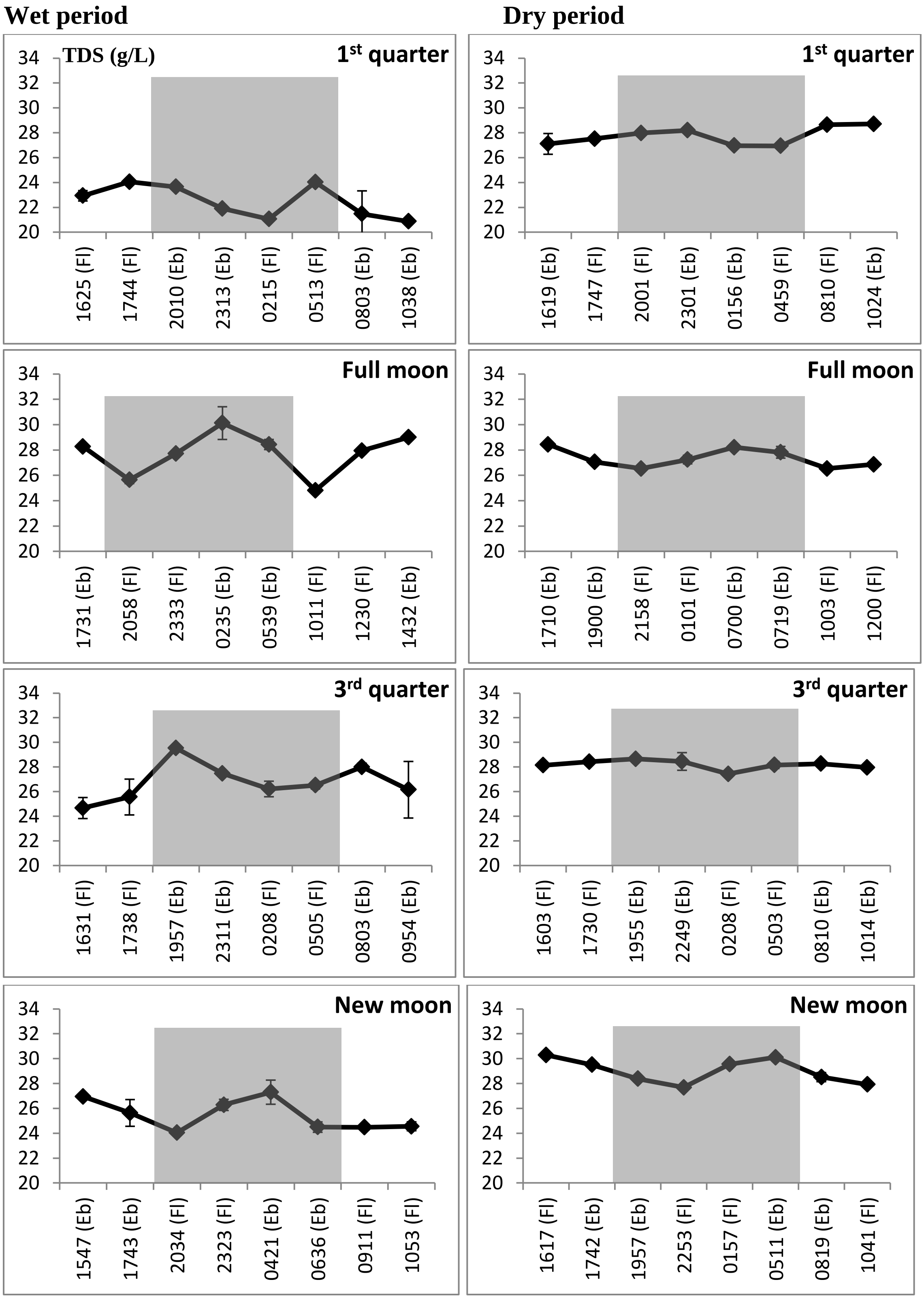


Fig. 3.1.8. Mean total dissolved solids (g/L) of bottom water recorded over 24 hours for four consecutive lunar phases during wet (December 2009) and dry (July/August 2010) periods. ‘Eb’ denotes ebb tide while ‘Fl’ denotes flood tide. Shaded column denotes night time.

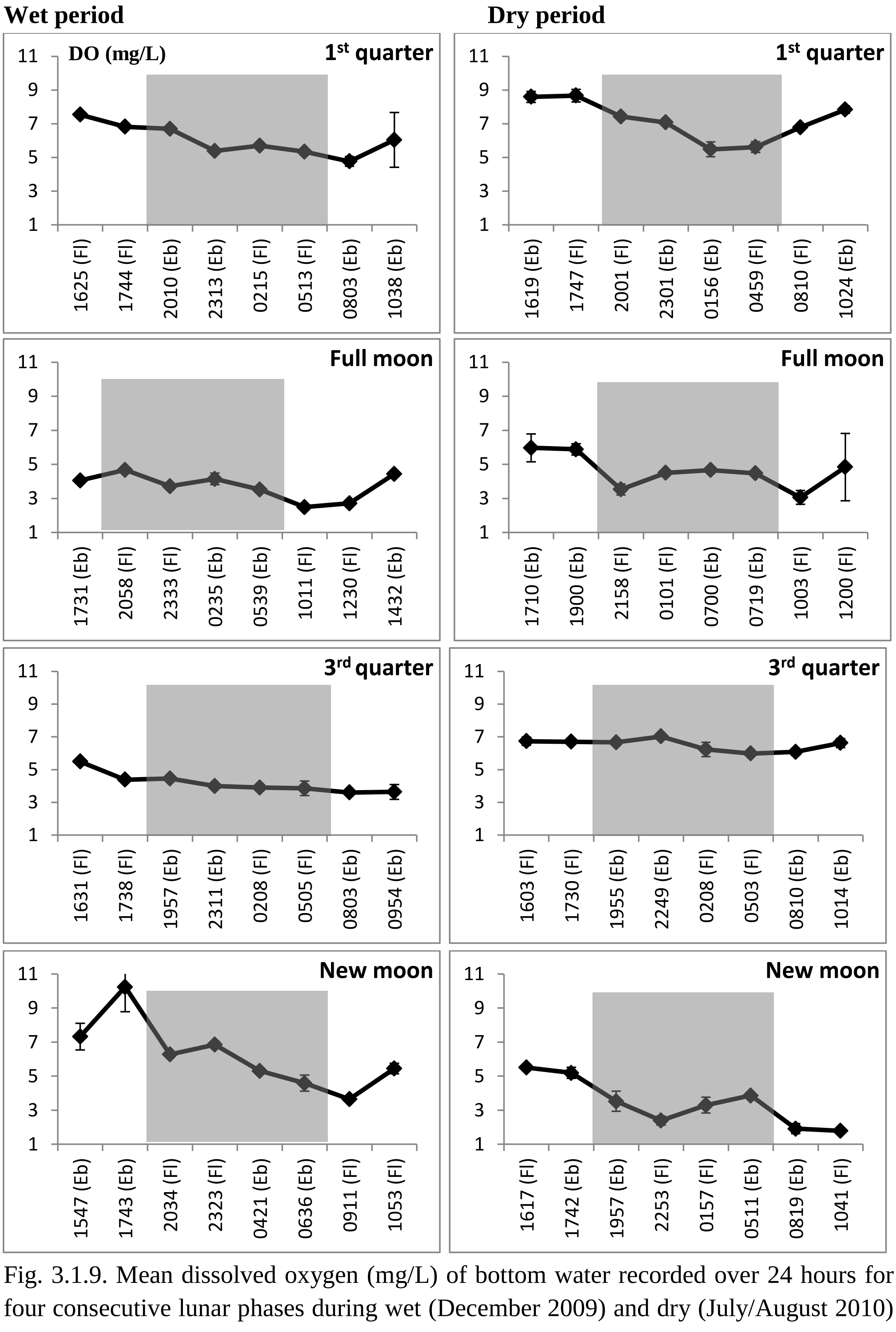


Fig. 3.1.9. Mean dissolved oxygen (mg/L) of bottom water recorded over 24 hours for four consecutive lunar phases during wet (December 2009) and dry (July/August 2010) periods. ‘Eb’ denotes ebb tide while ‘Fl’ denotes flood tide. Shaded column denotes night time.

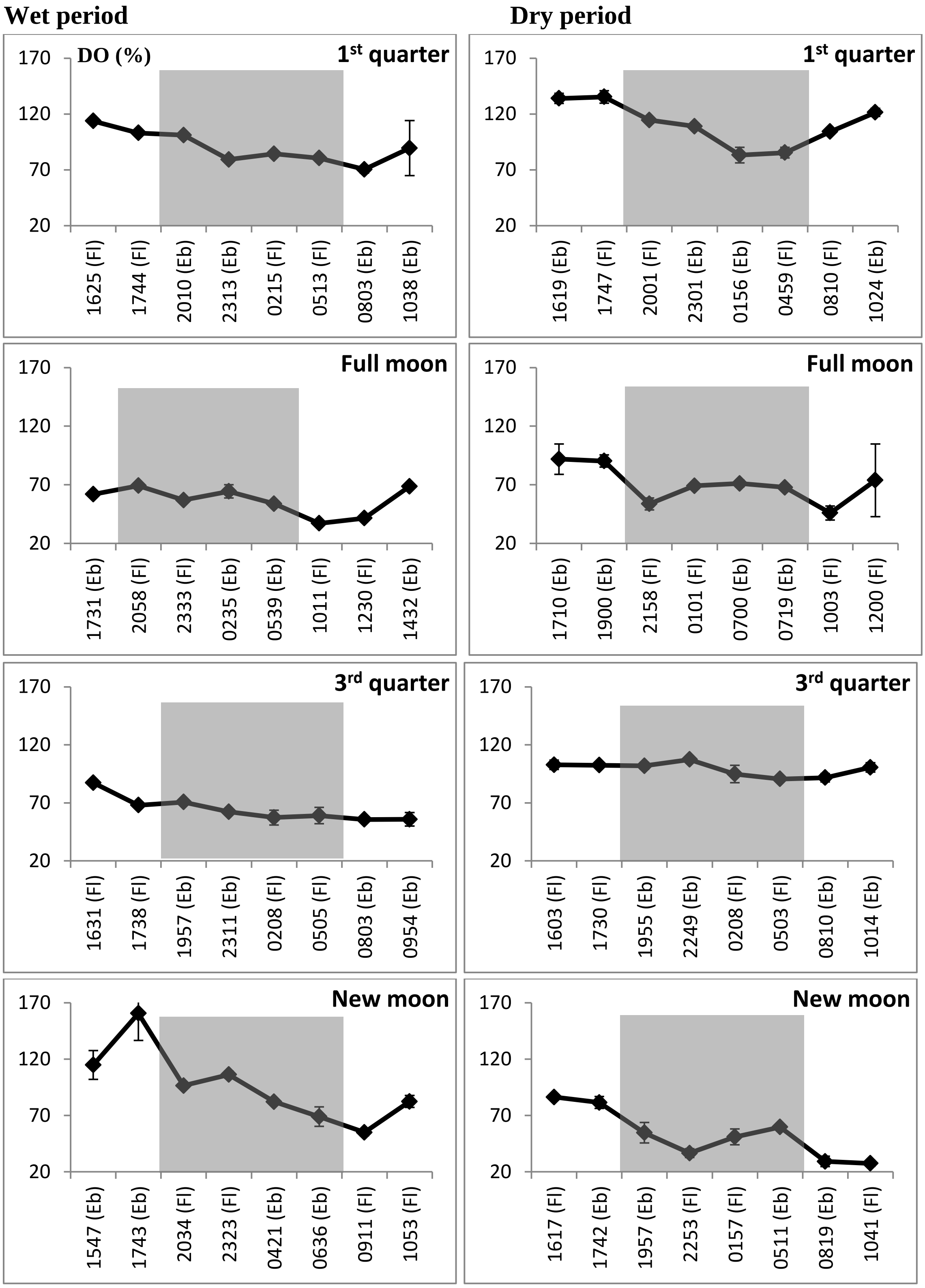


Fig. 3.1.10. Mean oxygen saturation (%) of bottom water recorded over 24 hours for four consecutive lunar phases during wet (December 2009) and dry (July/August 2010) periods. ‘Eb’ denotes ebb tide while ‘Fl’ denotes flood tide. Shaded column denotes night time.

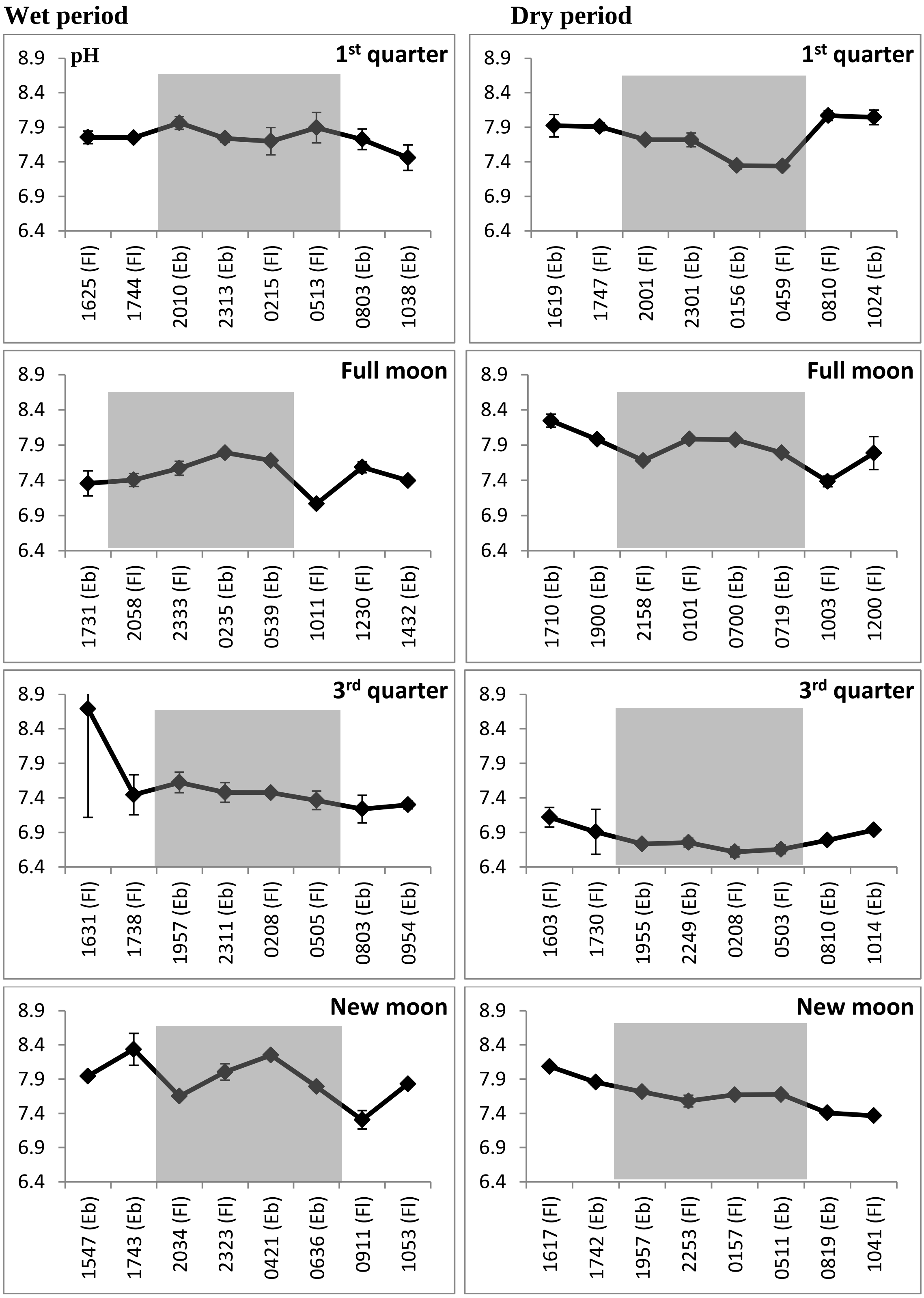


Fig. 3.1.11. Mean bottom pH of bottom water recorded over 24 hours for four consecutive lunar phases during wet (December 2009) and dry (July/August 2010) periods. ‘Eb’ denotes ebb tide while ‘Fl’ denotes flood tide. Shaded column denotes night time.

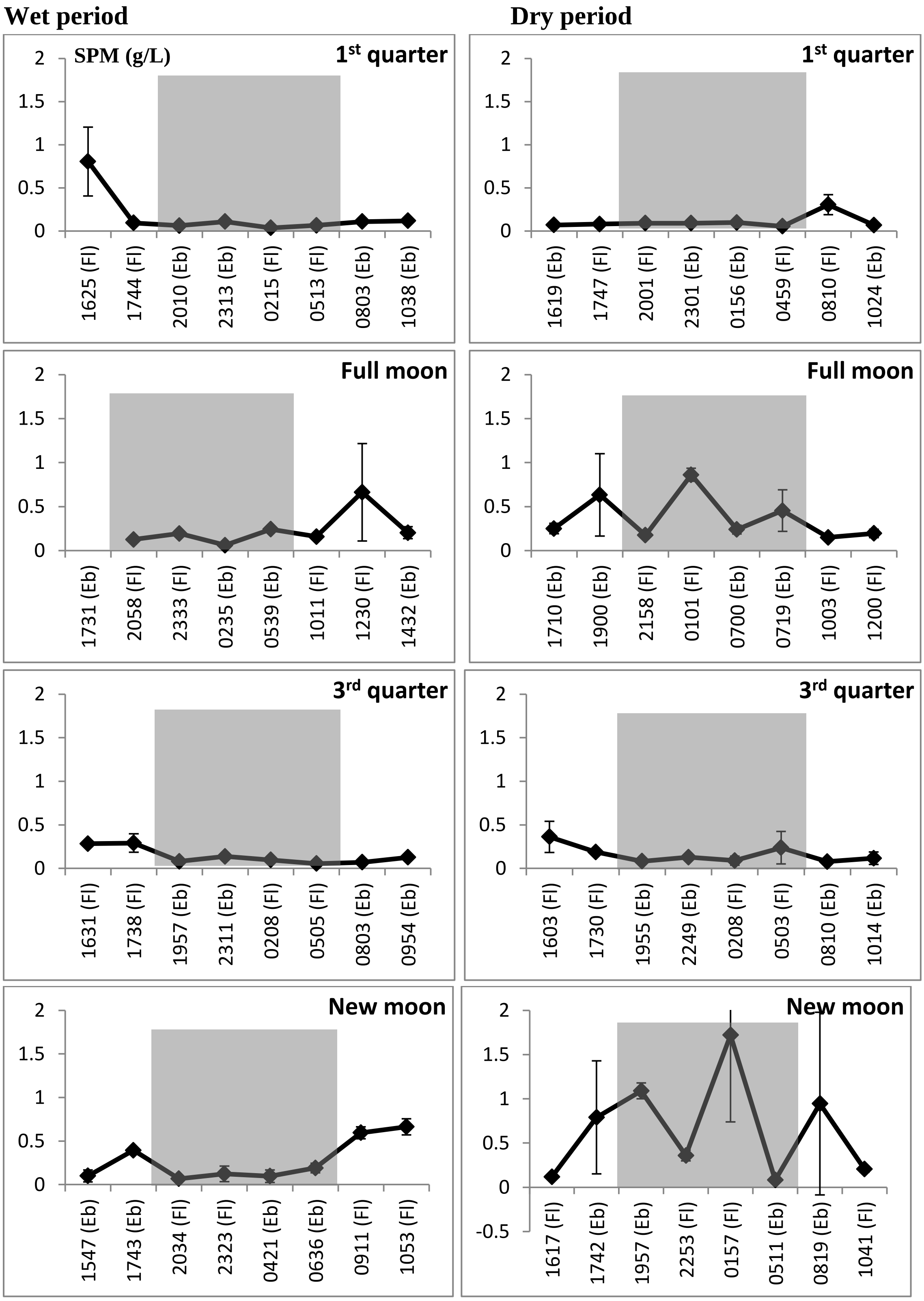


Fig. 3.1.12. Mean suspended particulate matter (g/L) of bottom water recorded over 24 hours for four consecutive lunar phases during wet (December 2009) and dry (July/August 2010) periods. 'Eb' denotes ebb tide while 'Fl' denotes flood tide. Shaded column denotes night time.

3.1.4 Discussion

Matang mangrove estuary can be considered as salt wedge estuary. Sasekumar et al. (1994) reported formation of temporal salt wedge due to freshwater inflow during neap tide when water current is weak and thus, less vertical mixing. This salt wedge has been observed to form over 10 km into the rivers (see Tanaka & Choo, 2000). Matang estuary is also characterised by water of high turbidity due to the mixing of the muddy substrate. This is more pronounced in area where water is shallow such as in the mudflat (mean depth = 2.2 m) and shoal (mean depth = 2.9 m) stations where mean concentration of suspended particulate matter were 395.40 mg/L and 339.91 mg/L respectively, about 2 folds more than in mid-estuary. The higher accretion rate of fine mud particles as indicated by relatively higher proportion of fine silt (about 26% at mudflat station) at the confluence of the Selinsing and Sangga Besar rivers have also contributed to the more turbid water at the subtidal mudflat station.

The organic content of sediment was significantly higher at mid-estuary (11.61±2.39%) and lowest at shoal station (8.31±1.61%). The proximity of mid-estuary station to mangrove fringe results in higher input of detrital matter from the mangrove forest to the sediment and thus, increase the organic content whereas shoal station is located further offshore and hence, a lower sediment organic content due to less detrital input from the mangroves. Both river mouth and mudflat stations had similar sediment organics which was less than mid-estuary but more than shoal station. This observation indicates the decreasing influence of mangrove detrital input on sediment organic matter from mid-estuary towards offshore.

It is important to note that the data on water parameters taken in the present study were instantaneous readings and were subjected to the weather on the day of sampling. Additionally, for the purpose of comparison, the water parameters measured during the routine monthly samplings covered only spring flood tides (or about 2 to 3 hours before the high slack water). Therefore, the data records may not necessarily be representative of the general water characteristics for the month.

In Matang, there is no clear wet and dry season i.e. each monsoon season is characterised by wet and dry periods (Fig. 3.1.3) whereas the intermonsoon (period when wind direction is variable) is typically characterized by more rainfall (Table 3.1.1). The influence of rainfall could be inferred from the salinity records throughout the sampling period. Drier months were recorded from June to August 2010 based on the standardised precipitation index (Fig. 3.1.3). This pattern was similarly followed by salinity particularly in mid-estuary, river mouth and mudflat where bottom salinity was higher during these months. In contrast, there were two salinity depression observed in the wetter months of November 2009 and 2010. Chong et al. (1999) showed that salinities were higher during drier periods compared to wetter periods. The fluctuation of salinity was more pronounced at mid-estuary where the largest range of salinities (10.79-28.58 ppt) was recorded. This is due to greater influence of freshwater at mid-estuary. At shoal station, salinity and other water parameters were subject to less fluctuation as indicated by the lower standard deviation since this station is situated farther offshore and subject to less riverine input. Hence, the shoal station hada higher mean salinity (28.19±1.80 ppt) compared to all other stations ($p<0.05$). Neap and spring tides had little effect on the salinity in the mudflat (where 24-hour samplings were carried out) since there is a mixed outcome. For example, during dry period, salinity at first quarter (neap) and full moon (spring) were significantly lower than third quarter (neap) and new moon (spring).

The mean bottom water temperature was more or less consistent throughout the study. However, variation in monthly temperature showed some similar trend with rainfall pattern. Relatively higher bottom water temperatures were recorded during the drier months (e.g. February and March 2010) whereas lower temperatures were recorded during wetter months (e.g. October and December 2009). This observation was also consistent with Singh (2003) which reported the tendency of water temperature to be lower during wetter months. The lower temperature could be caused by the cooler wind of the northeast/winter monsoon during the wetter months whereby the bottom water is also affected due to shallow water. Yap (1995) and Singh (2003) reported that temperature of Matang estuary (lower to upper reaches) was more or less homogeneous from surface to bottom water. On the other hand, Chong et al. (1999) did not find any relationship between water temperature and seasonality. The mid-estuary station had the lowest mean bottom temperature (30.24±1.23 ºC) among all stations. This could be related to the cooling effect caused by more mangrove tree cover and the narrower channel (Singh, 2003). Generally, water at study area was less alkaline than typical seawater (about pH 8.4) with pH in mid-estuary significantly lower than other stations. This is perhaps due to less influence of the more alkaline seawater in mid-estuary station.

The oxygen levels were significantly lower at mid-estuary station. This is perhaps due to the deeper and calmer water at this station where oxygen influx from surface water is minimal compared to the shallower water at mudflat and shoal stations. Chong et al. (1999) and Singh (2003) reported that oxygen level at surface water was generally higher than bottom water. Additionally, at the deeper water, the oxygen levels were noticeably lower compared to the shallower part of the same station. Deeper water also had less variability in oxygen content of bottom water (Table 3.1.3) in mid-estuary and river mouth stations compared to mudflat and shoal stations.

The diel variation in oxygen level is only available for mudflat station where 24-hour samplings were carried out. Dissolved oxygen level was significantly higher during neap tides (first and third quarter moon) compared to the spring tides in dry period. This is in agreement with pattern reported in Singh (2003) where oxygen levels were lower during the spring tides. The greater turbulence of water during the flood and ebb tides in spring conditions causes greater re-suspension of the anoxic sediment (high concentration of organic matter) that depresses the bottom DO levels at mudflat (Okamura et al., 2010). DO concentration was consistently highest in the late afternoon or evening. Alongi et al. (2003) reported the daytime increase and night time decrease in oxygen levels in Sangga Besar River. Similarly, Chong et al. (1999) and Sasekumar et al. (1994) also reported increase in DO level during daytime in Selinsing River. The increased oxygen level is likely due to increased photosynthetic activity during daytime which reaches peak in the late afternoon or evening whereas the lower oxygen level during night time could be attributed to higher demand of oxygen exerted by organisms.

As a conclusion, the spatial influence on water parameters is pronounced particularly at mid-estuary whereby the mean salinity, TDS, DO and pH were lower than mudflat and shoal area, whereas the sediment organic content at mid-estuary is much higher. With the exception of SPM, the overall water parameters were quite homogeneous temporally (monthly) as routine measurements were taken only during spring flood tide. However, amount of SPM fluctuated greatly at mudflat and shoal stations due to resuspension of mud during spring condition. Water condition particularly salinity and temperature level in the subtidal shoal station are less variable due to less tidal and freshwater influences. On the other hand, oxygen level at mid-estuary and river mouth is more stable due to deeper water. For diel water condition, temperatures were generally lower during night time with lowest temperature usually occurred during early morning (0500-0900 hour) whereas higher temperature usually occurred during afternoon and late morning (1100-1600 hour). DO levels were regularly lower at flood tide particularly during spring condition (full moon and new moon).

3.2 DISTRIBUTION AND ABUNDANCE OF HERMIT CRABS IN MATANG MANGROVE ESTUARY AND ADJACENT COASTAL WATERS

This section addresses objective 1 which is to determine the abundance and distribution of hermit crabs in relation to the abiotic factors. The study sought to answer the question of whether, and if so, how the different species of hermit crabs are spatially and temporally distributed along the environmental gradient of their habitats. To address the above objective, the abundance of hermit crabs and various water parameters (temperature, salinity, TDS, DO, pH and SPM) and sediment characteristics (organic content and particles size compositions) at four different stations at mid-estuary, river mouth, mudflat and shoal area of Matang waters were monitored and quantified over 20-month period. This study further explores the influence of tides on diel ingression of hermit crabs at the mudflat area by monitoring the abundance of hermit crabs at different tidal conditions. Statistical analyses such as univariate significant test, correlation and redundancy analyses were employed to examine the relationship between abundance of different species of hermit crabs and their environment.

3.2.1 Spatial abundance and distribution of hermit crabs

3.2.1.1 Density of hermit crabs

The hermit crab community along Sangga Besar River is mainly represented by three species; *Diogenes moosai* Rahayu & Forest, 1995, *D. lopochir* Morgan, 1989 and *Clibanarius infraspinatus*. All species belong to the family Diogenidae. There were however, two unidentified *Diogenes* species which were only present on one occasion at the mid-estuary station, and another species *Clibanarius padavensis* was present on four occasions at the mid-estuary station (one individual) and river mouth (three individuals). Overall, the hermit crab abundance showed a distinct increment towards the sea with highest mean density at shoal station (379.36±761.02 ind/ha) (F=42.39, p<0.05) followed by mudflat (122.36±88.12 ind/ha), mid-estuary (29.01±154.27 ind/ha) and river mouth (18.78±154.27 ind/ha) (Appendix VII).

Fig. 3.2.1 shows abundance of hermit crabs by species and stations. *C. infraspinatus* was dominant at the mid-estuary station (24.57±139.19 ind/ha), *D. moosai* was dominant at the river mouth (16.86 ind/ha±24.09) and mudflat (115.17±75.70 ind/ha)whereas *D. lopochir* was dominant at the shoal station (131.94±129.51 ind/ha). Both *C. infraspinatus* and *D. lopochir* recorded minimum mean density at river mouth with density of 1.58±2.47 ind/ha and 0.33±1.56 ind/ha respectively while minimum mean density of *D. moosai* was recorded at mid-estuary (3.65±12.50 ind/ha). Results of ANOVA showed that density of *D. moosai* at the mudflat and shoal stations were significantly (F=34.76, p<0.05) higher than both mid-estuary and river mouth, while density of *D. moosai* at river mouth was significantly (F=34.76, p<0.001) higher than at the mid-estuary. Density of *D. lopochir* at shoal station was significantly (F=73.37, p<0.001) higher than the mid-estuary, river mouth and mudflat whereas *C. infraspinatus* was widespread in the four stations (F=2.22, p>0.05) (Table 3.2.1) (Appendix VIIb-d).

3.2.1.2 Spatial distribution of hermit crabs in relation to environmental parameters

RDA triplots (Fig. 3.2.2) shows spatial separation of hermit crab species in relation to environmental gradients. *D.lopochir* was confined to shoal station where salinity was relatively high. *D. moosai* which is widespread in mudflat and shoal areas was more related to waters of higher salinity, DO and turbidity (SPM). On the other hand, *C. infraspinatus*, which was more abundant at mid-estuary, was more tolerant to waters of lower salinity and DO level. RDA triplots (Fig. 3.2.3) also shows association of *D. lopochir* to sediment with higher content of coarse silt and very fine sand at shoal area. *C. infraspinatus* was more associated with coarser sediments i.e. sediments with higher content of medium and coarse sand at mid-estuary and river mouth.

Table 3.2.1. Mean density (ind/ha), standard deviations and summary of one-way ANOVA and post hoc Tukey HSD tests on density of different species of hermit crabs between sampling stations in Matang mangrove estuary from September 2009 to March 2011.

Station		Species				
		Mid-estuary	River mouth	Mudflat	Shoal	p-level
D. moosai	Mean	3.65^{a}	16.86^{b}	$115.17^{c,d}$	131.94^{d}	<0.001
	SD	12.50	24.09	75.70	129.51	
	n	40	40	57	60	
	Min	0.00	0.00	0.00	0.00	
	Max	79.51	166.67	692.46	927.44	
D. lopochir	Mean	0.79^{a}	0.33^{a}	4.20^{a}	240.38^{b}	<0.001
	SD	2.58	1.56	5.83	624.64	
	n	40	40	57	60	
	Min	0.00	0.00	0.00	0.00	
	Max	14.18	9.24	36.55	4044.07	
C. infraspinatus	Mean	24.57	1.58	2.99	7.04	0.087
	SD	139.19	2.47	6.58	6.87	
	n	40	40	57	60	
	Min	0.00	0.00	0.00	0.00	
	Max	893.73	15.69	54.16	49.72	

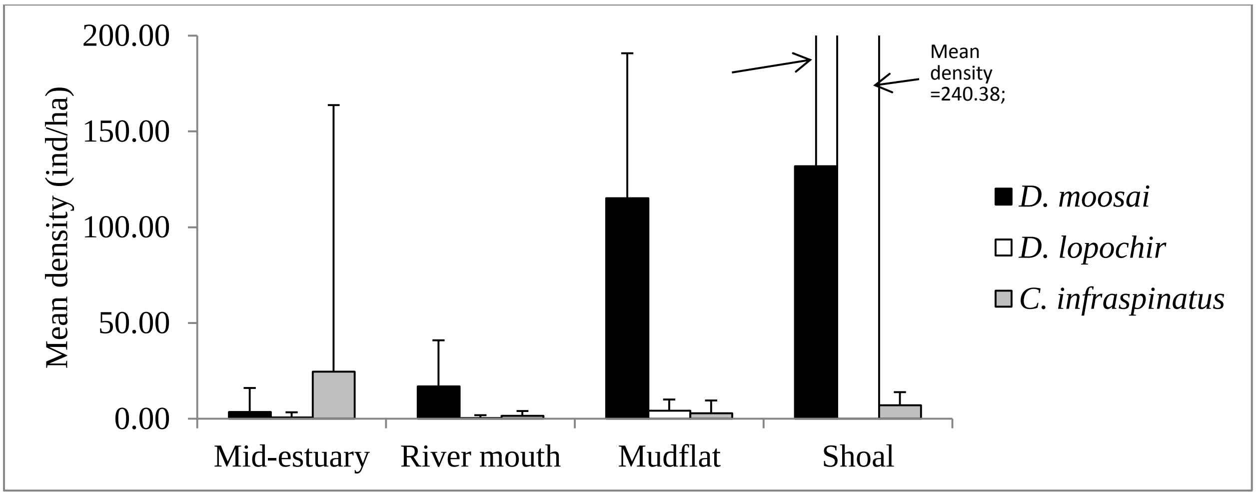


Fig. 3.2.1. Mean density (ind/ha) (vertical bar) and standard deviations (hairline) of hermit crabs at each each sampling station in Matang mangrove estuary from September 2009 to March 2011 (SD=standard deviation).

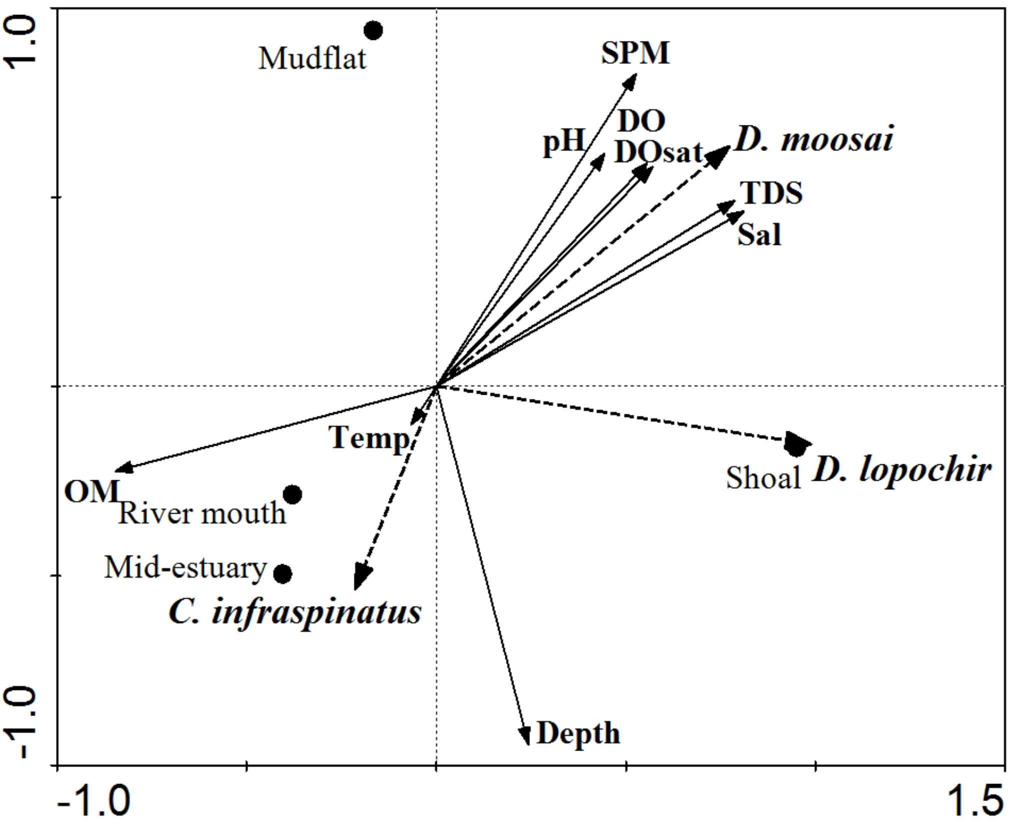


Fig. 3.2.2. Triplots from redundancy analysis (RDA) of abundance of three common species of hermit crabs (*D. lopochir*, *D. moosai* and *C. infraspinatus*) (dashed line arrows) at mid-estuary, river mouth, mudflat and shoal stations (solid circles) in relation to bottom water parameters (Temp=temperature; DOsat=oxygen saturation; DO=dissolved oxygen concentration; Sal=salinity; TDS=total dissolved solids; SPM=suspended particulate matter) (line arrows).

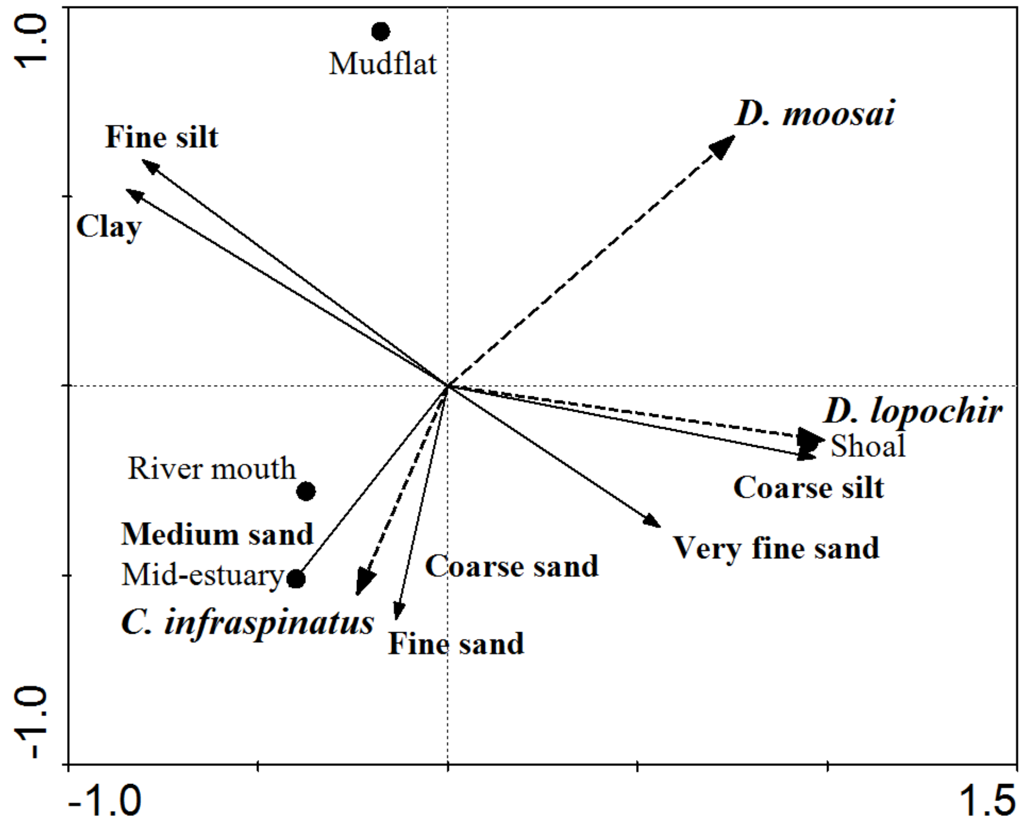


Fig. 3.2.3. Triplots from redundancy analysis (RDA) of abundance of three common species of hermit crabs (*D. lopochir*, *D. moosai* and *C. infraspinatus*) (dashed line arrows) at mid-estuary, river mouth, mudflat and shoal stations (solid circles) in relation to sediment particle size categories (clay, fine silt, coarse silt, very fine sand, fine sand, medium sand and coarse sand) (line arrows).

3.2.2 Temporal density of hermit crabs

3.2.2.1 Mid-estuary

Mean density of *C. infraspinatus* at mid-estuary was 24.57±139.19 ind/ha, the highest among the other species. This species was present in most of the sampling months from September 2009 to September 2010 in very low density except in November 2009 where exceptionally high density was recorded (451.83±624.95 ind/ha). There was no significant difference (F=1.24, p>0.05) in density of *C. infraspinatus* detected among months at the mid-estuary. Both *D. moosai* and *D. lopochir* were present in very low abundance at the mid-estuary. Highest density of *D. moosai* and *D. lopochir* were recorded in January 2010 (39.80 ind/ha) and November

2010 (3.20 ind/ha), respectively. (Fig. 3.2.4). There was no significant difference in density among months at mid-estuary station of both *D. moosai* (F=0.81, p>0.05) and *D. lopochir* (F=0.84, p>0.05). .

3.2.2.2 River mouth

The river mouth had the lowest abundance of hermit crabs among all stations with mean density of 18.78±28.13 ind/ha. Both *C. infraspinatus* and *D. lopochir* were rare and occurred in very low density with means of 1.58±2.47 ind/ha and 0.33±1.56 ind/ha respectively. Highest density of *C. infraspinatus* was recorded in May 2010 (10 ind/ha). *D. lopochir* was only present in two sampling months February 2010 (4.61±6.53 ind/ha) and October 2010 (2.03±2.87 ind/ha). *D. moosai* was the dominant species in the river mouth with mean density of 16.86±24.09 ind/ha. *D. moosai* was present in most sampling months with two distinct density peaks observed in August 2010 (65.50±60.62 ind/ha) and October 2010 (97.60±97.65 ind/ha) (Fig. 3.2.4). ANOVA results showed no significant difference in the density of *C. infraspinatus* (F=1.39, p.0.05), *D. lopochir* (F=0.95, p>0.05) and *D. moosai* (F=2.49, p>0.05) among months at the river mouth.

3.2.2.3 Mudflat

At the mudflat station, mean density of hermit crabs was 122.36±88.12 ind/ha. *D. moosai* was the dominant species with mean density of 115.17±75.70 ind/ha followed by *D. lopochir* (4.20±5.83 ind/ha) and *C. infraspinatus* (2.99±6.58 ind/ha). *D. moosai* was present in all sampling months with density that ranged from 3.00±2.67 ind/ha (November 2010) to 386.19±266.85 ind/ha (May 2010). Distinct density peaks of *D. moosai* were observed in September 2009 (324.53±1.49 ind/ha), May (386.19±266.85 ind/ha), June (304.43±193.93 ind/ha) and July (340.59±199.58 ind/ha) of 2010. Both *D. lopochir* and *C. infraspinatus* were present in very low abundance with highest density of observed in March 2011 (12.19±21.10 ind/ha) and May 2010 (25.52±25.48 ind/ha) respectively. There was no significant difference in density of both *D. lopochir* (F=0.51, p>0.05) and *C. infraspinatus* (F=1.22, p>0.05) among months at the mudflat (Fig. 3.2.4).

3.2.2.4 Shoal

At the shoal station, mean density of hermit crabs (379±761 ind/ha) was the highest among all stations. *D. lopochir* was the dominant species with mean density of 240±625 ind/ha followed by *D. moosai* (132±130 ind/ha) and *C. infraspinatus* (7±7 ind/ha). *D. lopochir* was present in all sampling months with density that ranged from 5±8 ind/ha to 1,399±2,291 ind/ha. Distinct density peaks of *D. lopochir* were observed in January (689.14±538.82 ind/ha), July (1,399±2,291 ind/ha), September (1,114±1,503 ind/ha) and October (650±1,059 ind/ha) of 2010, while lowest density was recorded in November 2009 (5±8 ind/ha). *C. infraspinatus* was present in relatively low abundancewith highest density observed in October 2009 (33±17 ind/ha). *D. moosai* was present in all sampling months except March 2011 with highest density observed at the end of June 2010 (657±398 ind/ha) (Fig. 3.2.4).

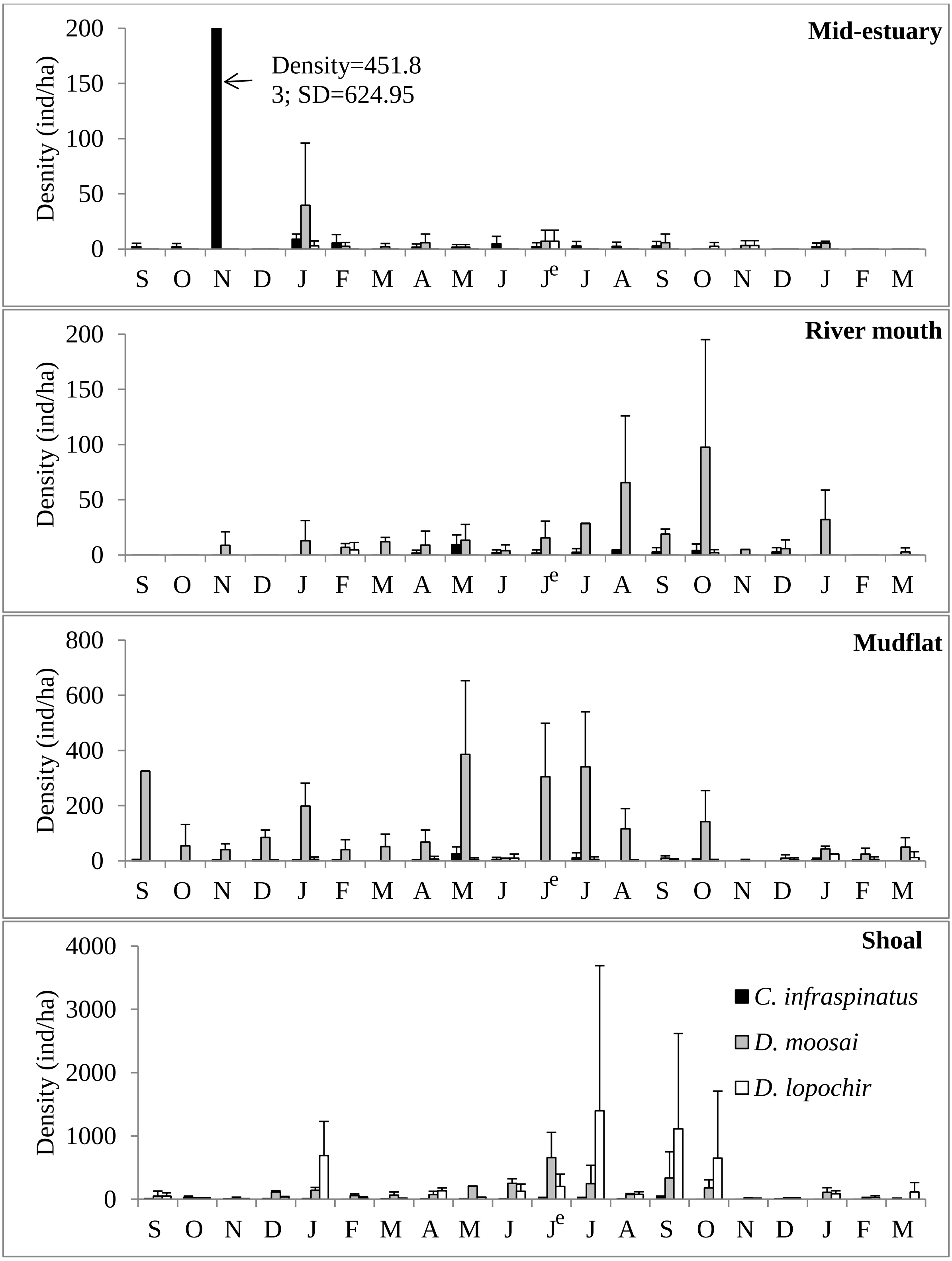


Fig. 3.2.4. Temporal density (ind/ha) of hermit crabs by species from September 2009 to March 2011 at each sampling stations in Matang mangrove estuary. (Note: different scale bars). 'J^{e}' indicates additional sampling at the end of June 2010.

3.2.3 Temporal distribution of hermit crabs in relation to environmental parameters

Correlation results of the temporal changes between the abundance of hermit crabs and environmental parameters (water characteristics and sediment organic content) are shown in Table 3.2.2. With exception of river mouth station, temporal changes in water parameters did not influence the abundance of hermit crabs ($p>0.05$). Abundance of the three species of hermit crabs did not fluctuate with temperature in all stations ($p>0.05$). At the river mouth, abundance of both *D. moosai* and *C. infraspinatus* were positively correlated ($p<0.05$) with salinity (R=0.4921 and 0.4461 respectively), DO concentration (R=0.5653 and 0.4970 respectively), DO saturation (R=0.5774 and 0.5333 respectively) and TDS (R=0.4959 and 0.4461 respectively). Significant positive correlation ($p<0.05$) was also detected between abundance of *D. lopochir* and sediment organic content (R=0.5488) but not with water parameters ($p>0.05$).

Table 3.2.2. Spearman rank correlation (R-value) between abundance of hermit crabs and various water parameters and sediment organic content by sampling stations. Asterisk '*' denotes significant correlation between two variables.

Parameters	Station	Species		
		D. moosai	*D. lopochir*	*C. infraspinatus*
Temperature (°C)	Mid-estuary	0.3293	0.0237	-0.0200
	River mouth	0.2664	0.2684	0.1350
	Mudflat	0.0496	-0.1260	0.1631
	Shoal	-0.1263	-0.3649	-0.1575
Salinity (ppt)	Mid-estuary	0.2354	-0.1689	0.0261
	River mouth	0.4921*	0.3117	0.4461*
	Mudflat	0.0075	-0.0507	-0.3690
	Shoal	0.3860	0.2509	0.0372
Dissolved oxygen (mg/L)	Mid-estuary	0.3078	0.2732	0.4164
	River mouth	0.5653*	0.0202	0.4790*
	Mudflat	0.0000	0.1414	0.1779
	Shoal	0.1632	0.0842	-0.1274
Dissolved oxygen (%)	Mid-estuary	0.3605	0.2506	0.4271
	River mouth	0.5774*	0.0476	0.5333*
	Mudflat	-0.0150	0.0922	0.1717
	Shoal	0.1491	0.0790	-0.1682
Total dissolved solid (mg/L)	Mid-estuary	0.2453	-0.1689	0.0184
	River mouth	0.4959*	0.3117	0.4461*

	Mudflat	-0.0075	-0.0261	-0.3659
	Shoal	0.3421	0.1684	0.0319
Sediment organic content (%)	Mid-estuary	-0.1045	0.0000	0.3380
	River mouth	0.1900	0.5488*	0.2727
	Mudflat	0.0162	-0.3758	0.1122
	Shoal	0.0677	0.0029	-0.1240

3.2.4 Seasonal abundance of hermit crabs

At mid-estuary, density of *D. moosai* and *C. infraspinatus* were highest during NE monsoon with means of 5.30±17.63 ind/ha and 46.83±199.38 ind/ha respectively. Highest density of *D. lopochir* occurred in SW monsoon (1.01±3.79 ind/ha). High mean density of *C. infraspinatus* during NE was caused by its exceptionally high abundance in November 2009. Mann-Whitney test showed no significant difference ($p>0.05$) in density of hermit crabs for all species between seasons at mid-estuary (Table 3.2.3) (Appendix VIIIa).

At river mouth, lowest mean density of *D. moosai* was observed during NE (8.53±12.33 ind/ha). However, there was no significant difference ($p>0.05$) detected between seasons. *D. lopochir* and *C. infraspinatus* were present in very low abundance at river mouth in all seasons. Mann-Whitney test showed that density of *C. infraspinatus* during NE was significantly lower ($p<0.05$) than SW (Table 3.2.4) (Appendix VIIIb).

At mudflat, density of *D. moosai* was significantly lower ($p<0.05$) during NE (52.10±62.86 ind/ha) compared to SW (207.13±202.03 ind/ha). Abundance of *D. lopochir* was highest during NE (4.56±9.60 ind/ha) while abundance of *C. infraspinatus* was highest during SW (6.18±13.84 ind/ha). Nevertheless, no significant difference ($p>0.05$) was detected between seasons in density for both species (Table 3.2.5) (Appendix VIIIc).

At shoal station, abundance of *D. moosai*, *D. lopochir* and *C. infrapsinatus* were significantly higher (p<0.05) during SW compared to NE. *D. lopochir* has the overall highest mean density during SW (426.01±1027.19 ind/ha) followed by *D. moosai* (240.16±292.40 ind/ha) and *C. infraspinatus* (10.57±13.07 ind/ha) (Table 3.2.6) (Appendix VIIId).

Table 3.2.3. Summary results of Mann-Whitney test (tested between NE and SW) and basic statistics on density (ind/ha) of different species of hermit crabs between seasons at mid-estuary station in Matang mangrove estuary from September 2009 to March 2011. SD=standard deviation; n=number of samples; Min=minimum; Max=maximum; ns=no significant.

Season		Species			
		NE	IN	SW	p-level
D. moosai	Mean	5.30	1.87	2.06	p=0.6200 (ns)
	SD	17.63	4.58	4.64	
	n	20	6	14	
	Min	0.00	0.00	0.00	
	Max	79.51	11.22	14.18	
D. lopochir	Mean	0.62	0.83	1.01	p=0.8311 (ns)
	SD	1.91	2.03	3.79	
	n	20	6	14	
	Min	0.00	0.00	0.00	
	Max	6.31	4.98	14.18	
C. infrapsinatus	Mean	46.83	0.62	2.73	p=0.5484 (ns)
	SD	199.38	1.53	3.12	
	n	20	6	14	
	Min	0.00	0.00	0.00	
	Max	893.73	3.74	9.46	

Table 3.2.4. Summary results of Mann-Whitney test (tested between NE and SW) and basic statistics on density (ind/ha) of different species of hermit crabs between seasons at river mouth station in Matang mangrove estuary from September 2009 to March 2011. SD=standard deviation; n=number of samples; Min=minimum; Max=maximum; ns=no significant.

Season		Species			p-level
		NE	IN	SW	
D. moosai	Mean	8.53	35.53	20.77	p=0.0751
	SD	12.33	65.33	27.58	(ns)
	n	20	6	14	
	Min	0.00	0.00	0.00	
	Max	50.99	166.67	108.35	
D. lopochir	Mean	0.46	0.68	0.00	p=0.4028
	SD	2.07	1.66	0.00	(ns)
	n	20	6	14	
	Min	0.00	0.00	0.00	
	Max	9.24	4.07	0.00	
C. infrapsinatus	Mean	0.28	1.95	3.28	p<0.01
	SD	1.23	3.35	4.20	
	n	20	6	14	
	Min	0.00	0.00	0.00	
	Max	5.51	8.13	15.69	

Table 3.2.5. Summary results of Mann-Whitney test (tested between NE and SW) and basic statistics on density (ind/ha) of different species of hermit crabs between seasons at mudflat station in Matang mangrove estuary from September 2009 to March 2011. SD=standard deviation; n=number of samples; Min=minimum; Max=maximum; ns=no significant.

Season		Species			p-level
		NE	IN	SW	
D. moosai	Mean	52.10	92.36	207.13	p<0.05
	SD	62.86	82.06	202.03	
	n	29	8	20	
	Min	0.00	0.00	0.00	
	Max	259.54	268.91	692.46	
D. lopochir	Mean	4.56	2.92	2.99	p=0.9141
	SD	9.60	6.31	6.13	(ns)
	n	29	8	20	
	Min	0.00	0.00	0.00	
	Max	36.55	17.78	20.73	
C. infrapsinatus	Mean	1.03	1.56	6.18	p=0.5262
	SD	2.16	2.95	13.84	(ns)
	n	29	8	20	
	Min	0.00	0.00	0.00	
	Max	7.95	7.33	54.16	

Table 3.2.6. Summary results of Mann-Whitney test (tested between NE and SW) and basic statistics on density (ind/ha) of different species of hermit crabs between seasons at shoal station in Matang mangrove estuary from September 2009 to march 2011. SD=standard deviation; n=number of samples; Min=minimum; Max=maximum; ns=no significant.

Season		Species			p-level
		NE	IN	SW	
D. moosai	Mean	55.70	87.95	240.16	p<0.05
	SD	56.14	100.74	292.40	
	n	30	9	21	
	Min	0.00	0.00	0.00	
	Max	194.00	301.89	927.45	
D. lopochir	Mean	96.78	266.39	426.01	p<0.05
	SD	249.92	605.08	1027.19	
	n	30	9	21	
	Min	0.00	0.00	0.00	
	Max	1045.55	1871.70	4044.07	
C. infrapsinatus	Mean	2.25	12.17	10.57	p<0.01
	SD	4.72	18.18	13.07	
	n	30	9	21	
	Min	0.00	0.00	0.00	
	Max	15.79	45.00	49.72	

3.2.5 Spatial and temporal density of juvenile hermit crabs

Recruited young juveniles were unidentifiable into species and therefore, the juvenile data represent the recruitment of the hermit crab community as a whole. Juveniles as defined in this study were crabs smaller than the smallest ovigerous female of *D. moosai* (i.e. <1.60mm shield length). The mean total juvenile density at mid-estuary, river mouth, mudflat and shoal stations was 104.2±482.2 ind/ha, 5,583±15,273 ind/ha, 2,847±7,651 ind/ha and 14,986±43,520 ind/ha, respectively. The abundance of juvenile hermit crabs was significantly lower (p<0.05) at the mid estuary compared to river mouth and mudflat (Kruskal-Wallis test, H=14.264, p<0.05). However, no significant difference (p>0.05) was detected between mid-estuary and shoal station despite the large difference in mean density (Appendix IXa). This was due to the high variability in juvenile density at the shoal area (Table 3.2.7).

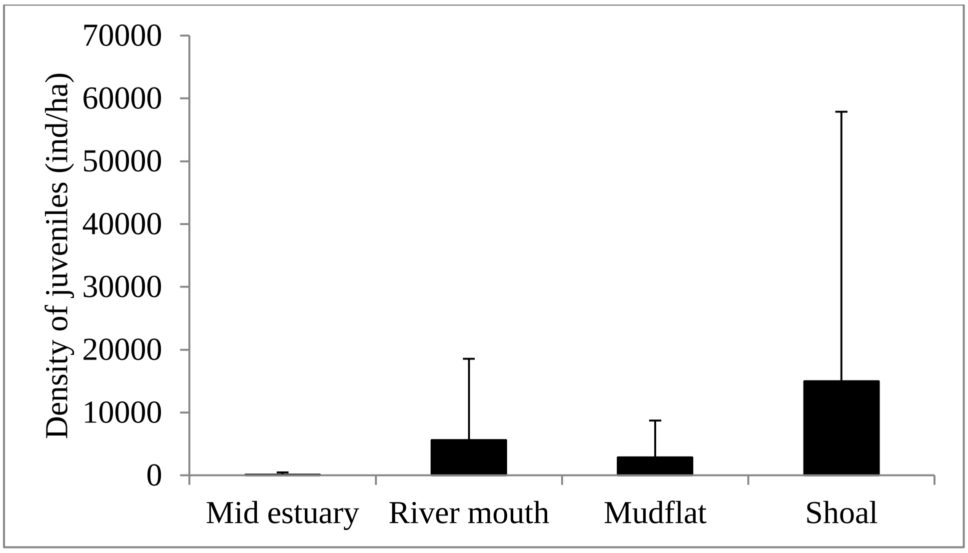


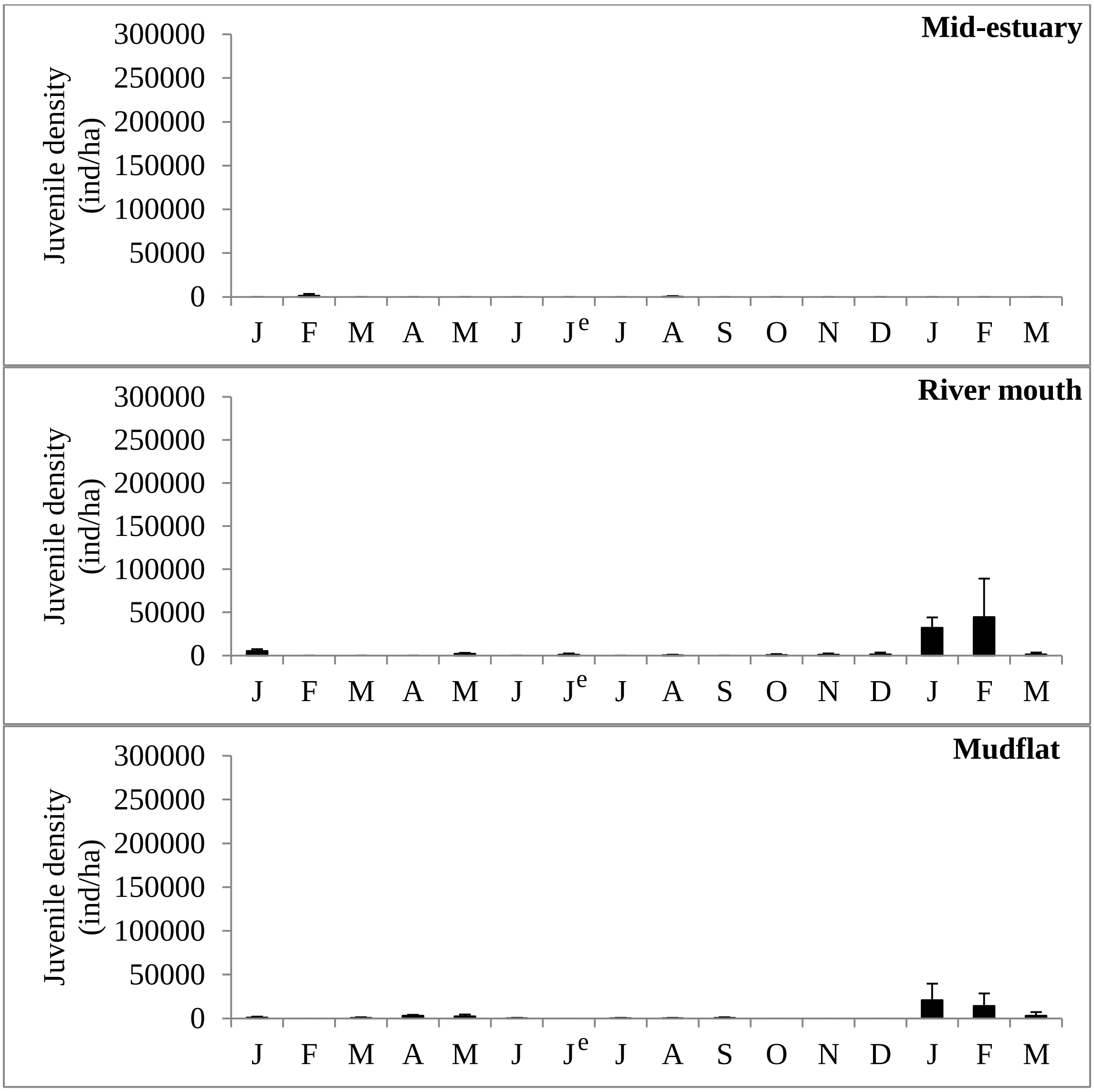
Fig. 3.2.5. Mean density (ind/ha) and standard deviation of juvenile hermit crabs at different sampling stations in Matang mangrove estuary caught between January 2010 to March 2011.

Table 3.2.7. Basic statistics and summary of Kruskal-Wallis test on density (ind/ha) of juvenile hermit crabs among sampling stations in Matang mangrove estuary from January 2010 to March 2011; SD=standard deviation; n=number of samples; Min=Minimum; Max=Maximum; ns=no significant; Superscript alphabets denote hierarchy after comparison test.

	Station				
	Mid-estuary	River mouth	Mudflat	Shoal	p-level
Mean	104.17^{a}	5,583.33^{b}	2,847.22^{b}	14,986.11^{a}	p<0.01
SD	482.21	15,272.67	7,650.45	43,520.27	
N	32	32	48	48	
Min	0.00	0.00	0.00	0.00	
Max	2666.67	76,000	42,000	202,000	

Temporal density of juvenile hermit crabs is shown in Fig. 3.2.6. Juveniles were absent from 5-7 months out of 15 months of juvenile samplings. Juveniles were generally present in relatively low numbers, except in January and February 2011 when they occurred in exceptionally high abundance at the river mouth, mudflat and shoal stations. Marked temporal variability in juvenile density was observed among sampling stations (Fig 4). The peak density of 202,000 ind/ha in January 2011 was recorded at the shoal station, while mean densities ranging from 14,000±14,422 ind/ha to 163,556±53,857 ind/ha were recorded from all stations. At the mid-estuary, juveniles were present only in February and August 2010 with mean density of 1,333±1886 ind/ha and 333±471 ind/ha respectively (Fig. 3.2.6).

Data of juvenile abundance were pooled by seasons; NE and SW and their summary statistics is shown in Table 3.2.8. Mean density of juvenile hermit crabs was higher during NE at all stations with highest abundance recorded at shoal station during NE with mean of 29,166.67±58,717.12 ind/ha. Mann-Whitney test revealed no significant difference (p>0.05) in density of juvenile hermit crabs between NE and SW in all sampling stations (Appendix IXb).



(Figure 3.2.6, continued)

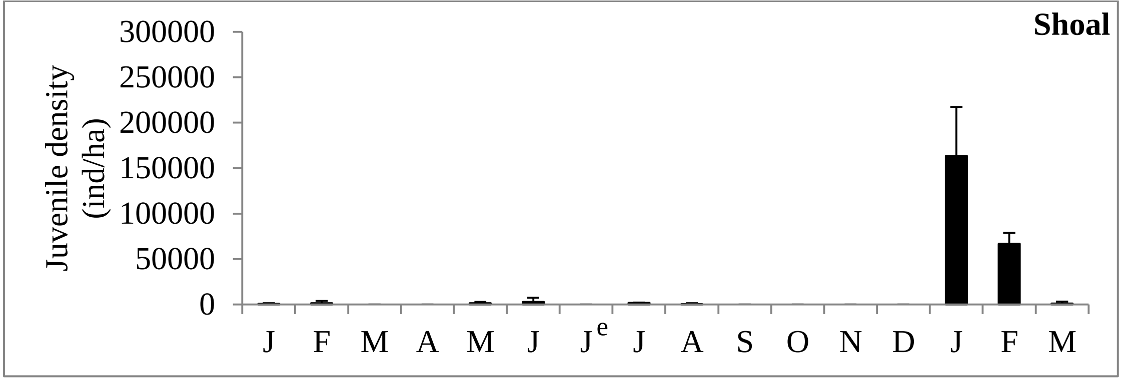


Fig. 3.2.6. Mean density (ind/ha) and standard deviation of juvenile hermit crabs at each sampling station in Matang mangrove estuary from January 2010 to March 2011. 'J^{e}' indicates additional sampling at the end of June 2010.

Table 3.2.8. Basic statistics and summary of Mann-Whitney test (tested between NE and SW) on density (ind/ha) of juvenile hermit crabs between seasons at each sampling stations in Matang mangrove estuary from January 2010 to March 2011; SD=standard deviation; n=number of samples; Min=Minimum; Max=Maximum; ns=no significant.

Season		Species			p-level
		NE	IN	SW	
Mid-estuary	Mean	166.67	0.00	55.56	p=0.8761
	SD	666.67	0.00	192.45	(ns)
	n	16	4	12	
	Min	0.00	0.00	0.00	
	Max	2,666.67	0.00	666.67	
River mouth	Mean	10,666.67	333.33	555.56	p=0.0583
	SD	20,644.43	666.67	935.64	(ns)
	n	16	4	12	
	Min	0.00	0.00	0.00	
	Max	76,000	1,333.33	2,666.67	
Mudflat	Mean	4,888.89	1,555.56	555.56	p=0.1421
	SD	10,444.55	1,821.68	1,102.58	(ns)
	n	24	6	18	
	Min	0.00	0.00	0.00	
	Max	42,000.00	4,000.00	4,000.00	
Shoal	Mean	29,166.67	0.00	1,074.07	p=0.5922
	SD	58,717.12	0.00	1,942.16	(ns)
	n	24	6	18	
	Min	0.00	0.00	0.00	
	Max	202,000.00	0.00	8,000.00	

3.2.6 Diel variability in occurrence of hermit crabs at subtidal zone of estuarine mudflat

3.2.6.1 Influence of lunar and tidal conditions on abundance of hermit crabs

A total of 2,369 hermit crabs comprising three species; *Diogenes moosai, D. lopochir* and *Clibanarius infraspinatus* were caught throughout samplings from both seasons. The hermit crabs assemblage was dominated by *D. moosai* (96%). Both *C. infraspinatus* and *D. lopochir* were present in very low density and represented only about 2.5% and 1.1% of all hermit crabs caught, respectively. Mean density of *D. moosai* in NE and SW seasons were 129.88±131.21 ind/ha and 89.14±71.95 ind/ha respectively. However, there was a marked difference in density observed for this species whereby the density ranged from 0.00 ind/ha to 780.75ind/ha. Such large difference in density was also shown in both *C. infrapsinatus* and *D. lopochir* where density ranged from 0.00 ind/ha to 42.93 ind/ha for *D. lopochir* and 0.00 to 25.63 ind/ha for *C. infraspinatus*. Mean density of both *C. infraspinatus* and *D. lopochir* was however, relatively low being only about 3 ind/ha and 1-2ind/ha respectively. Kruskal-Wallis test detected no significant difference ($p>0.05$) in density of all species between sampling seasons. Although very low in number, the occurrence of *C. infraspinatus* was relatively high with 40% (full moon), 30% (third quarter moon), 46.15% (new moon) and 31.2% (first quarter moon) during NE season and 35% (full moon), 26.32% (third quarter moon) and 53.33% (first quarter moon) with no occurrence at new moon during SW season (Table 3.2.9).

D. moosai was present in all trawls of 24 hour samplings (frequency of occurrence 100%). Highest mean density was observed in neap tides during first quarter moon and third quarter moon in the wet period with mean density of 172.01±99.00 ind/ha and 186.82±246.64 ind/ha respectively. The lowest abundance was recorded at full moon (61.77±41.72 ind/ha) during the same season (Table 3.2.9). Kruskal-Wallis test showed that density of *D. moosai* during full moon was significantly lower (H=10.664, $p<0.05$) than other moon phases. Tidal condition did not significantly affect (Kruskal-Wallis, $p>0.05$) the density of *D. moosai* during wet period (Table 3.2.10). In the dry period, higher mean density was recorded at spring tide during full moon (113.95±75.97 ind/ha) and new moon (105.90±87.90 ind/ha) while lower density was recorded during neap tide at first quarter (71.75±58.47 ind/ha) and third quarter moon (64.97±54.09 ind/ha). Tidal conditions (flood and ebb) did not significantly (H=0.017, $p>0.05$) affect density of *D. moosai* during neap tide (first and third quarter moon). However, during spring tide of full moon and new moon, density of *D. moosai* was significantly higher (H=16.571, $p<0.0001$) during ebb tide (Table 3.2.10) with mean density of 166.43±65.19 ind/ha compared to flood tide with mean density of 53±50 ind/ha (Appendix Xa).

Both *D. lopochir* and *C. infraspinatus* were present in very low density in all sampling occasions. In wet period, highest density of *C. infraspinatus* was observed in both full moon and new moon with mean density of 3.11±4.22 ind/ha and 3.40±5.12 ind/ha respectively. Frequency occurrences of *C. infraspinatus* were 40.0% and 46.1% respectively during both moon phases. *D. lopochir* was not present during the first quarter moon of the wet period, while density during other moon phases was only about 1 ind/ha (Table 3.2.9).

In the dry period, *C. infraspinatus* was absent during new moon while highest abundance was observed in first quarter and full moon with mean density of 4.48 ind/ha and 4.64 ind/ha respectively. Highest frequency of occurrence for *C. infraspinatus* was

53.3% recorded in first quarter moon (Table 3.2.9). Highest abundance of *D. lopochir* was recorded in new moon with mean density of only 3.35±10.89 ind/ha.

Table 3.2.9. Mean abundance (ind/ha), relative abundance (% Rel) and occurrence (% Occ) of *D. moosai*, *D. lopochir* and *C. infrapsinatus* at different lunar phases during two seasonal occasions of samplings at mudflat station in Matang mangrove estuary.

Season	Species	Moon phase											
		Full moon			Third quarter moon			New moon			First quarter moon		
		Mean	% Rel	% Occ	Mean	% Rel	% Occ	Mean	% Rel	% Occ	Mean	% Rel	% Occ
NE	*D. moosai*	61.77±41.72	95.82	100.00	186.82±246.64	99.25	100.00	90.14±77.09	96.46	100.00	172.02±99.01	99.10	100.00
	C. infraspinatus	3.11±4.22	3.83	40.00	1.21±1.75	0.51	30.00	3.40±5.12	3.26	46.15	2.26±2.91	0.90	31.25
	D. lopochir	0.37±1.11	0.35	7.69	0.63±1.17	0.24	18.18	0.41±1.47	0.28	5.56	0.00	0.00	0.00
SW	*D. moosai*	113.95±75.97	96.33	100.00	64.97±54.09	96.08	100.00	105.90±87.90	98.15	100	71.75±58.47	95.96	100.00
	C. infraspinatus	4.64±5.94	2.63	35.00	3.82±7.59	3.09	26.32	0.00	0.00	0.00	4.48±5.42	3.85	53.33
	D. lopochir	1.83±3.65	1.04	3.85	1.14±2.78	0.83	14.29	3.35±10.89	1.85	12.50	0.30±1.21	0.20	4.55

(NE = northeast monsoon; SW = southwest monsoon)

Table 3.2.10. Mean, standard deviations and non-parametric Kruskal-Wallis test on density (ind/ha) of *D. moosai*, *D. lopochir* and *C. infraspinatus* at different tidal conditions during two seasonal occasions of samplings at mudflat station in Matang mangrove estuary.

Season	Species	Spring tides			Neap tides		
		Flood	Ebb	p-value	Flood	Ebb	p-value
NE	*D. moosai*	54.93±43.35	98.20±75.32	p=0.2623 (ns)	234.92±198.37	118.98±74.15	p=0.0833 (ns)
	C. infraspinatus	3.04±4.40	3.49±5.07	p=0.9474 (ns)	1.97±2.81	1.71±2.32	p=0.8798 (ns)
	D. lopochir	0.00	0.72±1.73	p=0.5097 (ns)	0.21±0.71	0.21±0.74	p=0.9770 (ns)
SW	*D. moosai*	53.42±49.70	166.43±65.19	p<0.0001	73.38±61.24	63.34±50.65	p=0.8951 (ns)
	C. infraspinatus	1.65±3.55	2.99±5.76	p=0.7630 (ns)	4.69±7.91	3.60±4.90	p=0.8505 (ns)
	D. lopochir	4.71±10.95	0.48±1.91	p=0.2206 (ns)	1.19±2.85	0.25±1.01	p=0.5340 (ns)

(NE = northeast monsoon; SW = southwest monsoon)

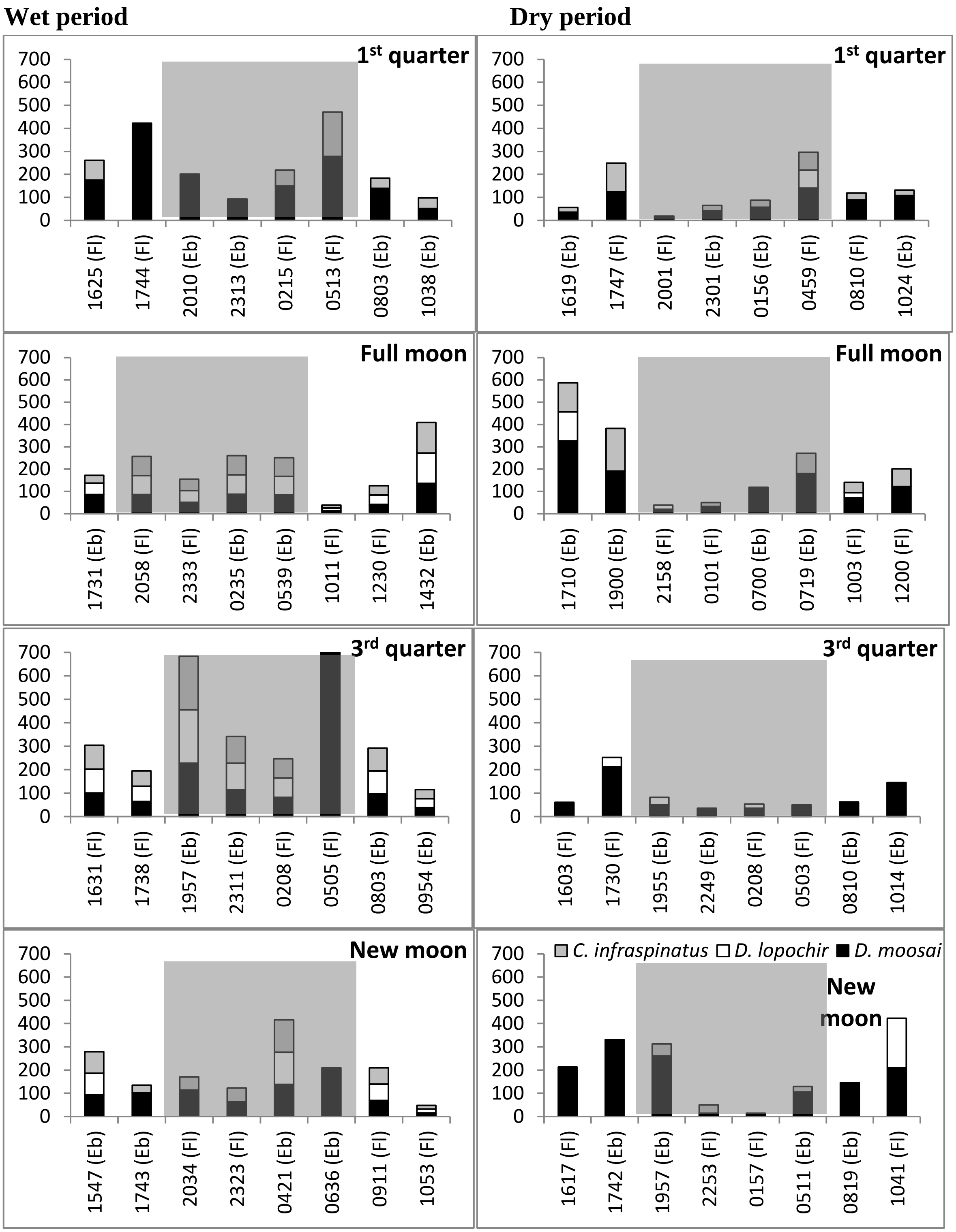


Fig. 3.2.7. Mean abundance (ind/ha) and compositions of hermit crabs caught over 24 hours in four consecutive lunar phases in both wet and dry periods at mudflat. 'Eb' denotes ebb tide while 'Fl' denotes flood tide.

3.2.6.2 Abundance by sex

The population of *D. moosai* was dominated by males with overall composition of 70.5%. This bias was slightly more pronounced during dry period (64.9%) compared to wet period (59.6%). Kruskal-Wallis test showed no significant difference ($p>0.05$) in composition of male and non-ovigerous female between both sampling periods while composition of ovigerous female in wet period was significantly higher ($H=4.308$, $p<0.05$) than dry period with highest composition being 81.8% that occurred during full moon. Mean density of male, non-ovigerous female and ovigerous female in wet period were 71.40±63.73 ind/ha, 16.89±35.07 ind/ha and 41.59±46.60 ind/ha respectively while in dry period, mean density were 54.59±41.75 ind/ha, 10.01±14.38 ind/ha and 24.55±32.31 ind/ha. Both male and non-ovigerous female were significantly (Kruskal-Wallis, $p<0.05$) more abundant in wet period than dry period.

In wet period, composition of male, non-ovigerous female and ovigerous female ranged from 18.2-100.0%, 0.0-50.0% and 0.0-81.8% respectively. Mean abundance of males was significantly higher ($H=10.703$, $p<0.05$) during periods of neap tides (first and third quarter moon) as compared to full moon. However, there was no significant difference ($H=0.923$, $p>0.05$) in composition of male between moon phases. Density of non-ovigerous female was significantly higher ($H=19.877$, $p<0.001$) during neap tides of first and third quarter moon. Similarly, composition of non-ovigerous female was significantly higher ($H=13.730$, $p<0.01$) in third quarter moon compared to both spring conditions of full moon and new moon. Higher mean composition but lower abundance of ovigerous female was observed during spring conditions (full moon and new moon), however, there was no significant difference (Kruskal-Wallis, $p>0.05$) between moon phases (Table 3.2.11 and 3.2.12).

In dry period, abundance and composition of male did not differ significantly (Kruskal-Wallis, $p>0.05$) among moon phases. Nonetheless, higher mean abundance was observed in full moon (78.06±53.12 ind/ha) and new moon (59.16±40.91 ind/ha). Composition of ovigerous female varied from 0.0-66.7%. Composition and abundance of non-ovigerous female in first quarter moon were significantly higher (Kruskal-Wallis, $p<0.001$) than both full moon and new moon. Kruskal-Wallis test revealed that abundance of ovigerous female was significantly higher ($H=11.535$, $p<0.01$) during new moon as compared to third quarter moon, while composition of ovigerous female during new moon was significantly higher ($H=15.135$, $p<0.01$) than both first and third quarter moon (Table 3.2.11 and 3.2.12).

Tidal conditions did not significantly (Kruskal-Wallis, $p>0.05$) affect density and composition of male and non-ovigerous female. During neap tide of wet period, density of ovigerous female during flood tide was significantly more ($H=4.813$, $p<0.05$) than ebb tide. On the other hand, during spring tide of dry period, density of ovigerous female during ebb tide was significantly higher ($H=15.125$, $p<0.001$) than flood tide. Tidal conditions also did not significantly (Kruskal-Wallis, $p>0.05$) affect composition of ovigerous female in both sampling periods (Table 3.2.14) (Appendix XI and XII). Both *Clibanarius infraspinatus* and *D. lopochir* were present in low abundance, nevertheless, majority of the individuals of both species were male with composition of male *C. infraspinatus* and *D. lopochir* being 91.07% and 96.67% respectively. Females of *C. infrapsinatus* were present in only few sampling occasions while ovigerous females were not recorded during the entire 24-hour samplings. In wet period, ovigerous female of *D. lopochir* was only recorded during ebb tide of last quarter moon with density of 2.56 ind/ha while in dry period, ovigerous female of *D. lopochir* was recorded in new moon during flood tide with density of 3.90±5.52 ind/ha (Fig. 3.2.9).

Table 3.2.11. Mean, standard deviations and non-parametric Kruskal-Wallis test on density (ind/ha) of male (M), non-ovigerous female (NF) and ovigerous female (OF) of *D. moosai* at different lunar phases during two seasonal occasions of samplings at mudflat station in Matang mangrove estuary.

Season	Species	Moon phase				
		Full moon	Third quarter	New moon	First quarter	
		Mean±SD	Mean±SD	Mean±SD	Mean±SD	p-value
NE	M	^{a}34.11±27.95	^{a,b}100.50±106.04	^{a,b}48.90±40.72	^{b}96.11±53.09	$p<0.05$
	NF	^{a}2.32±3.05	^{b}46.24±75.97	^{b}4.74±7.91	^{a}20.29±14.62	$p<0.001$
	OF	25.34±19.43	40.08±68.09	36.50±49.40	55.62±42.49	$p=0.1103$ (ns)
SW	M	78.06±53.12	41.84±29.93	59.16±40.91	39.28±29.92	$p=0.1036$ (ns)
	NF	^{a}2.82±5.66	^{a,b,c}13.09±15.74	^{a,c}6.00±10.32	^{b}18.12±18.17	$p<0.001$
	OF	^{a,b}33.07±28.71	^{a}10.03±13.67	^{b}40.74±4.95	^{a,b}14.35±16.85	$p<0.01$

(NE = northeast monsoon; SW = southwest monsoon; SD=standard deviation)

Table 3.2.12. Mean, standard deviations and non-parametric Kruskal-Wallis test on density (ind/ha) of male (M), non-ovigerous female (NF) and ovigerous female (OF) of *D. moosai* at different tidal conditions at each diel sampling occasion at mudflat station in Matang mangrove estuary.

Season	Species	Spring tides			Neap tides		
		Flood	Ebb		Flood	Ebb	
		Mean±SD	Mean±SD	p-value	Mean±SD	Mean±SD	p-value
NE	M	35.44±28.48	49.02±41.56	$p=0.6444$ (ns)	118.78±86.96	76.37±49.65	$p=0.1842$ (ns)
	NF	3.95±5.90	3.58±7.02	$p=0.7667$ (ns)	42.43±61.02	15.44±13.03	$p=0.0689$ (ns)
	OF	15.54±14.94	45.60±48.65	$p=0.0847$ (ns)	73.71±61.53	27.17±23.68	$p<0.05$
SW	M	37.23±34.80	99.99±37.06	$p=0.1842$ (ns)	41.69±31.57	39.42±28.19	$p=0.9549$ (ns)
	NF	1.14±2.56	7.67±10.70	$p=0.0765$ (ns)	18.80±19.34	12.41±13.97	$p=0.3080$ (ns)
	OF	15.04±15.15	58.77±44.75	$p<0.001$	12.88±16.59	11.50±14.31	$p=0.7203$ (ns)

(NE = northeast monsoon; SW = southwest monsoon)

Table 3.2.13. Mean, standard deviations and non-parametric Kruskal-Wallis tests on compositions (%) of male (M), non-ovigerous female (NF) and ovigerous female (OF) of *D. moosai* at different lunar phases during two seasonal occasions of samplings at mudflat station in Matang mangrove estuary.

Season	Species	Moon phase				
		Full moon (%)	Third quarter (%)	New moon (%)	First quarter (%)	
		Mean±SD	Mean±SD	Mean±SD	Mean±SD	p-value
NE	M	60.63±23.21	63.63±17.21	59.26±22.19	57.12±11.80	p=0.8198 (ns)
	NF	^{a}5.06±8.25	^{b}20.67±9.59	^{a,c}8.29±14.38	^{a,b,c}11.96±7.49	p<0.01
	OF	34.31±25.68	15.71±8.75	32.45±23.89	30.93±10.60	p=0.0489 (ns)
SW	M	72.82±17.37	71.41±19.07	63.31±20.29	51.88±22.20	p=0.0512 (ns)
	NF	^{a}1.65±3.14	^{b}16.45±13.60	^{a}3.46±5.46	^{b}31.87±25.96	p<0.0001
	OF	^{a,b}25.53±16.20	^{a}12.14±10.67	^{b}33.23±19.32	^{a}16.25±10.05	p<0.01

(NE = northeast monsoon; SW = southwest monsoon; SD=standard deviation)

Table 3.2.14. Mean, standard deviation and non-parametric Kruskal-Wallis tests on compositions (%) of male (M), non-ovigerous female (NF) and ovigerous female (OF) of *D. moosai* at different tidal conditions at each diel sampling occasion at mudflat station in Matang mangrove estuary.

Season	Species	Spring tides			Neap tides		
		Flood	Ebb		Flood	Ebb	
		Mean±SD	Mean±SD	p-value	Mean±SD	Mean±SD	p-value
NE	M	66.23±14.78	54.04±26.44	p=0.3069 (ns)	54.18±10.76	64.39±15.03	p=0.0941 (ns)
	NF	11.33±16.19	2.89±3.76	p=0.3242 (ns)	16.95±8.60	12.78±9.40	p=0.1840 (ns)
	OF	22.44±17.06	43.07±25.93	p=0.1131 (ns)	28.88±11.00	22.83±13.16	p=0.1939 (ns)
SW	M	74.54±21.01	61.59±15.20	p=0.0797 (ns)	56.53±26.19	66.75±17.84	p=0.2822 (ns)
	NF	1.01±2.27	4.10±5.58	p=0.0972 (ns)	30.33±26.84	17.99±13.56	p=0.2206 (ns)
	OF	24.46±20.60	34.31±13.82	p=0.1366 (ns)	13.13±10.80	15.26±10.24	p=0.6647 (ns)

(NE = northeast monsoon; SW = southwest monsoon; SD=standard deviation)

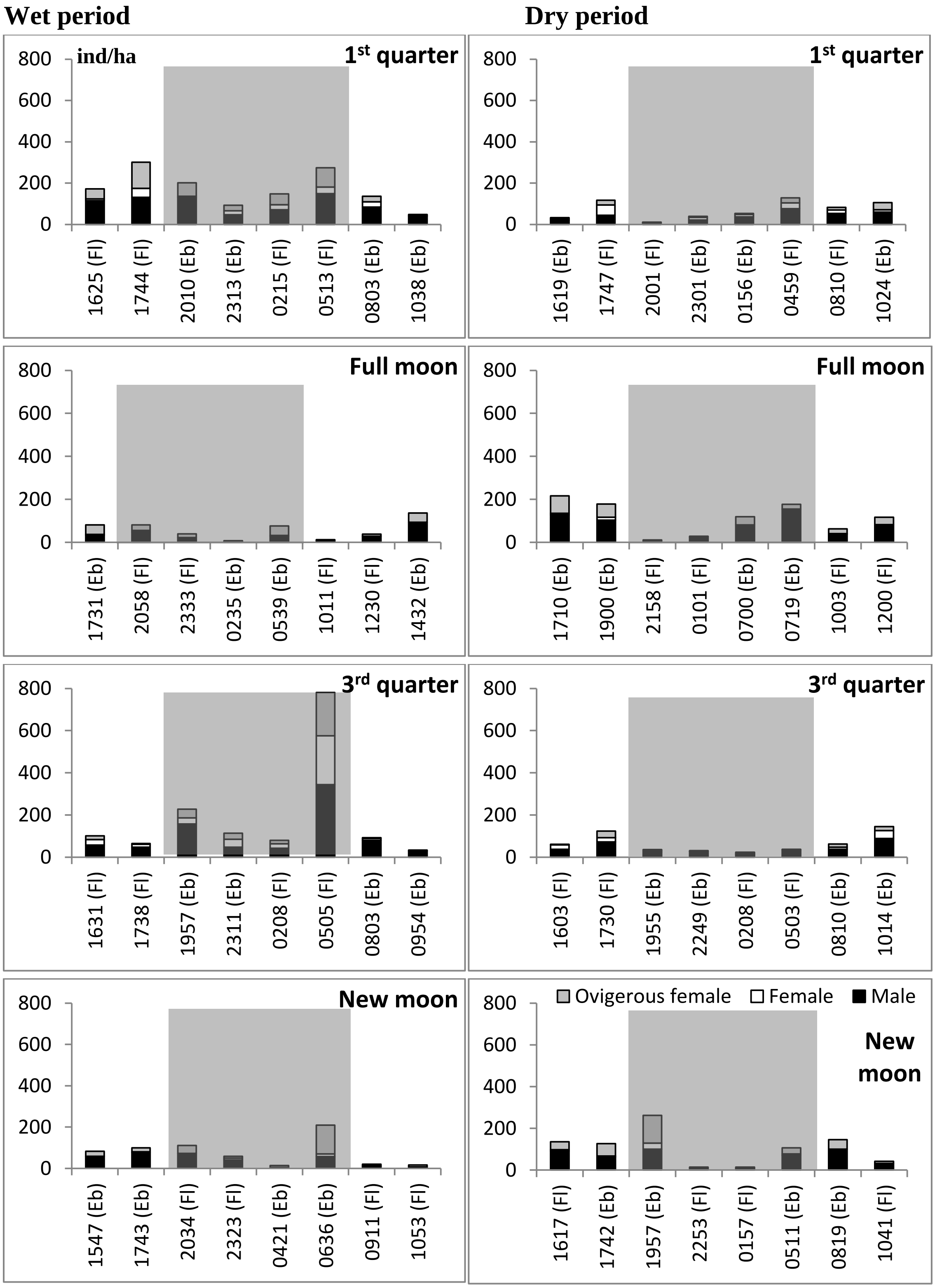


Fig. 3.2.8. Mean abundance (ind/ha) and sex compositions of *D. moosai* caught over 24 hours in four consecutive lunar phases in both wet and dry periods at mudflat. ‘Eb’ denotes ebb tide while ‘Fl’ denotes flood tide. Shaded column denotes night time.

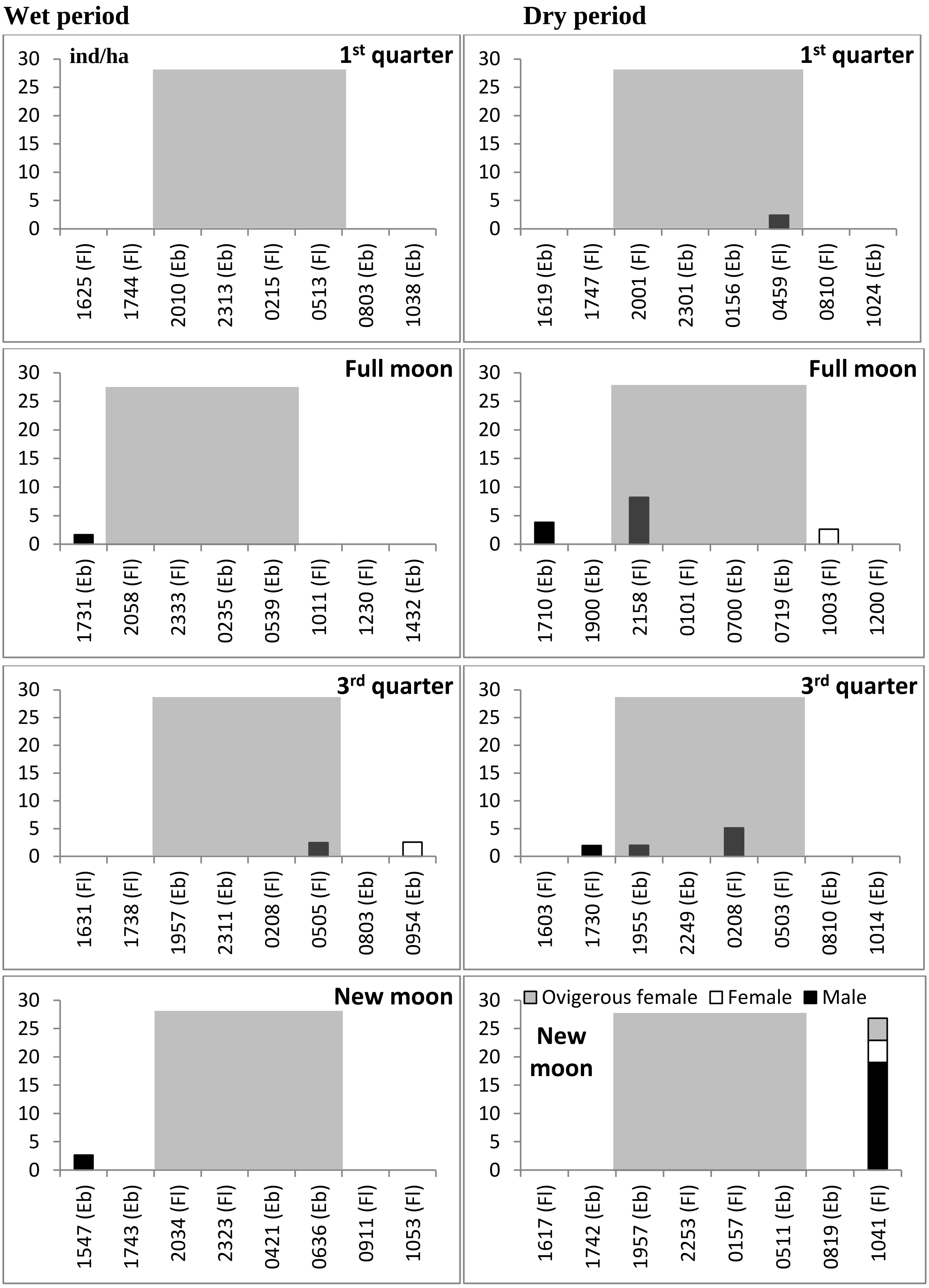


Fig. 3.2.9. Mean abundance (ind/ha) and sex compositions of *D. lopochir* caught over 24 hours in four consecutive lunar phases in both wet and dry periods at mudflat. 'Eb' denotes ebb tide while 'Fl' denotes flood tide. Shaded column denotes night time.

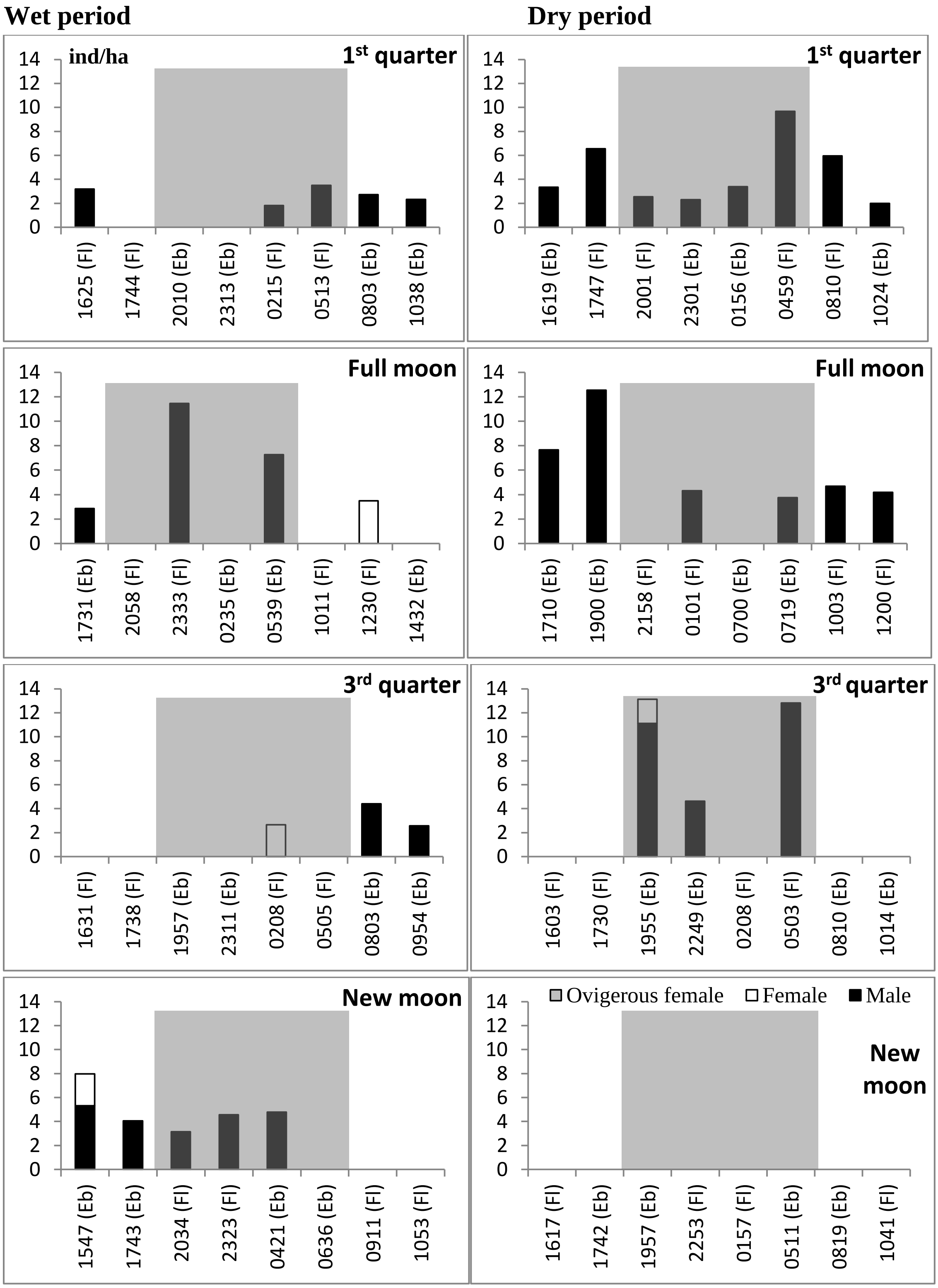


Fig. 3.2.10. Mean abundance (ind/ha) and sex compositions of *C. infraspinatus* caught over 24 hours in four consecutive lunar phases in both wet and dry periods at mudflat. ‘Eb’ denotes ebb tide while ‘Fl’ denotes flood tide. Shaded column denotes night time.

3.2.7 Discussion

3.2.7.1 Hermit crab diversity and abundance

Diogenes lopochir and *D. moosai* are found to be common in the estuaries of the Matang mangrove forest, Malaysia. *D. lopochir* has a distribution from Western Australia, Singapore (Rahayu, 2000) to Pakistan (Siddiqui et al., 2004) while *D. moosai* has been recorded in Java, Indonesia (Rahayu & Forest, 1995). Although mean density of hermit crabs in Matang estuary could be computed in this study, comparison of density with other studies is difficult as methods of sampling as well as habitat characteristics or systems where hermit crabs were sampled varied. Clustering behavior of most hermit crabs also complicates abundance comparison as a single cluster could comprise close to 300 individuals (Barnes & Arnold, 2001). In an infralittoral rocky shore of Brazilian coast, mean density of nine species of hermit crabs estimated from timed visual census was 4,052 ind/ha with *Paguristes tortugae* being the most abundant at 2,381 ind/ha (Mantellato & Garcia, 2002). In a study at coast of Irish Sea where water depth is 40m, average density of both *Pagurus bernhardus* and *P. prideaux* were estimated at 165 ind/ha and 137 ind/ha respectively (Ramsay et al., 1996). In a transect and quadrate survey at intertidal rocky flats in Sepangar Bay, Sabah during low tide, mean density of hermit crabs was estimated at 230,000 ind/ha comprising six species with highest density being *D. tumidus* recorded at 89,940 ind/ha (Teoh, 2008). Therefore, abundance of hermit crabs in this study could be considered very low with overall mean densities of *D. moosai*, *D. lopochir* and *C. infraspinatus* being only 67 ind/ha, 61 ind/ha and 9 ind/ha respectively with maximum density recorded at 4,044 ind/ha for *D. lopochir* at shoal station.

This low abundance of hermit crabs could be explained by their sparse distributions as argued in Barnes & Arnold (2001) given the example whereby abundance of the sparsely distributed *Dardanus* species may be low compared to gregarious species confined in narrow littoral zone. In addition, hermit crabs typically have the tendency to form clusters when exposed and becoming active and dispersed during immersion (Gherardi et al., 1994). Although hermit crabs in this study were less likely to form clusters since samplings were done during flood tide, there was still tendency of forming aggregations. The sparse yet patchy distribution of hermit crabs is shown by the regularly high standard deviation between replicates and high density range for all species whereby density for *D. moosai*, *D. lopochir* and *C. infraspinatus* could range from 0 ind/ha to 927, 4,044 and 894 ind/ha respectively. Problem of patchiness, spatial distributions and adequacy of sampling efforts were also encountered in a macrobenthos study at mid-estuary and river mouth of Sg. Sangga Besar and Sg. Selinsing by Muhammad Ali (2004) where despite having higher macrobenthos catches at river mouth, nevertheless, the density of macrobenthos at river mouth ranged from 0-700Nm^{-2}. In addition, the density of hermit crabs in this study may be underestimated since escapement factor is not considered i.e hermit crabs may escape through the meshes or when the net bounced off the bottom. The consistent use of the trawling method in this study however, allows spatial and temporal comparison of hermit crabs abundance.

The wide variations in diversity and density of hermit crabs is probably more related to heterogeneity of habitats given that rocky and coral reefs settings seemed to host higher diversity and density of hermit crabs compared to mangroves or estuarine settings. Based on a review of hermit crabs of southern Thailand by McLaughlin (2002), a total of sixteen species of hermit crabs are associated with corals and nine species are associated with rocky shores while only seven species are associated with mangroves, mudflats or river mouth. In a review by Rahayu (2000) on hermit crabs from South

China Sea, 24 species of hermit crabs are associated with corals, 19 species with rocky shores while only seven species are associated with mangroves and mudflats. Mantellato & Garcia (2002) collected nine species of hermit crabs in rocky shore of Anchieta Island, Brazil. In Ubatuba coastal zone in Brazil, 13 species of hermit crabs belonging to seven genera from families Diogenidae and Paguridae were recorded with highest abundance of hermit crabs observed in the sheltered areas near rocky shore where water was deeper while highest diversity index was recorded at shallower sites near rocky shores (Fransozo et al., 2008).

The disparity in abundance and distribution of hermit crabs could be explained by the layout complexity of rocky and coral habitats with irregular surfaces and substrates and presence of crevices that serve as ideal hideout for these animals. Differential use of space that allows coexistence of various species may be made possible by presence of different type of substrates (Mantellato & Garcia, 2002). De Grave & Barnes (2001) in a study in Quirimba Island, Mozambique, found that smaller islands with less heterogenous shores were dominated by *Clibanarius virescens* while in larger islands adorned by diverse type of habitats such as mangroves, sand, reef, seagrass and rock had more complex distributional patterns.

Therefore, this may also explicate the lack of diversity and density of hermit crabs in this study due to homogeneity of muddy bottom of mangrove estuary. It is also possible that mangrove forest may host higher abundance of hermit crabs than the estuarine and river sites due to its complex root system which form an ideal shelter for hermit crabs (Gherardi & Vannini, 1991). Despite lack of diversity, interspecific habitat partitions of hermit crabs in this study are apparent. This pattern of distribution may be advantageous as habitat segregations may alleviate competition pressures (Abrams, 1980).

The regularly low abundance of *C. infraspinatus* throughout this study may suggest solitary behavior of this species. Large male hermit crabs have the tendency of solitary behavior. Gherardi & Vannini (1991) noted that hermit crab individuals separated from clusters were the largest in size. Turra & Leite (2000a) found that scattered individuals of *C. antillensis* were larger than clustered individuals. In a Mediterranean rocky shore, aggregations of *C. erythropus* composed mostly females (Benvenuato & Gherardi, 2001). Fig. 3.2.11 shows size frequency of all males of *C. infraspinatus*. The consistently low catch of *C. infraspinatus* were composed mostly of larger sized individuals with highest frequency in size class 7.01-8.00mm (34 individuals) and this may suggest solitary behavior of larger size individuals. In addition, 70% of *C. infraspinatus* caught in this study were males. However, the possibility of solitary behavior of larger males may not be conclusive without examination of cluster characteristics (size class and sex composition) of this species and compared with solitary individuals.

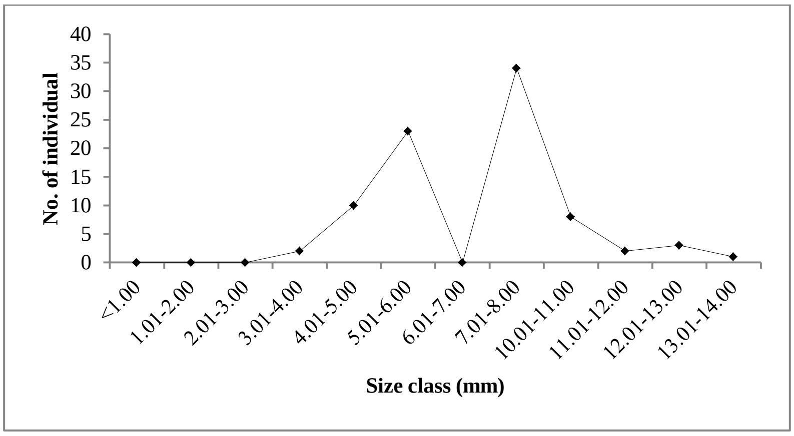


Fig. 3.2.11. Size frequency of male *C. infraspinatus* (with exception of November 2009 catch).

3.2.7.2 Spatial distribution and abundance of hermit crabs in relation to environmental parameters

There were a total of six species of hermit crabs caught throughout the sampling period all belonging to the family Diogenidae. However, only *D. moosai, D. lopochir* and *C. infraspinatus* occurred in high abundance. This indicates that the diversity of hermit crabs community was low as the remaining three species represented less than 1% of total hermit crabs sampled. Nonetheless, this representation may not reflect the overall number of species in Matang Mangroves Forest Reserve as there may be more species residing in the mangrove forest. As a comparison, Rahayu (2000) reported 102 species belonging to the family Diogenidae (eight genera), Paraguridae and Parapaguridae in South China Sea which are associated with coral reefs, coral rubbles, rocky platform, sand-mud bottom, sand flat, littoral and sublittoral waters and mangroves habitats. Both *D. lopochir* and *C. infraspinatus* were also noted in mangrove areas. McLaughlin (2002) reviewed the hermit crab fauna in Southern Thailand which included 39 species from Diogenidae with 12 species each in genera *Clibanarius* and *Diogenes*.

The pattern of precipitation in Peninsular Malaysia is largely related to the prevalence of the northeast monsoon (NE) which is usually associated with heavy rainfall and southwest monsoon (SW) which is associated with drier period. However, wind and precipitation pattern can be localized. Typical rainfall pattern in Peninsular Malaysia is characterized by two periods of maximum rainfall separated by two periods of minimum rainfall. Primary maximum rainfall usually occurs between October-November while secondary maximum rainfall usually occurs between April-May. Over study area in the northwestern region, the period of primary minimum rainfall generally occurs in January-February while secondary minimum generally occurs between June-

July (Malaysia Meteorological Department). With the exception of temperature, all water parameters showed significant spatial differences (Table 3.1.3).

Hermit crabs are affected by the abiotic factors of environmental dynamics. The mid-estuary station is characterised by lower salinity, higher depth and lower dissolved oxygen content as compared to the shoal station which is characterised by higher salinity, more turbid water, shallower depth and less variability in its water parameters. The river mouth and mudflat represent the intermediate of the water characteristics between mid-estuary and shoal waters.

The spatial separation of hermit crabs in Matang estuary was pronounced. *D. moosai* and *D. lopochir* were dominant at mudflat and shoal stations respectively (Table 3.2.1 and Fig. 3.2.1) while *C. infraspinatus* regularly occurred in all stations in low abundance except for November 2009 at mid-estuary where unusually high abundance of this species was recorded with density of 452±625 ind/ha (Fig. 3.2.4). This could be an indication of euryhaline nature of *C. infraspinatus* where it could tolerate wide fluctuations of salinity which ranged from 10.79 to 28.58 ppt in the mid-estuary station (Table 3.1.3). On the other hand, both *D. moosai* and *D. lopochir* preferred the saline environment of the mudflat and shoal stations. Preference of different species of hermit crabs for a range of salinity has been shown experimentally and by field observation by Dunbar et al. (2003) where they found that *C. taeniatus* survived better than *C. virescens* when experimentally subjected to diluted seawater (8ppt) over an extended period of time. From a field survey at Queensland coast, Australia, they revealed that *C. taeniatus* tended to be more abundant in areas influenced by freshwater, while *C. virescens* was more dominant at a site not influenced by freshwater. Sant' Anna et al. (2006) found strong correlation between spatial distributions of three sympatric hermit crabs of *C. vittatus*, *Loxopagurus loxochelis* and *Isocheles sawayai* with water salinity and thus, they considered this parameter as important limiting factor regulating distribution of hermit crabs in the estuary. Higher abundance of *C. infraspinatus* at mid-estuary water could also suggest tolerance of this species towards lower concentration and saturation of oxygen which were the characteristics of the deeper bottom water of mid-estuary station while both *D. moosai* and *D. lopochir* were more adapted to higher oxygen levels in shallow water at the mudflat and shoal stations. Crustaceans are often known to be able to regulate oxygen consumption when exposed to low oxygen level to reduce risk of hypoxia (McMahon 2001).

Although organic content of sediment is relatively low at sites where *D. moosai* and *D. lopochir* are abundant food does not appear to be a limiting factor because *Diogenes* hermit crabs are capable of deposit feeding. In the laboratory, these two species had been observed to actively pump out from the sediment (personal observation). Efficiency of deposit feeding by both hermit crab species is less likely to be affected sediment texture despite the differences in organic matter content since particle size compositions are similar in all stations with coarse silt having the highest composition (15.6-62 µm). Despite the subtle differences in sediment texture among stations, RDA (Fig. 3.2.3) showed association of *C. infraspinatus* with sediment of larger particle size (medium sand and coarsed sand) and higher organic content, affinity of *D. lopochir* for very fine sand and coarse silt, and affinity of *D. moosai* for fine silt and clay. Influence of sediment texture on distribution of hermit crabs has been shown in previous studies (e.g. Fransozo et al. 2008; Turra and Denadai, 2002; Fantucci et al., 2009). Fransozo et al. (2008) reported an association between *Dardanus insignis* and fine and very fine sand substrate with higher organic content, whereas *Petrochirus* *diogenes* was found at sites with higher composition of larger grains with substantial amount of organic content.

3.2.7.3 Temporal distribution and abundance of hermit crabs in relation to environmental parameters

At mudflat and shoal stations where both *D. moosai* and *D. lopochir* are abundant, the temporal variation in water parameters and sediment organic content did not appear to modulate the temporal abundance of both *Diogenes* species based on the non-significant results ($p>0.05$) of the correlation test (Table 3.2.2). This could be explained as both stations are located farther offshore and thus, had the least variability in temperature and salinity of bottom water as reflected by the low standard deviations of the two parameters at both stations. This homogenous environment is attributed to the shallow water with higher turbulence and in addition, less influence of freshwater in both stations compared to mid-estuary and river mouth stations. The consistently higher and less fluctuation in salinity of water particularly in shoal station (Fig. 3.1.4) may reflect the stenohaline nature of *D. lopochir* which is spatially confined at shoal station. On the other hand, *D. moosai* may tolerate wider range of salinity compared to *D. lopochir* since the former is not only dominant at mudflat but also occurred in substantial number in river mouth and shoal stations throughout most of the sampling months.

Although the mean salinity at river mouth station is similar to mudflat station ($p>0.05$), the abundance of *D. moosai* at river mouth showed significant positive correlation ($p<0.05$) with salinity (Table 3.2.2). This could be due to larger fluctuation of salinity in river mouth compared to mudflat as the former is subject to greater influence of freshwater. Therefore, the fluctuation in abundance of *D. moosai* along the salinity gradient is more obvious for example, abundance of *D. moosai* at river mouth was highest in August and October 2010 which coincided with the highest monthly salinity recorded at the station. Abundance of *D. moosai* also showed significant positive correlation ($p<0.05$) with oxygen level (Table 3.2.2) which may suggest that this species is less tolerant to lower oxygen level.

Pooled data (northeast monsoon and southwest moonsoon) of hermit crab abundance between seasons at both mudflat and shoal stations showed that *D. moosai* and *D. lopochir* at each respective station where they were dominant was significantly more abundant during southwest monsoon (Table 3.2.5 and 3.2.6), a period characterized by lower rainfall. This observation concerned with monthly abundance data showing that the temporal variation in abundance of both species was obvious with peak abundance during the drier months at both mudflat (May, end of June and July 2010) and shoal (January, July and September 2010) stations (Fig. 3.2.4).

3.2.7.4 Spatial and temporal abundance of juvenile hermit crabs

In this study, recruited juveniles were not sorted into species and therefore, the juvenile data represent the recruitment of hermit crab community as a whole. High abundance of juvenile hermit crabs at river mouth, mudflat and shoal stations (Fig. 3.2.6) implied the use of the estuarine area as nursery ground, the same habitat the adults are distributed. Litulo (2005a) also reported recruitment to the same site occupied by adult of *C. longitarsus* in southern Mozambique which he attributed to the high nutrient runoff that is important for production and thus, larval development. Immigration of megalopae or juveniles from coastal water to nearer shore is the only mechanism for restoring the adult population (González-Gordillo et al., 2003). Abundance of juveniles was exceptionally high in the shoal station in January and

February 2011 (Fig. 3.2.6) which was about 7 to 8 months after the highest occurence of ovigerous females observed in both species (Fig. 3.5.3). The high recruitment of juveniles during this period results from the high reproductive activity during the onset of southwest monsoon in June and July 2010. However, no study has been done to observe the larval development of *D. moosai* and *D. lopochir* and time taken for the larvae to develop into juvenile stage. Garcia & Mantellato (2001) reported continuous recruitment of *Pagurus erythrops* in Anchieta Island, Brazil with peak recruitment of juvenile being observed six to nine months after peak occurence of ovigerous.

3.2.7.5 Short term variation in abundance and assemblages of hermit crabs

Although previous studies have shown the association between circatidal or circadian rhythms with distributional and activity patterns of hermit crabs (e.g. Bertness, 1981a; Gherardi & Vannini, 1989, 1993, 1994; Barnes, 2001, 2003; Turra & Denadai, 2003; De Grave & Barnes, 2001), this was less obvious for hermit crabs in the present study (e.g. Table 3.2.9). There was no diel variation in hermit crab abundance. However, the consistent presence of hermit crabs could be due to homogeneity of habitats, which were characterized by narrow variation in environmental conditions. Further, diel samplings were carried out at the subtidal region of the mudflat and therefore, not subjected to environmental extremities as in the intertidal zone. An interesting observation is that *D. lopochir* was more abundant at the mudflat during spring flood tide showing that this species could have been tidally transported from the shoal station where they were more abundant. It has been shown that animals may rely on either the ebb or flood tide current as a passive transport mechanism to move them from one location to the other (Tankersley et al., 2002). According to Gherardi & Vannini (1991), hermit crabs adopt two strategies in space utilization; first by remaining along a narrow belt where they are undirected by the periodic submergence and emergence caused by tides, and second by their reliance upon tides for their daily movements.

The majority of *Clibanarius infraspinatus* that were caught in mudflat were males (average relative abundance 91.07%). Apart from the hypothesis that the disproportionate sex composition is a result of the interplay between predation pressure and reproductive strategy, it may also suggest that the male of *C. infrapsinatus* is predominantly migratory investing more energy on locomotion to reach richer and higher quality foraging ground which compensates for the energy spent. In contrast, the female is less mobile and spent more of its energy in egg production. Migratory tendency of male has also been noted by Hunter & Naylor (1993) in a study on intertidal migration of the shore crab, *Carcinus maenas*. In addition, body size could play a significant role in habitat segregation of hermit crabs in two ways. Firstly, larger crabs (e.g. *C. infraspinatus*) have higher locomotory capabilities and are capable of faster movement than their smaller conspecifics (e.g. *D. moosai*), probably a consequence related to their greater muscle development and lever length. Secondly, smaller individuals have a greater surface to volume ratio and are more susceptible to dessication than larger crabs (Gherardi & Vannini, 1993). Thus, in the context of habitat segregation, the occupation of the lower zone by smaller *D. moosai* may confer lower risk of dessication during ebb tide.

Sparse distribution of hermit crabs at mudflat may present bias due to patchiness and zonation such that the abundance of *C. infraspinatus* may be underestimated due to its solitary nature especially males (commonly one or two individuals present in a single trawl). *C. infraspinatus* were sparsely distributed as compared to *D. moosai* which may have formed aggregated clusters confined to the lower zone of the mudflat and thus, caught in high abundance. Barnes & Arnold (2001) raised such questions of density estimation due to the sparse and clustering nature among different species of hermit crabs. They noted that many species of hermit crabs aggregated, their estimated abundance estimation might be low if species are sparsely distributed over wide subtidal shelf areas.

Literature reviews on the diel activities of hermit crabs have reiterated that activities of hermit crabs are often initiated during submergence where feeding and other social activities ensued (Gherardi & Vannini, 1993). Although consistent patterns of hermit crab density were observed throughout samplings, some variations are distinguishable in the present study. Density peaks were recorded during neap tides (first quarter moon and third quarter moon) during the northeast monsoon, but at the southwest monsoon, density peaks were noted at spring tides (full moon and new moon) (Fig. 3.2.7).

These combined patterns of hermit crabs ingression by season and lunar phase are not clear but could be related to interplay of predation pressure, feeding intensity, reproduction strategy, availability of shells and rainfall. The peaks at northeast monsoon could correspond to the influx of nutrients due to higher rainfall which subsequently increasing concentration of phytoplankton. This condition could have triggered reproduction in hermit crabs including aggregations for mating and release of larvae which is energetically beneficial as food source is abundant. Chew (2011) recorded phytoplankton bloom in the study area in January 2003 during the period of the northeast monsoon. Hermit crab density peaks at night flood of the last quarter moon during northeast monsoon and new moon during southwest monsoon may be related to the decrease in predation pressure as the peaks coincided with low densities of both ariid and sciaenid fishes. Presence of predators can affect the distribution of mobile intertidal prey invertebrates as they seek the safer zone in intertidal areas (Rochette & Dill, 2000).

The high standard deviations of crab density data in all stations in the present study suggests aggregations and patchy distribution of hermit crabs. Since empty shells are a limiting resource at the study site, shell exchange between similar-sized individual hermit crabs would enhance the probability of achieving appropriate shell fit (see Barnes & Arnold, 2001). However, the frequent shell exchanges among hermit crabs would put them at higher risk of predation (Rotjan et al., 2010). This is plausible since ‘naked’ hermit crabs were observed in the stomach of sciaenid fishes.

Although ovigerous females were present in all moon phases and tidal conditions in both seasons, there are two interesting patterns. Firstly, the percentage of ovigerous females was relatively higher during spring tides (full moon and new moon) compared to neap tides (first quarter moon and third quarter moon) at both seasons. Secondly, the percentage of ovigerous females was regularly higher at ebb tide. Both patterns could be explained by crab behaviour to release and disperse larvae at the highest and swiftest tide. Hence, *D. moosai* likely uses the strong ebb tidal current during spring tide to disperse their larvae offshore. It is been known that megalopae of some decapod crustaceans use tidal stream as a mode of passive transport (Gonzales-Gordillo et al., 2003). To do so, females synchronise their larval release to the changing tidal phase; high ebb tide for larvae to drift out and low flood tide for them to be retained (Drake et al., 1998).

Estuarine crabs commonly employ two patterns of larval dispersal in which the larvae are either retained in estuary or dispersed elsewhere (Morgan, 1987). According to Chew (2012), decapod larvae (mainly Sergestidae, Brachyura, Diogenidae and Luciferidae) were found to be 3 to 8 times greater at shoal water compared to mangrove waters. This observation suggests that hermit crabs are similar to other common decapods releasing their larvae offshore instead of retaining them inside the estuary. The advantages of dispersive larval stages in marine benthic invertebrates are the avoidance of competition with adults for resources and higher ability to withstand local extinction (Pechenik, 1999). Therefore, the dispersive ability of hermit crabs is presumed to allow them to colonise environment within the limits of physiological tolerance rendering them ubiquitous along mangrove coastline.

3.2.8 Conclusion

Although the number of hermit crab species was generally low in Matang mangrove estuary due to the homogeneous estuarine habitat characterised by muddy substrate, spatial separation and variability in temporal abundance of each species are apparent. *C. infraspinatus* is dominant at the mid-estuary, *D. moosai* is dominant at the river mouth, mudflat and shoal area and *D. lopochir* is dominant at the shoal area. *C. infraspinatus* is associated with less saline and deeper water and able to tolerate low dissolved oxygen whereas *D. moosai* and *D. lopochir* are associated with higher salinity water. Temporally, significant influence of salinity and DO on abundance of hermit crabs (*D. moosai* and *C. infraspinatus*) was observed only at river mouth. Additionally, temporal abundance of *C. infraspinatus* consistently shows the crab’s affinity to period of less saline water. The high abundance of juvenile hermit crabs at river mouth, mudflat and shoal stations implied the use of the estuarine area as nursery ground, the same habitat the adults are distributed. This is advantageous for the newly recruited hermit crabs as shell resource is readily available. Percentage of ovigerous females was relatively higher during spring tides (full moon and new moon) compared to neap tides (first quarter moon and third quarter moon) at both seasons and in addition, percentage of ovigerous females is regularly higher at ebbing of water during the spring tides. These two observations suggest the use of tidal stream as mode of larval dispersal by hermit crabs (*D. moosai*).

3.3 POPULATION DYNAMICS OF HERMIT CRABS COMMUNITY IN MATANG MANGROVE ESTUARY AND ADJACENT COASTAL WATERS

(Part of the results of this section has been published in Teoh & Chong (2014a); see Appendix I)

This section addresses objective 2 which is to study the population dynamics of hermit crabs. The study describes the length-frequency distribution and length-weight relationship among hermit crab species. Length-frequency data were used to determine various parameters of the population dynamics of *Diogenes moosai* and *D. lopochir*, the two most dominant species. These included the growth rate, growth performance index, asymptotic length, lifespan, total mortality and recruitment pattern. These parameters were estimated by VBGF fitted length-frequency histograms using the Fisat ii software.

3.3.1 Size of hermit crabs

Mean shield lengths of *C. infraspinatus*, *C. padavensis*, *D. lopochir* and *D. moosai* were 6.87±1.84mm, 5.73±1.68mm, 3.10±0.69mm and 2.63±0.49mm respectively (Fig. 3.3.1). Kruskal-Wallis test showed that *D. moosai* was the smallest species (H=1029.70, p<0.001). *D. lopochir* was significantly smaller (p<0.001) than *C. infraspinatus* (Appendix XIIIa). Size of *D. moosai* varied subtly among sampling stations (p>0.05) with means that ranged from 2.46±0.38mm to 2.70±0.75mm. *D. lopochir* at mid-estuary was slightly larger (3.98±1.02mm) (p>0.05) compared to other stations which ranged from 2.96±1.32mm to 3.10±0.67mm (Fig. 3.3.2). *C. infraspinatus* at shoal area was significantly smaller (6.24±1.93mm) (H=18.73, p<0.001) than all other sampling stations (Table 3.3.1) (Appendix XIIIb).

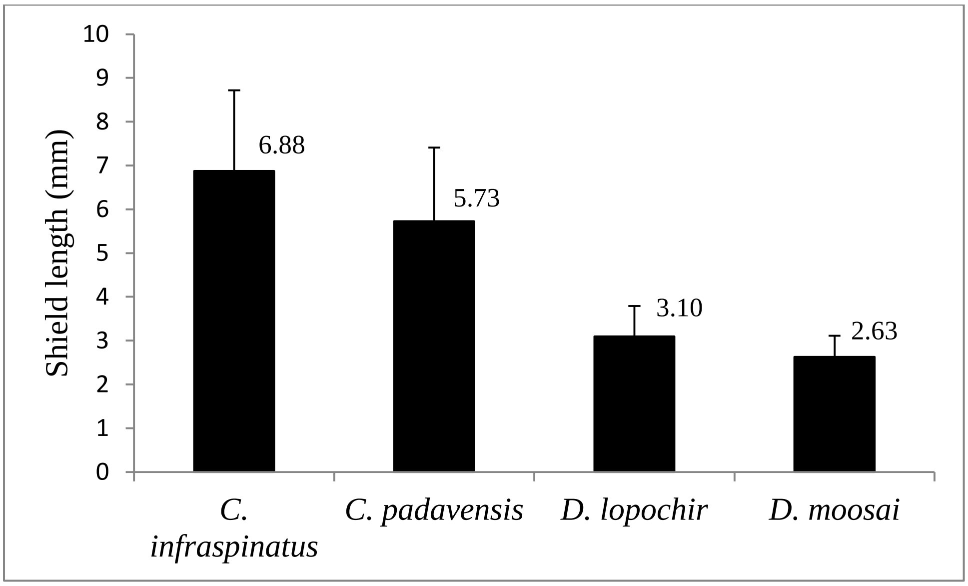


Fig. 3.3.1. Mean shield length (mm) and standard deviations of different species of hermit crabs in Matang mangrove estuary.

Table 3.3.1. Basic statistics and results of Kruskal-Wallis test on shield length (mm) of different species of hermit crabs between sampling stations in Matang mangrove estuary; SD=standard deviations; n=number of samples; ns=no significant; similar superscripts of a or b indicates homogenous group.

Species		Station				
		Mid-estuary	River mouth	Mudflat	Shoal	p-level
D. moosai	Mean	2.46	2.70	2.62	2.63	p=0.2884 (ns)
	SD	0.38	0.75	0.46	0.45	
	n	27	153	1004	695	
	Min	1.52	1.33	1.20	1.25	
	Max	3.19	4.85	4.82	6.32	
D. lopochir	Mean	3.98	2.96	2.98	3.10	p=0.1234 (ns)
	SD	1.02	1.32	0.93	0.67	
	n	6	3	40	708	
	Min	2.70	1.78	0.98	1.24	
	Max	5.13	4.38	5.18	5.13	
C. infraspinatus	Mean	6.90^{a}	8.04^{a}	7.75^{a}	6.24^{b}	$p<0.001$
	SD	1.65	2.61	1.90	1.93	
	n	184	13	25	63	
	Min	3.17	5.01	5.58	3.48	
	Max	12.38	13.55	12.84	11.86	

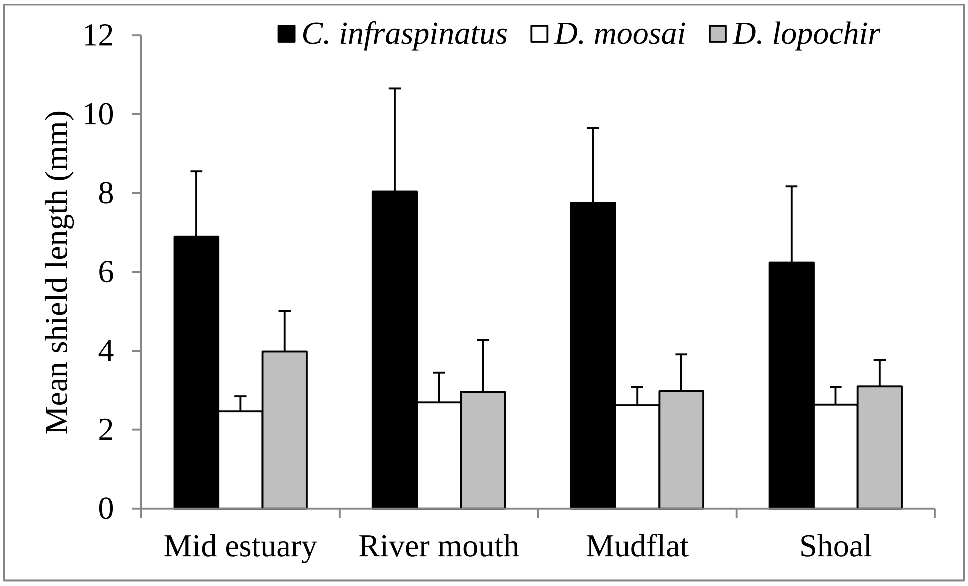


Fig. 3.3.2. Mean shield length and standard deviations of different species of hermit crabs at each sampling stations in Matang mangrove estuary.

All three major species showed distinct sexual dimorphism where adult males were generally larger than adult females. Largest adult male and female of *D. moosai* were 6.32 mm and 4.01mm respectively. The mean shield lengths for male, non-ovigerous female and ovigerous females of *D. moosai* were 2.81±0.47mm, 2.10±0.34mm and 2.32±0.24mm respectively (H=677.98, $p<0.001$). Adult males of *D. lopochir* was significantly (H=88.93, $p<0.001$) larger than the females with maximum shield length of 5.18mm and 3.65mm respectively while no significant difference ($p>0.05$) was detected between ovigerous and non-ovigerous females. Largest male and female of *C. infraspinatus* were 13.55mm and 9.53mm respectively. Males of *C. infraspinatus* was significantly larger (H=26.36, $p<0.001$) than non-ovigerous females (Table 3.3.2) (Appendix XIIIc).

Table 3.3.2. Basic statistics and results of Kruskal-Wallis test on shield length (mm) of different species of hermit crabs between sexes; SD=standard deviations; n=number of samples; ns=no significant; similar superscripts of a, b or c indicates homogenous group.

Species		Sex			
		Male	Non-ovigerous female	Ovigerous female	p-level
D. moosai	Mean	2.81^{a}	2.10^{b}	2.32^{c}	p<0.001
	SD	0.47	0.34	0.24	
	n	1261	138	482	
	Min	1.20	1.29	1.60	
	Max	8.94	4.01	3.16	
D. lopochir	Mean	3.24^{a}	2.74^{b}	2.95^{b}	p<0.001
	SD	0.75	0.45	0.26	
	n	508	178	71	
	Min	0.98	1.64	2.39	
	Max	5.18	3.65	3.47	
C. infraspinatus	Mean	7.23^{a}	5.96^{a}	$6.48^{a,b}$	p<0.001
	SD	1.95	1.12	1.36	
	n	203	76	6	
	Min	3.63	3.17	5.03	
	Max	13.55	9.53	8.72	

Mean chelae size of male, non-ovigerous female and ovigerous female *D. moosai* were 4.81±0.089mm, 3.30±0.40mm and 3.48±0.40mm respectively whereas for *D.* lopochir, mean chelae sizes were 5.70±1.61mm, 3.78±0.58mm and 3.95±0.34mm respectively. Males of both species possessed significantly (F=11.741, p<0.05) larger chelae than their respective females. Overall, *D. moosai* possessed larger chelae relative to shield length than *D. lopochir* (F=91.671, p<0.001) whereas male *D. lopochir* had significantly (F=16.295, p<0.001) larger chelae relative to shield length than female *D. moosai* (Fig. 3.3.3) (Appendix XIIId).

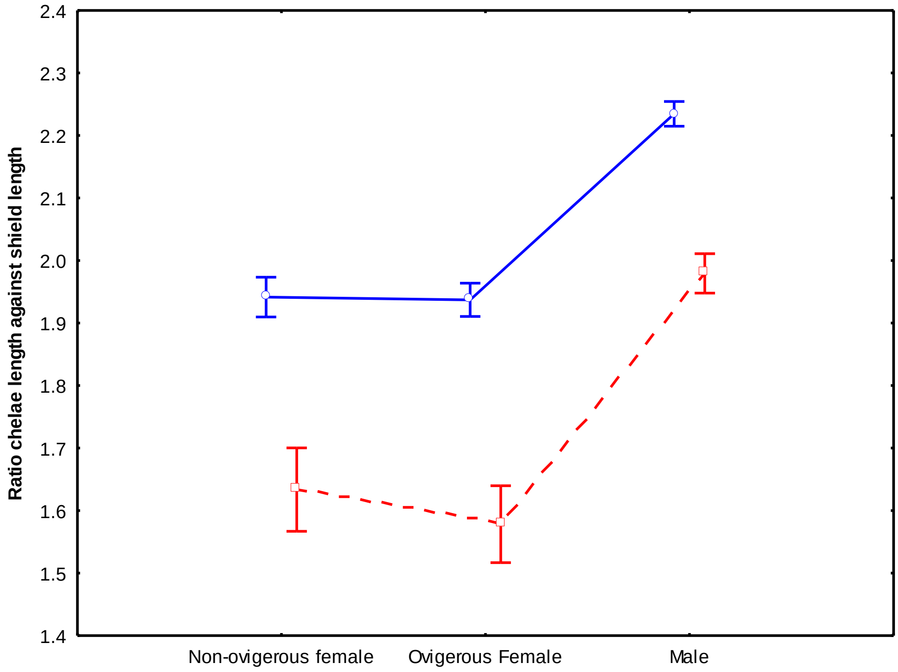


Fig. 3.3.3. Chelae length in relation to shield length hermit crabs by species and sex. *D. lopochir* is indicated by solid line while *D. moosai* is indicated by dotted line.

3.3.1.1 Length frequency distributions

Fig. 3.3.4 shows the size (shield length) frequency distributions of hermit crabs by species and sex in Matang mangrove estuary. All the three hermit crab species had unimodal pattern of distributions in their sizes. Most *D. moosai* fell in the size class of 2.51-3.00mm. However, there was distinct variation between sexes as size class of the smaller non-ovigerous and ovigerous female *D. moosai* was 2.01-2.50mm, but absent in subsequent size classes. *D. lopochir* was generally larger than *D. moosai* with common size class of 3.01-3.50mm. Size of most non-ovigerous female *D. lopochir* was between 2.51-3.00mm with the largest size class of 3.51-4.00mm whereas size of most ovigerous female *D. lopochir* laid between size classes of 2.51-3.00mm and 3.01-3.50mm. However, ovigerous female *D. lopochir* was absent in subsequent size classes. *C. infraspinatus* could grow larger compared to both *Diogenes* species as individuals with shield length of more than 13.00mm had been observed, while overall size prevailed between 6.01-6.50mm.

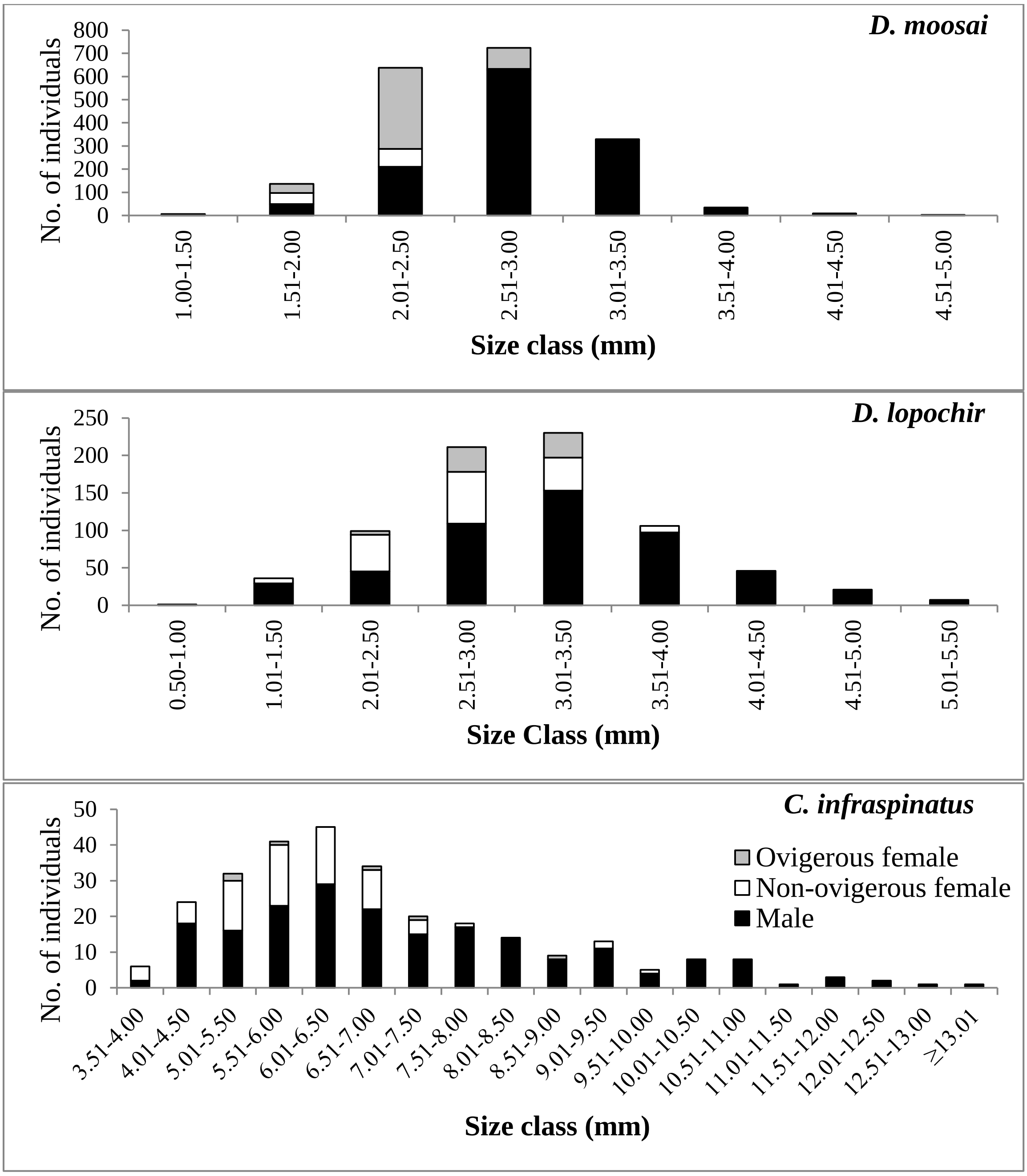
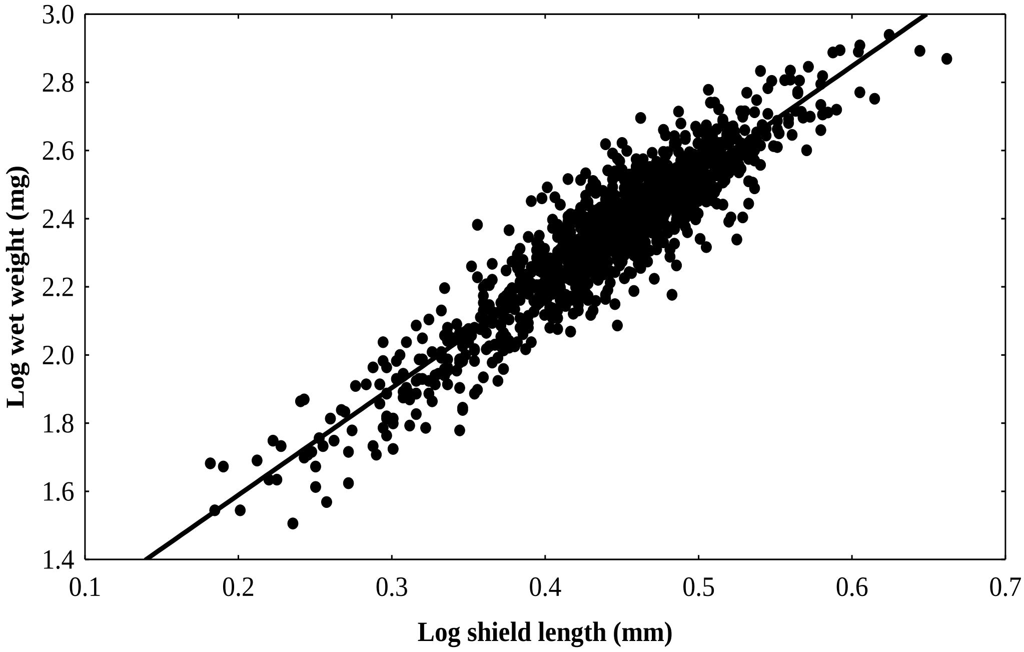


Fig. 3.3.4. Shield length (mm) frequency distribution of hermit crabs by species and sex (males, non-ovigerous females and ovigerous females) in Matang mangrove estuary (note the different scales used in X and Y axes for different graphs).

3.3.1.2 Length-weight relationship

Log length-log weight relationships of *D. moosai*, *D. lopochir* and *C. infraspinatus* were estimated using generalised linear model as shown in Fig. 3.3.5, 3.3.6 and 3.3.7 respectively. All species and sex of hermit crabs showed significant positive relationships ($p<0.01$) between length and weight with the generated log linear regression explaining about 76% to 93% of the variability as indicated by R^2 values.

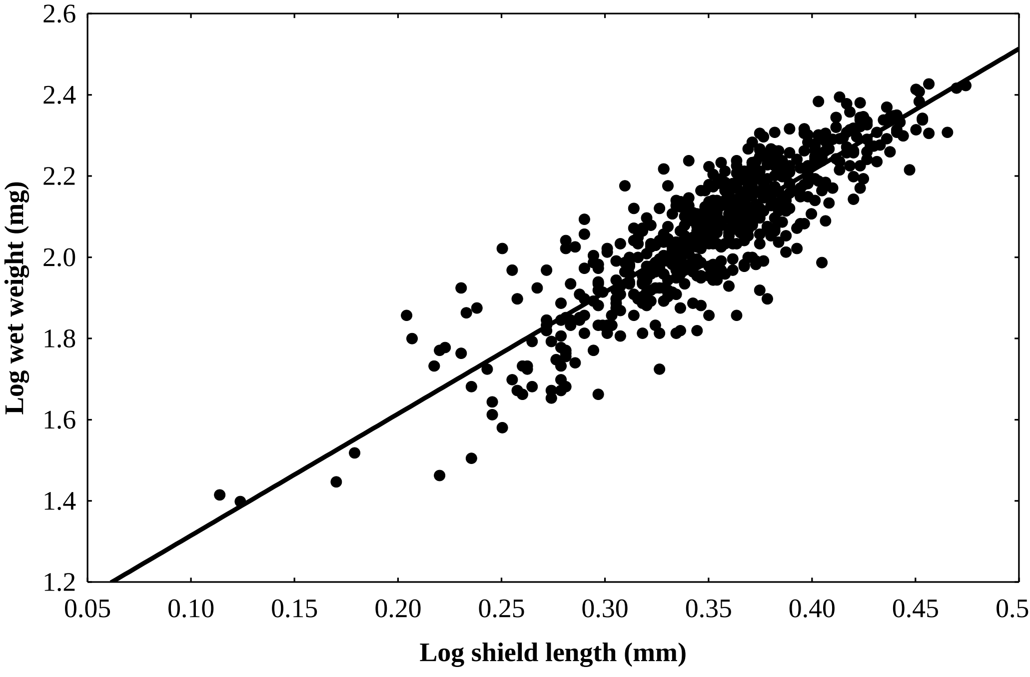
Student t-test revealed significant differences ($p<0.05$) of slopes (b) between sexes for all species (Table 3.3.3a). The length-weight relationship follows the equation; $W = aL^b$, and basic statistics by species and sex of hermit crabs are shown in Table 3.3.3b. Overall, the slopes (b) ranged between 2.67 to 3.28 with both *Diogenes* species having similar rate of weight increment (b values ranged from 2.97 to 3.28) whereas *C. infraspinatus* has the lowest b value (male=2.77; female=2.67). Males of all species had greater slopes ($p<0.05$) compared to the females, indicating of higher rate of weight increment of males than females as it grows.



Male *D. moosai*

Log wet weight = .96004 + 3.1456 * **Log shield length**

Correlation: r = .92498

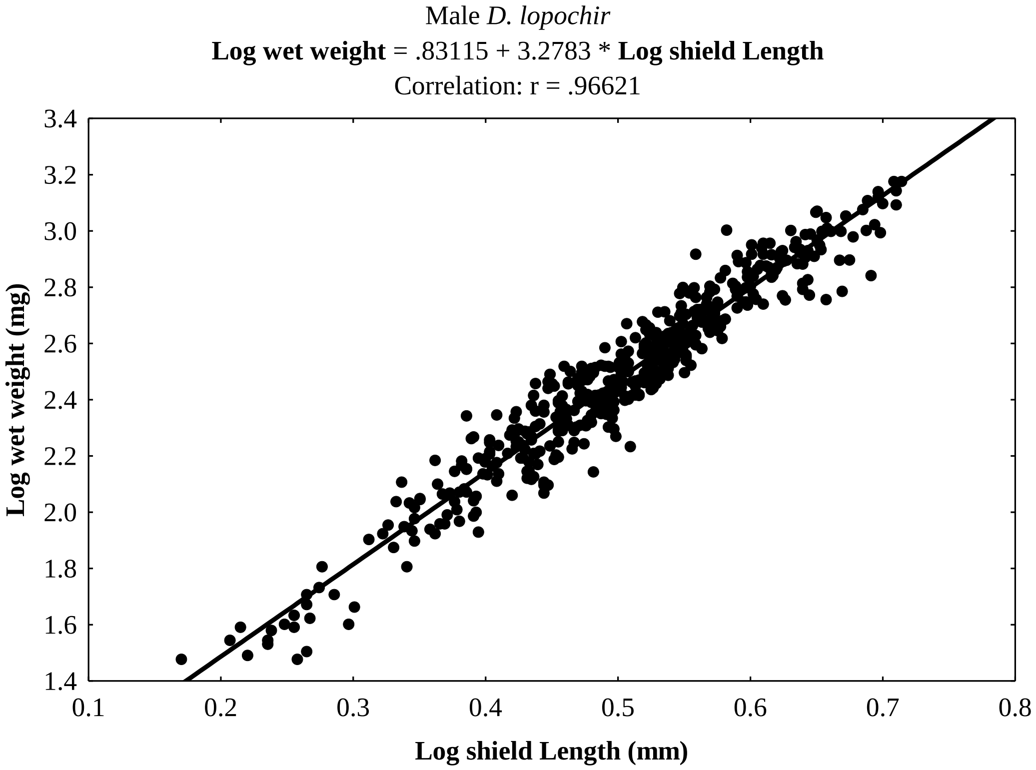


Female *D. moosai*

Log wet weight = 1.0150 + 2.9966 * **Log shield length**

Correlation: r = .86971

Fig. 3.3.5. Relationship between log shield length (mm) and log wet weight (g) of male and female of *D. moosai*.



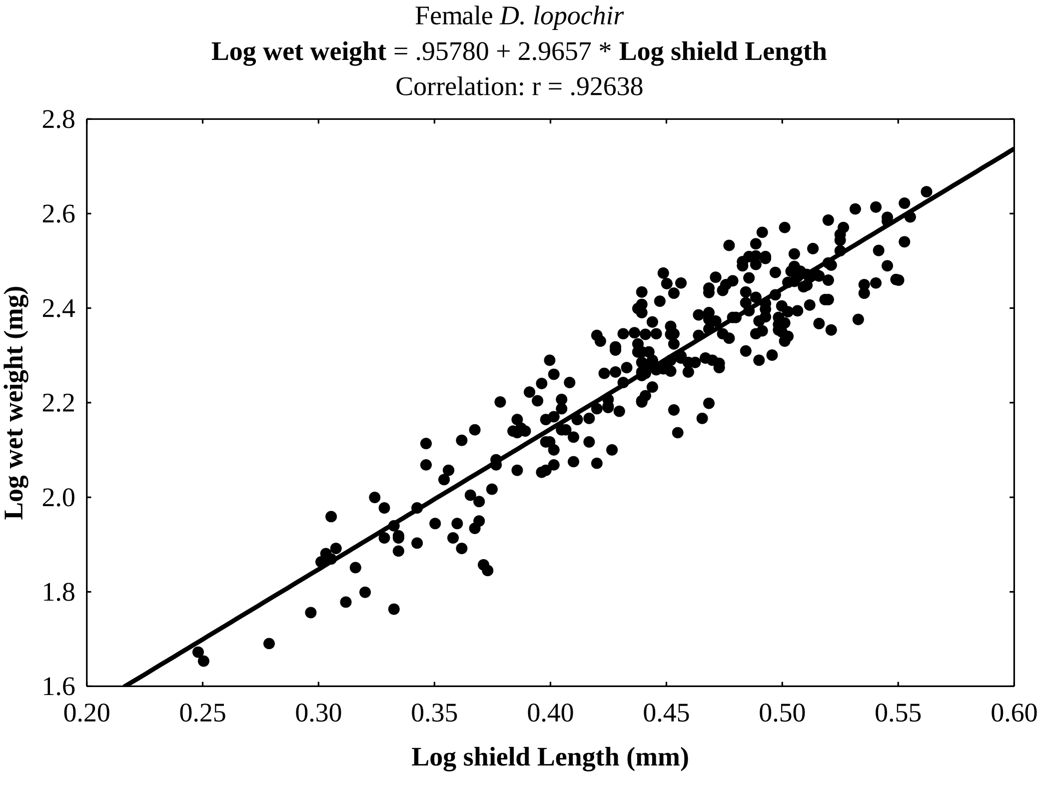
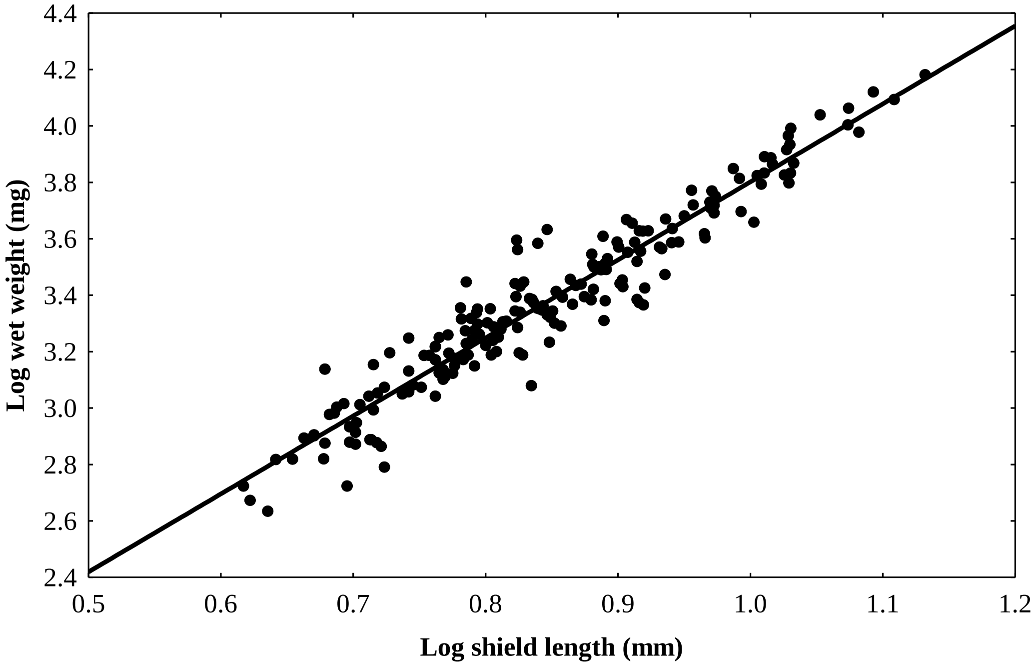
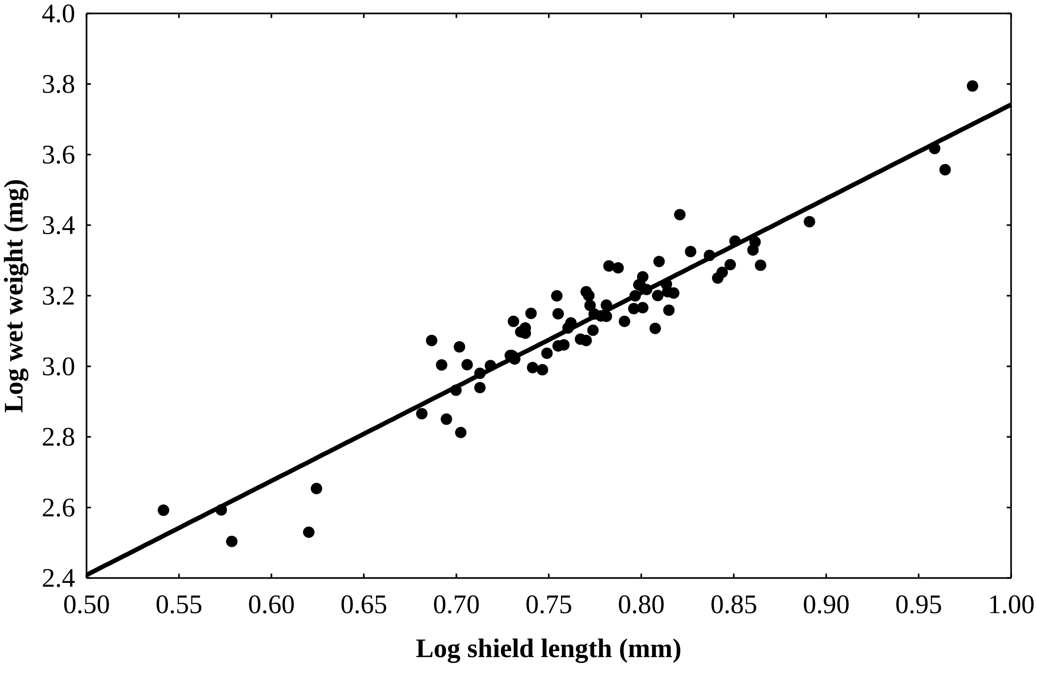


Fig. 3.3.6. Relationship between log shield length (mm) and log wet weight (g) of male and female of *D. lopochir*.



Male *C. infraspinatus*
Log wet weight = 1.0367 + 2.7649 * **Log shield length**
Correlation: r = .95847



Female *C. infraspinatus*
Log wet weight = 1.0753 + 2.6667 * **Log shield length**
Correlation: r = .94790

Fig. 3.3.7. Relationship between log shield length (mm) and log wet weight (g) of male and female of *C. infraspinatus*.

Table 3.3.3a. Log linear relationship between length and weight by species and sex of hermit crabs in Matang mangrove estuary; SL=shield length; W=crab wet weight; M=male; F= female; CI=confidence interval for relationship.

Species	Sex	Linear equation	R^2	sig-p (CI=95%)	Significance of slopes between sexes	t-value
D. moosai	M	Log W = 3.1456Log SL + 0.9600	0.8556	<0.01	$p<0.05$	24.9709
	F	Log W = 2.9966Log SL + 1.0150	0.7564	<0.01		
D. lopochir	M	Log W = 3.2783Log SL + 0.8312	0.9336	<0.01	$p<0.05$	6.7604
	F	Log W = 2.9657Log SL + 0.9578	0.8582	<0.01		
C. infraspinatus	M	Log W = 2.7649Log SL + 1.0367	0.9187	<0.01	$p<0.05$	3.2611
	F	Log W = 2.6667Log SL + 1.0753	0.8985	<0.01		

Table 3.3.3b. Length-weight relationship by species and sex of hermit crabs in Matang mangrove estuary; L=shield length; W=crab wet weight; n=number of samples; Min=minimum; Max=maximum; M=male; F= female; a=y-intercept; b=slope.

			SL (mm)		Weight (mg)					Length-weight relationship
Species	Sex	n	Min	Max	Min	Max	Log a	a	b	$W=aL^b$
D. moosai	M	1209	1.52	4.59	32	870	0.9600	9.1201	3.1456	$W = 9.1201L^{3.1456}$
	F	599	1.30	2.98	25	267	1.0150	10.3514	2.9966	$W = 10.3514L^{2.9966}$
D. lopochir	M	481	1.48	5.18	30	1501	0.8312	6.7795	3.2783	$W = 6.7795L^{3.2783}$
	F	235	1.77	3.65	45	443	0.9578	9.0740	2.9657	$W = 9.0740L^{2.9657}$
C. infraspinatus	M	190	4.14	13.55	431	15211	1.0367	10.8818	2.7649	$W = 10.8818L^{2.7649}$
	F	75	3.48	9.53	319	6236	1.0753	11.8932	2.6667	$W = 11.8932L^{2.6667}$

3.3.2 Growth, mortality and recruitment patterns

The VBGF fitted length frequency histogram for *D. moosai* and *D. lopochir* populations are shown in Fig. 3.3.8. Goodness of fit (Rn) values for *D. moosai* and *D. lopochir* were 0.124 and 0.158 respectively. The generated VBGF curve for *D. moosai* had an asymptote shield length (L_∞) of 5.12 mm and growth constant (K) of 1.40. For *D. lopochir*, the curve yielded a L_∞ of 5.39 mm and K of 1.30. For both species, the starting sample was set at January 2011. The life spans of *D. moosai* and *D. lopochir* were estimated at 25.7 months and 27.7 months respectively. Growth performance index (ϕ') for *D. moosai* and *D. lopochir* were 1.53 and 1.61 respectively. Total mortality (Z) of hermit crabs as estimated from the length-converted catch curve (Fig. 3.3.9) was 7.06 year^{-1} (r^2=0.9635) and 3.71 year^{-1} (r^2=0.9628) for *D. moosai* and *D. lopochir* respectively. The M values yielded were 3.76 year^{-1} and 3.54 year^{-1} for *D. moosai* and *D. lopochir* respectively. The recruitment pattern as reconstructed from data of length-frequencies showed one major and one minor pulse in a year for *D. moosai* and *D. lopochir* (Fig. 3.3.10).

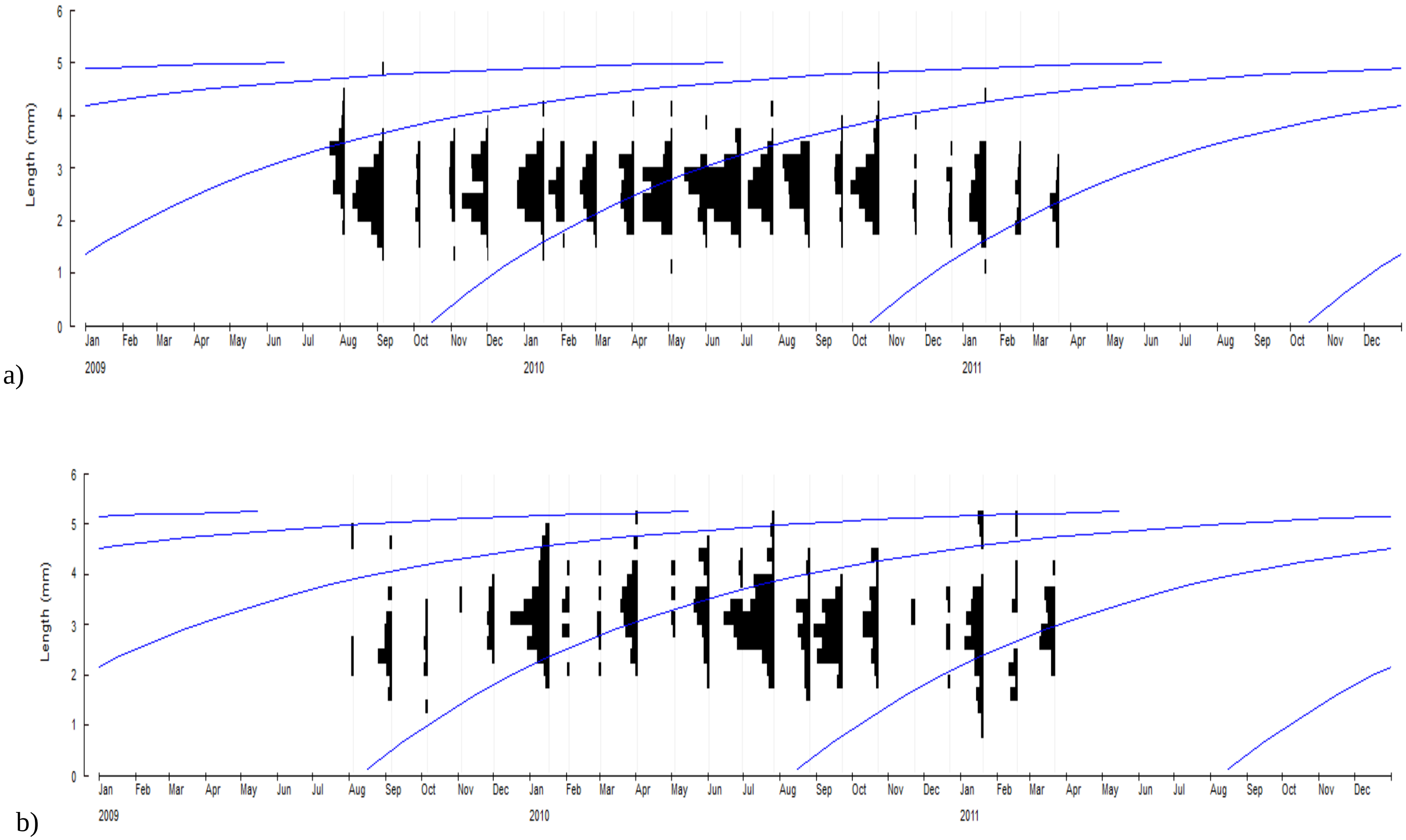
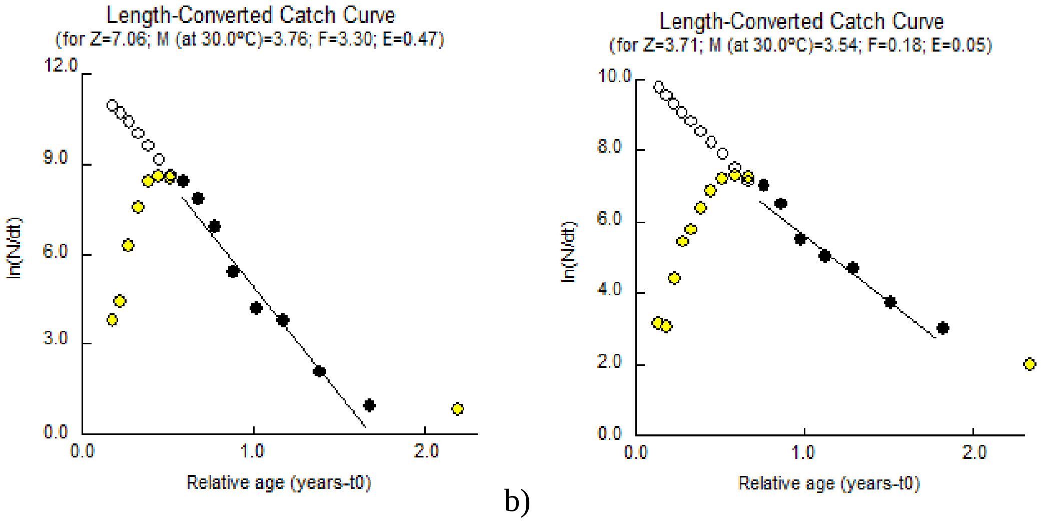
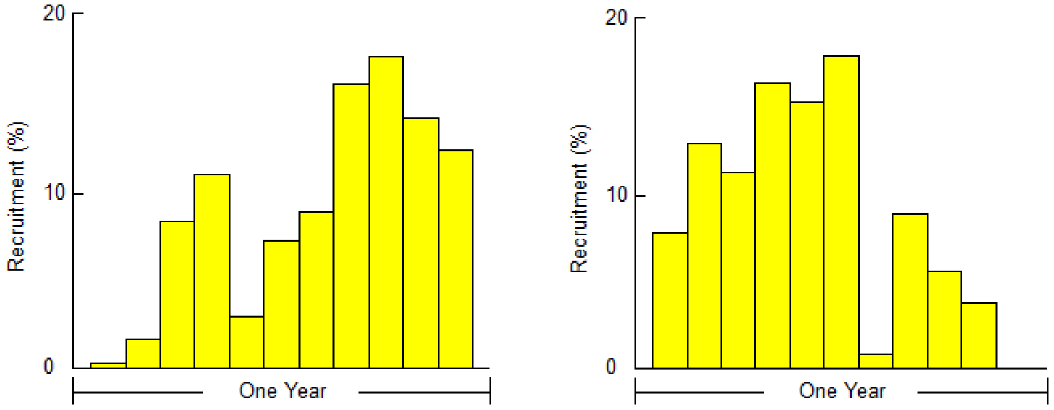


Fig 3.3.8. Von Bertalanffy growth curve (VBGF) best fitted to the length frequency histogram from August 2009 to March 2011 of a) *D. moosai* (L∞=5.12, K=1.40, Rn=0.124) and b) *D. lopochir* (L∞=5.39, K=1.30, Rn=0.158) populations at Matang mangrove estuary.



a) b)

Fig. 3.3.9. Length converted catch curve of a) *D. moosai* and b) *D. lopochir* populations with extrapolated points used to estimate probability of catch and values of total mortality, Z, natural mortality, M and fishing mortality, F.



a) b)

Fig. 3.3.10. Recruitment patterns plotted from length frequency data of a) *D. moosai* and b) *D. lopochir* populations at Matang mangrove estuary.

3.3.3 Discussion

3.3.3.1 Size and morphometry of hermit crabs

Hermit crabs of the genus *Clibanarius* and *Diogenes* were morphologically different whereby the latter possessed an elongated left compared to the right cheliped while the former had similar sized chelipeds. In term of size, *Diogenes* is a smaller genus based on shield length. Sexual dimorphism was apparent in all the three common species whereby males were larger (Table 3.3.2). Such feature is common in other hermit crab populations as reported for *Clibanarius erythropus* (Benvenuato & Gherardi, 2001), *Clibanarius vittatus* (Sampaio & Masunari, 2010) and *Clibanarius laevimanus* (Gherardi et al., 1994). Larger males may suggest differential use in energy whereby males utilised more energy for growth in larger body size, an advantage in agonistic encounters against competitors during mating, while females use energy for egg production and incubation. Also, the sexual divergence in growth rate and hence, body size may help to reduce potential competition for shell (Abrams, 1988).

Size of hermit crabs did not differ significantly among sites, except for *C. infraspinatus* whereby individuals found at shoal station were generally smaller than other stations (Table 3.3.1). This could be due to more *C. infraspinatus* juveniles at shoal station where recruitment occurred. *C. infraspinatus* could grow significantly larger than *Diogenes* species and thus, the large individuals of *C. infraspinatus* move upriver where larger shells like *Murex occa* are more available.

The length-frequency histograms of both *D. moosai* and *D. lopochir* show unimodal pattern (Fig. 3.3.4). According to Mantellato et al. (2007), unimodal pattern of size distribution is common in tropical and subtropical hermit crabs. However, such observation pertained mainly for pagurids. It is also suggested that such a distribution pattern is attributed to a stable population with continuous recruitment and constant mortality (Mantellato et al., 2007). Litulo (2005a) reported bi- and polymodality of the overall size-frequency distribution of *Clibanarius longitarsus* in southern Mozambique and suggested that such a distribution portrays differential patterns of recruitment, mortality rates and behavioural differences. Garcia & Mantellato (2001) reported general unimodality in the size frequency distribution of *Pagurus erythropus* in Southern Brazil, except that males were observed to have bimodal and even trimodal patterns. They suggested that this was due to migration for shell resources in males which also have differential life spans.

The lack of larger individuals can be reflected by the more equal sex ratio for *D. lopochir* in smaller size class (2.51-3.00mm) while subsequent size classes were dominated by the males. Similarly, female *D. moosai* were dominant in the smaller size class from 1.00-2.50mm while male *D. moosai* predominated in larger size class. There was an abrupt change in female-biased sex ratio in size class 2.01-2.50mm to male-biased sex ratio in size class 2.51-3.00mm of *D. moosai*. Right skewness of size distribution was evident in *C. infraspinatus* for both male and female (Fig. 3.3.4). Litulo (2005b) reported right skewness for both sexes of *Dardanus deformis* caught at Southern Mozambique which may be indicative of high mortality rates of the population. On the other hand, Branco et al. (2002) suggested that the lack of larger individuals might result from the shortage of shell supply. In this study, the lack of larger *C. infraspinatus* may result from the low availability of larger shells like *M. occa* and *P. cochlidium* compared to other smaller gastropods like the nassarids. Gherardi et al. (1994) suggested that the abrupt change in female-biased to male-biased sex ratio in the larger size class is an indication of occupancy of shells by the males that were not favourable to females.

3.3.3.2 Population dynamics of hermit crabs

The asymptote length of *D. moosai* and *D. lopochir* was 5.12mm and 5.39mm respectively. These values were higher than *D. pugilator* (4.70-5.08mm) in a Mediterranean shore as reported by Manjón-Cabeza and Garcia-Raso (1998) but much lower than larger species such as *Dardanus insignis* (20.75mm) in southern Brazil (Branco et al., 2002) and three sympatric species of *Clibanarius* in southern Brazil with asymptote lengths of between 7.39mm to 12.70mm (Turra and Leite, 2000b).

Growth rate (K) of both *D. moosai* and *D. lopochir* (1.3mm/year and 1.4mm/year respectively) were much higher compared to other reported tropical species on Brazilian shores; *D. insignis* (K=0.6) (Branco et al., 2002), *C. antillensis* (K=0.9), *C. sclopectarius* (K=0.65), *C. vittatus* (K=0.96) (Turra and Leite, 2000b) and temperate Mediterranean shore; *D. pugilator* (K=0.14-0.27) (Manjón-Cabeza & Garcia-Raso, 1998). The higher growth of both *D. moosai* and *D. lopochir* could suggest good food supply in the Matang mangrove estuary. However, both *D. moosai* and *D. lopochir* have shorter lifespans estimated at 26 months and 28 months respectively, as compared to larger species such as *Dardanus* (Branco et al., 2002) and *Clibanarius* (Turra & Leite, 2000b) with life spans that ranged from 42-47 months. A closely related species, *D. pugilator* has a similar lifespan of between 24 to 27 months (Manjón-Cabeza & Garcia-Raso, 1998).

The higher natural mortality of both species of *Diogenes*, M per year (*D. moosai* = 3.76 year^{-1}; *D. lopochir* = 3.54 year^{-1}) could be offset by continuous reproduction in particular *D. moosai* to replenish the population (see section 3.5). As a comparison, the total mortality estimated in this study was much higher compared to what was reported by Branco et al. (2002) for *Dardanus insignis*, a larger species which has a total mortality, Z (i.e natural mortality + fishing mortality) of only 2.21 year^{-1}. Fishing mortality (F) in both species (*D. moosai* = 3.30; *D. lopochir* = 0.18) despite their non-commercial value is explained by cockle dredging activity imposing coincidental fishing mortality on hermit crabs especially *D. moosai* which is dominant on the mudflat area. In contrast, *D. lopochir* found more at the shoal station where there is less cockle harvesting activity had a lower value of F.

3.3.4 Conclusion

Sexual dimorphism occurs in all three major species (*C. infraspinatus*, *D. moosai* and *D. lopochir*) with the male being generally larger than female. The overall length-frequency for both *D. moosai* and *D. lopochir* showed unimodal pattern, which is common in tropical and subtropical hermit crabs. Length weight relationship yielded the parameter b (or slopes) that ranged from 2.67 to 3.28 with males of both *Diogenes* species having significantly higher rate of weight increment as they grow compared to the females. The fitted VBGF estimated the growth constant (K) for *D. moosai* and *D. lopochir* at 1.4 and 1.3 respectively which are much higher than other recorded tropical species (e.g. *D. insignis*, *C. antillensis*, *C. sclopectarius* and *C. vittatus*). The recruitment pattern showed one major and one minor pulse in a year for *D. moosai* and *D. lopochir*. Both *D. moosai* and *D. lopochir* have much lower lifespan (2.14 years and 2.31 years respectively) compared to other larger species such as *Dardanus* and *Clibanarius* (42 to 47 months) but similar lifespan with closely related species, *D. pugilator* (24 to 27 months). *D. moosai* suffered higher total mortality (7.06 year^{-1}) compared to *D. lopochir* (3.71 year^{-1}) suggesting influence of cockle harvesting activity at the mudflat where *D. moosai* is abundant.

3.4 SHELL USE BY HERMIT CRABS

(Part of the results of this section has been published in Teoh & Chong (2014b); see Appendix II)

This section addresses objective 3 which is to determine the shell use pattern of hermit crabs and the factors affecting shell selection. The study sought to answer how sympatric hermit crab species share or compete for similar shell resources inter- and intraspecifically. It is hypothesised that shell use by hermit crabs is modulated by three factors: shell size, shape (species) and availability. To address the above objective and hypothesis, morphometric measurements of the occupied gastropod shells (shell height, shell width, aperture length, aperture width and shell weight) and hermit crabs (shield length, shield width, length of left chela and width of left chela) were measured and spatial distribution of live gastropods at mid-estuary, river mouth, mudflat and shoal area of Matang waters were quantified. The study elucidates how sympatric hermit crabs are partitioned in terms of shell use pattern based on the three factors and to further answer the following specific research questions; (1) are high densities of hermit crabs matched by equally abundant gastropod shells of suitable sizes? (2) is (and how) shell use pattern affected by interspecific and intraspecific (sex and size) interactions? (3) how and what attributes (size and shape) of occupied shells are matched to that of the crabs? Statistical analyses such as chi-square test, discriminant analysis, canonical correlation analysis, Spearman rank correlation and Kruskal-Wallis test were used to test for significant differences and relationships.

3.4.1 Shell use by species and sex of hermit crabs

A total of 19 species of gastropod shells were used by *Diogenes moosai*, *D. lopochir* and *Clibanarius infraspinatus*. Table 3.4.1 shows list of shell species and composition of hermit crabs by species and sex based on their shell occupancy. Male *D. moosai* occupied mainly shells of *N. jacksoniasus* (41.10%) and *N. cf. olivaceus* (27.82%) while the females used mainly shells of *N. cf. olivaceus* (51.05%) and *C. cingulata* (32.05%). Male *D. lopochir* occupied mainly shells of *N. jacksoniasus* (34.44%) and *T. malayensis* (33.07%) while majority of the females used shells of *N. jacksoniasus* (59.27%) particularly the ovigerous female (78.87%). Most of *C. infraspinatus* (37.50% male and 41.46% female) used *M. occa* shells. This was followed by *P. cochlidium* which mostly used by the males (21.00%) and *N. dorsatus*, mostly used by the females (17.07%).

Table 3.4.1. List of gastropod species used by different species and sex of hermit crabs from Matang mangrove estuary (M=male;F=non-ovigerous female; OF=ovigerous female; AF=all females '*' denotes top two most common shells used by each species and sex).

	Clibanarius infraspinatus				*Diogenes lopochir*				*Diogenes moosai*			
Shell type	**M**	**F**	**OF**	**AF**	**M**	**F**	**OF**	**AF**	**M**	**F**	**OF**	**AF**
Buffonaria sp.	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cerithidea cingulata	0.00	0.00	0.00	0.00	3.13	11.86	9.86*	11.29	6.68	26.09*	33.75*	32.05*
Littorina melanostoma	0.00	0.00	0.00	0.00	0.39	0.56	0.00	0.40	0.16	0.00	0.00	0.00
Littorina scabra	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.72	0.00	0.16
Pugilina cochlidium	21.00*	6.58	16.67	7.32	0.59	0.00	0.00	0.00	0.08	0.00	0.00	0.00
Melongena ternatana	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Murex occa	37.50*	42.11*	33.33*	41.46*	3.72	0.56	0.00	0.40	0.48	0.00	0.00	0.00
Nassarius coronatus	0.00	0.00	0.00	0.00	0.20	0.00	0.00	0.00	1.43	0.72	0.41	0.48
Nassarius dorsatus	7.50	17.11*	16.67	17.07*	3.72	3.39	1.41	2.82	9.78	1.45	2.28	2.09
Nassarius jacksoniasus	0.50	1.32	0.00	1.22	34.44*	51.41*	78.87*	59.27*	41.10*	13.77	10.97	11.59
Nassarius cf. olivaceus	0.00	0.00	0.00	0.00	6.26	15.82*	5.63	12.90*	27.82*	52.17*	50.72*	51.05*
Natica tigrina	8.50	13.16	0.00	12.20	9.59	1.69	0.00	1.21	2.86	0.72	0.00	0.16
Planaxis sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00
Prunum sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.72	0.00	0.16
Thais lacera	14.00	13.16*	33.33*	14.63	3.52	0.00	0.00	0.00	0.16	0.00	0.00	0.00
Thais malayensis	7.00	6.58	0.00	6.10	33.07*	10.17	1.41	7.66	6.52	2.17	1.04	1.29
Trigonafera costifera	0.00	0.00	0.00	0.00	0.39	4.52	2.82	4.03	2.86	1.45	0.83	0.97
Turricula javana	0.50	0.00	0.00	0.00	0.98	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Turricula duplicata	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

3.4.2 Spatial variations in shell use

Both *Diogenes moosai* and *D. lopochir* utilized the shells of 14 gastropod species, but only four shell species were frequently utilized, or with more than 20% shell occupancy; these were *Cerithidea cingulata*, *Nassarius jacksonianus*, *N. cf. olivaceous* and *Thais malayensis* (Fig. 3.4.1 and 3.4.2). Log-linear analysis shows good fit (to observed cell frequencies) for the *D. lopochir*'s model with shell use related to site (two-way association) and shell use related to sex (maximum log likelihood χ^2 = 5.34, df=4, p=0.254). The fitted model for *D. moosai* also had a good fit, with similar two-way associations (maximum log likelihood χ^2 = 2.72, df=4, p=0.606).

At mudflat, *D. moosai* females equally occupied either *N. cf. olivaceus* (non-ovigerous females 51.43%, ovigerous females 43.87%) or *C. cingulata* (non-ovigerous females 38.57%, ovigerous females 44.19%) while male utilized mostly *N. cf. olivaceus* (29.97%) and *N. jacksonianus* (32.21%) (Fig. 3.4.1). *D. lopochir* occurred in very low abundance at mudflat; only 40 individuals were collected from a total of 57 trawls from August 2009 to March 2011. Non-ovigerous females (15 individuals) of *D. lopochir* occupied equally *N. jacksonianus*, *N. cf. olivaceus* and *C. cingulata* (26.67 %) while majority of ovigerous females (5 individuals) occupied *N. jacksonianus*. Majority of males (20 individuals) occupied equally between *N. cf. olivaceus* and *T. malayensis* (25.00% each) (Fig. 3.4.2).

At shoal area, male *D. moosai* occupied mostly *N. jacksonianus* (56.49%) while majority of females occupied *N. cf. olivaceus* (non-ovigerous female 53.33% and ovigerous female 62.42%) shells (Fig. 3.4.1). Most male *D. lopochir* occupied either *N. jacksonianus* (35.28%) or *T. malayensis* (33.82%) shells, while majority of females occupied *N. jacksonianus* (non-ovigerous female 53.70%, ovigerous female 78.79%) shells (Fig. 3.4.2).

Majority of *C. infraspinatus* occupied *M. occa* shells in all sampling stations (Fig. 3.4.3). At mid-estuary, similar proportion of male (42.19%) and non-ovigerous (37.50%) *C. infraspinatus* occupied shells of *M. occa*. However, majority ovigerous *C. infraspinatus* (40.00%) occupied *T. lacera* shells. At shoal area, male *C. infraspinatus* occupied equally shells of *M. occa* (27.66%), *T. lacera* (21.28%) and *T. malayensis* (21.28%) whereas all ovigerous females occupied *M. occa* shells (Fig. 3.4.3).

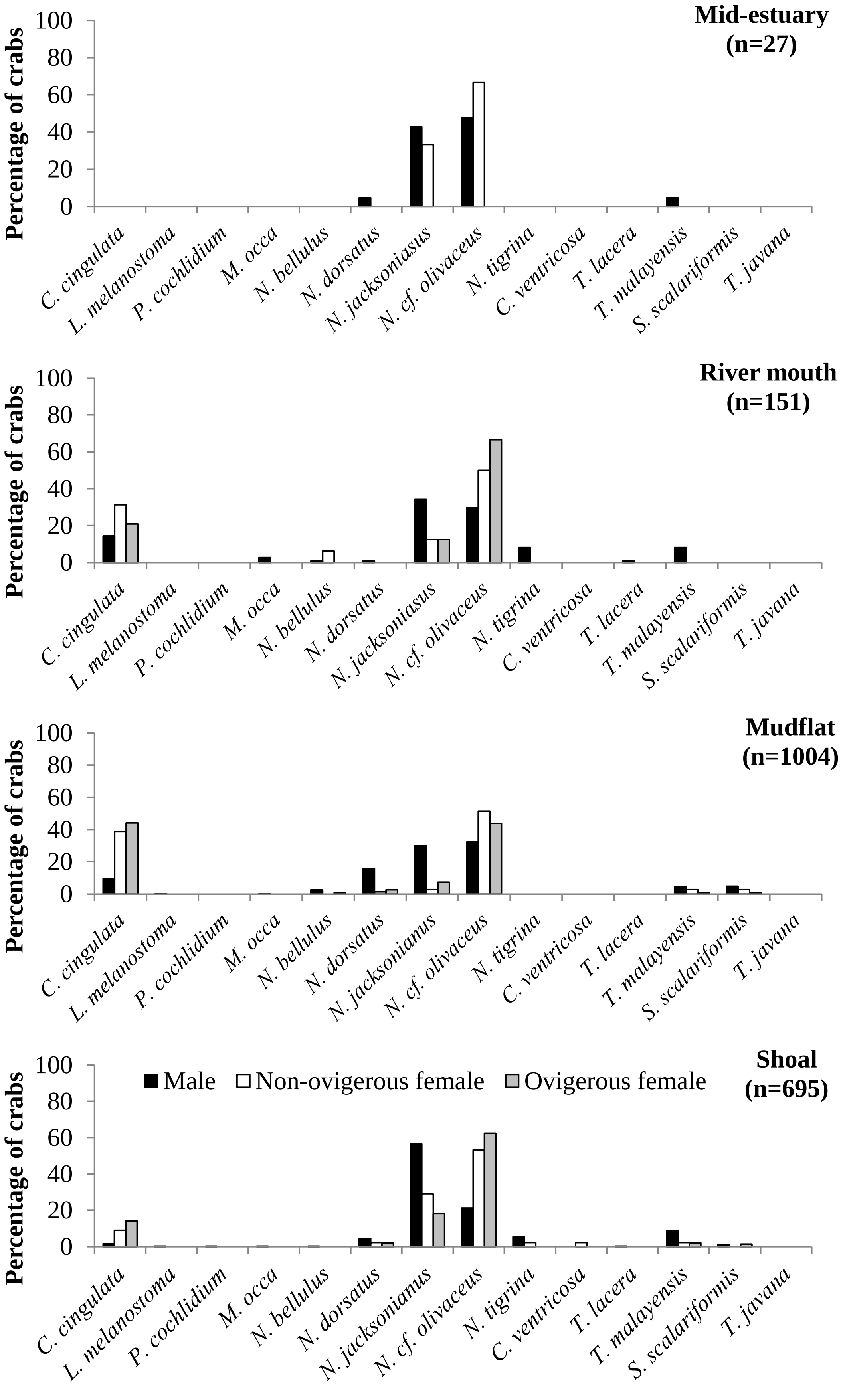


Fig. 3.4.1. Frequency of males, non-ovigerous females and ovigerous females by shell type for *D. moosai* at different sampling stations. Filled black bars = male, hollow bars = non-ovigerous female, filled grey bars = ovigerous females; n = sample size.

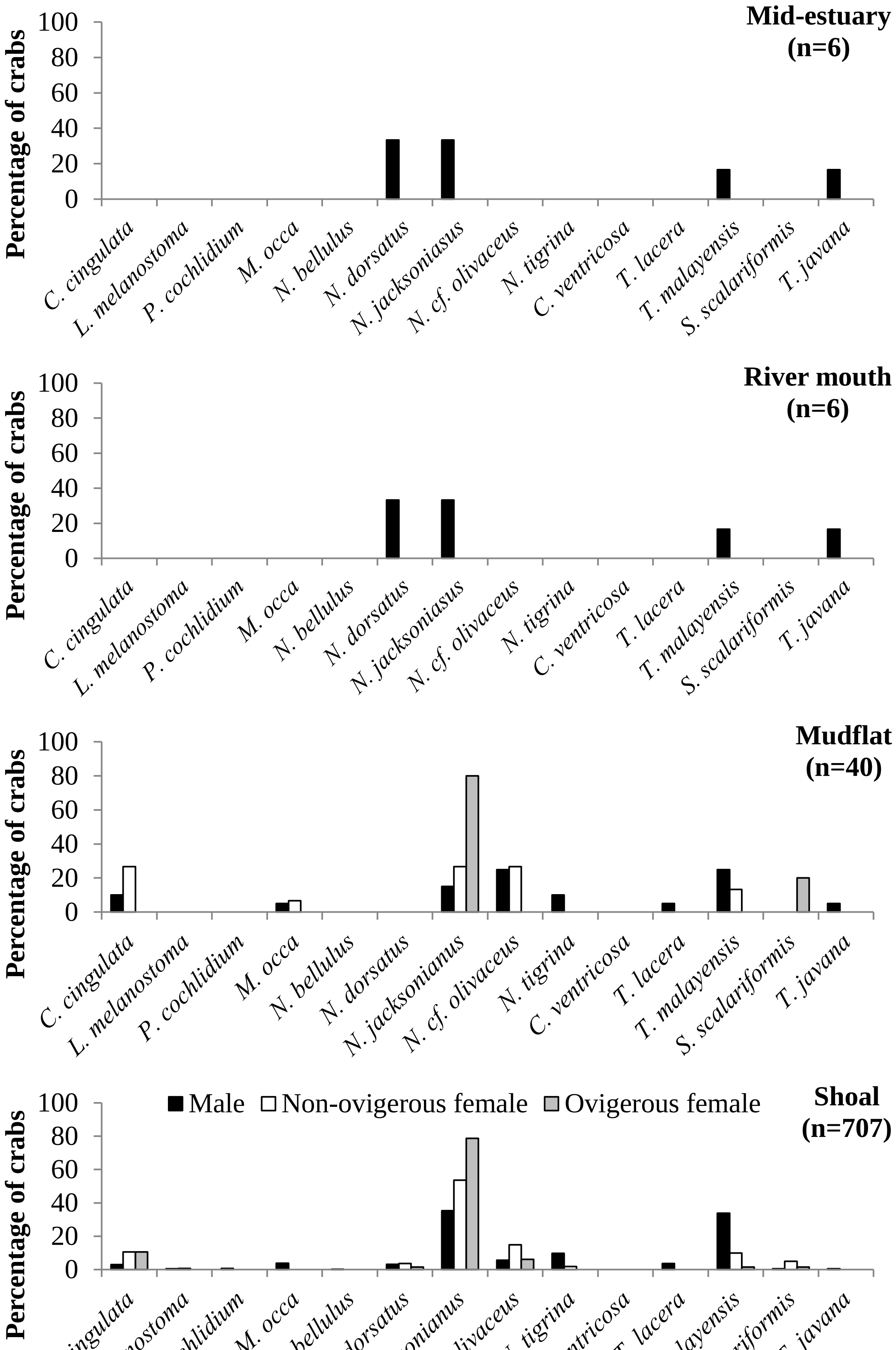


Fig. 3.4.2. Frequency of males, non-ovigerous females and ovigerous females by shell type for *D. lopochir* at different sampling stations. Filled black bars = male, hollow bars = non-ovigerous female, filled grey bars = ovigerous females; n = sample size.

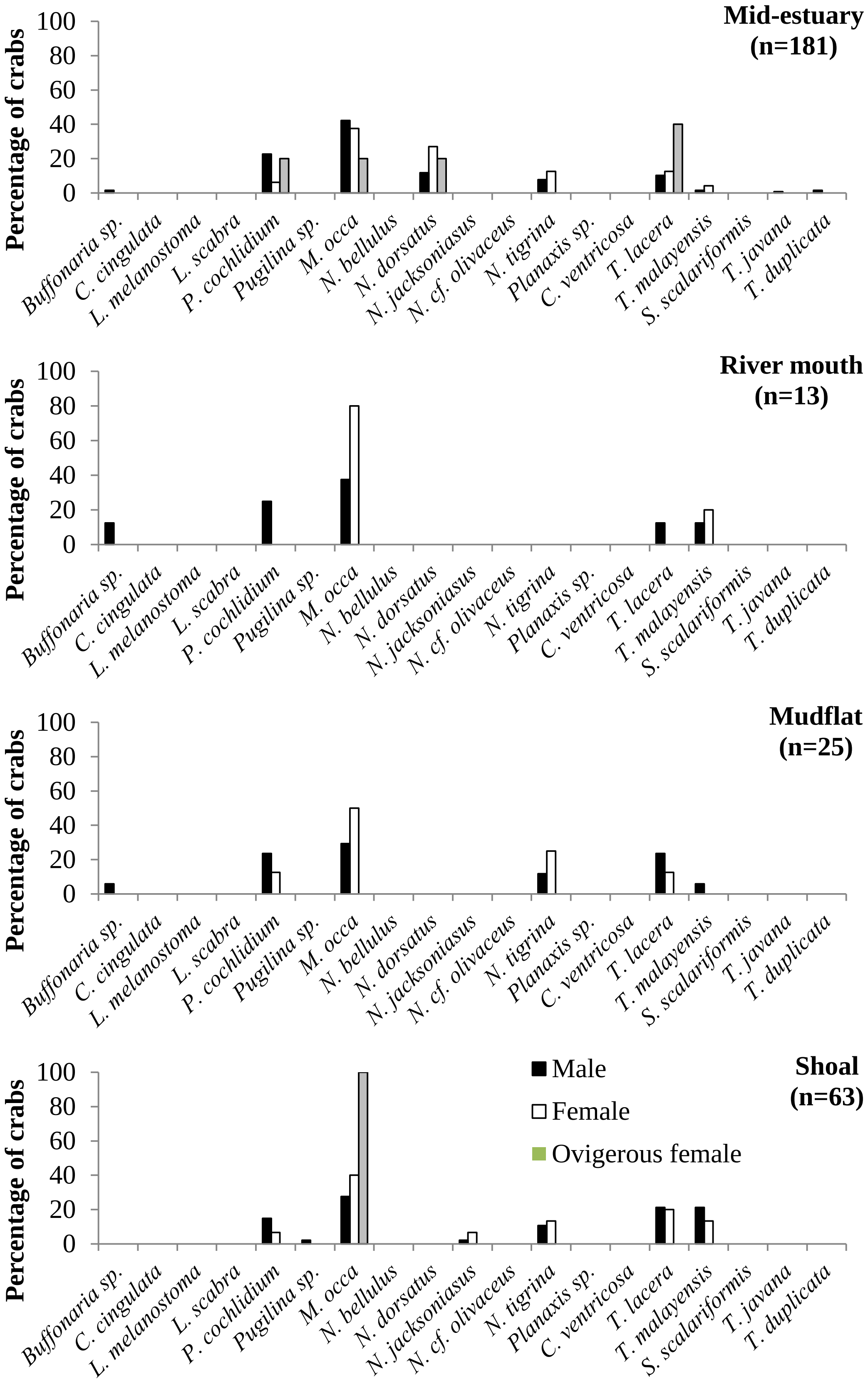


Fig. 3.4.3. Frequency of males, non-ovigerous females and ovigerous females by shell type for *C. infraspinatus* at different sampling stations. Filled black bars = male, hollow bars = non-ovigerous female, filled grey bars = ovigerous females; n = sample size.

3.4.3 Shell characteristics by species

Discriminant analysis (DA) of the shell characteristics indicates that the seven types of occupied gastropod shells by both *Diogenes* species could reasonably be distinguished based on the first two canonical roots which explained 93.1% of the total variation. The occupied shells show either large or subtle differences in shell size and shape (shell and aperture elongation). *C. cingulata*, *T. malayensis* and *N. tigrina* were well separated from each other while large *C. cingulata* and small *T. malayensis* overlapped with the three species of *Nassarius* in term of shell morphometry (Fig. 3.4.4). The shell morphometrics of *T. lacera* however strongly overlapped with *T. malayensis*. The standardized coefficients of the first root which accounted for 70.2% of the total variation (eigenvalue=7.21) loaded heaviest on the variable ShW (1.25), and ShH (-1.22); therefore, *N. tigrina*, *T. lacera* and *T. malayensis* had the largest shell width (more globose shell), while *C. cingulata* had the shortest shell width but the longest shell height (more elongated shell). Since the second root (eigenvalue=2.36) loaded heaviest on AW (1.32) and AL (-1.93), *N. cf. olivaceus* and *N. bellulus* thus had the longest aperture length, but shortest aperture width compared to the other five species (Table 3.4.2).

Table 3.4.2. Standardised coefficients for canonical variables of most common shells used by *D. lopochir* and *D. moosai* based on discriminant analysis (AL=aperture length; AW=aperture length; ShH=shell height; ShW=shell width; ShWt=shell weight).

Variable	Root 1	Root 2	Root 3
AL	0.40069	-1.92655	-0.39375
AW	0.24674	1.31524	-1.35111
ShH	-1.21913	0.66211	-0.05658
ShW	1.25399	0.67835	2.13332
ShWt	-0.19820	-0.41710	-0.79993
Eigenvalue	7.21164	2.36058	0.63643
Cumulative proportion	0.70154	0.93117	0.99309

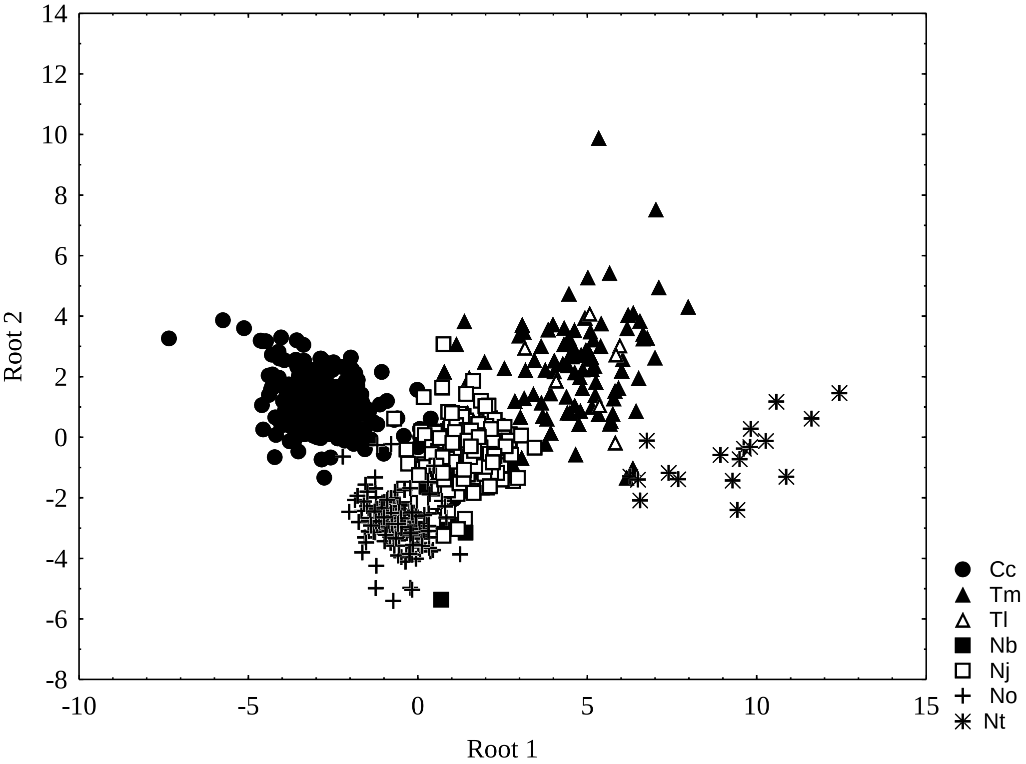
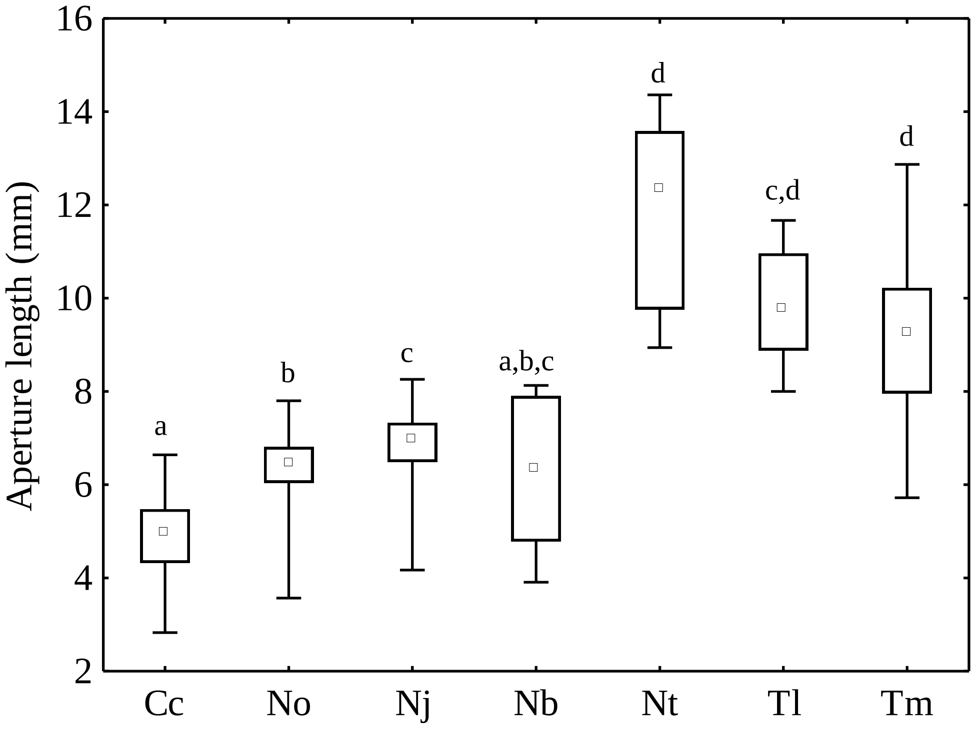


Fig. 3.4.4. Plots of canonical scores derived from discriminant analysis of shell parameters (aperture length, aperture width, shell height, shell length and shell weight) of seven gastropod species used by both *Diogenes* species. Filled circles = *Cerithidea cingulata* (Cc), hollow squares = *Nassarius jacksonianus* (Nj); filled squares = *Nassarius bellulus* (Nb); crosses = *Nassarius cf. olivaceus* (No); filled triangles = *Thais malayensis* (Tm); hollow triangles = *Thais lacera* (Tl); asterisks = *Natica tigrina* (Nt).

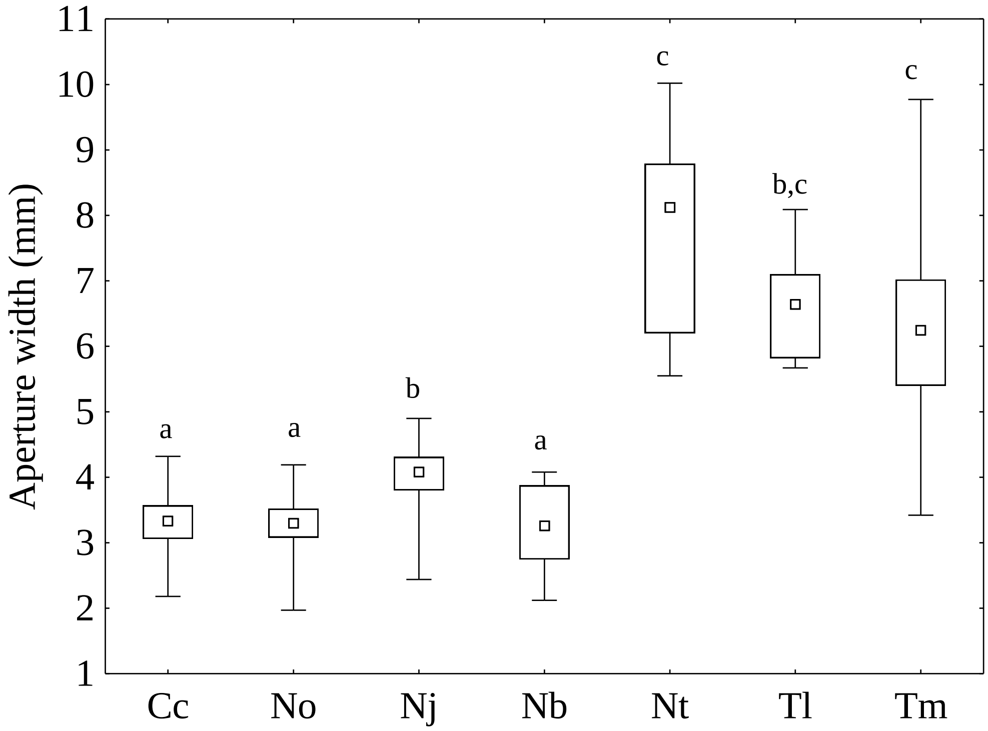
The four morphometric parameters (ShH, ShW, AL and AW) that distinguished the occupied shell species are depicted in Fig. 3.4.5. The four most occupied shell species, *C. cingulata*, *N . jacksonianus*, *N. cf. olivaceus* and *T. malayensis* ranged widely in their lengths from 2.83-12.87 mm (AL), 1.97-9.77 mm (AW), 8.09-30.19 mm (ShH) and 4.37-20.13 mm (ShW), indicating that the shells of both small and large snails were occupied. *C. cingulata* and *T. malayensis* were respectively the smaller and larger values of these parameters with no overlaps. Intermediate values of these shell parameters were however covered by the two nassarid species.

T. malayensis had a significantly larger aperture length (H_{964} = 686.69, p<0.001), aperture width (H_{964} = 610.67, p<0.001), shell height (H_{964} = 310.68, p<0.001) and shell width (H_{964} = 655.10, p<0.001) than the other three common shell species. *N. jacksonianus* was the larger (p<0.001) of the two common nassarids in terms of aperture width and shell width whereas *C. cingulata* had significantly smaller (p<0.001) aperture length, aperture width and shell width than *N. jacksonianus*. The aperture length, aperture width and shell width of the rarely used larger shells like *T. lacera* and *N. tigrina* were significantly larger (p<0.001) than those of *N. cf. olivaceus* and *C. cingulata* but overlapped with those of *T. malayensis* (Fig. 3.4.5). The shells of the *Thais* and *Natica* species were relatively thicker or denser than that of nassarids (Fig. 3.4.5e) (Appendix XIV).



(a)

(Figure 3.4.5, continued)



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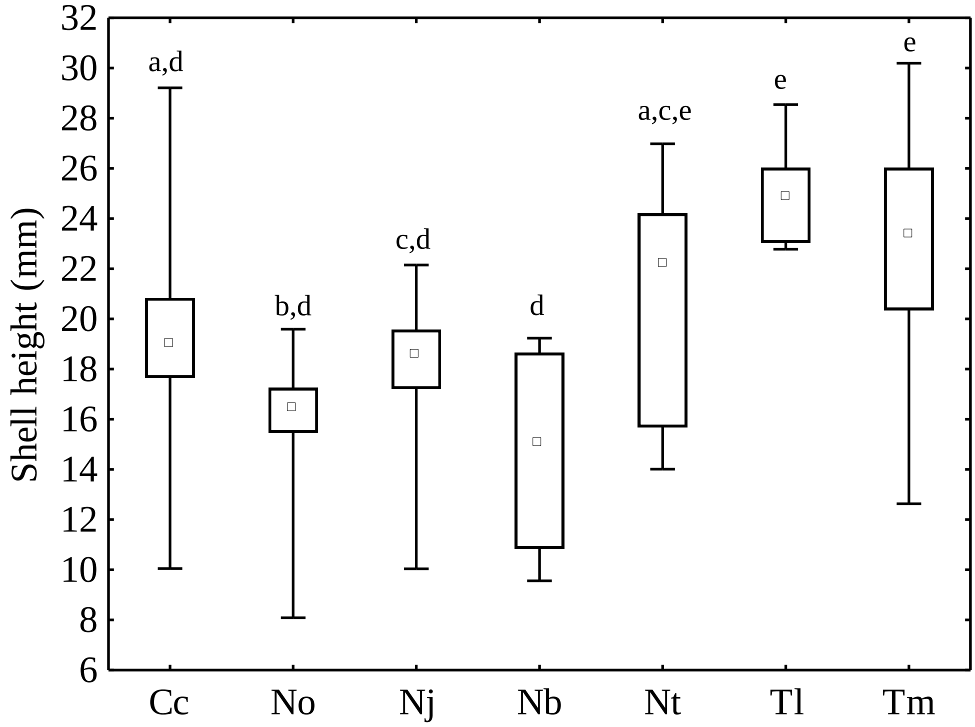
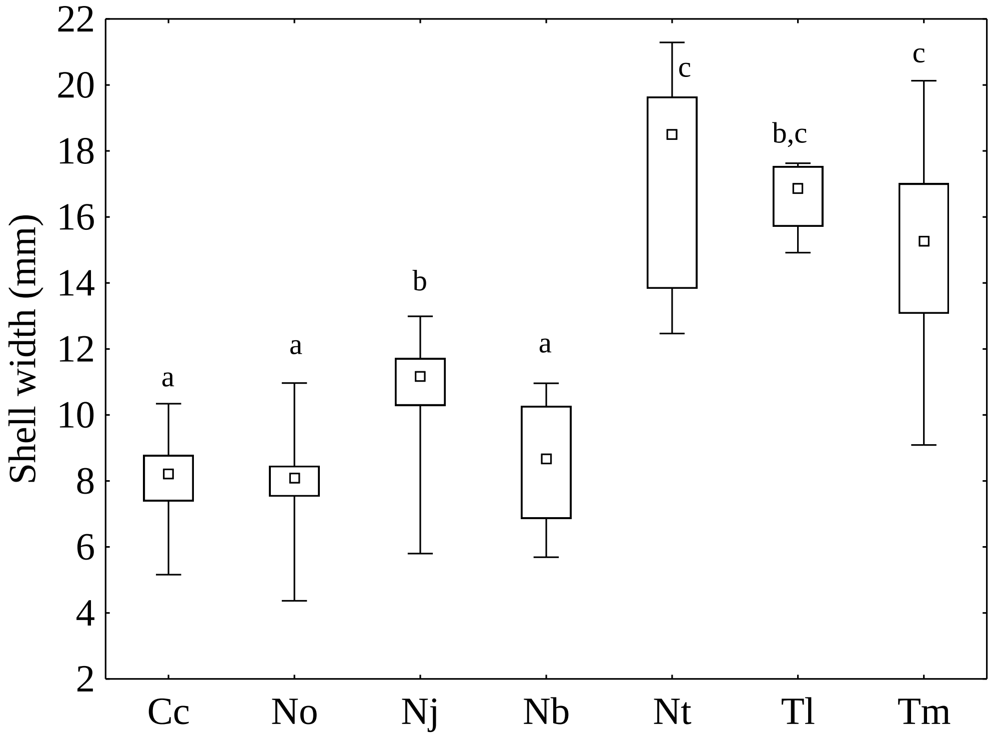
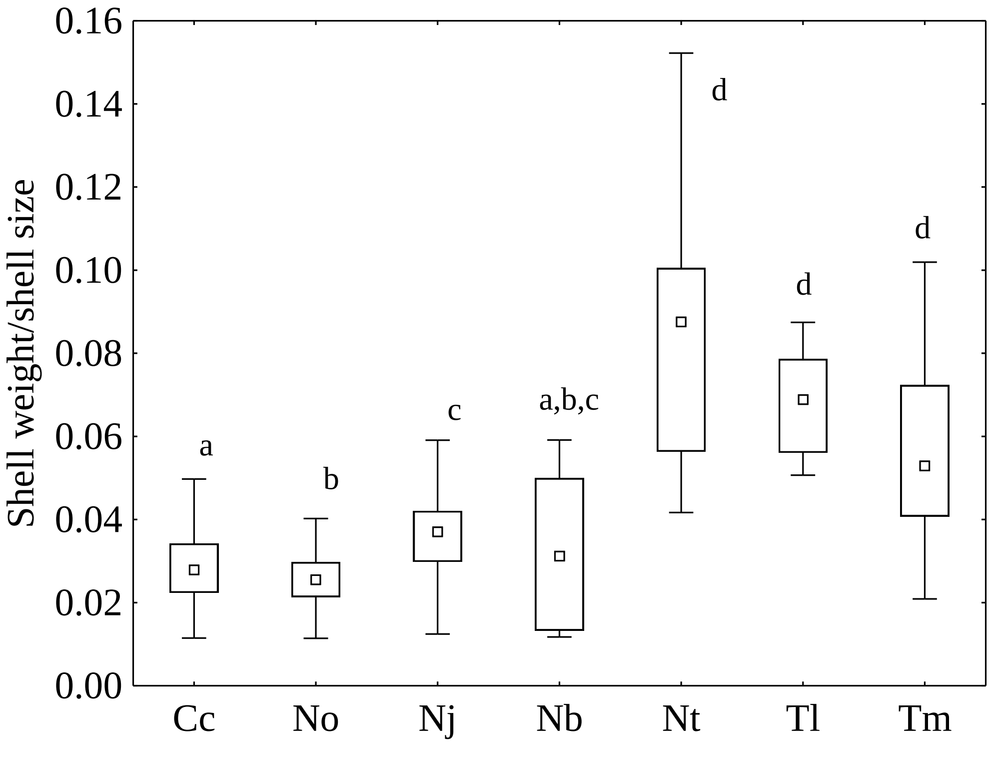


(c)

(Figure 3.4.5, continued)



(d)



(e)

Fig. 3.4.5. Box and whisker plots of (a) aperture length, (b) aperture width, (c) shell height and (d) shell width of seven shells used by male and female *Diogenes moosai* and *D. lopochir*. Cc=*Cerithidea cingulata*, No=*Nassarius cf. olivaceus*, Nj=*Nassarius jacksonianus*, Nb=*Nassarius bellulus*, Nt=*Natica tigrina*, Tl=*Thais lacera*, Tm=*Thais malayensis*; Box = 25th and 75th percentiles, midpoint = median, whiskers = minimum and maximum; Letters over bars denote the hierarchy after Multiple Comparison tests.

3.4.4 Relationship between crab and shell attributes

For both species and sex, the overall canonical correlation, R (root 1) was highly significant ($p<0.001$) between the two sets of crab and shell variables. Extracted variance and redundancy results of root 1 and all (total) roots are presented in Table 3.4.3. Redundancy analysis shows quite a strong relationship between variables of the crab and shell data sets (Table 3.4.3). Based on all canonical roots for female *D. lopochir*, the set of shell variables accounted for 48.2% of the variance from the set of crab variables, while crab variables accounted for 42.4% of the variance from shell variables. For male *D. lopochir*, these were 55.2% and 50.1% respectively.

The first root (R1) however extracted an average of 82% of the total variance from the crab variables or 70% of total variance from the shell variables for female *D. lopochir*. Hence, based on the first root, canonical weights of crab variables in female *D. lopochir* were further evaluated; they were highest for wet weight and chela width, whereas for shell variables, canonical weights were highest in aperture width, aperture length and shell weight (Table 3.4.4). Similar interpretation of the first root for male *D. lopochir*, which accounted for 80% or more of the total variance for crab and shell variables (Table 3.4.3), indicated canonical weights of crab variables were highest for shield width, chelal length and wet weight whereas for shell variables, canonical weights were highest in shell height, shell width and shell weight (Table 3.4.4).

Redundancy results for male and female *D. moosai* similarly indicate that the set of crab variables was strongly related to the set of shell variables (Table 3.4.3). Based on the first root, canonical weights of crab variables in female *D. moosai* were highest for shield width and wet weight whereas for shell variables, canonical weights were highest for aperture length, shell width and shell weight. For male *D. moosai*, canonical weights of crab variables were highest in shield width and wet weight whereas for shell variables, canonical weights were highest in aperture length, aperture width and shell width (Table 3.4.4).

For male *C. infraspinatus*, overall canonical R was 0.7421 indicating substantial correlation between variables of hermit crabs and shells. Redundancy analysis showed that both set of crab and shell variables accounting for 47% and 46% of the variance of the other. The first root extracted an average of 80% of the variance from the crab variables and 79% of the shell variables (Table 3.4.4). Based on the first root, canonical weights of crab variables in *C. infraspinatus* were highest for chelae length (ChL=-1.1043), wet weight (WW=0.9681) and shield width (SW=1.1734) whereas for shell variables, canonical weights were highest for aperture width (AW=0.7552), shell height (ShH=0.5213) and shell width (ShW=-0.2835) (Table 3.4.4).

Table 3.4.3. Variance extracted (%) and redundancy (%) results of root 1 and the total from canonical analysis of left set (crab variables) and right set (shell variables) data of male (M) and female (F) *D. moosai*, *D. lopochir* and *C. infraspinatus* (sex data pooled).

Species	[a]Sex	Canonical R	Chi^2 (25)	Variance extracted (%)				Redundancy (%)			
				Left set		Right set		Left set		Right set	
				Root 1	Total	Root 1	Total	Root 1	Total	Root 1	Total
D. moosai	M	0.8632	617.23	89.39	100.00	68.06	100.00	66.60	67.45	50.71	53.31
	F	0.7887	397.99	76.21	100.00	61.55	100.00	47.41	47.91	38.29	40.53
D. lopochir	M	0.7860	175.50	88.16	100.00	79.55	100.00	54.47	55.24	49.15	50.14
	F	0.7586	81.07	81.84	100.00	70.08	100.00	47.09	48.23	40.32	42.36
C. infraspinatus		0.7421	72.86	80.04	100.00	78.76	100.00	44.08	47.04	43.37	46.08

Table 3.4.4. Canonical weights of the most statistically significant root (root 1) for morphometrics of male (M) and female (F) *D. moosai*, *D. lopochir* and *C. infraspinatus* (sex data pooled) and their occupied gastropod shell.

		Canonical Weights				
		D. moosai		*D. lopochir*		*C. infraspinatus*
Variable	[b]Morphometrics	M	F	M	F	Pooled
Crab (left set)	SL	-0.0182	-0.1344	-0.1628	-0.0850	-0.3067
	SW	0.4733*	0.3826*	0.7472*	0.0086	1.1734*
	ChL	0.0425	0.1022	-0.8290*	0.1620	-1.1043*
	ChW	0.0137	0.0625	0.6088	0.3598*	0.2145
	WW	0.5129*	0.6507*	0.6281	0.6073*	0.9681*
Shell (right set)	AL	0.3885*	0.3903*	-0.0735	0.2628*	-0.1440
	AW	-0.2629*	-0.0648	0.1798	0.4657*	0.7552*
	ShH	0.0769	0.0153	0.4329*	0.1806	0.5213*
	ShW	0.9404*	0.5969*	0.8471*	0.2230*	-0.2835*
	SWt	-0.1060	0.2233*	-0.3918*	-0.0042	0.1636

(SL=shield length; SW=shield width; ChL=chelae length; ChW=chelae width; WW=wet weight; AL=aperture length; AW=aperture width; ShH=shell height; ShW=shell width; SWt=shell weight; '*' indicates morphometrics with higher magnitude of canonical weight.

Factorial (2-way) ANOVA revealed that female *D. moosai* occupied shells with significantly smaller mean aperture length ($F_{(2,969)}=6.15$, $p<0.001$), aperture width ($F_{(2,969)}=32.28$, $p<0.001$) shell width ($F_{(2,969)}=9.14$, $p<0.001$) and shell weight ($F_{(2,969)}=14.05$, $p<0.05$) than those of male *D. moosai* and both male and female *D. lopochir*. Male *D. moosai* overlapped with female *D. lopochir* in terms of their aperture length ($p>0.05$), aperture width ($p>0.05$) and shell width ($p>0.05$). On the other hand, male *D. lopochir* occupied shells with significantly larger mean shell height ($F_{(2,969)}=20.49$, $p<0.001$) than female *D. lopochir* and both male and female *D. moosai* (Appendix XV).

The degree of shell elongation could be expressed by the ratio of the shell height to shell width (Edgell & Miyashita, 2009). Generally, *D. lopochir* used shells with a lower height to width ratio i.e. more globose shells, whereas *D. moosai* used relatively more elongated shells, i.e. larger height to width ratio. However, females of both species tended to occupy relatively more elongated shells than males which occupied more globose shells (Fig. 3.4.6).

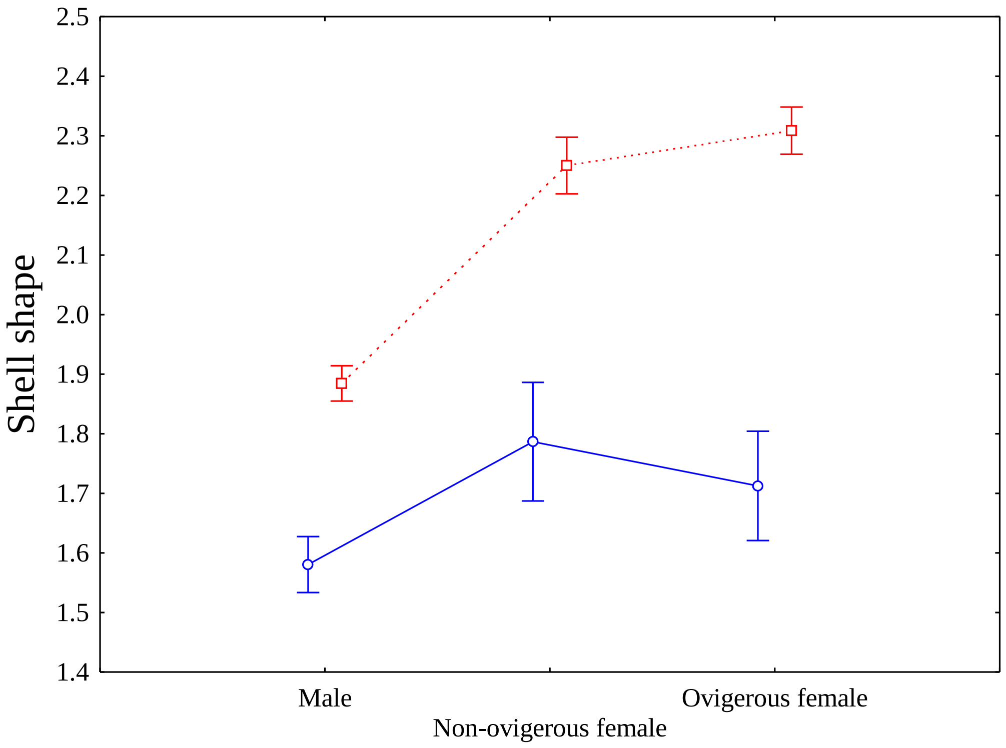


Fig. 3.4.6. Shell shape by sex (male, non-ovigerous female/female and ovigerous female) of *D. moosai* (dotted line) and *D. lopochir* (solid line).

3.4.5 Shell use by hermit crabs: Influence of shell attributes

The CCA results (Fig. 3.4.7) revealed that smaller sized males (MoM1 and MoM2) and females (MoF1 and MoF2) of *D. moosai* occupied short narrow shells with small elongated apertures such as *N. cf. olivaceus*, *N. bellulus* and *Cerithidea cingulata*. Smaller sized *D. lopochir* including males (LoM1 and LoM2) and females (LoF2 and LoF3) may also occupy such shells, but most of them occupied the more globose shells of *N. jacksonianus*. Larger individuals (LoM3 and LoM4) used larger shells with larger apertures i.e. larger globose shells with more rounded apertures e.g. *Thais malayensis*, *T. lacera*, *Pugilina cochlidium*, *Natica tigrina* and *Murex occa*.

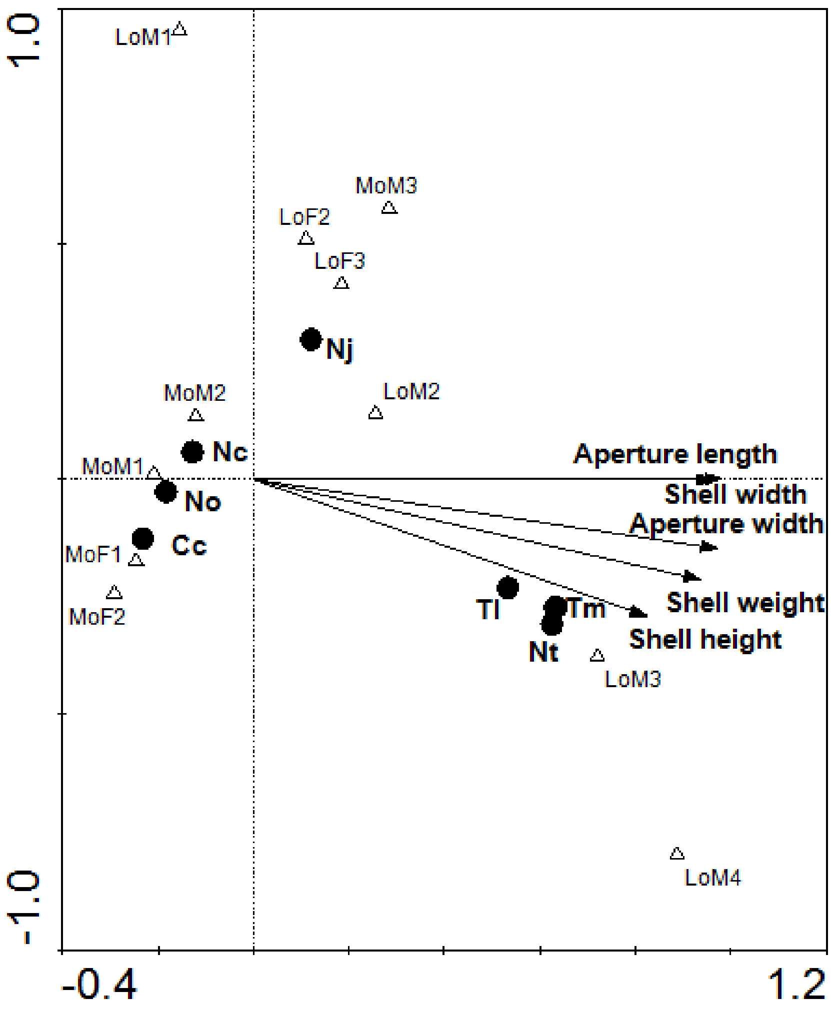


Fig. 3.4.7. Triplots from canonical correspondence analysis (CCA) of shell use by *D. lopochir* and *D. moosai* of different size classes as influenced by shell attributes. First axis is horizontal, second axis vertical. Filled circles indicate shell species; Cc = *Cerithidea cingulata*, No = *Nassarius cf. olivaceus*, Nj = *Nassarius jacksonianus*, Nc = *Nassarius bellulus*, Tm = *Thais malayensis*, Tl = *Thais lacera*, Nt = *Natica tigrina*. Arrows indicate shell attributes in direction of increasing magnitude. Open triangles indicate hermit crab species (Mo = *D. moosai*, Lo = *D. lopochir*) by sex (M = male, F = female) and size class (numeral, please refer to Table 3.4.5 for explanation).

Table 3.4.5. Groupings of hermit crabs based on species, sex and size classes (shield length, mm) with their annotated codes for canonical correspondence analysis (CCA).

Species	Sex	Size class (mm)	Code	n
D. moosai	Female	1.00-2.00	MoF1	53
		2.01-3.00	MoF2	311
	Male	1.00-2.00	MoM1	14
		2.01-3.00	MoM2	252
		3.01-4.00	MoM3	119
D. lopochir	Female	2.01-3.00	LoF2	50
		3.01-4.00	LoF3	24
	Male	1.00-2.00	LoM1	2
		2.01-3.00	LoM2	34
		3.01-4.00	LoM3	82
		4.01-5.00	LoM4	34

3.4.6 Shell quality

Proportion of hermit crabs by species and sex based on their shell conditions are shown in Fig. 3.4.8. Male *D. moosai*, occupied significantly (H_{84} = 59.16, p<0.01) more undamaged shells (50%) than damaged (10 %) and highly damaged shells (2%). Non-ovigerous females occupied 65% (H_{84} = 25.87, p<0.05) and ovigerous female 73% (H_{84} = 49.50, p<0.05) of slightly damaged shells. Male *D. lopochir* occupied more evenly among undamaged (28%), slightly damaged (28%) and damaged (38%) shells (H_{84} = 16.18, p>0.05). However, ovigerous and non-ovigerous females of *D. lopochir* occupied 65% (H_{84} = 16.53, p<0.01) and 73% (H_{84} = 30.46, p<0.01) of undamaged shells, respectively (Appendix XVI).

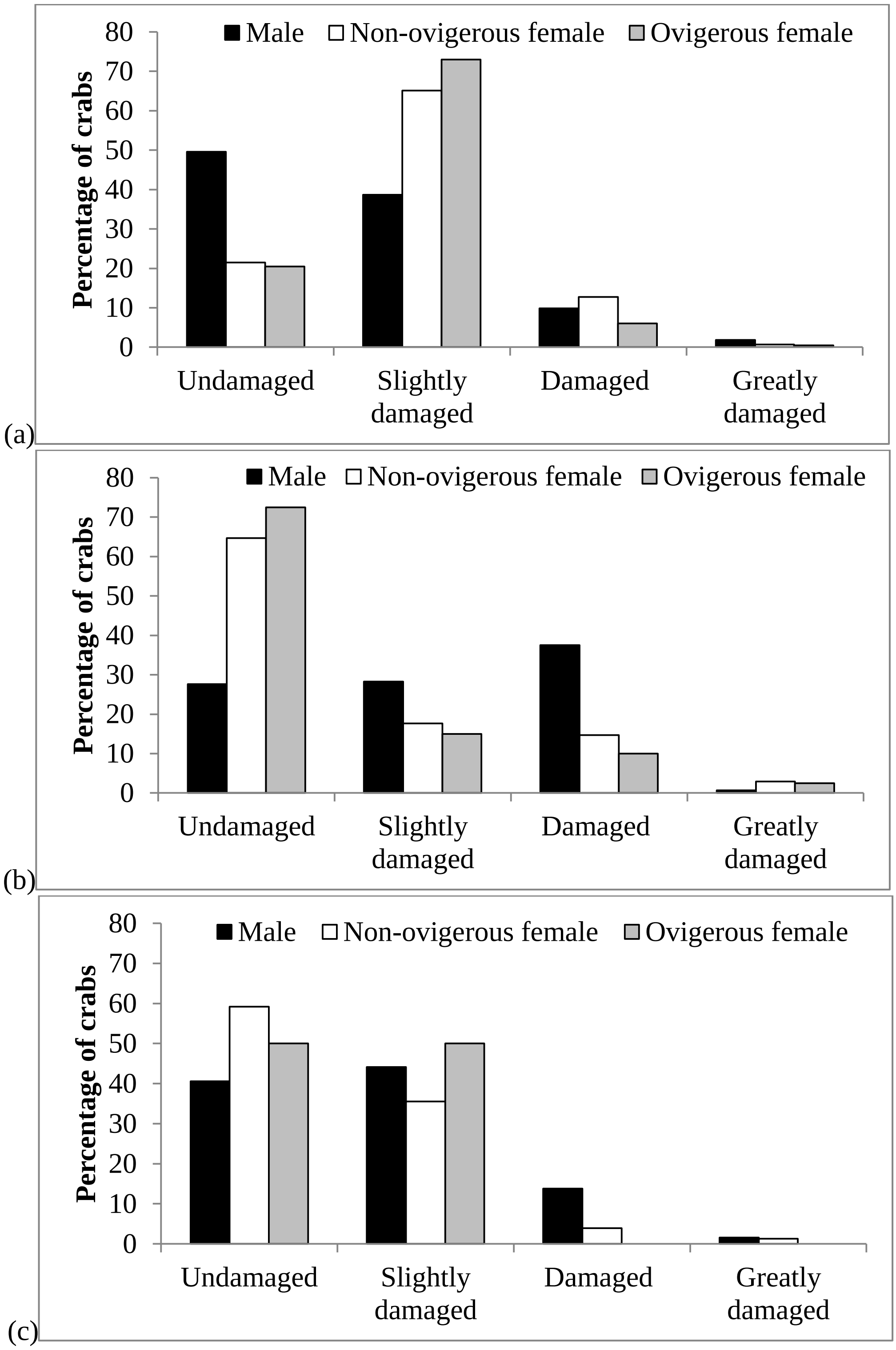


Fig. 3.4.8. Proportion of males, non-ovigerous females and ovigerous females by degree of shell breakage for (a) *D.* moosai, (b) *D. lopochir* and (c) C. *infraspinatus.*

3.4.7 Distribution patterns of live gastropod species

Abundance of live gastropod species; *T. malayensis*, *T. lacera*, *N. cf. olivaceus*, *N. jacksoniasus*, *N. tigrina*, *C. cingulata*, *P. cochlidium* and *M. occa* at each sampling station is shown in Table 3.4.6. Abundance of live gastropod was used as proxy to shell availability as unoccupied shells were very few or rare (and in poor state). A strong positive correlation existed between the abundance of *D. moosai* with the living gastropods (*C. cingulata* and *Nassarius* spp.) at mudflat (R_s=0.768, $p<0.0001$, n=20) and shoal area (R_s=0.718, $p<0.001$, n=19), and similarly between *D. lopochir* and living gastropods (*Nassarius* spp. and *T. malayensis*) at site B (R_s=0.781, $p<0.0001$, n=19).

Overall, abundance of live gastropods at mid-estuary and river mouth stations were relatively low compared to mudflat and shoal stations. At shoal station, *N. jacksonianus* was the most dominant (321.81±508.11 ind/ha), followed by *N. cf. olivaceus* (147.86±249.66 ind/ha) and *T. malayensis* (86.10±159.78 ind/ha). Kruskal-Wallis test showed that density of *T. malayensis* and *N. jacksoniasus* were significantly higher ($p<0.001$) at shoal station compared to mid-estuary, river mouth and mudflat stations. The most abundant gastropod species at mudflat was *N. cf. olivaceus* (230.23±303.89 ind/ha) followed by *C. cingulata* (130.42±514.35) and *N. jacksonianus* (66.27±77.64). The numbers of *N. cf. olivaceus* were about equal in both mudflat and shoal stations (H=72.42, $p>0.05$) but significantly higher (H=72.42, $p<0.001$) than both mid-estuary and river mouth stations (Appendix XVII). *Cerithidea cingulata* found abundantly in mudflat station (130.42±514.35 ind/ha) but was completely absent in mid-estuary and shoal stations. Other gastropods (*T. lacera*, *P. cochlidium*, *N. tigrina* and *M. occa*) whose shells were rarely occupied by both *Diogenes* species but commonly used by *C. infraspinatus*, were relatively low in abundance in all stations.

Table 3.4.6. Basic statistics and summary of Kruskal-Wallis test (significant at 5% level of significance) on density (ind/ha) of gastropod species where their shells were most commonly used by hermit crabs between sampling stations in Matang mangrove estuary from September 2009 to March 2011; SD=standard deviation; n=number of samples; Min=Minimum; Max=Maximum; ns=no significant.

Species		Station				p-level
		Mid-estuary	River mouth	Mudflat	Shoal	
T. malayensis	Mean	6.69^{a}	4.28^{a}	17.06^{b}	86.10^{c}	p<0.001
	SD	36.61	9.58	52.88	159.78	
	n	39	38	55	57	
	Min	0.00	0.00	0.00	0.00	
	Max	228.88	36.59	393.75	1,026.42	
T. lacera	Mean	0.70^{a}	0.11^{a}	0.89^{a}	18.92^{b}	p<0.001
	SD	4.36	0.66	3.22	38.67	
	n	39	38	55	57	
	Min	0.00	0.00	0.00	0.00	
	Max	27.25	4.07	16.26	188.68	
N. cf. olivaceus	Mean	2.57^{a}	46.67^{b}	230.23^{c}	147.86^{b,c}	p<0.001
	SD	6.88	64.57	303.89	249.66	
	n	39	38	55	57	
	Min	0.00	0.00	0.00	0.00	
	Max	27.03	248.87	1,378.15	1,024.85	
N. jacksoniaus	Mean	2.64^{a}	20.92^{a}	66.27^{b}	321.81^{c}	p<0.001
	SD	6.31	44.10	77.64	508.11	
	n	39	38	55	57	
	Min	0.00	0.00	0.00	0.00	
	Max	26.17	223.58	320.82	2,229.81	
N. tigrina	Mean	0.84^{a}	0.09^{a}	8.59^{a,b}	17.43^{b}	p<0.001
	SD	2.37	0.58	22.00	34.11	
	n	39	38	55	57	
	Min	0.00	0.00	0.00	0.00	
	Max	10.90	3.58	112.00	173.59	
C. cingulata	Mean	0.00	0.75	130.42	0.00	p=0.0830 (ns)
	SD	0.00	2.40	514.35	0.00	
	n	39	38	55	57	
	Min	0.00	0.00	0.00	0.00	
	Max	0.00	11.77	3,018.74	0.00	
P. cochlidium	Mean	0.16^{a}	0.00^{a}	1.82^{a,b}	3.73^{b}	p<0.001
	SD	0.98	0.00	9.00	7.19	
	n	39	38	55	57	
	Min	0.00	0.00	0.00	0.00	
	Max	6.12	0.00	65.93	43.39	
M. occa	Mean	2.09	0.23	1.43	1.18	p=0.4243 (ns)
	SD	7.79	1.00	4.86	3.91	

n	39	38	55	57
Min	0.00	0.00	0.00	0.00
Max	43.60	4.65	33.33	20.36

3.4.8 Discussion

There were a total of 19 shell species used by hermit crabs however, only few shells were commonly occupied (i.e. shell species occupied by >20% of hermit crabs) despite the wide range of shell choices available; *D. moosai* commonly used *N. jacksnonianus*, *N. olivaceus* and *C. cingulata* shells, most *D. lopochir* used *N. jacksonianus* and *T. malayensis* shells whereas the larger *C. infraspinatus* occupied mostly *M. occa* and *T. lacera* shells and therefore, showed no overlap in shell use with *Diogenes* species. With exception of terrestrial hermit crabs (Laidre & Vermeij, 2012), previous works have shown that marine hermit crabs occupied few species of shells in spite of the many types of shells available (see Benvenuto & Gherardi, 2001; Ismail, 2010). Sant' Anna et al. (2006) reported that *Clibanarius vittatus* in a Brazilian estuary occupied 13 species of gastropod shells, however, only three shell species represented 98% of shells used. Ismail (2010) reported utilization of 39 species of gastropod shells by *Calcinus latens* and *Clibanarius signatus* on the Red Sea Coast (Egypt) however, three shell species represented 45% and 37% of total shells used by *C. latens* and *C. signatus* respectively. Benvenuto & Gherardi (2001) reported 20 species of shells used by *Clibanarius erythropus* in an Italian rocky shore, however only two gastropod species comprised about 83% of shells used.

Shell use by hermit crabs thus appears to be a selected rather than a random choice. However, the use of shells by reason of preference or availability is equivocal, depending on the hermit crab species (Floeter et al., 2000; Dominciano et al., 2009). In a laboratory study of the effect of shell preference versus shell availability on shell use by hermit crabs, Floeter et al. (2000) showed that shell availability rather than preference is more important in *Calcinus tibicen*, although this seems to depend on species since another coexisting species, *Clibanarius antillensis*, was found closer to its preferred shells than to the most common shells. Another study by Dominciano et al. (2009) shows that the pattern of shell use by *P. brevidactylus* was dependent on site, while shell use by *P. criniticornis* was more dependent on shell preference. Preference for the most suitable shells appears to satisfy a security reason at least for some hermit crabs. For instance, *Calcinus elegans* which occupied unusually shaped shells like cowrie shells (lacking spire or extremely elongate aperture) in tide pools were more easily dislodged by surge compared to those that occupied shells with more standard shell shape (Bach and Hazlett 2009).

D. lopochir is the larger of the two sympatric species of small diogenid hermit crabs inhabiting the subtidal edge of tropical coastal mudflat. Sexual dimorphism in size was apparent in both *D. lopochir* and *D. moosai* whereby males were larger than females (Table 3.3.2). This has also been reported in other species of Diogenidae, for examples *Clibanarius erythropus* (Benvenuato & Gherardi, 2001), *Clibanarius vittatus* (Sampaio & Masunari, 2010) and *Clibanarius laevimanus* (Gherardi et al., 1994). Since crab size strongly correlates with shell size (Fig. 3.4.5 and Fig. 3.4.7), the small size (<5mm shield length) of these two species of hermit crabs therefore limits usage of shells belonging to small gastropods. Among the 14 species of shells that were used by both species of hermit crabs, more than 85% of the shells belonged to only four species of small gastropods (<31mm shell height), namely, *N. jacksonianus*, *N. cf. olivaceus, C. cingulata* and *T. malayensis*. Different species were also utilized by male and female hermit crabs. The results thus provide evidence of both inter- and intraspecific differences in shell use among the two species of *Diogenes* hermit crabs. The most commonly used gastropods were present in relatively high densities in the lower estuary and coastal mudflat area (see Table 3.4.6). It is possible that differences in shell occupancy result from different competitive ability between species and sex at each site (see Yoshino and Goshima, 2002).

The four most occupied gastropod shells differ in their shell morphometrics, particularly aperture length, shell height and shell width (Fig. 3.4.5). *T. malayensis* is more globose, *C. cingulata* is narrow and elongated while *N. cf. olivaceus* has distinctively elongated aperture length. Together these shells formed an assortment of shell types with globose and elongated shells which covered a wide range of aperture lengths (2.83mm-14.92mm), and widths (1.97mm-10.02mm) and shell widths (4.37mm-24.10mm), hence, offering a wide choice of occupancy by small to large hermit crabs. While *C. cingulata* and *T. malayensis* shells fulfilled the requirments of small and large hermit crabs respectively, nassarids shells were commonly used by both hermit crabs of intermediate sizes (2.01-4.00mm). Except *T. malayensis*, the nassariids and cerithiid are herbivorous detritivores, feeding on the rich benthic microalgae and detritus on the mudflat (Broom, 1982). *T. malayensis* is a predator feeding on the abundant fauna of bivalves. Thus, both *D. moosai* and *D. lopochir* appear well adapted and closely associated with the mollusk community living on the mudflat. The shell use pattern of these hermit crabs indicates that the occupied shell resource is proportionally dependent on the species and abundance of gastropod populations in the area. Given the four most occupied shell species of choice and that both coexisting hermit crab species are quite similar in size, a question that begs answer is how are they ecologically partitioned so as to reduce interspecific and intraspecific competition?

In the Matang mudflat, *D. lopochir*, the larger of the two species, was found more at shoal station (65%) than on the mudflat (4%), while the smaller *D. moosai* had a wider distribution from the mudflat (96%) to the shoal station (35%). The smaller number of *D. lopochir* at the subtidal mudflat could be due to lower salinity tolerance, although it also appears to be due to the shortage of their preferred larger shells as provided by *N. jacksonianus* (for females) and *T. malayensis* (males). These shells were however very abundant at shoal station where the hermit crabs used them. In contrast, *D. moosai* dominated in the mudflat because smaller shells of *C. cingulata* and *N. cf. olivaceus* were highly available and their competitor *D. lopochir* were much reduced in numbers here. Thus, spatial confinement affected by the availability of their occupied shells helps reduce and modulate interspecific and intraspecific (male vs female) competition among these hermit crabs. Where competition for shell resources is likely more intense as when both species were equally dominant in a particular area (shoal station), the coexistence of the two hermit crabs is still possible apparently by using shell resources that subtly differ in their characteristics (Fig. 3.4.4, 3.4.5 and 3.4.7). At shoal station, the smaller *D. moosai*, now without *C. cingulata* shells, shifted their shell use to mostly nassariids that were abundant in the shoal station; *N. cf. olivaceus* by females and *N. jacksonianus* by males. This sexual differences in choice of nassariid shells however put *D. moosai* males in direct competition with *D. lopochir* females (Fig. 3.4.7). Interestingly, despite the more intense competition between male *D. moosai* and female *D. lopochir* for the same shells of *N. jacksonianus*, occupied shells of both hermit crabs were mostly in good condition, an indication that the shell resource was not in short supply. The exception was observed in large male *D. lopochir,* where nearly 40% of them occupied damaged shells. This is an indication that good quality, large shells of *Thais malayensis* were limited in numbers. When shell numbers are limited, active competition for shells can influence shell quality (Bertness, 1981b). These results indicate that intense competition for the same shell resource may not be harmful or to the exclusion of the weaker species, if the shell resource is not limiting.

Shell use by hermit crabs is however not a random process even if the shell resource is not a limiting factor (Grant & Ulmer, 1974). It is a process of selection associated with the biometrics of both shell and hermit crab which must be compatible in such a way that will maximize the utilisation of available shell resources (Elwood et al., 1995; Caruso & Chemello, 2009). Interestingly, terrestrial hermit crabs, e.g. *Coenobita compressus*, can remodel the interior architecture of their shells (so-called niche construction) so that they become specialised for living in such remodelled shells (Laidre, 2012). The differences in shell occupancy are possible because the size of hermit crabs varies considerably between species, sexes, as well as spatially across the geographical boundary of their habitats (Barnes, 2005). Thus, despite the wide choice of shells available to them, the good fit between crab and shell dimensions suggests that crabs must choose the right shells to wear. As an examples, shell size variables (shell width, shell height and shell weight) are the most important variables in shell selection for male *D. lopochir* which matched the shield width, chelae length and body weight of the crab (Table 3.4.4). The larger male *D. lopochir* used the best fitted larger shell of mostly *T. malayensis* but not the smaller shells like *N. cf. olivaceus*. Nevertheless, the larger shells of *P. cochlidium, M. occa* and *N. tigrina* were also used by male *D. lopochir* at shoal station, hence, substantiating the limited presence of *T. malayensis* shells. Heavier shells are more stable in position and are less likely to crack from knock impacts due to strong waves and currents. However, the heavy shell may be energetically costly to carry or its larger aperture exposes the hermit crab to higher predation risk.

The weight of hermit crab is correlated to its shell weight in particular female *D. moosai* and male *D. lopochir*, or shell size (Table 3.4.4). Hermit crabs are known to be able to distinguish slightest weight variations in shells (Elwood & Stewart, 1985; Jackson & Elwood, 1989; Mesce, 1993). The energetic cost of carrying a shell as shelter has been demonstrated (Osorno et al., 2005). When carrying a shell, the terrestrial hermit crab, *Coenobita compressus* consumed 50% more oxygen than when 'naked' (Herreid & Full, 1986). Therefore, mechanisms to save energy should be favoured by hermit crabs to ensure optimum growth and recruitment (Osorno et al., 1998). For submerged marine hermit crabs, water buoyancy offers the advantage of reduced energy cost when heavy shells are carried (Briffa & Elwood, 2005). Thus, female *D. moosai* may save more energy from carrying lighter shells than males, and this saved energy could be invested in egg production (see Benvenuto & Gherardi, 2001). For male *D. lopochir*, the possible trade off of using heavy shell is better protection against predator whereas the lighter shell allows for higher growth (Osorno et al., 2005).

The degree of shell elongation or spiralization can be an important factor in shell selection by hermit crabs. Highly spiraled or elongated shells conserve more water preventing risk of dessication during exposure, while less spiraled but often tougher and thicker walled shells offer better protection from predators (Osorno et al., 2005). This could explain why *C. cingulata* (with elongated shell) was heavily used by small hermit crabs like *D. moosai* at the subtidal edge of the mudflat where there is higher risk of exposure during low water. On the other hand, the globose but thicker shells of *T. malayensis* and *N. tigrina* were more used by *D. lopochir* at the subtidal region where there is higher risk of predation by fish. Stomach content analysis indicates that in the Matang study area, both species of hermit crabs were heavily predated by sciaenid and ariid fishes (Yap et al. 1994). Males of both *D. moosai* and *D. lopochir* occupied relatively more globose shells than the smaller females. This observation agrees with a study by Caruso & Chemello (2009) who found males of *Clibanarius erythropus* used more frequently globose shells, although they conceded that such preference might not be dictated by shell shape but rather the large resource of globose shells.

In female *D. lopochir* and male *D. moosai*, the size of the large chela (chela width) of the first pereopod is well matched to the aperture size (length and width) of their shells (Table 3.4.4). Hermit crabs are known to use their enlarged chela as a weapon during fights or in threat display (Elwood et al., 2006; Laidre & Elwood, 2008; Laidre, 2009). It also likely functions as a sealing structure for the shell opening to reduce dessication or/and to protect against predator strike. Therefore, compatible size between the chela and shell aperture may confer an added advantage to female *D. lopochir* and male *D. moosai* through greater protection against predation. In contrast, female *D. moosai* which occupied the elongate shell of *C. cingulata*, could retreat farther back into the shell apex in the face of danger. The result of this is that it apparently allows for the faster growth of its larger left cheliped, a phenomenon that was also reported in male *P. longicarpus* when they were reared in small, high spired shells (Blackstone, 1985).

3.4.9 Conclusion

Shell partitioning between species and sex of the two hermit crabs was evident. The shell use pattern is possible because of size differences between species and sex. Coexistence of the two species of hermit crabs is possible through the use of shell resources that differ subtly in their characteristics, hence reducing interspecific and intraspecific competition. There is clear evidence of differential use of shell species by hermit crab species; these shells differ in terms of shell shape and aperture size.

Nonetheless, these occupied shells satisfy the requirements of size compatibility between shell and crab dimension. Also, the shell aperture length is correlated to the size of the enlarged left chela of particularly females. Although the availability of preferred shells may limit hermit crab species distribution, high shell species diversity and abundance can help reduce intense inter- and intraspecific competition for similar resources. Although not studied, shell species recognition by hermit crabs seems possible from evidence of shell use and the fact that random trial-and-error occupation of shells would be energetically costly. Further studies based on laboratory experiments are necessary to elucidate this.

3.5 REPRODUCTION OF *Diogenes* HERMIT CRABS IN MATANG MANGROVE ESTUARY AND ADJACENT COASTAL WATERS

(Part of the results of this section has been published in Teoh & Chong (2014a); see Appendix I)

This section addresses objective 4 which is to determine the spatial and temporal reproductive pattern of hermit crabs. It is further hypothesised that sympatric species of *Diogenes* hermit crabs adopt different reproductive strategies to avoid/reduce competition for similar resources by their young. To address the above objective and hypothesis, spatial and temporal presence (density and proportion) of ovigerous female at mid-estuary, river mouth, mudflat and shoal area of Matang waters were monitored and quantified over a 20-month period. Univariate significant tests such as Kruskal-Wallis and Wilcoxon matched pair tests were used to test for significant difference in spatial occurrence of the ovigerous females.

3.5.1 Sex ratio and spatial density of ovigerous females

Mean abundance of ovigerous female *D. moosai* at both mudflat and shoal stations were 32.15±43.96 ind/ha and 30.64±84.04 ind/ha respectively which were significantly higher (H=71.5074, p<0.001) than at the river mouth (2.47±8.48 ind/ha). Ovigerous *D. moosai* was absent at mid-estuary station (Table 3.5.1). Proportion of ovigerous female *D. moosai* was higher than non-ovigerous female at river mouth, mudflat and shoal (Fig. 3.5.1). Ovigerous *D. lopochir* was absent in both mid-estuary and river mouth stations while highest density was recorded at shoal station (23.15±148.66 ind/ha). Kruskal-Wallis test showed that density of ovigerous *D. lopochir* at shoal station (23.15±148.66 ind/ha) was significantly higher (H=29.4115, p<0.001) than at the mudflat (0.35±2.15 ind/ha) (Appendix XVIII). Ovigerous *C. infraspinatus* was absent at the river mouth and mudflat while present in very low density at the mid-estuary (0.52±2.67 ind/ha) and shoal stations (0.09±0.66 ind/ha) (Table 3.5.1).

Sex ratio of all hermit crab species was male biased. Average male composition for *D. moosai*, *D. lopochir* and *C. infraspinatus* were 66.67%, 67.02% and 71.02% respectively. Composition of female *D. moosai* was lowest at mid-estuary while female *D. lopochir* was absent at mid-estuary. Highest female composition for both *D. moosai* and *D. lopochir* was observed at mudflat. Composition of ovigerous *D. moosai* was highest at mudflat (31.87%) followed by shoal station (21.27%) and river mouth station (14.77%). Composition of ovigerous *D. lopochir* at the mudflat (12.5%) and shoal station (9.25%) were lower compared to *D. moosai* Ovigerous *C. infraspinatus* composed only small proportion of the population at the mid-estuary (2.26%) and shoal stations (1.59%) (Fig. 3.5.1).

Table 3.5.1. Summary results Kruskal-Wallis test and basic statistics on density of ovigerous females of hermit crabs among sampling stations in Matang mangrove estuary from September 2009 to March 2011. SD=standard deviation; Min=Minimum; Max=Maximum; ns=no significant; similar superscripts of a or b denotes homogenous groups.

Station		Species				
		Mid-estuary	River mouth	Mudflat	Shoal	p-level
D. moosai	Mean	0.00	2.47^{a}	32.15^{b}	30.64^{b}	p<0.001
	SD	0.00	8.48	43.96	84.04	
	n	39	38	58	60	
	Min	0.00	0.00	0.00	0.00	
	Max	0.00	48.78	208.00	592.59	
D. lopochir	Mean	0.00	0.00	0.35^{a}	23.15^{b}	p<0.001
	SD	0.00	0.00	2.15	148.66	
	n	39	38	58	60	
	Min	0.00	0.00	0.00	0.00	
	Max	0.00	0.00	15.91	1152.54	
C. infraspinatus	Mean	0.52	0.00	0.00	0.09	p=0.1871 (ns)
	SD	2.67	0.00	0.00	0.66	
	n	39	38	58	60	
	Min	0.00	0.00	0.00	0.00	
	Max	16.35	0.00	0.00	5.09	

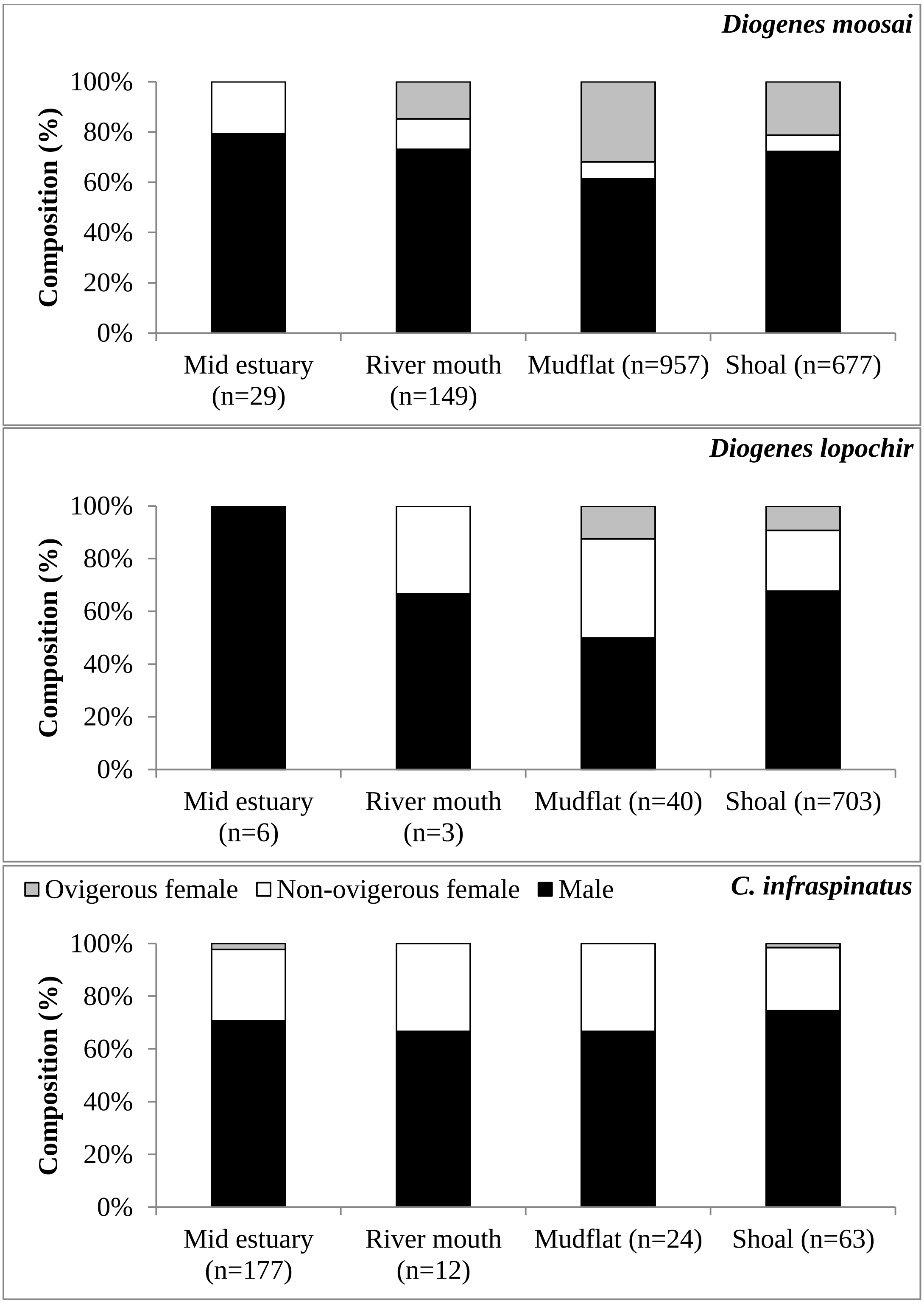


Fig. 3.5.1. Compositions of male, non-ovigerous female and ovigerous female of different species of hermit crabs at each sampling station in Matang mangrove estuary from September 2009 to March 2011 (n=number of samples).

3.5.2 Temporal density of ovigerous females

At mid-estuary station, ovigerous *C. infraspinatus* was present only in November 2009 (0.82±3.66 ind/ha) and April 2010 (0.75±1.67 ind/ha). At the river mouth, highest density of ovigerous *D. moosai* was recorded in October 2010 (1.79±2.53 ind/ha) . Ovigerous *D. moosai* was present in most of sampling months in the mudflat except early June, September and November 2010 with density peaks observed in September 2009 (91.52±4.46 ind/ha) and July 2010 (130.14±78.73 ind/ha). At the mudflat, ovigerous *D. lopochir* was present only in January 2011 (6.70±8.24 ind/ha). At shoal station, ovigerous *D. moosai* was also present in most sampling months except November 2009 and 2010 and March 2011. Density peak was observed at the end of June 2010 (306.39±262.88 ind/ha), while other months with higher density were also observed in October 2010 (58.14±57.75 ind/ha) and January 2011 (40.38±57.52 ind/ha). Density peak of ovigerous *D. lopochir* at shoal station was recorded in July 2010 (390.53±659.99 ind/ha) (Fig. 3.5.2).

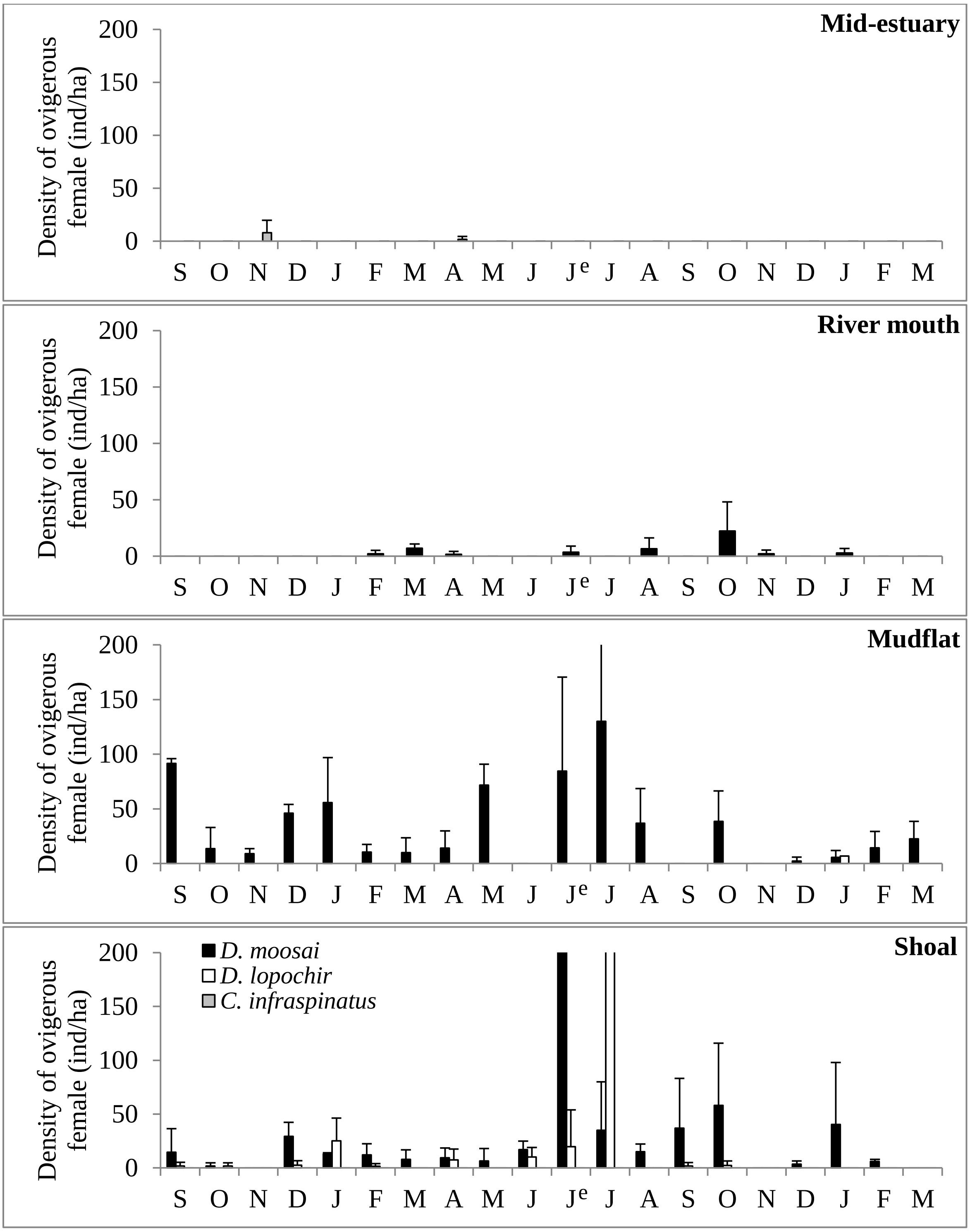


Fig. 3.5.2. Mean density (ind/ha) and standard deviations of ovigerous female by species of hermit crabs at each sampling station in Matang mangrove estuary, from September 2009 to March 2011. ‘J^{e}’’ indicates additional sampling at the end of June 2010.

3.5.3 Monthly proportion of ovigerous females

Wilcoxon matched pairs test revealed that ovigerous *D. moosai* at both mudflat and shoal areas where their populations were equally abundant likely belonged to the same population (T=81.00, p=0.8446). Hence, the monthly proportions of ovigerous females present in the *D. moosai* population in both areas were pooled together and their monthly variations are displayed in Fig. 3.5.3. The mean proportion of ovigerous *D. moosai* for the study period was high (74%), which was significantly higher (H=23.90, p<0.001) than for *D. lopochir* (13%). Also, ovigerous *D. moosai* were present throughout the sampling period with major peaks occurring twice a year, from January to March and from June to August. In contrast, ovigerous *D. lopochir* were absent in various months, while ovigerous females if present were generally low in numbers (<15%), except in January and July 2010.

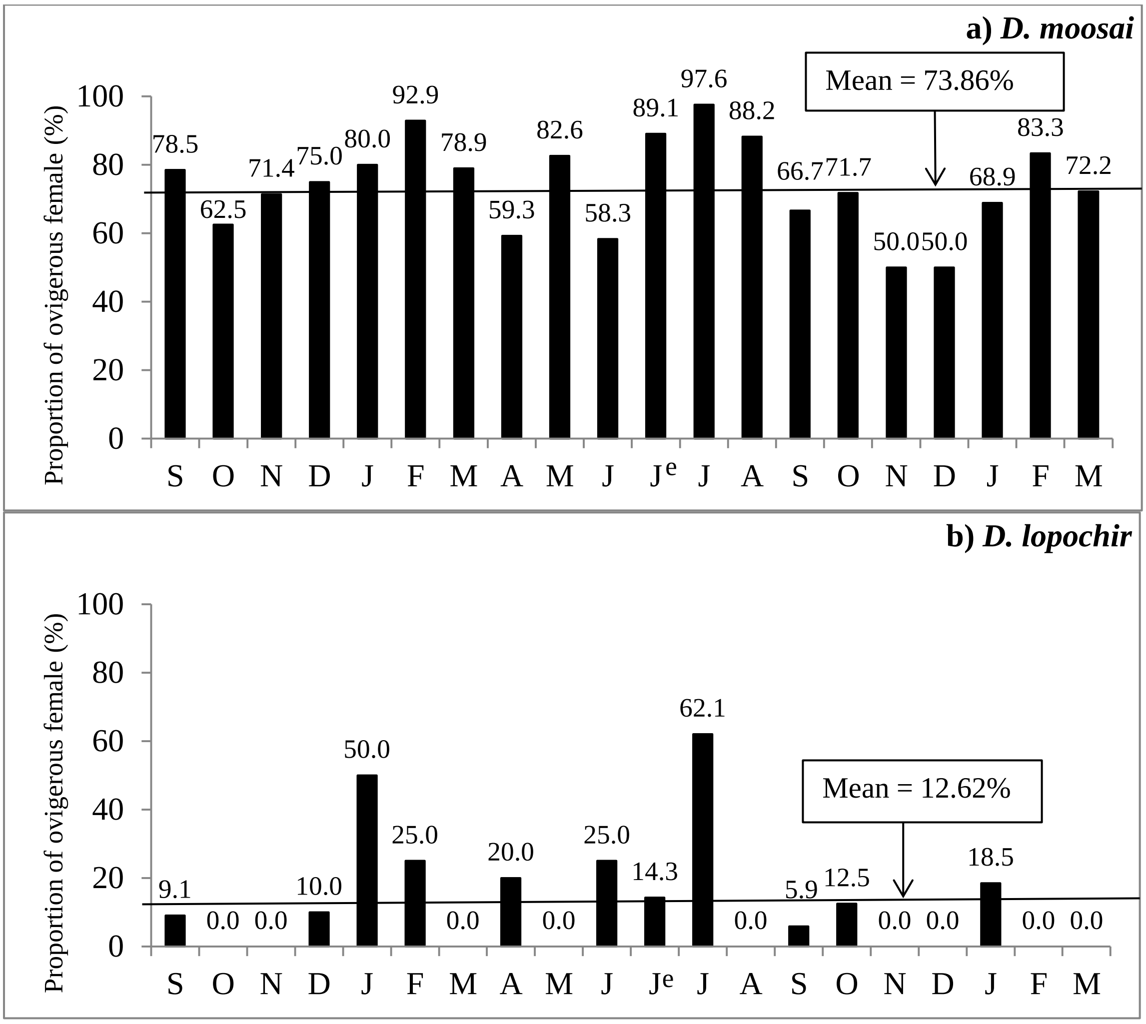


Fig. 3.5.3. Proportion of ovigerous female (%) in female population (pooled from mudflat and shoal stations) of a) *D. moosai* and b) *D. lopochir* from September 2009 to March 2011. Mean proportion denotes the average of all ovigerous female proportions for the entire study. ‘J^{e}’ indicates additional sampling at the end of June 2010.

3.5.4 Discussion

In term of proportion, both mudflat and shoal station had more ovigerous hermit crabs of both species. This suggests that regions farther out from the river are more suitable for their reproduction. The spatial confinement of *Diogenes* hermit crabs to the mudflat and shoal area where the salinity fluctuated between 21-31 ppt as compared to mid-estuary where salinity could fall to 10ppt further suggests the stenohaline nature of these *Diogenes* hermit crabs. However, shell supply may play a more important role in determining spatial distribution of hermit crabs as shells commonly used by both species (*Nassarius cf. olivaceus*, *N. jacksonianus*, *Cerithidea cingulata* and *Thais* *malayensis*) were found in high abundance at or near the subtidal region of mudflat (Table 3.5.1).

D. moosai from the mudflat to subtidal shoal reproduces all year round whereas *D. lopochir* largely on the subtidal shoal shows irregular spawning episodes (Fig. 3.5.3). Although reproduction of hermit crabs in the western Indo-Pacific region has not been reported before, continuous reproduction has been reported for other tropical hermit crabs. *Dardanus deformis* reproduces throughout the year in Southern Mozambique, Indian Ocean (Litulo, 2005b). Among three hermit crab species living in the Boso peninsula (Japan), *Pagurus geminus* reproduces for 11 months, the longest reported for any intertidal decapods in Japan and adjacent waters (Imazu & Asakura 1994). Year round reproductive season has also been reported for hermit crabs on the eastern Pacific and Atlantic coasts such as *Clibanarius zebra*, *Calcinus laevimanus* and *Calcinus latens* (Reese, 1968), *Clibanarius chapini* and *Clibanarius senegalensis* (Ameyaw-Akumfi, 1975) and *Clibanarius clibanarius* (Varadarajan & Subramoniam, 1982) and for the European species, *Pagurus bernhardus* (Lancaster, 1990). Mura et al. (2006) also reported the year round presence of ovigerous females of the deep sea hermit crab, *P. excavatus* in the Mediterranean Sea.

In the present study, both *Diogenes* species showed two major spawning activity in January and July, respectively two months after the onset of northeast and southwest monsoon season (Fig. 3.5.3). These major spawnings resulted in one major and one minor recruitment pulse in a year for both species (see section 3.3.2). Both length frequency analysis and field data on juvenile abundance (Table 3.2.7) however indicate poor recruitment from the July spawning despite its high intensity. Periodicity in reproduction as exhibited by both species may be important to ensure optimum larval growth under the most favourable environment conditions. According to Turra & Leite (2000b), seasonal reproduction in temperate and tropical hermit crabs is an important life cycle strategy resulting from their evolutionary history as modulated by the dynamics of local processes. The two reproduction peaks observed in the present study interestingly, matched the period of peak phytoplankton concentration (Jan and July) as reported by Chew (2012) in the same study area. Stable isotope tracers ($\delta^{13}C$) of juvenile and adult hermit crab nutrition (-20.6‰ to -17.2‰, Table 3.6.2) indicate that phytoplankton (-22.8‰, Chew et al., 2012) and microphytobenthos (-17.3‰, Okamura et al., 2010) are the two major primary sources. Spawning peaks of marine organisms matched to periods of food abundance may not be an unusual phenomenon in tropical waters. This has been reported in tropical anchovies (Sarpedonti & Chong, 2008). However, the larvae of coral reef fishes (mostly damselfishes and wrasses) in the Philippines have been reported to survive better when water temperatures are warmest and when local winds are weakest, i.e., during the southwest monsoon and inter-monsoonal periods (Abesamis & Russ, 2010). Pauly & Navaluna (1983) hypothesized that although tropical fishes breed throughout the year the generally two recruitment peaks may reflect a "survival window" opened for a short period, in this case, during the southwest and northeast monsoons. In India, the crab *Paratelphusa hydrodromus* has been reported to breed during the northeast monsoon (Pillai & Subramonian, 1984).

The continuous reproduction strategy adopted by *D. moosai* may be a strategy to ensure continuous larval supply (see Litulo, 2005b) to buffer against high mortality and possible recruitment failures in certain months (Fig. 3.2.6). Tides at Matang are semi-diurnal with maximum tidal amplitudes of 3.3m. Hence, *D. moosai* on and near to the intertidal mudflat and at greater risk of exposure to extreme physical conditions during spring low tide, spreads its recruitment over the year. On the other hand, *D. lopochir* a more subtidal species reproduces less regularly but at the most favourable period of high primary productivity. This reproductive strategy not only ensures high larval survival, but also conserves the reproductive and energy resources of adults, and perhaps crucially, reduces predation. Hermit crabs must bring out their abdomen from the shell (back and forth) to release their young (see Ziegler & Forward, 2006), and this is the time when they are most vulnerable to predation. Sciaenid and ariid fishes are the major predators of these two species of diogenid hermit crabs. Hermit crabs constituted 22.9% and 3.7% of the mean volumetric composition of the stomach contents of sciaenid fishes that fed in the subtidal shoal and mudflat (Fig. 3.6.4).

The high variability in juvenile density in particular at the shoal area (Table 3.2.7) is due to the irregular spawning of *D. lopochir*. During favourable periods, many ovigerous *D. lopochir* together release high concentration of larvae giving rise to high densities of juveniles of as high as 200,000 ind/ha. On the other hand, there could be no juvenile at all (Table 3.2.7). Despite the large scale recruitment in January/February in river mouth, mudflat and shoal area, many of these juveniles may not survive to adulthood as evidenced by the substantially lower density of adult populations. The limitation in empty shell resources could be a crucial factor that impedes the survival of juveniles. In fact, most juveniles caught in this study were ‘naked’ and vulnerable to predation (subtidal shoal area) and desiccation (mudflat). While competition for empty shells is less likely to occur at river mouth and mudflat, *D. moosai* living at the shoal area are in direct competition with the dominant, larger *D. lopochir*. Despite having coincident reproduction peaks, *D. lopochir* has a faster growth (ϕ’=1.61) than *D. moosai* (ϕ’=1.53) which indicates that the former attain size to occupy available shells faster than the latter. Additionally, the larger size of *D. lopochir* gives it a greater advantage over *D. moosai* in agonistic encounter to acquire shells (see Elwood & Glass, 1981). On the other hand, continuous spawning in *D. moosai* may alleviate the risk of being outcompeted by *D. lopochir*. Segregation of reproductive traits among sympatric species of hermit crabs has been hypothesized to reduce interspecific larval competition for important resources such as empty shells (Reese, 1968).

3.5.5 Conclusion

The coastal mudflat hermit crab species, *D. moosai* reproduces year round, whereas its larger, sympatric congener *D. lopochir* reproduces discontinuously. However, reproduction in both species tends to intensify in biannual peaks, each peak occurring two months after the onset of the summer and winter monsoon. These two spawning peaks resulted in two major recruitment pulses for *D. moosai* and *D. lopochir*. Despite the year-round spawnings observed especially in *D. moosai,* recruitment of young juveniles (shield length <1.6mm) appears patchy and discontinuous, suggesting often recruitment failures. *D. moosai* and *D. lopochir* are dominant at mudflat and subtidal area respectively and thus, experience different external pressures such as tidal emersion (in intertidal mudflat), predation and/or competition (greater at subtidal area), causing high mortality and the adoption of different reproduction strategies. It could be summarised that reproduction and recruitment periodicity is well adapted by both species as evidenced by their high abundance in Matang mangrove estuary.

3.6 HERMIT CRAB TROPHODYNAMICS BASED ON STABLE ISOTOPE ANALYSIS AND FISH PREDATION

This section addresses objective 5 which is to elucidate the trophodynamics of hermit crabs. The study sought to determine the trophic role played by hermit crabs in the coastal food web. It is hypothesised that small diogenid hermit crabs serve as prey organisms to large predators. To address the above objective, stable isotope signature of major primary producers (microphytobenthos, phytoplankton and mangroves), hermit crabs (juveniles and adult from mudflat and shoal areas) and common predatory fishes (ariid and sciaenid fishes) were determined. Stable Isotope Analysis using R-Program (SIAR) was used to analysis the stable isotope readings to determine the proportional contribution of primary sources (from $\delta^{13}C$) and the trophic position (from $\delta^{15}N$) of hermit crabs. Stomach content and stable isotopes of ariid and sciaenid fishes were further quantified to determine the extent of hermit crabs being predated by these predatory fishes.

3.6.1 Stable isotopes

3.6.1.1 Primary producers

Stable isotope results of primary producers in Matang mangrove estuary; mangrove leaves, seston and microphytobenthos were based on Chew (2011), Okamura et al. (2010), Hayase et al. (1999) and Newell et al. (1995) (Table 3.6.1). Senescent mangrove leaves had means of $\delta^{13}C$ that ranged from -29.1±1.4‰ to -28.3±0.9‰ which were lower than the seston (-18.8‰ to -18.1‰) and microphytobenthos (-20.6‰ to -12.1‰). Senescent mangrove leaves also had the lowest mean $\delta^{15}N$ values which ranged from 4.1±1.3‰ to 4.4±0.2‰. This is followed by seston (4.9±1.2‰) and micophytobenthos (3.4 to 3.6‰).

Table 3.6.1. Mean value of $\delta^{13}C$ from primary producers; mangrove leaves; seston and microphytobenthos at shoal waters of Matang mangrove estuary based on literatures.

	$\delta^{13}C$ (‰)	**$\delta^{15}N$ (‰)**	**Source**
Senescent mangrove leaves	-28.3±0.9	4.1±1.8	Chew (2012)
	-28.7 to -26.7	4.4±0.2	Hayase et al. (1999)
	-29.1±1.4	4.1±1.3	Okamura et al. (2010)
Seston (phytoplankton)	-18.8±2.2	4.9±1.2	Chew (2012)
	-18.1 to -17.9	-	Hayase et al. (1999)
Microphytobenthos	-19 to -16	3.4 to 3.6	Okamura et al. (2010)
	15.6 (mean)	-	Newell et al. (1995)

(Sources: Chew (2012); Okamura et al. (2010); Hayase et al. (1999); Newell et al. (1995))

3.6.1.2 Hermit crabs

Hermit crabs were selected from mudflat and shoal stations based on the dominance of species at the sampling stations. Overall, hermit crabs had means of $\delta^{13}C$ ranging from 17.2‰ to 20.6‰. *D. moosai* at mudflat had $\delta^{13}C$ ranging from -19.9‰ to -20.2‰ and mean of -20.1±0.1‰, which was slightly lower than *D. lopochir* at shoal station (-18.9±0.2‰) where $\delta^{13}C$ ranged from -18.8‰ to -19.2‰. Mean $\delta^{13}C$ for ovigerous female at mudflat (*D. moosai*) and shoal (*D. lopochir*) stations were -20.6‰ and -19.4‰ respectively. On the other hand, values of $\delta^{13}C$ were consistently higher for juvenile *Diogenes* sp. at mudflat and shoal stations with means of -18.2‰ and -17.3‰ respectively. Juvenile *Diogenes* sp. at shoal station recorded highest $\delta^{13}C$ values which ranged from -17.2‰ to -17.3‰. Values of $\delta^{15}N$ were also quite similar in adults for both *D. moosai* and *d. lopochir* with mean ranged from 8.6‰ to 9.2‰ while juvenile *Diogenes* sp. had slightly lower $\delta^{15}N$ with means ranged from 7.7‰ to 8.3‰. Juveniles at shoal station had the lowest $\delta^{15}N$ values which varied from 7.3‰ to 8.1‰ (Table 3.6.2).

Table 3.6.2. Mean values and basic statistics of δ^{13}C, δ^{15}N and C:N ratio for *D. moosai*, *D. lopochir* and juvenile *Diogenes* sp. collected at Matang mangrove estuary; SL=shield length (mm); SD=standard deviation; n=number of samples.

Samples	**SL (mm)**	**Station**		**δ^{13}C (‰)**	**δ^{15}N (‰)**	**C:N**
D. moosai (mixed male and female)	1.80-3.40mm	Mudflat	Mean	-20.1	8.6	5.17
			SD	0.1	0.4	0.14
			n	3	3	3
			Min	-20.2	8.3	5.06
			Max	-19.9	9.0	5.32
D. lopochir (mixed male and female)	2.40-3.40mm	Shoal	Mean	-18.9	9.2	5.11
			SD	0.2	0.3	0.19
			n	4	4	4
			Min	-19.2	8.7	4.92
			Max	-18.8	9.5	5.37
Ovigerous *D. moosai*	NA	Mudlat	Mean	-20.6	9.1	5.36
			SD	0.0	0.3	0.08
			n	2	2	2
			Min	-20.6	8.9	5.30
			Max	-20.6	9.3	5.41
Ovigerous *D. lopochir*	NA	Shoal	Mean	-19.4	8.7	5.51
			SD	0.3	0.2	0.11
			n	2	2	2
			Min	-19.6	8.6	5.43
			Max	-19.3	8.8	5.59
Juvenile *Diogenes* sp.	<1.0mm	Mudflat	Mean	-18.2	8.3	5.26
			SD	0.3	0.2	0.03
			n	2	2	2
			Min	-18.4	8.1	5.23
			Max	-18.0	8.6	5.28
Juvenile *Diogenes* sp.	<1.0mm	Shoal	Mean	-17.3	7.7	5.49
			SD	0.1	0.6	0.05
			n	4	4	4
			Min	-17.3	7.3	5.45
			Max	-17.2	8.1	5.56

3.6.1.3 Predators

For analysis of stable isotope, only predatory fishes that were found to consume hermit crabs were selected. Results of the analysis are shown in Table 3.6.3. Values of δ^{13}C of selected fishes did not differ much with means that ranged from -20.7‰ to -22.3‰. Highest variation in δ^{13}C values was recorded for *J. belangerii* which ranged from -18.7‰ to -23.7‰. Highest of these values was observed in *J. belangerii* of standard length 12.0cm (-18.7‰) Values of δ^{15}N were quite similar for all fish species with means ranging from 14.4‰ to 14.7‰.

Table 3.6.3. Mean values and basic statistics of δ^{13}C, δ^{15}N and C:N ratio for some species of predatory fishes from family Ariidae and Sciaenidae collected at Matang mangrove estuary; SL=shield length (mm); SD=standard deviation; n=number of samples.

Family	**Species**	**Size range (cm)**		**δ^{13}C** (‰)	**δ^{15}N** (‰)	**C:N**
Ariidae	*Arius venosus*	11.6-18.5	Mean	-22.2	14.5	3.89
			SD	1.5	0.0	0.04
			n	2	2	2
			Min	-23.3	14.5	3.89
			Max	-21.2	14.5	3.94
Sciaenidae	*Johnius belangerii*	8.2-17.0	Mean	-21.2	14.4	3.79
			SD	2.8	0.1	0.09
			n	3	3	3
			Min	-23.7	14.3	3.72
			Max	-18.2	14.5	3.89
	Johnius carouna	12.5	Mean	-20.7	14.7	3.82
			SD	-	-	-
			n	1	1	1
			Min	-	-	-
			Max	-	-	-
	Johnius weberii	11.8-13.6	Mean	-22.3	14.5	3.77
			SD	0.9	0.2	0.04
			n	2	2	2
			Min	-22.9	14.4	3.77
			Max	-21.7	14.6	3.83

3.6.1.4 Proportional contribution of primary sources and trophic position of hermit crabs

The SIAR results showed greater mean proportional contribution of microphytobenthos in all analysed groups (Table 3.6.4). Microphytobenthos had the highest overall mean proportion (49.9%±14.6%) followed by phytoplankton (27.6%±9.3%) and mangroves (22.5%±7.7%). The dependency on microphytobenthos as primary source was more pronounced at shoal area for juvenile *Diogenes* (between

41.7% and 85.7%; mean = 70.3%) and adult *D. lopochir* (between 24.9% and 72.2%; mean = 50.5%). Contribution of phytoplankton at shoal area for both juvenile *Diogenes* (mean = 16.2%) and adult *D. lopochir* (mean = 25.9%) was slightly greater than mangrove (mean = 13.6% and 23.6% respectively). At mudflat, contribution of microphytobenthos and phytoplankton were equally important for juvenile *Diogenes* (40.6% and 38.7% respectively). Nutrition of adult *D. moosai* derived from mangrove, phytoplankton and microphytobenthos was equally important in mudflat (32.1%, 29.6% and 38.3% respectively) (Table 3.6.4).

Trophic positions of primary sources, hermit crabs and predatory fishes are shown in Fig. 3.6.1 which reflects the general greater dependency of hermit crabs towards microphytobenthos and phytoplankton. Hermit crabs (adult and juveniles) are at the intermediate position between primary sources and predatory fishes. However, the trophic link between hermit crabs and the predatory fishes could not be established without ascertaining the predation on hermit crabs by these fishes. Therefore, examination of stomach contents of the predatory fishes is required to complement the stable isotope data.

Table 3.6.4. Mode, mean and range (95% Bayesian confidence interval) of proportional contribution of mangroves, microphytobenthos and phytoplankton on *D. moosai* (mudflat), *D. lopochir* (shoal station) and juvenile *Diogenes* from mudflat and shoal station.

Group	Primary source	Low 95%	High 95%	Mode	Mean
D. moosai (mudflat)	Mangroves	0.1597	0.4526	0.3522	0.3211
	Phytoplankton	0.0000	0.6168	0.3221	0.2958
	Microphytobenthos	0.1086	0.6260	0.3809	0.3831
D. lopochir (shoal station)	Mangroves	0.1136	0.3245	0.2629	0.2357
	Phytoplankton	0.0000	0.5764	0.0999	0.2594
	Microphytobenthos	0.2488	0.7222	0.6260	0.5049
Juvenile *Diogenes* (mudflat)	Mangroves	0.0000	0.4557	0.2009	0.2073
	Phytoplankton	0.0088	0.7439	0.4102	0.3866
	Microphytobenthos	0.0414	0.7237	0.4173	0.4061

Juvenile	Mangroves	0.0358	0.1877	0.1608	0.1355
Diogenes	Phytoplankton	0.0000	0.5101	0.0369	0.1620
(shoal)	Microphytobenthos	0.4171	0.8568	0.7992	0.7025

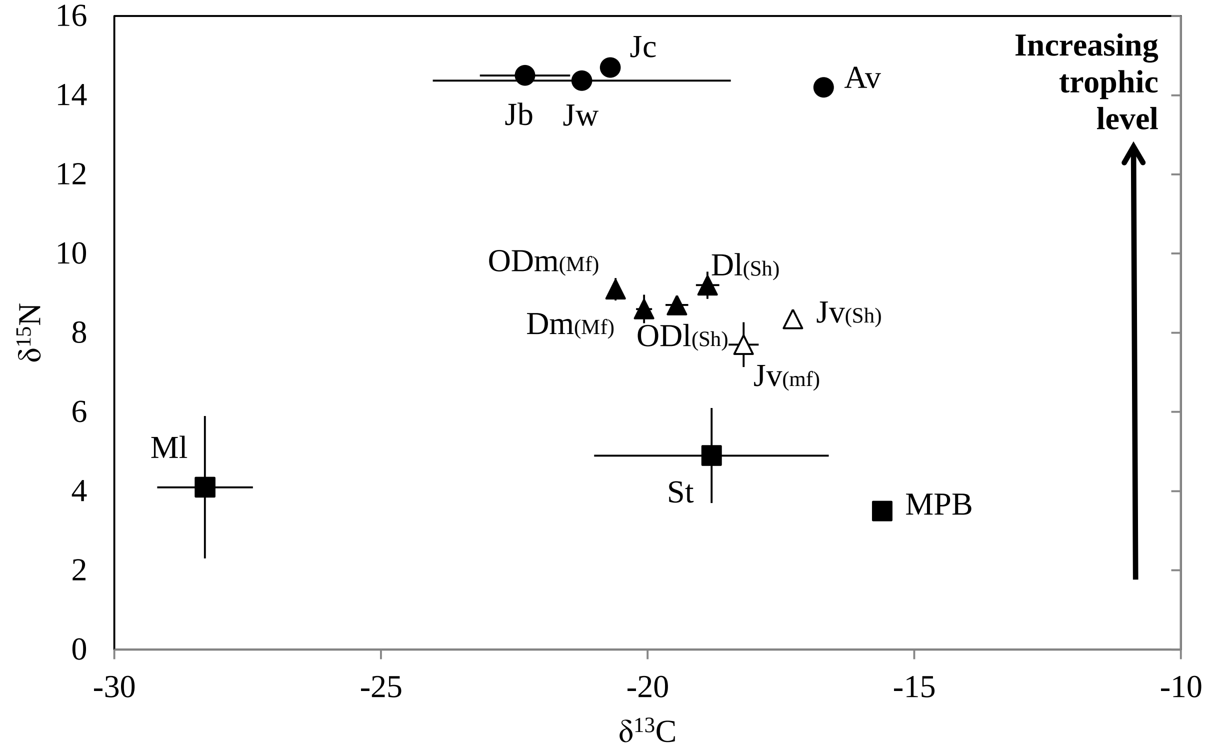


Fig. 3.6.1. Plots of unadjusted δ^{13}C and δ^{15}N mean values of various primary producers, hermit crabs and fishes in Matang mangrove estuary and adjacent coastal waters based on Table 3.6.1, 3.6.2 and 3.6.3. Primary producers (■): Ml = senescent mangrove leaves, St = seston, MPB = microphytobenthos. Adult hermit crabs (▲): Dm = *D. moosai*, Dl = *D. lopochir*, ODm = Ovigerous *D. moosai*, ODl = Ovigerous *D. lopochir*. Juvenile hermit crabs (Δ): Jv = Juvenile *Diogenes*. Fish predators (●): Jb = *J. belangerii*, Jw = *J. weberii*, Jc = *J. carouna* and Av = *A. venosus*. 'Mf' and 'Sh' in brackets indicate mudflat and shoal stations respectively. Standard deviations are indicated by error bars. Dark arrow indicates increasing trophic level.

3.6.2 Stomach content analysis of common predatory fishes

None of the fishes examined had empty stomachs. Six individuals of ariids were observed to have stomachs with 1/4 fullness while four individuals had full stomach. Majority of sciaenids (47.5%) had 1/4 stomach fullness. Sciaenids with full stomachs represented only about 6.6% of individuals analysed while sciaenids with 1/2 and 3/4 stomach fullness comprised 27.0% and 18.3% respectively of individuals examined.

Composition of individuals based on stomach fullness and their respective size range (standard length) for each species of predatory fish are shown in Table 3.6.5.

Table 3.6.5. Composition (%) of stomach fullness and size range of some common predatory fishes caught at river mouth, mudflat and shoal stations in Matang mangrove estuary. n=number of sample; com=percentage composition; SL=size range based on standard length (cm); '-' denotes non-presence of sample.

Family	Species	n	Stomach fullness							
			1/4		1/2		3/4		Full	
			com	SL	com	SL	com	SL	com	SL
Ariidae	*A. sagor*	3	33.3	13.5	-	-	-	-	66.7	12.0-15.4
	A. caelatus	4	25.0	21.0	25.0	10.5	25.0	13.8	25.0	12.4
	A. venosus	3	66.7	17.2-17.5	-	-	-	-	33.3	17.5
	C. truncatus	1	-	-	100	9.5	-	-	-	-
	O. militaris	2	50	11.0	-	-	50	15.2	-	-
Sciaenidae	*J. belangerii*	78	41.0	5.2-17.1	33.3	9.7-16.8	19.2	7.3-15.1	6.4	11.3-16.2
	J. carouna	39	56.4	7.3-13.2	23.1	8.4-13.6	18.0	9.7-12.9	2.6	13.8
	J. weberii	20	55.0	9.8-15.4	10.0	13.2-14.8	20.0	12.7-13.8	15.0	12.3-14.7

A total of 52 prey items from stomach content analysis were identified to the lowest taxa. However, most of the prey taxa contributed a minor portion of the diet composition with 17 taxa contributing ≥ 1% of overall diet volume. Unidentified organic materials composed the major portion of the volumetric composition with 46% with the highest frequency of occurrence of 35%. This category composed of prey items that were undistinguishable such as organic clumps and partly digested flesh. All prey taxa were pooled into broader taxa for clarity of results in the presentation. Prey items categorized as 'others' include egg sacs, some small solid objects and fine spicules that were unidentifiable. These prey items however, only composed about 1% of total volumetric compositions. Fish scales and gill rakers were not grouped as teleost since presence of these items is not necessarily associated with food instead presence of fish scales might be a results of aggressive interactions between fishes (Winemiller, 1989). Unidentified prawn and shrimp were collectively categorized as "unidentified decapods", while remnants of crustacean appendages were broadly categorized as "unidentified crustaceans". Both *D. moosai* and *D. lopchir* were identified based on the presence of the larger left cheliped although intact individuals were also found in the stomachs examined. All hermit crabs together with remnants of unidentifiable *Diogenes* sp. were categorized as Diogenidae (Table 3.6.6).

Brachyuran and Diogenidae were most important prey taxa particularly for sciaenid fishes. These taxa comprised 16.2% and 10.5% of volumetric composition of stomach contents, with frequency of occurrence of 17% and 13% respectively. Identified taxa of Brachyura in order of volumetric composition were Pinnotheridae (5.2%), some unidentified crabs (3.6%), *Phylira* sp. (3.5%), Xanthidae (3.1%) and *Neodorippe callida* (0.8%). For hermit crabs, *D. moosai* and *D. lopochir* formed 2.8% and 6.2% by volumetric composition respectively. Frequency of occurrence of both species was 8.7% and 13.3% respectively. *D. lopochir* ranked second after organic matter in term of composition and frequency of occurrence, while *D. moosai* ranked 8th in term of composition and 5th in term of frequency of occurrence. Unidentified *Diogenes* sp. comprised 1.5% (ranked 13) of the diet composition and 4.7% (ranked 11) of frequency of occurrence. Juvenile *Diogenes* sp. formed less than 1% of diet composition and frequency of occurrence and ranked last (Table 3.6.6). Although, hermit crab was one of the most frequent prey items, they were the smaller *Diogenes* sp., and larger hermit crabs such as *Clibanarius* sp. were absent. Other important decapod taxa in order of volumetric composition included Penaeidae (4.0%), other unidentified decapods (2.9%), Sergestidae (1.3%) and Alpheidae (1.1%). Unidentified crustaceans, Gastropoda, Polychaeta and teleost fish comprised 3.8%, 3.6%, 2.3% and

1.9% of the total volume respectively. Other distinguishable taxa such as Isopoda, Bivalvia, Ostracoda, Scaphopoda, Nematoda, Amphipoda, Ophiuroidea, Octopoda and Cirripedia each made up ≤1% of total diet composition (Fig. 3.6.3).

Table 3.6.6. List of prey items of all examined stomachs of sciaenids and ariids identified to the lowest taxa with their groupings, frequency of occurrence (FO) and volumetric composition (VC) of each taxa with rankings based on these values. '*' denotes hermit crabs as prey item.

		FO (%)		**VC (%)**	
Prey item	**Taxa grouping**	**Mean**	**Rank**	**Mean**	**Rank**
Acetes sp.	Sergestidae	2.0	15	1.3	14
Alpheus sp.	Alpheidae	1.3	19	1.1	16
Amphipoda	Amphipoda	2.7	14	0.1	26
Barnacles	Cirripedia	0.7	20	0.2	25
Bivalve	Bivalvia	0.7	20	0.1	26
Crab	Brachyura	12.7	3	3.6	5
Crassatellidae	Bivalvia	3.3	13	0.8	19
Unidentified crustacean	Crustacean	10.7	4	3.8	4
D. lopochir	Diogenidae	13.3*	2*	6.2*	2*
D. moosai	Diogenidae	8.7*	5*	2.8*	8*
Decapod zoea	Decapod larvae	1.4	18	0.1	26
Dentalium sp.	Scaphopoda	1.3	19	0.0	27
Diogenes sp.	Diogenidae	4.7*	11*	1.5*	13*
Diopatra sp.	Polychaeta	2.0	15	1.6	12
Egg sacs	Others	0.7	20	0.7	20
Fish	Teleost	0.7	20	0.0	27
Fish gill rakers	Gill rakers	0.7	20	0.2	25
Fish scale	Fish scales	2.7	14	0.5	22
Gammaridea	Amphipoda	0.7	20	0.1	26
Gastropod	Gastropoda	5.3	9	3.3	6
Isopoda	Isopoda	2.7	14	1.0	17
Juvenile Diogenes sp.	Diogenidae	0.7*	20*	0.0*	27*
M. affinis	Penaeidae	1.3	19	0.9	18
M. brevicornis	Penaeidae	1.3	19	0.6	21
Maldanidae	Polychaeta	0.7	20	0.0	27
N. callida	Brachyura	1.3	19	0.8	19
Nassarius sp.	Gastropoda	0.7	20	0.3	24
Nematode	Nematoda	2.0	16	0.1	26
Octopoda	Octopoda	0.7	20	0.3	24
Ophiuroidea	Ophiuroidea	4.7	11	1.2	15
Organic matter	Organic matter	75.3	1	46.0	1
Ostracoda	Ostracoda	3.3	13	0.3	24
P. trigona	Bivalvia	0.7	20	0.1	26
Palatine plate	Teleost	0.7	20	0.4	23
Penaeidae	Penaeidae	4.0	12	2.4	10
Phylira sp. 1	Brachyura	3.3	13	1.1	16

Phylira sp. 2	Brachyura	0.7	20	0.1	26
Phylira sp. 3	Brachyura	6.0	7	2.3	11
Pinnotheridae	Brachyura	7.3	6	5.2	3
Plant detritus	Detritus	0.7	20	0.7	20
Polychaete	Polychaeta	2.0	17	0.7	20
Unidentified prawn	Decapoda	4.7	11	2.6	9
Round things	Others	0.7	20	0.0	27
S. baganensis	Teleost	1.3	19	1.3	14
Salmacis sp.	Echinodermata	0.7	20	0.1	26
Sciaenid juvenile	Teleost	0.7	20	0.2	25
UnidentfiedShrimp	Decapoda	2.0	17	0.3	24
Spicules	Others	0.7	20	0.1	26
Stomatopoda	Stomatopoda	0.7	20	0.1	26
Tanaid	Tanaidacea	0.7	20	0.0	27
Tellinidae	Bivalvia	0.7	20	0.0	27
Xanthidae	Brachyura	5.3	8	3.1	7

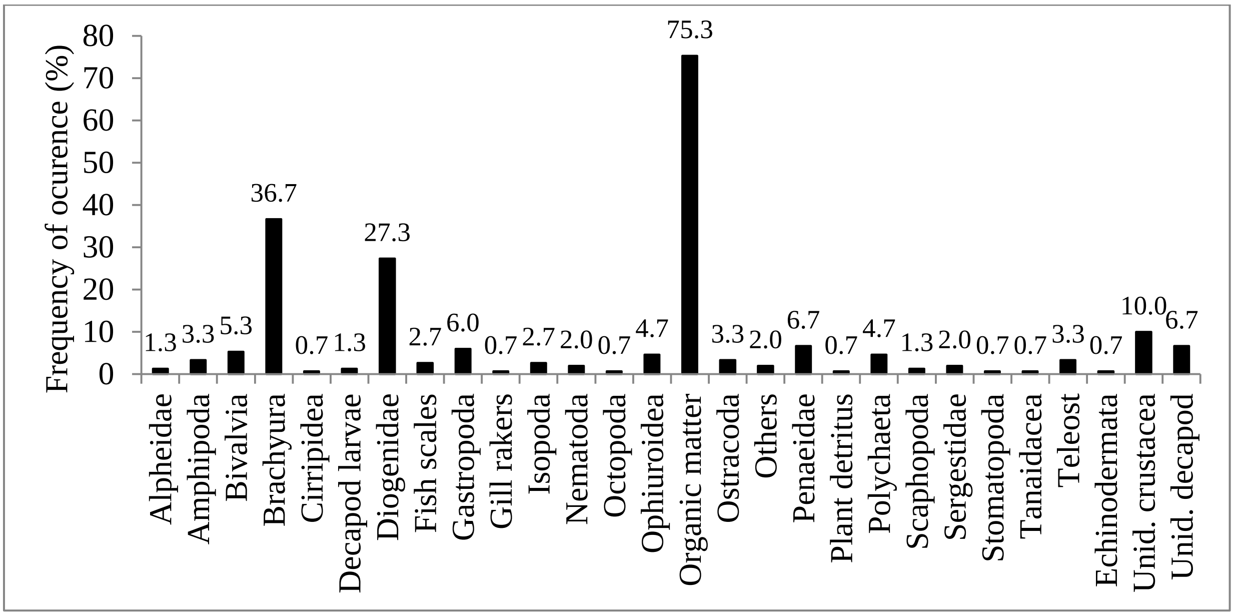


Fig. 3.6.2. Frequency of occurrence (%) of some major prey taxa found in stomachs of predatory Sciaenidae and Ariidae fishes caught at river mouth, mudflat and shoal stations in Matang mangrove estuary.

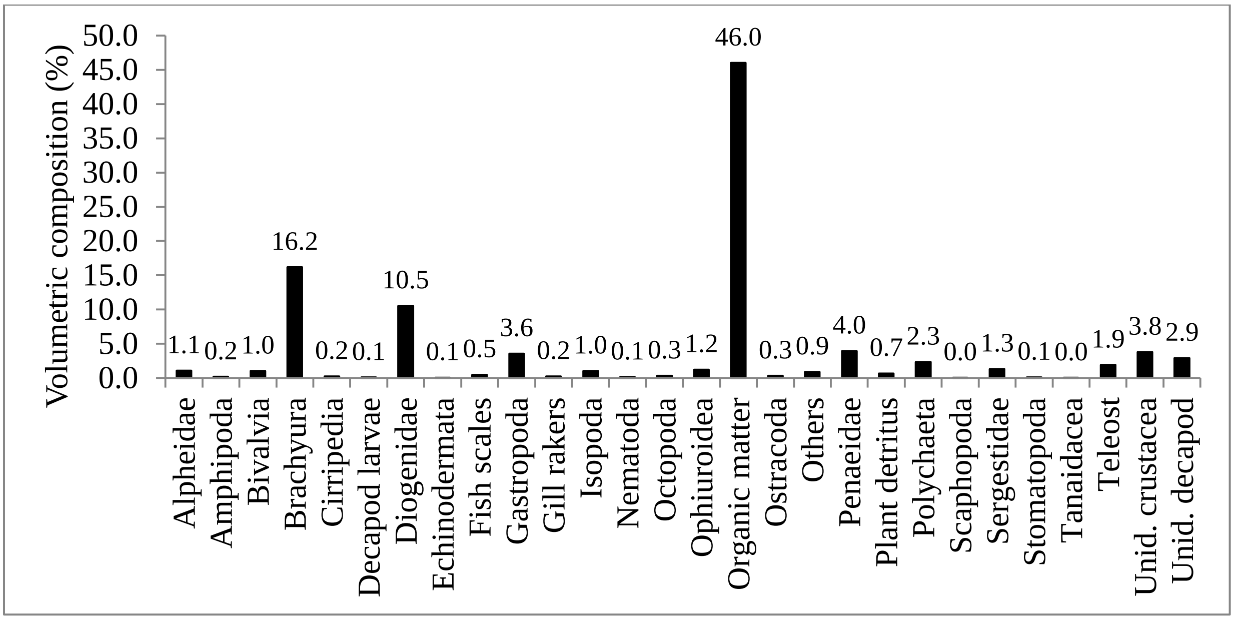


Fig. 3.6.3. Mean volumetric compositions (%) of some major prey taxa found in stomachs of predatory Sciaenidae and Ariidae fishes caught at river mouth, mudflat and shoal stations in Matang mangrove estuary.

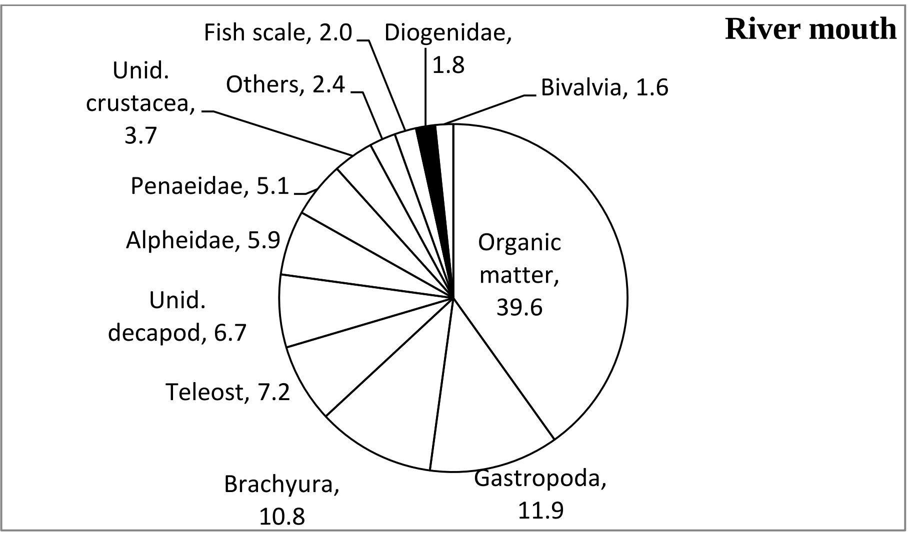
Fig. 3.6.4 shows that the mean volumetric composition of major prey taxa by stations irrespective of predator groups. Contribution of hermit crabs in diet of sciaenids was more pronounced at the shoal station with 22.9% which was the highest of all identifiable taxa (see Table 3.6.7 for breakdown of the Diogenid prey item). This was followed by Brachyura (11.0%) and Penaeidae (4.0%). At mudflat, unidentified organic matter made up majority of the volume of stomach content with 51.7% while Diogenidae composed 3.7% which was ranked third among discernible taxa behind Brachyura (22.3%) and other crustacean (3.7%). Hermit crabs at the river mouth contributed the least of the diet contents with 1.8% which was ranked 8th among all taxa, excluding organic matter. The latter made up the major portion (39.6%) of the diet contents. Highest contributors to sciaenid and ariid food in this station were Gastropoda (11.9%) followed by Brachyura (10.8%) and teleost (7.2%).

Fig. 3.6.5 shows the volumetric compositions of the top 10 prey taxa from stomach contents of three common sciaenid species. *Johnius belangerii* was the major sciaenid predator that preyed upon hermit crab. Diogenidae made up the highest portion of the diet at 18.8% for *J. belangerii*'s, except organic matter (47.3%). This was followed by Brachyura (14.6%) and Polychaeta (4.0%). Size of *J. belangerii* that fed upon hermit crabs ranged from 5.0cm to 15.0cm standard length (SL). The highest consumption of diogenid (33.6%) occurred in size class 11.1-13.0cm SL (Fig. 3.6.7a). Hermit crabs made up only 0.2% of *J. carouna's* diet ranked at 16. Highest contributor of *J. carouna*'s diet was Brachyura at 14.8%, followed by Penaeidae and Gastropoda each contributing 6.7%. Sergestids and unidentified decapods made up 2.7% and 6.0% respectively. Stomach content of *J. carouna* contained of hermit crabs only in size class 7.1-9.0cm SL with 1.3% composition (Fig. 3.6.7b). Hermit crabs made up 5.3% of the volumetric composition of stomach content of *J. weberii*. Hermit crabs ranked third among all discernible taxa. This was followed by Alpheidae which made up 5.0% of the composition. Highest diet contributor of *J. weberii,* except unidentified organic matter, was Brachyura at 32.4% followed by unidentified decapods at 6.7%. Diogenid crabs were only consumed by *J. weberii* of 13.1-15.0cm SL, comprising 10.6% of stomach content (Fig. 3.6.7c).

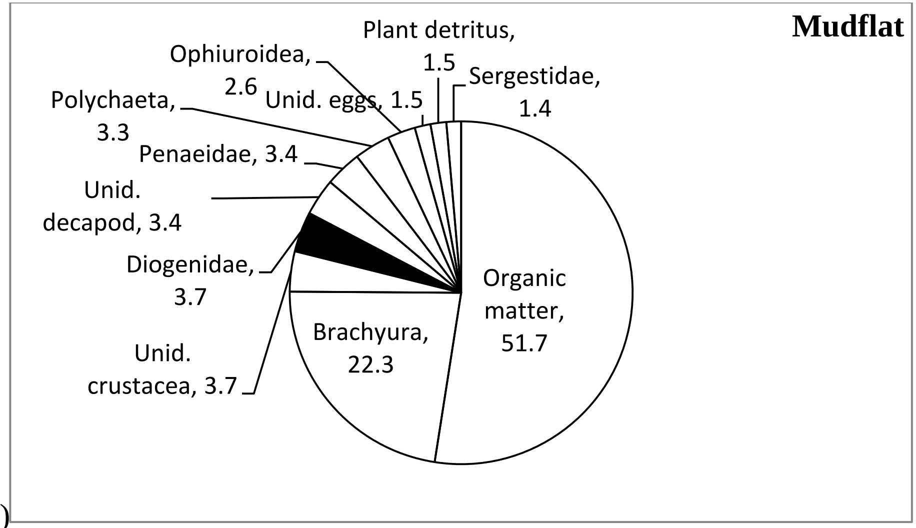
Majority of ariid fishes intended for stomach content examination were caught from river mouth since mudflat and shoal stations have relatively low abundance of ariids. Due to low sample size of each ariid species, data was therefore, pooled as Ariidae. Hermit crabs made up 0.4% of ariid diet and was ranked 11th among all discernible taxa. With the exception of organic matter, teleosts made up the highest diet composition of ariids at 15.0% followed by Penaeidae (13.6%) and Gastropoda (7.7%). Other decapods include Alpheidae and Brachyura which comprised 4.6% and 3.1% of ariid diet respectively (Fig. 3.6.6).

Table 3.6.7. Breakdown of the proportion (%) of Diogenid prey item by species/categories from stomachs of predatory fishes at each station.

Station	Diogenid species/categories				
	D. lopochir	*D. moosai*	Unidentified *Diogenes* sp.	Juvenile *Diogenes*	Total
River mouth	0.3	1.5	0.0	0.0	1.8
Mudflat	1.7	1.0	1.0	0.0	3.7
Shoal station	14.4	5.7	2.6	0.1	22.9

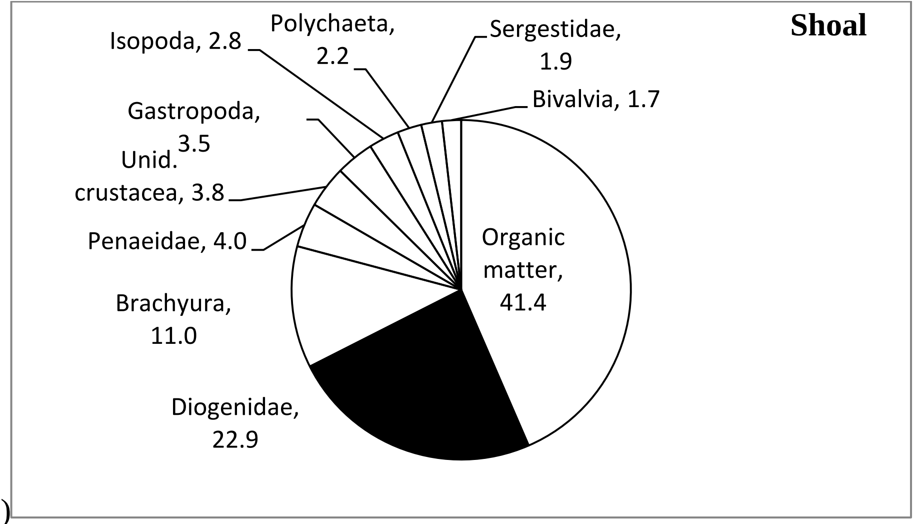


(a)



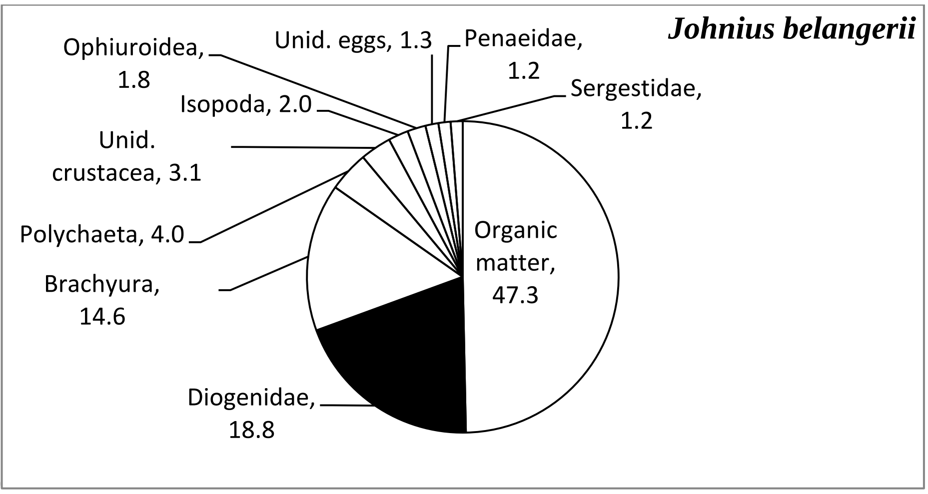
(b)

(Figure 3.6.4, continued)

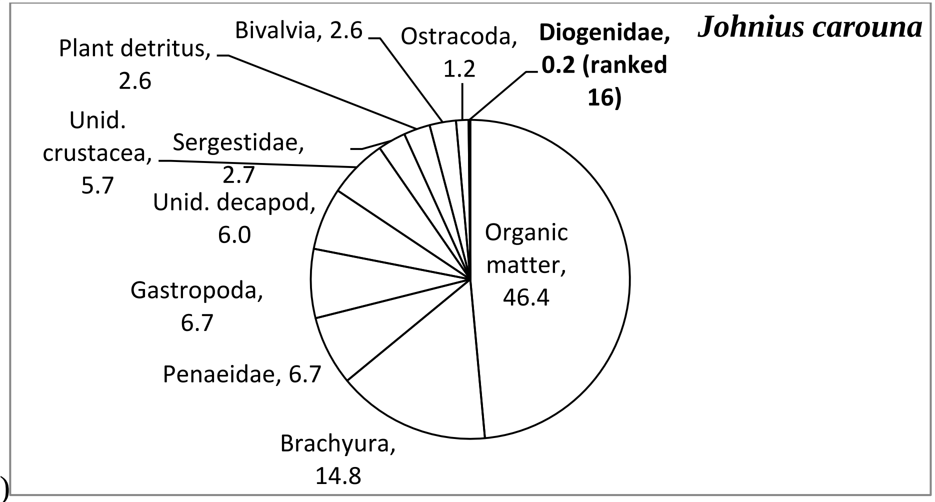


(c)

Fig. 3.6.4. Mean volumetric compositions (%) of major prey taxa (≥1% composition) irrespective of predator groups at (a) river mouth, (b) mudflat and (c) shoal stations in Matang mangrove estuary (solid pie indicates composition of hermit crabs).

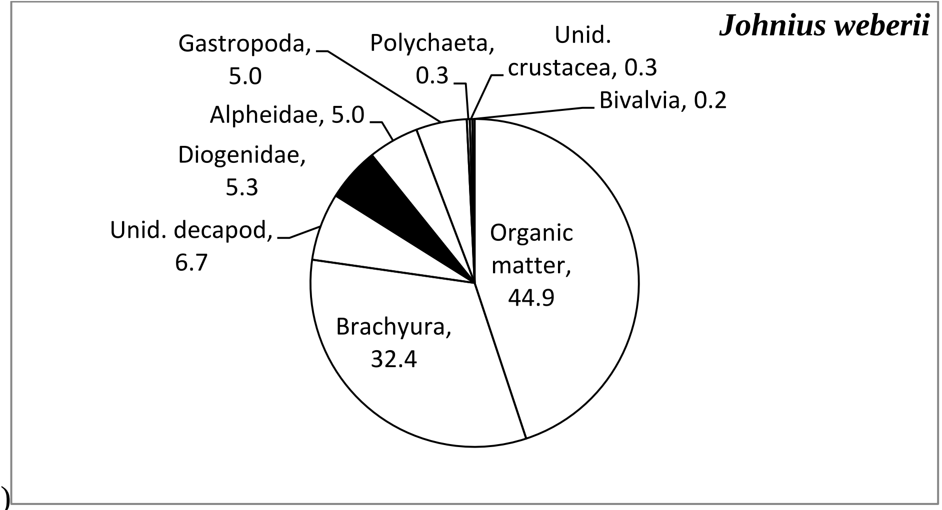


(a)



(b)

(Figure 3.6.5, continued)



(c)

Fig. 3.6.5. Mean volumetric compositions (%) of major prey taxa (only the top ten taxa were selected for clarity of presentation) of major sciaenid species; (a) *Johnius belangerii*, (b) *J. carouna* and (c) *J. weberii* in Matang mangrove estuary (solid pie indicates composition of hermit crabs).

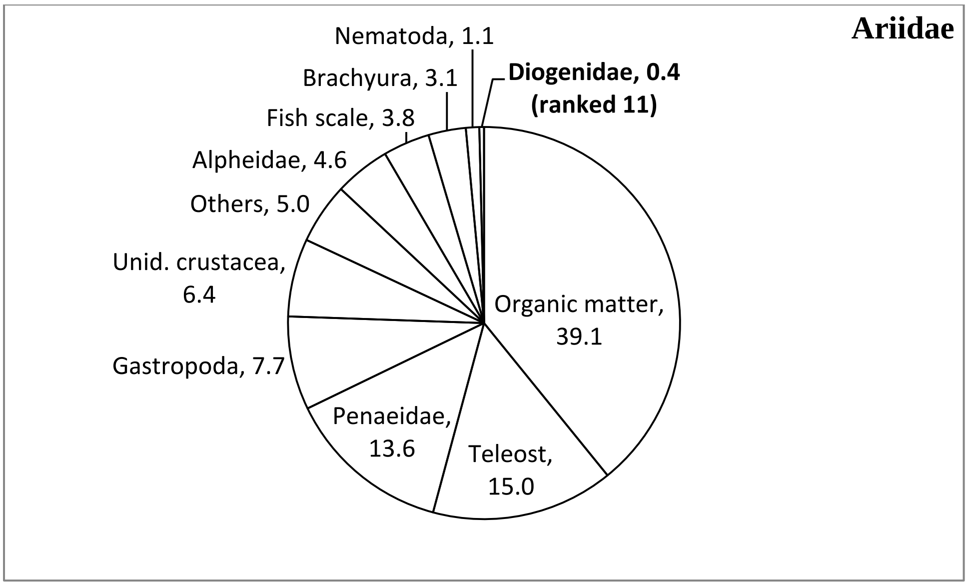


Fig. 3.6.6. Mean volumetric compositions (%) of major prey taxa (only the top ten taxa were selected for clarity of presentation) of Aridae in Matang mangrove estuary (solid pie indicates composition of hermit crabs).

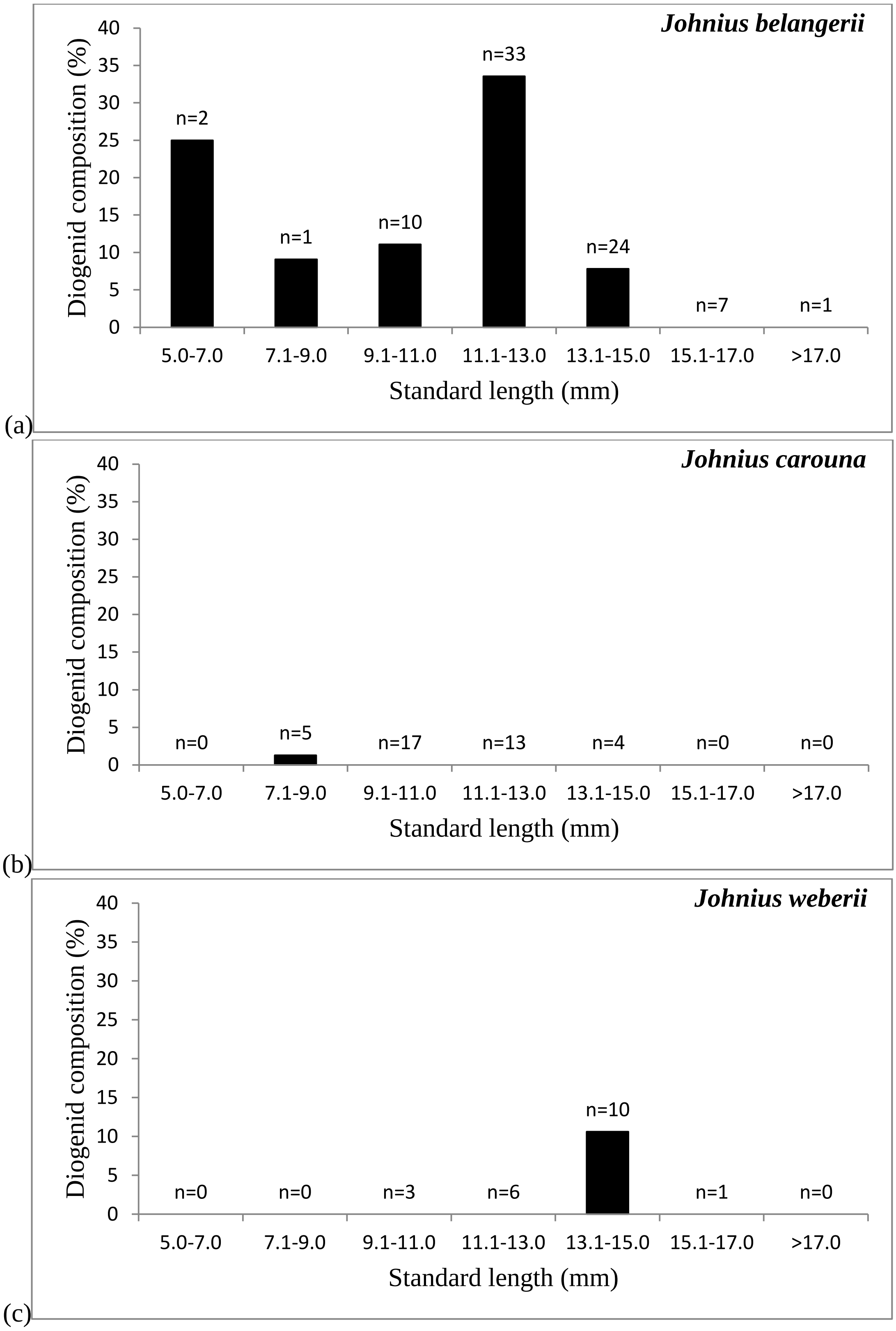


Fig. 3.6.7. Composition (%) of Diogenidae in the diet of (a) *Johnius belangerii*, (b) *J. carouna* and (c) *J. weberii* in Matang mangrove estuary; n = no. of individual fishes.

3.6.3 Spatial and temporal distribution patterns of predatory fishes

The sciaenid fishes at mudflat and shoal stations are represented by *Johnius weberii*, *J. carouna* and *J. belangerii* which composed collectively of about 92.19% and 99.32% of all sciaenid fishes caught at mudflat and shoal stations respectively during monthly samplings. Comparatively, ariid fishes were less abundant than sciaenids at all sampling stations. Common species of ariids included *Arius venosus*, *A. maculatus*, *A. sagor*, *A. caelatus*, *A. truncatus* and *Osteogeneiosus militaris*. Spatial and temporal abundance of these predatory fishes were described as shown in Table 3.6.8, Fig. 3.6.8 (mudflat) and Fig. 3.6.9 (shoal station). Mean density of ariids at mid-estuary and river mouth stations were both significantly higher ($H=49.39$, $p<0.001$) than mudflat and shoal stations while density at mudflat was significantly higher ($H=49.387$, $p<0.001$) than shoal station. Abundance of sciaenids were significantly higher ($H=56.854$, $p<0.001$) at both mid-estuary and shoal station with means of 520.51±457.67 ind/ha and 534.36±560.10 ind/ha respectively (Appendix XIXa). At mudflat, density peaks of sciaenids were apparent in April, June and December 2010 and January 2011, while density peaks of Ariidae were apparent in April and July 2010. At the shoal station, density peaks of sciaenids were observable in October 2009, January and end of June 2010 and January 2011, while exceptionally high density of ariids was recorded in April 2010. Pearson correlation test and lag analysis did not show any significant correlation ($p>0.05$) between density of both sciaenids and ariids with density of hermit crabs in mudflat and shoal stations (Table 3.6.9).

Table 3.6.8. Basic statistics and summary results of Kruskal-Wallis test on density (ind/ha) of fishes from family Ariidae and Sciaenidae between sampling stations in Matang mangrove estuary from September 2009 to March 2011.

Family		Station				
		Mid-estuary	River mouth	Mudflat	Shoal	p-level
Ariidae	Mean	79.02^a	78.05^a	22.74^b	11.45^c	p<0.001
	SD	66.76	145.08	43.84	52.79	
	n	16	25	58	57	
	Min	0.00	0.00	0.00	0.00	
	Max	269.72	668.09	199.09	396.93	
Sciaenidae	Mean	520.51^a	136.17^b	111.84^b	534.36^a	p<0.001
	SD	457.67	284.91	248.00	560.10	
	n	17	25	58	57	
	Min	0.00	0.00	0.00	0.00	
	Max	1,567.43	1,469.57	1,429.43	2,173.49	

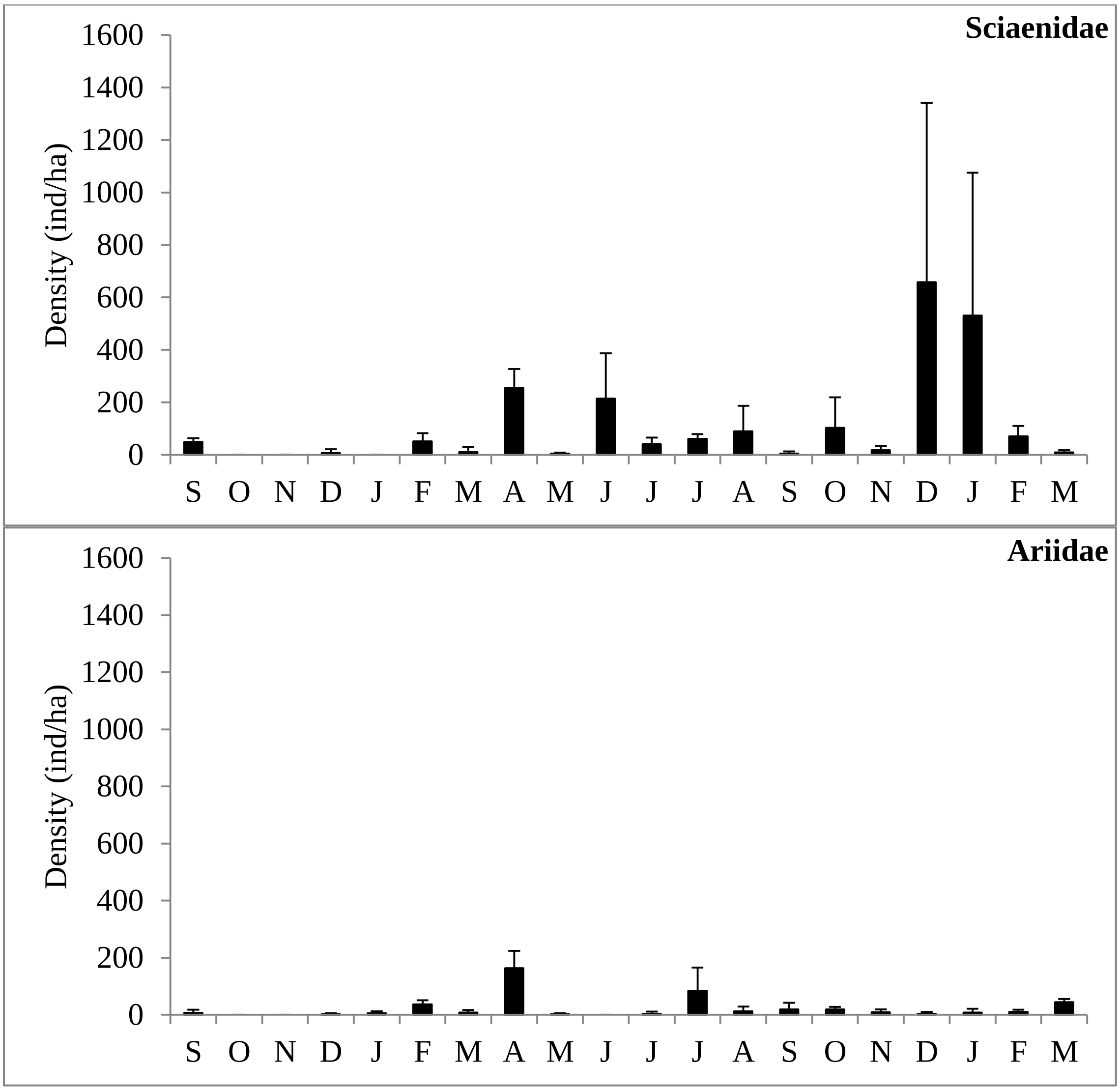


Fig. 3.6.8. Mean density (ind/ha) and standard deviations of hermit crab predators from family Sciaenidae and Ariidae at mudflat station in Matang mangrove estuary from September 2009 to March 2011.

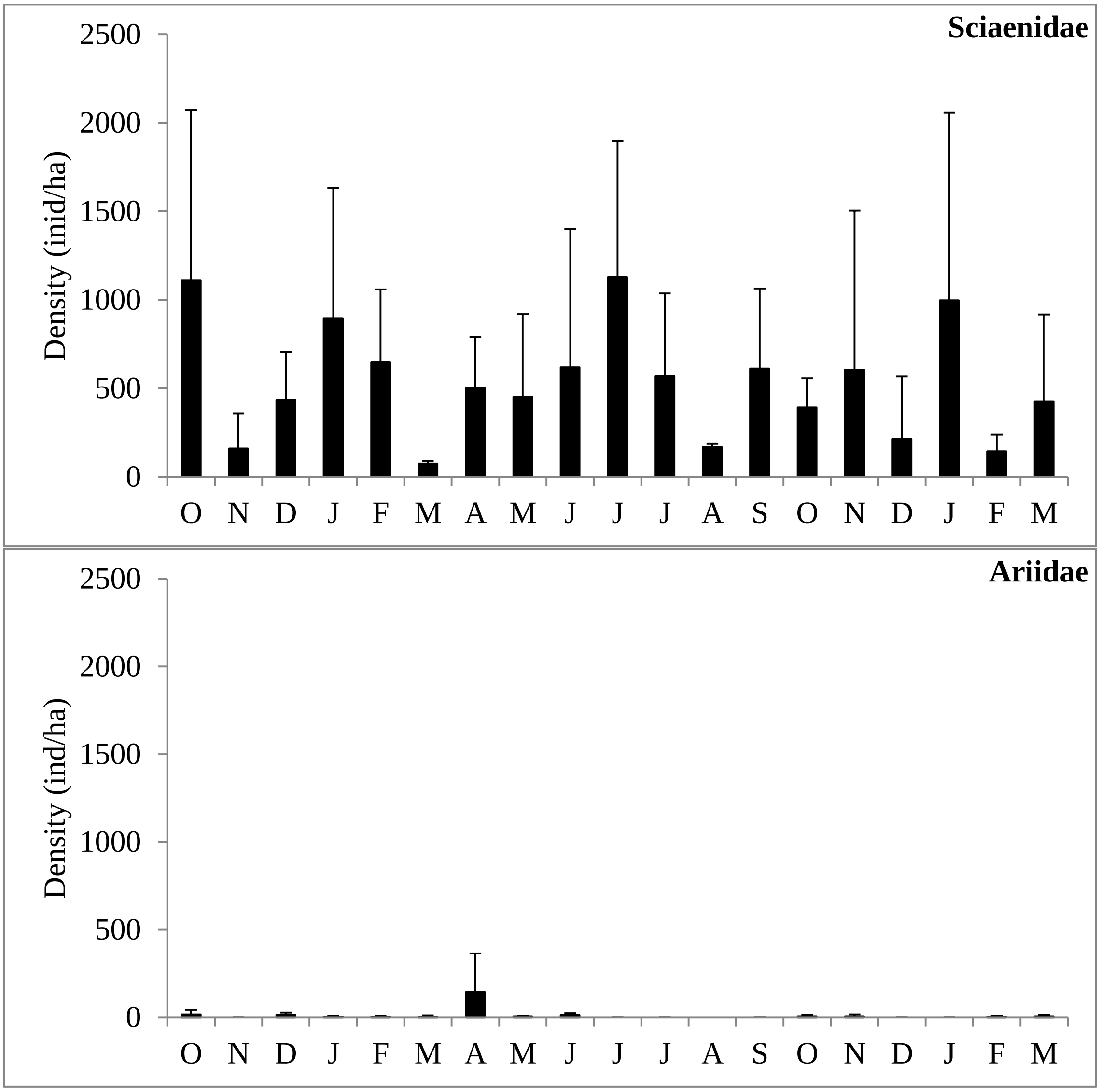


Fig. 3.6.9. Mean density (ind/ha) and standard deviations of hermit crab predators from family Sciaenidae and its juvenile and Ariidae at shoal station in Matang mangrove estuary from October 2009 to March 2011.

Table 3.6.9. (a) Pearson's correlation coeficients and (b) distributed lag analysis (one-month and two month) results between density (log transformed) of hermit crabs and fishes from family Ariidae and Sciaenidae which were the most abundant predatory fish of hermit crabs at mudflat and shoal stations in Matang mangrove estuary from September 2009 to March 2011; n=number of pairwise (significant at 5% level of significance).

(a)

Station	Predators	Species					
		D. moosai		*D. lopochir*		*C. infraspinatus*	
		Pearson, r	p-level	Pearson, r	p-level	Pearson, r	p-level
Mudflat	Ariidae	0.1656	p=0.485	0.3005	p=0.198	0.0234	p=0.922
(n=20)	Sciaenidae	-0.1785	p=0.451	0.3841	p=0.094	0.0699	p=0.770
Shoal	Ariidae	0.2708	p=0.262	0.4088	p=0.082	0.3284	p=0.170
(n=19)	Sciaenidae	-0.1756	p=0.472	-0.1161	p=0.636	-0.0240	p=0.922

(b)

Station	Predators	Lag length	Species					
			D. moosai		*D. lopochir*		*C. infraspinatus*	
			R-value	p-value	R-value	p-value	R-value	p-value
Mudflat	Ariidae	One-month	0.4690	0.2931	0.4986	0.6679	0.3020	0.9708
		Two-month		0.7531		0.5122		0.4995
	Sciaenidae	One-month	0.3175	0.5095	0.7139	0.8456	0.2974	0.3790
		Two-month		0.5426		0.1961		0.7088
Shoal	Ariidae	One-month	0.1465	0.9603	0.0941	0.9405	0.1461	0.8527
		Two-month		0.8864		0.9821		0.8962
	Sciaenidae	One-month	0.8248	0.6923	0.6325	0.3619	0.7339	0.2310
		Two-month		0.4895		0.5501		0.3998

3.6.4 Diel variations in abundance of predatory fishes

Ariidae and Sciaenidae were two common families of predatory fishes present during diel samplings. Common species of ariids caught during diel samplings included *Arius sagor*, *A. venosus*, *A. maculatus*, *A. caelatus*, *A. truncatus*, *A. utik*, *Osteogeneiosus militaris* and *Ketengus typus*, while the common Sciaenidae included *Johnius belangerii*, *J. weberii*, *J. carouna*, *J. borneensis*, *Pennahia anea*, *Aspericorvina jubata* and *Panna microdon*. Diel distribution patterns of these predatory fishes were described and compared by means of correlation with abundance of hermit crabs to determine the possibility of matching distribution patterns.

Mean density of sciaenids during wet and dry periods were 48.96±29.75 ind/ha and 158.17±114.66 ind/ha respectively whereas mean density of ariids during NE and SW were 24.19±16.80 ind/ha and 52.01±10.42 ind/ha respectively. Density ranged from 0.00 ind/ha to 410.46 ind/ha for ariids and 0.00 ind/ha to 1,466.31 ind/ha for sciaenids. Highest abundance of ariids was recorded during first quarter moon in both wet and dry periods with means of 48.78±103.47 ind/ha and 66.65±49.79 ind/ha. Highest abundance of sciaenids at wet and dry periods occurred during first quarter (87.05±114.16 ind/ha) and third quarter moon (290.03±424.28 ind/ha) respectively (Table 3.6.10). Kruskal-Wallis test did not detect any significant difference ($p>0.05$) in density of ariids between moon phases during both periods. Density of sciaenids during new moon was significantly lower ($H=14.406$, $p<0.01$) than other moon phases in dry period (Appendix XIXb). Diel variations in abundance of *D. moosai*, sciaenids and ariids are shown in Fig. 3.6.10.

Pearson correlation test showed that density of *D. moosai* during first quarter moon in wet period was negatively correlated ($r = -0.8230$, $p<0.05$) with density of ariids. Density of *D. moosai* during new moon in wet period was significantly positively correlated ($r = 0.7749$, $p<0.05$) with density of sciaenids while in dry period, density of *D. moosai* during third quarter moon was significantly negatively correlated ($r = -0.7076$, $p<0.05$) with density of sciaenids (Table 3.6.11).

Table 3.6.10. Basic statistics and summary of Kruskal-Wallis test on density (ind/ha) of Ariidae and Sciaenidae fishes between different moon phases in northeast and southwest monsoons. Max=maximum; Min=minimum; SD=standard deviation; ns= no significant; similar superscripts of a or b indicates homogenous group.

Family		Season									
		Northeast monsoon				p value	Southwest monsoon				p value
		First quarter	Full moon	Third quarter	New moon		First quarter	Full moon	Third quarter	New moon	
Ariidae	Mean	48.78	12.52	14.36	21.09	p=0.7253	66.65	51.89	46.41	43.08	p=0.3004
	SD	103.47	15.05	11.37	25.92	(ns)	49.79	40.05	40.77	53.89	(ns)
	n	16	9	8	14		16	16	16	16	
	Min	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	
	Max	410.46	38.25	35.89	96.83		165.74	146.63	153.81	147.10	
Sciaenidae	Mean	87.05	14.65	43.97	50.18	p=0.1387	95.54^{a}	212.26^{a}	290.03^{a}	34.86^{b}	$p<0.01$
	SD	114.16	21.30	39.19	68.37	(ns)	66.05	339.38	424.28	21.11	
	n	16	9	8	14		16	16	16	16	
	Min	0.00	0.00	0.00	0.00		0.00	0.00	28.33	0.00	
	Max	360.62	60.47	106.87	254.98		245.62	1,368.58	1,466.31	77.27	

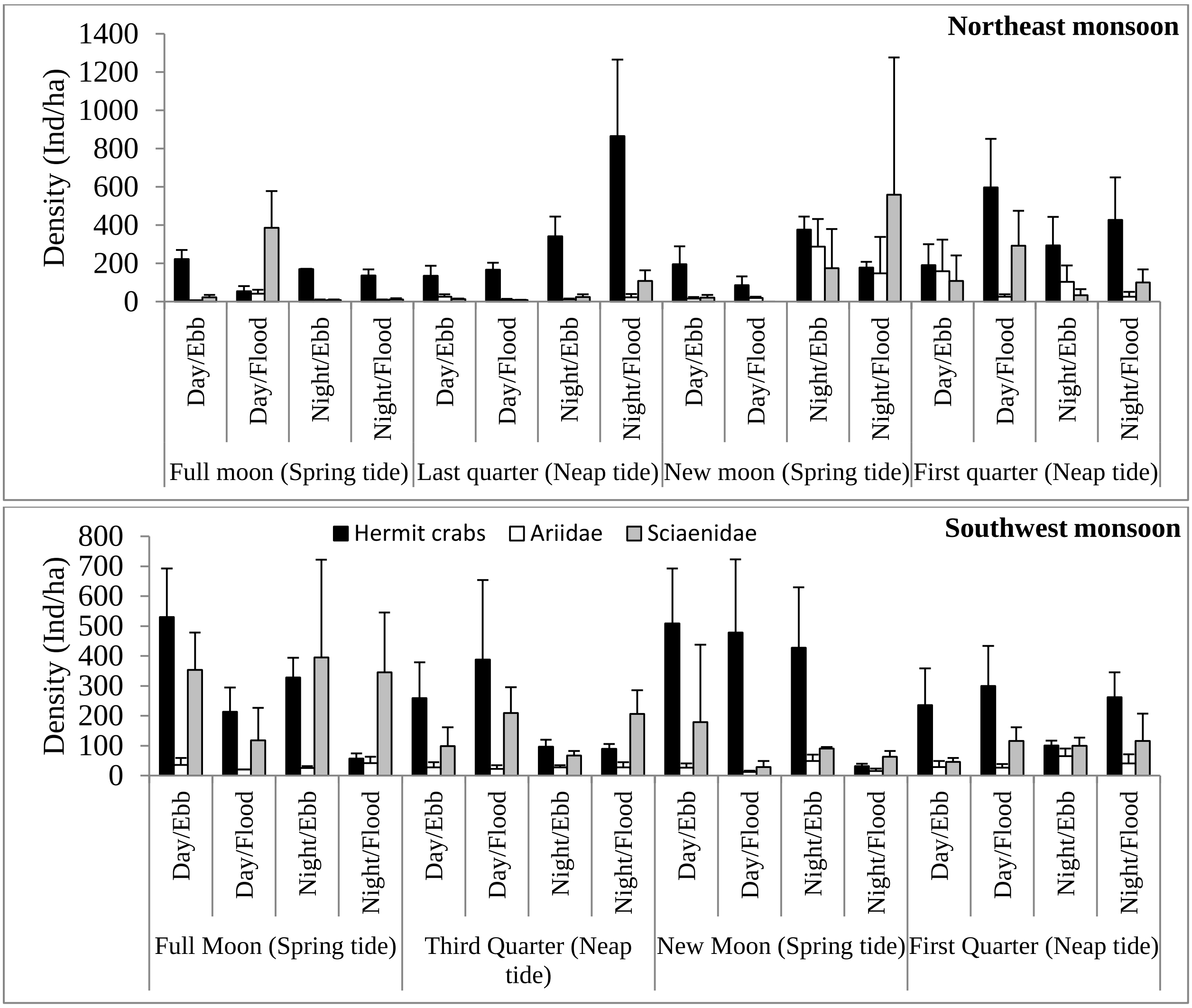


Fig. 3.6.10. Mean density (ind/ha) and standard deviation of hermit crabs, Ariidae and Sciaenidae at different moon phases and tidal conditions at mudflat of Matang mangrove estuary during northeast monsoon and southwest monsoon (note the difference in scales).

Table 3.6.11. Pearson's correlation coefficients (r) between density (log transformed) of *D. moosai* and predatory Ariidae and Sciaenidae fishes at different moon phases of two seasonal diel sampling occasions during northeast and southwest monsoon in Matang mangrove estuary; n=number of pairwise (significant at 5% level of significance).

Season	Moon phase	n	Species			
			Ariidae		Sciaenidae	
			Pearson, r	p value	Pearson, r	p value
Northeast monsoon	First quarter	8	-0.8230	p<0.05	0.0462	p=0.913
	Full moon	8	0.3240	p=0.434	-0.4704	p=0.240
	Third quarter	8	-0.2332	p=0.578	-0.1795	p=0.671
	New moon	8	-0.1155	p=0.785	0.7749	p<0.05
Southwest monsoon	First quarter	8	-0.2066	p=0.623	-0.6383	p=0.089
	Full moon	8	-0.4654	p=0.245	-0.3899	p=0.340
	Third quarter	8	-0.4833	p=0.225	-0.7076	p<0.05
	New moon	8	0.3746	p=0.361	0.0544	p=0.0898

3.6.5 Discussion

The feeding modes of hermit crabs have been generalized by Schembri (1982) as deposit-feeders feeding on benthic particulate, detrital and macroscopic material. This was based on observation of 15 species of hermit crabs in southeastern New Zealand. He further elaborated that there was no obvious correlation between taxonomic group and their feeding behavior suggesting employment of several similar feeding mechanisms by different species of hermit crabs. Laboratory observation on *D. moosai* and *D. lopochir* revealed their capability in deposit feeding. In the laboratory, individuals of these species were observed to constantly pump out the mud sediment taken from their natural habitat. This implies the reliance of these species on ingestion of organic material from the sediment.

However, hermit crabs are known also to be able to employ different modes of feeding depending on availability of different food sources (Schembri, 1982) i.e. planktonic microorganisms and detrital matter via filter feeding mechanism (Boltt, 1961; Gerlach et al., 1976), scavenging on carrion and predation (Hazlett, 1981).

Therefore, stable isotope analysis technique is used in this study to trace the relative contribution of mangrove, seston and microphytobenthos derived food sources to hermit crab nutrition. Since larger predators like sciaenid fishes cannot neither directly feed on microscopic organism nor having the ability to extract organic material from sediment therefore, such information is crucial in understanding the energy flow from primary producers to larger predators.

SIAR results showed that microphytobenthos (overall mean proportion = 49.9%±14.6%) is major contributor to the nutrition of hermit crabs (both juveniles and adults) followed by phytoplankton (27.6%±9.3%) and mangrove (22.5%±7.7%). Both phytoplankton (16.2%) and mangrove (13.2%) have little effects on trophodynamics of juvenile hermit crabs at shoal water in Matang mangrove estuary (Table 3.6.4). *D. moosai* and *D. lopochir* which are dominant at mudflat and shoal station respectively, showed higher nutritional dependency towards microphytobenthos (Table 3.6.4). This tendency was more pronounced for juveniles collected from shoal station which showed high dependency towards microphytobenthos (70.3%) as primary food source. This result supports the findings of Chew et al. (2012) who reported that benthic diatoms and phytoplankton were the major primary source contributors in adjacent coastal waters. Chong et al. (2011) reported that mollusks, fish and prawns depend primarily on microphytobenthos and phytoplankton and that there was little influence of mangrove on the trophodynamics of coastal mudflats with respect to these animals.

However, in relative term, lower value of $\delta^{13}C$ for *D. moosai* (-20.1±0.1‰) and juveniles of *Diogenes* (-18.2±0.3‰) at mudflat indicates increasing dependency towards mangrove-derived material from shoal to mudflat stations. In fact, SIAR results showed comparable proportion of mangrove contribution (32.1%) with phytoplankton

(29.6%) and microphytobenthos (38.3%) on nutrition of *D. moosai* at mudflat (see Table 3.6.4). This could be explained by the proximity of mudflat station to mangrove fringe and hence, greater influence by the detrital input from mangroves on sediments. However, Chew et al. (2012) reported high contribution of phytoplankton (70% - 84%) on zooplankton in river mouth and mangrove estuary while proportion of mangrove primary source remains low (<11%). This perhaps due to variation in feeding mode and vertical distribution between zooplankton and hermit crabs. Zooplankton being planktonic are more effective in utilizing phytoplankton as primary source whereas hermit crabs which are bottom feeders are more effective in utilizing microphytobenthos and mangrove as primary sources.

Both sciaenids and ariids are the major predatory fishes of Matang mangrove estuary (Chong et al. 2011). At mudflat and shoal areas, sciaenids are abundant with maximum density of 1,429 ind/ha and 2,173 ind/ha respectively whereas abundance of ariids is generally lower at these two areas compared to mid-estuary and river mouth (Table 3.6.8). Sciaenidae is the largest group of fish at Sangga Besar River which comprised about 41% of the total catch and this is followed by the ariids at 29% (Amy, 2008). Based on the stable isotope data (Table 3.6.3), sciaenids and ariids occupied the fourth trophic level which is two trophic levels higher than hermit crabs (trophic level 2) (see section 2.4.11 for calculation). Both sciaenids and ariids are therefore, indirectly dependent on phytoplankton, microphytobenthos and mangroves as these primary sources are fed directly by primary consumers including hermit crabs which are then predated by these fishes.

Stomach content analysis results showed that sciaenids and ariids fed mainly on crustaceans with overall volumetric composition of 42.6% and 28.1% respectively.

Sciaenids as crustacean feeders have been reported by Yap (1995). Chew (2012) reported higher crustacean contents in stomachs of juvenile of *A. venosus* (46.6%), *J. belangerii* (78.2%) and *J. weberii* (60.1%) although the proportion of diogenid as prey item was not specified. In contrast, Singh (2003) reported that *A. caelatus* and *A. venosus* fed mainly on teleosts whereas 99% of *C. truncatus* diet comprised of polychaetes. The variation in diet preference of ariids could be due to site differences since the ariids in Singh (2003) were captured in the mid- and upper estuary whereas in this study, the ariids were sampled from mudflat and shoal areas. Other predators such as portunid crabs particularly *Charybdis affinis* which occurred in substantial abundance in mudflat (21.1±31.8 ind/ha) and shoal stations (44.8±51.9 ind/ha) may also prey on hermit crabs. However, analysis of stomach content of portunid crabs is omitted in this study due to the difficulty in identifying the prey items since these portunid crabs masticate their food before ingestion (Williams, 1981).

The variability in proportion of hermit crab prey in stomachs of predatory fishes is likely resulted from spatial differences in abundance of hermit crabs and their predators. *D. moosai* and *D. lopochir* are abundant on the mudflat and shoal area respectively (Table 3.2.1) whereas sciaenids are more abundant at shoal area compared to at the mudflat (Table 3.6.8). This could explain the overall higher composition of *D. lopochir* as prey item (VC = 6.2%), compared to *D. moosai* (VC = 2.8%), in the stomachs of the sciaenids. On the other hand, both sciaenids and ariids were less abundant at mudflat and thus, less predation on *D. moosai*. Although sciaenids and ariids were relatively more abundant at mid- estuary and river mouth, hermit crabs were less abundant here. *C. infraspinatus* was not found in the diet of both groups of fish probably due to the large size of this species. In addition, most of *C. infraspinatus* occupied tougher shells of *Murex occa*, *Natica tigrina* and *Pugilina cochlidium* that offer better protection from predatory fishes.

Size of *J. belangerii* that fed on hermit crabs ranged from 5.0-15.0 cm (largest specimen examined was 17.0 cm) suggesting that young and adult of this species could predate on hermit crabs. Although size class with highest composition of diogenids prey item of *J. belangerii* was between 11.1 cm to 13.0 cm, the high presence of diogenids in stomachs of smaller specimens (5.0-7.0 cm) infers the importance of hermit crabs for growing individuals of *J. belangerii* (Fig. 3.6.7).

Although there were no significant correlations even with lag time consideration, in abundance between sciaenids and hermit crabs (Table 3.6.9), the higher densities of sciaenids regularly coincided with the drier periods, except October 2009 (based on SPI values in Fig. 3.1.3). This explains the high predation on hermit crabs at shoal area when density of both sciaenids and hermit crabs are highest. The non-significant correlation abundance between hermit crabs and predators in diel samplings at the mudflat area (Table 3.6.11) may further suggest that hermit crabs (particularly *D. moosai* which formed 96% of total hermit crabs caught at the mudflat area) are an optional prey target and that presence of predators is not a determinant factor modulating presence of hermit crabs at the mudflat area.

Gregarious behavior of hermit crabs as suggested by the high standard deviations of abundance data confers an added opportunity for predatory fishes to obtain easy meal. The method used by these fishes to extract hermit crabs from their shells is however not known. An idea emerged that hermit crabs aggregate for the purpose of shell exchange (Gherardi et al, 1994) and during this time, hermit crabs may go astray and become ‘naked’ when available shells are not quickly found and this would expose themselves to predators. It is also possible that maxillae protrusion of predatory fishes is fast enough to bit off the thoracic region of the hermit crab before it can retrieve into the shell. However, both of these hypotheses remain untested in this study. Diogenids formed a substantial diet of *J. belangerii* (Fig. 3.6.5) and although hermit crabs may not form the significant diet of the other predatory fishes like *J. weberii*, *J. carouna* and ariids, the presence of hermit crabs broaden the food option for these fishes.

3.6.6 Conclusion

Stable isotope analysis results showed that microphytobenthos (overall mean proportion = 49.9%±14.6%) is the major primary producer contributing to the nutrition of hermit crabs followed by phytoplankton (27.6%±9.3%) and mangroves (22.5%±7.7%). The reliance on type of primary sources is probably site dependent and varied along the estuarine gradient as evidenced by the increasing dependency on mangrove derived carbon by hermit crabs from coastal water to upriver. Stomach content analysis of Sciaenidae and Ariidae, the major fish predators in Matang estuary, revealed consumption of hermit crabs; *Johnius belangerii* had the highest diogenid prey items in terms of volumetric composition (18.8%). Hermit crabs face the greatest predation at subtidal shoal area (22.9% by volumetric composition of total prey items identified) compared to mudflat (3.7%) and river mouth (1.8%). The incorporation of stable isotope and stomach content results reflect the trophic role of hermit crabs as intermediary, transferring energy from primary producers to animals of higher trophic level.

CHAPTER 4

GENERAL DISCUSSION AND CONCLUSION

4.1 A conceptual model of the interactions among three hermit crab species with the abiotic and biotic factors in Matang mangrove estuary and adjacent coastal waters

From the synthesis of the findings of the present study, the distribution of the three major species of hermit crab in relation to the environment and biological interactions is shown in a schematic diagram in Fig. 4.1. The availability of empty gastropod shells will limits the distribution and abundance of hermit crabs. This study reveals shell use partition among the three species of hermit crabs; *Diogenes moosai*, *D. lopochir* and *Clibanarius infraspinatus*. The partition in shell use is possible since different species and sex of hermit crabs differ in their body sizes. Females are smaller than males in all species. Size compatibility between hermit crabs and their shells is crucial to their choice of particular shells; for example, the nassarid shells are preferred by the smaller diogenids (section 3.4). Therefore, the smaller *Diogenes* species and the larger *C. infraspinatus* show little overlap in the type of shells used (Table 3.4.1, pg. 148). Hence, inter- and intraspecific competition for shell resource appears to be reduced.

Both *Diogenes* species thrive in the mudflat and offshore shoal area, given the high availability of cerithiid and nasariid shells. Some degree of spatial separation of these two species is apparent with *D. moosai* and *D. lopochir* dominating in the mudflat and the shoal area respectively. *D. moosai* appears to be more physiologically tolerant to the harsher intertidal conditions as a result of periodic tidal emersion. The harsh intertidal conditions are the cause of high total mortality of *D. moosai* (Z=7.06 year^{-1}). However, *D. moosai* exploits the large numbers of *C. cingulata* shells found on the coastal mudflats. The long narrow shell of this gastropod is more compatible to the smaller size of *D.moosai*, where it could also retreat into the apex of the shell. On the other hand, *D. lopochir* appears to be less tolerant of the intertidal conditions, being found in more subtidal waters at the offshore shoal. *D. moosai* also occurred here but in lesser numbers. Since both species use the common nassariid shells found here, competition for these shells between the two diogenids is expected in the subtidal waters. Intense competition is more likely between male *D. moosai* and female *D. lopochir* (which overlapped in their size) for shells of *N. jacksonianus*.

Although availability of shells appears to modulate the spatial distribution of hermit crabs, other interplaying factors such as predation and bottom water characteristics likely contribute to determining distribution. With the exception of *C. infraspinatus*, hermit crabs are less abundant in mid-estuary (Table 3.2.1, pg. 86). The deeper and sheltered water at mid-estuary however has lower level of dissolved oxygen and salinity (ranging from 10.79 ppt to 28.58 ppt) which incurs physiological stress to *Diogenes* hermit crabs. On the other hand, the coastal waters are temporally more homogenous due to lesser riverine but higher marine influence. The smaller confined area of the mid-estuary with high abundance of ariid and sciaenid fishes is likely to expose hermit crabs to higher predation risk. Additionally, the availability of suitable small shells (e.g. *N. cf. olivaceus*, *N. jacksonianus* and *C. cingulata*) declines towards the upper estuary (Table 3.4.6, pg. 168). Therefore, these conditions are not favourable to sustain a resilient population of *Diogenes* species in the estuary.

In contrast, *C. infraspinatus* is more widespread ($p>0.05$) in all sampling stations and dominant at mid-estuary where the highest mean density was observed (Table 3.2.1, pg. 86). This indicates that this species is hardier and can adapt to the wide fluctuations in environmental conditions. The larger size of *C. infraspinatus* and their occupancy of the larger and tougher shells of mainly *M. occa* and *P. cochlidium* (Table 3.4.1, pg. 148) may substantially reduce the risk of being predated by fishes. Stomach content analysis of both ariid and sciaenid fishes caught at the river mouth, mudflat and shoal areas revealed no remnants of *C. infraspinatus*. Also, at mid-estuary, the habitat is more heterogeneous with the complex root system of the mangrove forest which offers many hiding places for *C. infraspinatus*.

The adaptability of both *Diogenes* species to their common shells may not always be advantageous. At the shoal area where *T. malayensis* (whose shells are commonly occupied by *D. lopochir*) are abundant (Table 3.4.6, pg. 168), *D. lopochir* are heavily predated by sciaenid fishes. At the shoal area, *D. lopochir* comprised 14.4% of the mean volumetric composition of the stomach contents of sciaenid fishes compared to *D. moosai* at 5.7% (Table 3.6.7, pg. 200). However, higher shell availability at the shoal area appears to outweigh the risk of higher predation. On the other hand, *D. moosai* experiences less predation at the mudflat due to regular exposure during low tide and shallow water during high tide. However, during low water it is at greater risk of exposure to dessication and high water temperature. Food availability on the other hand, may not dictate the distribution and abundance of hermit crabs since hermit crabs are known to employ different modes of feeding such as scavenging and deposit feeding (Schembri, 1982) and hence, able to utilise any available food sources.

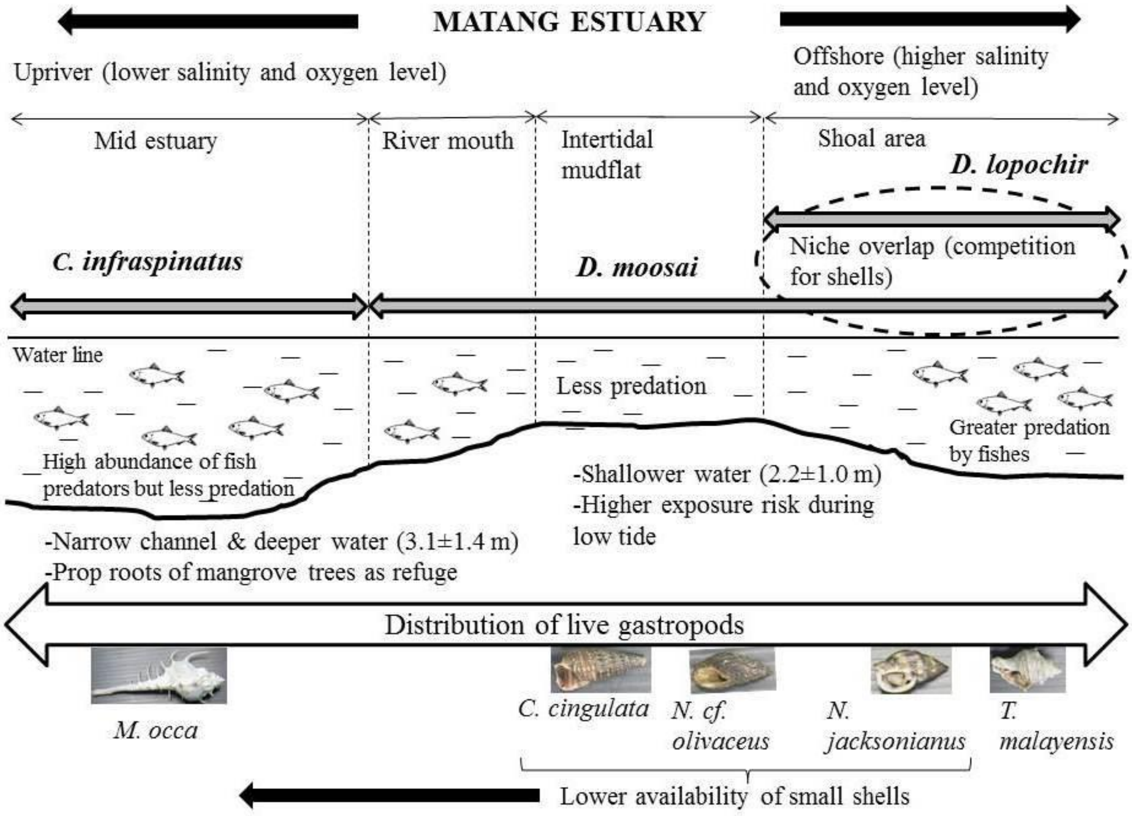


Fig. 4.1. Schematic diagram (not to scale) of the distribution of three common species of hermit crabs (*C. infraspinatus*, *D. moosai* and *D. lopochir*) from mid-estuary to offshore shoal area, in relation to the environment, and biological interactions (in Matang mangrove estuary. Double sided grey arrows indicate the range where the species of hermit crab is dominant or is substantially abundant (>30% of the total abundance of hermit crabs at the site). The distribution of live gastropods indicates where they are most abundant. Shell availability has been shown to correlate with live gastropod abundance (Section 3.4.7, pg. 167).

4.2 Trophic role of hermit crabs

Fig. 4.2 shows a generalised schematic diagram of the trophic role of hermit crabs as intermediary linking primary producers to predatory fishes in the estuarine food web. Predation on hermit crabs is greater at the subtidal shoal area (Fig. 3.6.4, pg. 200) where both hermit crabs, *D. moosai* (131.94±129.51 ind/ha) and *D. lopochir* (240.38±624.64 ind/ha) occurred together, and where sciaenid fish (534.36±560.10 ind/ha) are most abundant. The predation on hermit crabs appears to be density dependent (both prey and predator) i.e. the higher the abundance of hermit crabs, the higher the predation by fishes. The high abundance of hermit crabs particularly *D. lopochir* at shoal area provides a consistent alternative food for the commercially-important sciaenid fishes. Additionally, hermit crabs are able to utilise different primary food sources which include microphytobenthos (49.9±14.6%), phytoplankton (27.6±9.3%) and mangrove (22.5±7.7%), an assurance of continuous food supply.

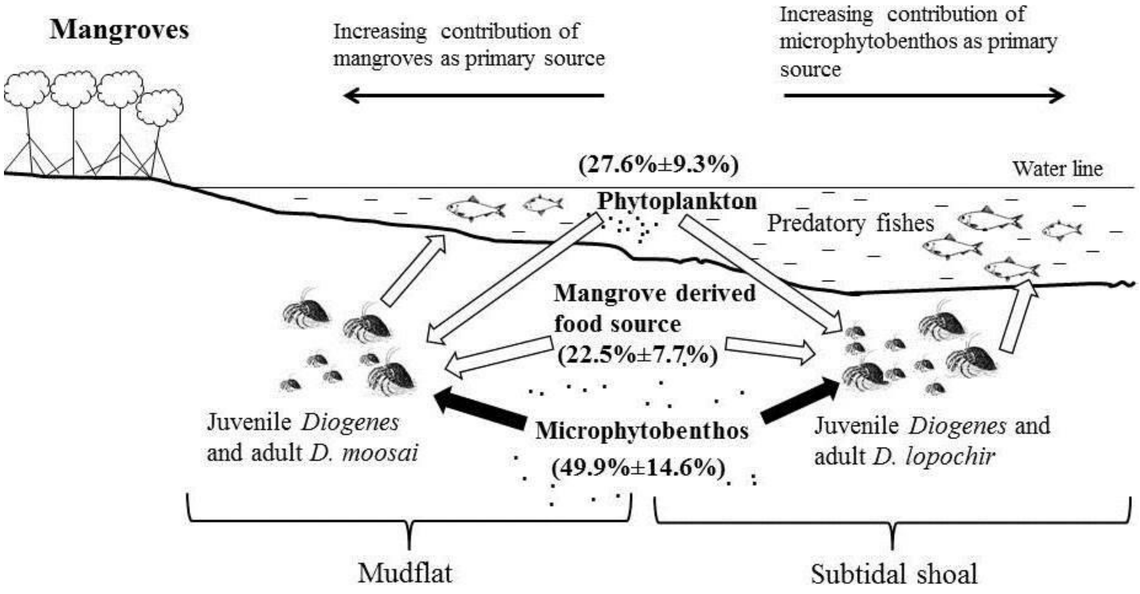


Fig. 4.2. Schematic diagram (not to scale) of relationship between primary producers (mangroves, microphytobenthos and phytoplankton), hermit crabs and predatory fishes based on this study; thick solid arrow indicates major primary source for hermit crabs; hollow arrows indicate minor primary sources and fish predation on hermit crabs. Percentage indicates overall proportion contribution of each primary source based on SIAR results.

The stomach content analysis and stable isotope analyses in this study are limited to two groups of fishes; Sciaenidae and Ariidae which are the most abundant predatory fishes in Matang mangrove estuary (Then, 2008). Other fish species that are known to consume hermit crabs included *Illisha melastoma*, *Upeneus sulphurous*, *Pomadasys kakaan*, *Lutjanus johnii*, *Eleutheronema tetradactylum*, *Arius maculatus*, *Dendrophyssa russelli*, *Johnius borneensis* and carangids (Chew, 2012). A conceptual diagram of the relationships between these fish species, hermit crabs and primary producers and their trophic position is shown in Fig. 4.3.

The noteworthy predator of hermit crabs is *Johnius belangerii*, the fish species which consumes the most hermit crabs (18.8%). High aggregations of *D. moosai* and *D. lopochir* in the shoal area (as indicated by the high standard deviations) (Table 3.2.1, pg. 86) may explain why they are heavily predated by *J belangerii*. However, other crustacean groups such as penaeids and brachyurans also formed the diet of *J. belangerii*, as well as *J. weberii* , *J. carouna* and ariid catfishes.

According to Chew (2012), juveniles of ariids (*A. maculatus*, *C. truncatus* and *A. venosus*) relied on zooplankton (e.g. copepods, chaetognaths and cirriped larvae) as major prey items while hermit crabs, penaeids and brachyurans also contributed substantially (10%-50%). The diet of juveniles of other common fishes such as *I. melastoma*, *Upeneus sulphureus*, carangids, *P. kakaan*, *L. johniis* and *E. tetradactylum* which also fed on hermit crabs, relied on hyperbenthic shrimps (e.g. *Acetes* species and mysids) as major prey items (Chew, 2012). Therefore, other prey groups at the 2nd or 3rd trophic level (Penaeidae, Brachyura, zooplankton and hyperbenthic shrimps) share the common predators with hermit crabs. Stable isotope results in the present study as well as Chew (2012) show the trophic dependency of hermit crabs for microphytobenthos and phytoplankton at the lower reaches of the estuary and shallow coastal area.

Mangrove derived carbon source may have less influence on hermit crabs in coastal waters. However, reliance on the type of primary sources is site dependent and varied along the estuarine gradient (Chew, 2012). Okamura et al. (2010) reported that mangrove-derived carbon in the sediment is significantly lower in coastal waters of Matang as compared to tidal creeks and upper reaches of the estuary. In this study, the mean $\delta^{13}C$ value of juvenile *Diogenes* decreased from shoal area to mudflat, while the $\delta^{13}C$ value of *D. lopochir* from shoal area was higher than *D. moosai* from mudflat

(Table 3.6.2, pg. 190). This indicates the increasing dependency on mangrove derived carbon by hermit crabs from coastal waters (shoal station = -18.56±7.06 ‰) to estuary (mudflat = -26.42±8.05 ‰). Thus, there is high dependency of consumers on microphytobenthos and phytoplankton in nearshore coastal waters as compared to consumers in the upper estuary, as also reported by Chew (2012) and Chong et al. (2011).

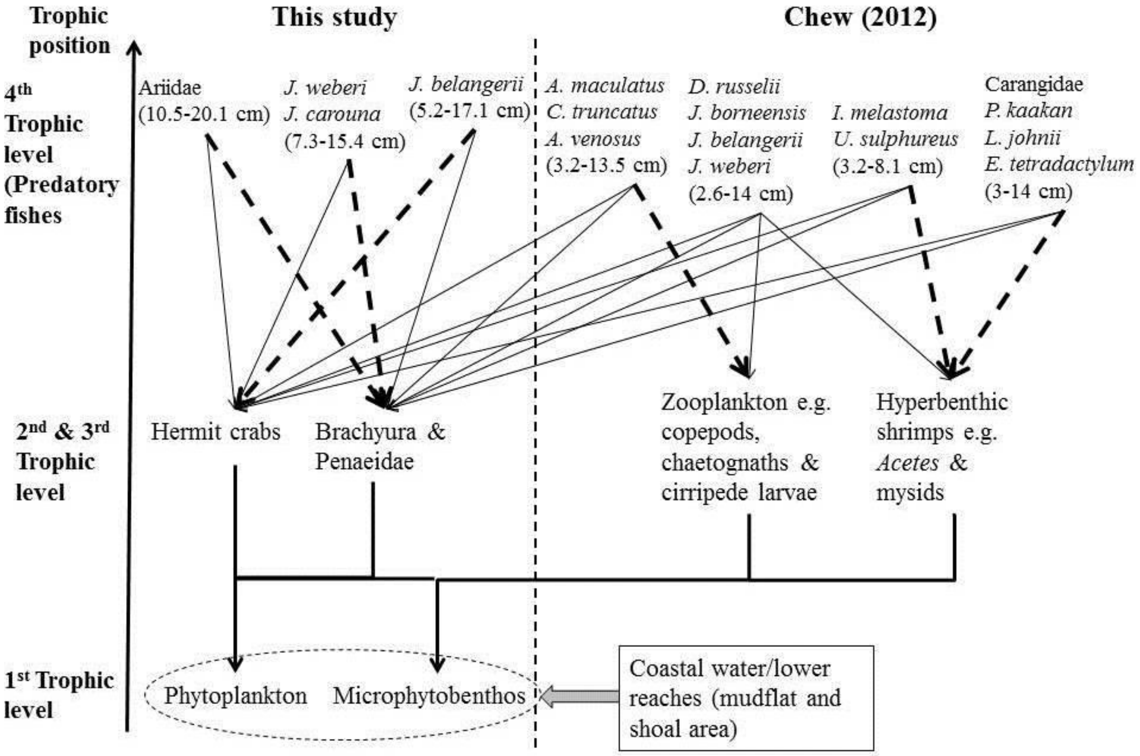


Fig. 4.3. Schematic trophic relationships of some common predatory fish species, their prey items and primary producers (microphytobenthos and phytoplankton) based on present study and Chew (2012). Major diet of the predatory fishes is indicated by thick broken arrows while thin arrows indicate food items that contributed 10% to 50% of the dietary compositions of the fishes. Values in parenthesis indicate size range (standard length) of fishes.

The ability of hermit crabs to utilize mangrove carbon (ca. 20%) as evident from the stable isotope analysis is however interesting. This is in view of the fact that few marine organisms can digest or utilize the largely refractory or cellulosic material of mangrove detritus (see Chong, 2007; Niiyama et al., 2012). The few reported organisms with this ability are mysids (Tanimura et al., 2012), penaeid shrimps (Newell et al., 1995; Chong et al., 2001), intertidal shelled molluscs (Niiyama et al., 2012), and brachyuran crabs (see Rodelli et al., 1984) all occurring inside or just outside the mangrove estuary. However, outside the estuary and in offshore waters, their ability to utilize mangrove carbon may diminish with ontogeny (e.g. Newell et al., 1995), thus explaining the lack of such organisms in marine waters. Thus, the diogenid hermit crabs which are largely distributed in the coastal areas away from mangrove forests could be among the few marine organisms capable of channelling (refractory) mangrove carbon to coastal food webs.

4.3 The role of predation on hermit crab interactions

Predation can be a potential selection pressure that modulates the assemblage (Bertness, 1981) and shell use (Rossi & Parisi, 1972; Bertness, 1981) of hermit crabs. Although fish and brachyuran crabs are known to crush the gastropod shells of hermit crabs during predation (Bertness & Cunningham, 1981; Bertness, 1982), other predators including gastropods, fishes and crabs have been known to extract hermit crabs without inflicting extensive damage to the shells (Bertness, 1981). Hence, predation can return the supply of good condition shells. The hermit crabs of both *Diogenes* species found in the stomachs of the sciaenid fishes were 'naked', suggesting two possibilities; either the hermit crabs were predated when astray without their shells, e.g. during shell exchange, or the sciaenid fishes were able to extract the hermit crabs from their shells. In any case, the continuous predation by either fish or other predatory crustaceans on hermit crabs and gastropods could have opened up or created empty niches for hermit crabs to occupy. For example, in this study, about 1.6% of hermit crabs caught at both mudflat and shoal area, occupied shells with boring holes, indicating creation of shell supply resulting from gastropod predation. Wilber Jr. et al. (1984) reported that the occupancy of new shells of the marsh periwinkle (*Littorina irrorata*) by the hermit crab, *Pagurus longicarpus* is the result of periwinkle predation by the predatory gastropod, *Melongena corona*.

At the offshore shoal area, both coexisting *Diogenes* species are exposed to greater predation by fish (22.9% volumetric composition of all examined stomachs of fishes at shoal area) than on the mudflat (3.7%). At the shoal area competition for common shell resource is also expected between the hermit crabs. However, the higher abundance (Table 3.2.1, pg. 86) and the overall larger body size (Fig. 3.3.1, pg. 129) and cheliped (Fig. 3.3.3, pg. 132) of *D. lopochir* give it an advantage over *D. moosai* when competing for the similar pool of shell resources. Thus, assuming no predation, it is likely that the larger and more aggressive *D. lopochir* will triumph over its smaller counterpart in shell fights, and thus gain higher access to more shell resources. However, in the presence of predation which can significantly cull the numbers of the dominant species, the result could be surprisingly different. The hypothesis that predation on the dominant competitor species could alleviate the adverse impact of competition and increase community diversity by removing the monopoly of the dominant species was first proposed by Paine (1966) which was further demonstrated by Vance (1974) in the comprehensive one predator two prey model communities, showing that a species that is less vulnerable to predator could coexist with its superior competitor. Similar model was also proposed by Leibold (1996) to explain coexistence among species sharing same resource and a common predator.

In the shoal area, the greater predation on *D. lopochir* (14.4% of sciaenid fish stomach contents) as compared to *D. moosai* (5.7%) similarly keeps the numbers of *D. lopochir* in check and therefore, reduces the likelihood of competitive exclusion of *D.*

moosai. Nevertheless, the presence of the dominant species also restricts the spatial and complete dominance of *D. moosai* in coastal waters. The higher vulnerability of *D. lopochir* to predation by sciaenid fishes could be the result of their aggregated or clumped distribution (variance/mean > 3) (see Table 3.2.1, pg. 86). Therefore, it is hypothesized that predation (on hermit crabs) is also an important factor that ameliorates the adverse effect of interspecific competition between the two *Diogenes* species in offshore waters allowing their coexistence. This hypothesis is testable using manipulative experiments in the field.

4.4 Reproduction and recruitment strategies of hermit crabs

Fig. 4.4 shows the schematic diagram of the reproduction strategies adopted by the two main species of *Diogenes* hermit crabs in Matang estuary. The high predation on *D. lopochir* by fish at the shoal area and the high mortality due to harsh environmental conditions at the mudflat explain their high natural mortality rate (*D. moosai* = 3.76 year^{-1}; *D. lopochir* = 3.54 year^{-1}). However, *D. moosai* had higher total mortality ($Z = 7.06$ year^{-1}) compared to *D. lopochir* ($Z = 3.71$ year^{-1}) (see section 3.3.2, pg. 139). The total mortality of both *Diogenes* species is much higher than the diogenid, *Dardanus insignis* ($Z = 2.21$ year^{-1}) as reported by Branco et al. (2002). *D. moosai* suffers high fishing mortality ($F= 3.30$) on the coastal mudflat where it is incidentally harvested by intensive cockle dredging. In contrast, *D. lopochir* does not ($F=0.17$) because the offshore shoal area is not dredged. Nevertheless, the high natural mortality of both species (M for *D. moosai* = 3.76 year^{-1}; *D. lopochir* = 3.54 year^{-1}) appears to be induced in different ways that resulted in adoption of different reproduction strategies by both *Diogenes* species. *D. lopochir* suffers higher predation in subtidal waters as revealed by fish predation, while *D. moosai* in shallow waters is periodically exposed to tidal emersion and extreme environmental conditions. For instance, stomachs of sciaenid fishes contained 14.4% *D. lopochir* but only 5.7% *D. moosai* (Table 3.6.7, pg. 200). In the mudflat area, monthly bottom water temperature, salinity and DO during tidal inundation have been reported to fluctuate between 26.7-31.6 ^{o}C, 20.6-28.7 ppt and 0.69-5.49 mg/L respectively (Ramarn et al., 2012).

Since predation is a potential factor suppressing reproductive activity, as for e.g. in *Clibanarius vittatus* (Hazlett & Rittschof, 2000) and also in fishes (Fraser & Gilliam, 1992), the higher predation on *D. lopochir* could restrict its reproduction to the most favourable period. On the other hand, the very high total mortality of *D. moosai* as a result of fishing removal may elicit more frequent spawnings. Chew (2012) reported the occurrence of diogenid zoeae throughout the year in Matang nearshore waters, with mean monthly density of 312 ind/m^3. Assuming all larvae settle down in nearshore waters of 3.3m depth, the expected post-metamorphic settlement density would be 1029 ind/m^2. However, the mean monthly juvenile hermit crab density in nearshore waters has been estimated at 0.029 ind/m^2 (mudflat area) to 0.150 ind/m^2 (shoal area) in the present study (Table 3.2.7, pg. 97). This extremely large discrepancy between planktonic and benthic abundance suggests very high larval mortality, consistent with the contention of high natural mortality. Compensatory response in reproduction to stabilise population size has been reported for the bay anchovy, *Anchoa mitchilli* based on field data and simulation models (Cowan et al., 1999), for pinnotherid crabs (Hines, 1992) and for other fishes (Rose et al., 2001). Therefore, the high proportion of female spawning (ovigerous females) combined with frequent spawnings in *D. moosai* are probably necessary to offset the high mortality of both adult and larvae.

The subtidal shoal area is the major recruitment site of *Diogenes* hermit crabs where relatively high numbers of juveniles have been recorded (Table 3.2.7, pg. 97).

The shoal area is shared by both hermit crab juveniles and adults as nursery and maturation ground. This is advantageous for the growing juveniles since shells are more readily available either from dead gastropods or the recycled shells after the adults died. On the other hand, the mudflat areas may be a less favourable environment for the new recruits due to higher risk of exposure during low tide as well as fluctuating water conditions including salinity, DO and temperature. Unlike the adults, most of the juveniles observed in this study were ‘naked’ and may not be able to tolerate the harsh, drier and warmer environment of the mudflat during emersion. At the mid-estuary, availability of shell resources may be insufficient for the growing juvenile hermit crabs.

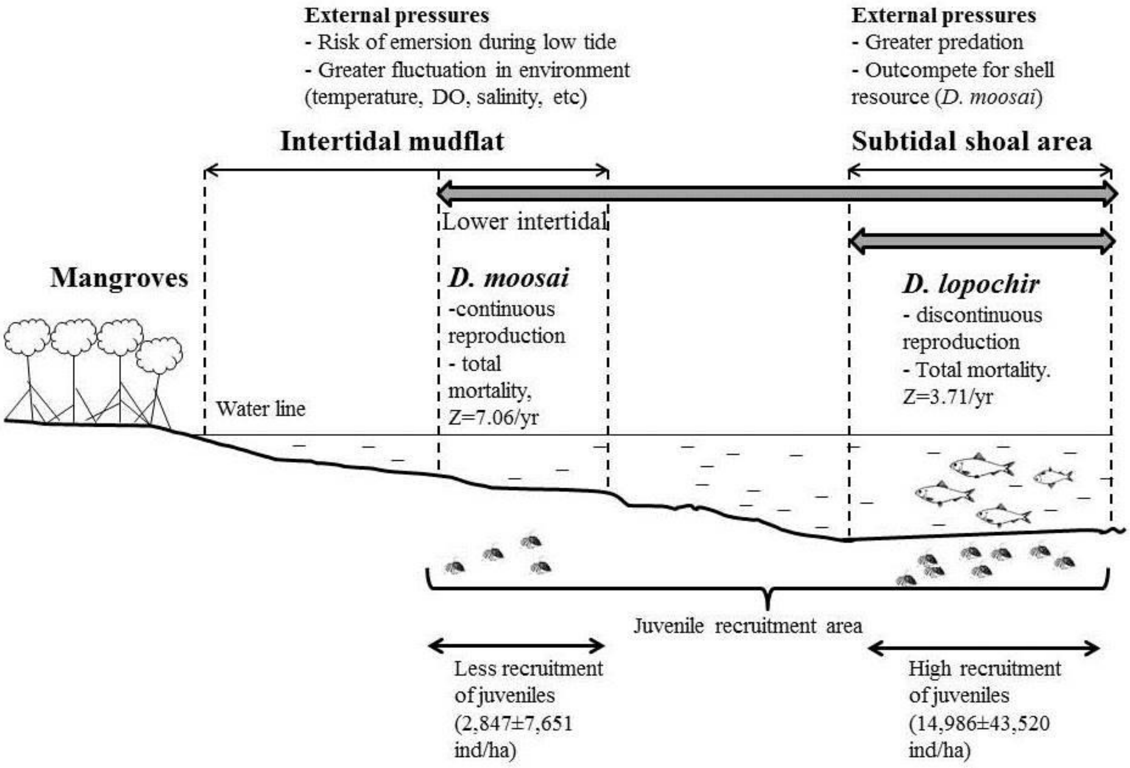


Fig. 4.4. Schematic diagram (not to scale) of reproduction strategies adopted by *D. moosai* and *D. lopochir*, given the different external pressures face by these hermit crabs. Double sided grey arrows indicate the range where the species of hermit crab is dominant or is substantially abundant (>30% of the total abundance of hermit crabs at the site).

4.5 Limitations in this study and future work

In this study, the abundance and distribution of the common hermit crabs (*C. infraspinatus*, *D. moosai* and *D. lopochir*) in Matang mangrove estuary as influenced by bottom water parameters (temperature, salinity, pH and oxygen level) and sediment characteristics (organic content and particle size) have been elucidated. However, this study had focused only on hermit crabs inhabiting the estuarine nearshore habitat characterised by muddy substrates. Although much information on tropical hermit crab ecology have been revealed in this study, the scientific knowledge of hermit crabs in this region is still much less than desired given the diversity of tropical marine habitats, hermit crabs and their gastropod hosts. It is therefore, an interesting prospect for future studies to cover more habitat settings. Within the scope of this study, there are still limitations that give rise to some uncertainties. These limitations serve to provide suggestions and ideas for further work on hermit crabs and as the basis to form new hypotheses that can be tested in future studies. The limitations and suggestions for future works are elaborated as follows:

1) Smaller hermit crabs and gastropods may escape through the mesh of the trawl net and thus, some bias in estimate of density of hermit crabs and gastropods is expected as the retention factor of 1.0 (i.e. assuming full retention or no escapement) was used. Although this assumption is justified in this study for the purpose of comparison (among species and sites), it is also because the hermit crabs and the gastropods are practically sedentary (or slow in their mobility), and there has been no experimental determination of epibenthic shell retention by a trawl net. Furthermore, the quantitative sampling of epibenthic fauna on soft bottom subtidal habitats poses a great challenge. The bottom trawl net operable during high tide has the advantage of covering a large area of sampling within a

short period. For the reason that the trawl net may be suitable to sample hermit crabs and other epibenthic fauna, future work should attempt to estimate the escapement rate of these epibenthic organisms when trawled. Such information would enhance the accuracy of density estimation of hermit crabs and their gastropod hosts.

2) In this study, the routine monthly samplings were performed during spring tide. Although there was no systematic survey on the effectiveness of otter trawl at different tidal condition (i.e spring and neap tides). The 24-hour sampling studies for four consecutive weeks at the mudflat showed that density of *D. moosai* caught during spring tide was consistently higher (nearly twice) than neap tide. It is not known however, if the tidal condition would influence the efficiency of the otter trawl at mid-estuary, river mouth and shoal areas. Nevertheless, all routine samplings were done consistently under the same tidal condition throughout the study and therefore, the spatial and temporal distribution patterns of hermit crabs could be compared.

3) Although there is spatial partitioning of hermit crabs in relation to salinity, this may not reflect the animal's limit of physiological tolerance or indicate the range of salinity preferred by these hermit crabs. Laboratory experiments could be conducted to verify the optimum conditions preferred by these hermit crabs. *D. moosai* which is abundant on the mudflat is able to tolerate harsher environment resulting from exposure and intense heat or higher temperature during low tide. Future work should consider experimental work on temperature and exposure tolerance of both diogenid species to verify the idea/hypothesis of higher tolerance by *D. moosai*. Future studies should also consider other factors

potentially modulating the temporal abundance of hermit crabs such as migration and competition.

4) Although reproduction intensity and recruitment to the population could be indicated by the presence of ovigerous female and juveniles, such information provides very little knowledge on the life cycle of hermit crabs. Future studies should describe egg development and life stages of larvae to juvenile. For instance, larval abundance could provide a more accurate estimation of reproduction pulses and recruitment pattern of hermit crabs.

5) The present study of shell use and partition of hermit crabs as influenced by shell size, shape and availability was based on field observations. Thus, it is not known if the type of shell occupied by hermit crabs is due to selection (preference) or shell availability. Ideally, the field observations could be supplemented with controlled laboratory experiments, such as shell selection experiments where the hermit crab could be offered a variety of shell choices. . Incorporating such information (preferred shells) with data from the present study (shells used and their abundance in the natural environment) would provide more concrete evidence on the inter- and intraspecific interactions among hermit crabs as modulated by shell availability in their natural environment.

6) Abundance of live gastropods was used as proxy to shell availability. The availability of empty shells may not be constant, and expected to be influenced by local hydrodynamics as there may be substantial import and/or export of empty shells by water current. However, our area of study is a low energy, major

depositional mudflat area and ‘empty’ shells are filled inside with mud. Moreover, all empty or occupied shells also belonged to those species living on site, including their juveniles and adults (Fig. 3.4.1-3.4.3, pg. 151-153 and Table 3.4.6, pg. 168). I did enumerate unoccupied shells in the samples, but they were very few or rare (and in poor state) suggesting very high occupancy of the available good shells. Empty shells could also be removed from the resource pool via burial in soft sediment, but both flood and ebb tidal currents also constantly disturb the soft mud surface to expose them. Our trawl net also scoured quite deep into the mud.

7) The trophic role of hermit crabs has been elucidated based on the results of stable isotope and gut content analysis of predatory fishes whereby hermit crabs serve the role of intermediary between primary food sources and higher trophic levels (i.e. predatory fishes). However, such results only provide a gross and limited view of the trophic contribution of hermit crabs. In future study, stomach content analysis should also include hermit crabs. This could provide a concrete evidence to support the current results on the dependency of hermit crabs on different primary sources. Study on this aspect could also be broadened to include feeding behaviour of both *D. moosai* and *D. lopochir*. As observed from laboratory, these hermit crabs are likely to be able to employ different feeding modes (Schembri, 1982) such as suspension feeding, scavenging and predation. Experimental based observation could be carried out to explicate the mechanisms and factors that induce employment of different feeding strategies of hermit crabs in Matang mangrove estuary.

8) As for predators of hermit crabs, this study only focused on two groups of fishes that fed on hermit crabs; sciaenids and ariids. Future studies should also include other potential predators of hermit crabs such as stomatopods, portunid crabs (particularly *Charybdis affinis*) and sting rays. These additional data would supplement the findings of the present study in order to better estimate the rate of predation on hermit crabs. Future work should also focus on experimental work to elucidate whether one or both diogenid species are equally vulnerable to fish predation and to test the hypothesis that predation of the dominant species allows the coexistence of the hermit crab species. This hypothesis can be tested in the field by using carefully designed caged and control experiments. Further experiments should also be designed to enable observation of the mechanisms involved on how fish predate on hermit crabs since no intact gastropod shells were found in the stomachs of these fishes. Some research questions asked could be: (a) Is the fish capable of breaking the shell?; (b) can the fish pull out the hermit crab using its mouth or by suction?; (c) is there a strategy to entice the hermit crab out of its shell? (d) are hermit crabs vulnerable to predation during shell exchanges?

4.6 Conclusion

This study is the first comprehensive attempt to clarify the ecology and adaptations of soft bottom hermit crabs in Malaysia. The small diogenid hermit crabs often occur gregariously in high numbers in estuaries and coastal waters despite their low diversity. The three major species of hermit crabs (*C. infraspinatus, Diogenes moosai*, *D. lopochir* and *C. infraspinatus*) are spatially distributed along a salinity gradient from brackish water estuaries, via coastal mudflats to rather marine coastal waters. However, tolerance to harsher conditions in the intertidal mudflat may be a driving force to their distribution; here, *D. moosai* which has a wider distribution appears to be more tolerant of such conditions. The availability of gastropod shells is an important biotic factor modulating the distribution and abundance of hermit crabs, since empty shells are rather few and even broken shells are occupied. Shells of 14 gastropod species were used by the two *Diogenes* species but >85% comprised shells of four main species, *Cerithidea cingulata*, *Nassarius cf. olivaceus*, *N. jacksonianus*, and *Thais malayensis*. It is further revealed that the size compatibility between hermit crabs and their shells determines the shell use pattern and explains the partitioning between species and sex of hermit crabs. However, interspecific competition between *D. moosai* and *D. lopochir* where their distribution overlaps in offshore waters, appears to be modulated by predation thus allowing coexistence. *Diogenes* hermit crabs are fed upon by predatory fishes particularly sciaenids. Stable isotope analysis provides evidence of the intermediary role played by hermit crabs in the Matang coastal food chain from three primary sources (phytoplankton, microphytobenthos, mangrove) to higher trophic levels. Both *Diogenes* hermit crabs adopted different reproduction strategies which may be related to their high mortality rate caused by different external pressures. *D. moosai* which suffers very high total mortality rate reproduces all year round whereas *D. lopochir* with a lower mortality rate concentrates reproduction to a few months. Nevertheless, both species display two reproductive peaks approximately two months after the onset of the northeast and southwest monsoon resulting in one major and one minor recruitment pulse.

SUMMARY

1. The bottom water characteristics at sampling sites in this study could be generalised as follow; mid-estuary station is characterised by lower salinity, deeper water and lower oxygen level compared to shoal station which is characterised by higher salinity, chalkier and shallower water whereas river mouth and mudflat represent the intermediate of the water characteristics. Although sediment organic content was significantly higher at mid-estuary compared to river mouth and mudflat, composition of particle size showed similar patterns in all stations with coarse silt having the highest composition.
2. Distribution pattern of hermit crabs showed apparent spatial separation with *C. infraspinatus* being dominant at mid-estuary, *D. moosai* is dominant at river mouth and mudflat stations whereas *D. lopochir* is dominant at shoal station. *C. infraspinatus* is associated with deeper and less saline water, coarser sediment with higher organic content and could tolerate lower oxygen level in water whereas *D. moosai* and *D. lopochir* is associated with water of higher salinity and DO, and finer sediment.
3. Abundance of juvenile hermit crabs are highest at shoal area followed by river mouth and mudflat, implying the use of the estuarine area as nursery ground, the same habitat the adults are distributed.
4. Temporal abundance of *D. moosai* and *D. lopochir* at mudflat and shoal areas did not varied in relation to environmental parameters. However, at river mouth, where *D. moosai* occurred in substantial number, salinity and DO appear to positively correlated with abundance of *D. moosai* and *C. infraspinatus* ($p<0.05$), indicating greater influence of freshwater.
5. Despite no significant correlation between water parameters and temporal abundance of *D. moosai* (mudflat and shoal) and *D. lopochir* (shoal), both

species had abundance peaks during drier months (as referred to monthly SPI values in Fig. 3.1.3, pg. 53) at both mudflat (May, end of June and July 2010) and shoal station (January, July and September 2010).

6. Based on SPI values, the period of diel sampling during northeast monsoon (December 2009) is relatively wetter than period of diel sampling during southwest monsoon (mid July to mid August 2010). Hermit crabs assemblage at mudflat station during diel samplings was dominated by *D. moosai* with over 96% of hermit crabs caught belonged to this species. Both *C. infraspinatus* and *D. lopochir* were presence in very low density and represented only about 2.5% and 1.1% of all hermit crabs caught. Both *C. infraspinatus* and *D. lopochir* were presence in low abundance and majority of the ingressed individuals were male with composition of male *C. infraspinatus* and *D. lopochir* being 91.07% and 96.67% respectively.

7. Tidal conditions (ebb/flood) did not significantly influence (Kruskal-Wallis, $p>0.05$) the density of *D. moosai* during wet period. However, during dry period, density of *D. moosai* was significantly higher ($H=16.571$, $p<0.001$) during spring ebb tide with mean density of 166.43±65.19 ind/ha compared to spring flood tide with mean density of 53±50 ind/ha. Similarly, during spring tide of dry period, density of ovigerous female during ebb tide was significantly higher ($H=15.125$, $p<0.001$) than during flood tide. Both observed patterns could be explained in the aspect of larval dispersal tendency and in this case, ovigerous female *D. moosai* may have used the strong tidal current to disperse their larvae shoal.

8. Length-frequency histogram showed unimodal pattern of both *D. moosai* and *D. lopochir*. *C. infraspinatus* is the largest of all species of hermit crabs sampled in Matang estuary. Sexual dimorphism occurs in all three major species (*C.*

infraspinatus, *D. moosai* and *D. lopochir*) with the male being generally larger than female. Length weight relationship yielded the parameter b (or slopes) that ranged from 2.67 to 3.28. Males of all species had greater slopes ($p<0.05$) compared to the females, indicating of higher rate of weight increment of males than females as they grow.

10. The fitted von Bertalanffy growth function (VBGF) yielded the following parameters for each species; K=1.4, L_∞=5.12 (*D. moosai*) and K=1.3, L_∞=5.39 (*D. lopochir*). Life span of both *D. moosai* and *D. lopochir* were estimated at 26 months and 28 months respectively. Total mortality, Z was estimated at 7.06 and 3.54 respectively for *D. moosai* and *D. lopochir*. The values of fishing mortality, F for both species (*D. moosai* = 3.30; *D. lopochir* = 0.18) despite their non-commercial value could be explained by the cockle dredging activity carried out especially at mudflat station where *D. moosai* was a dominant species.
11. Presence of ovigerous female *D. moosai* throughout most sampling months indicates that this species reproduce all year round but with differing intensities. On the other hand, temporal presence of ovigerous female *D. lopochir* was discontinuous. At shoal station where *D. lopochir* was abundant, ovigerous female was absent in almost half of the sampling months. Nevertheless, both species has biannual peaks in reproduction intensity about two months after the onset of the northeast and southwest monsoon which resulted in two recruitment pulses. The difference in reproduction strategies adopted by both *Diogenes* species reflects their exposure to different external pressures (risk of emersion, predation and competition).
12. There were a total of 19 shell species used by the three hermit crab species nevertheless, only few shell species were commonly occupied by hermit crabs despite the wide range of shell choices available; *D. moosai* commonly used

shells of *N. jacksnonianus*, *N. olivaceus* and *C. cingulata* shells, *D. lopochir* commonly used shells of *N. jacksonianus* and *T. malayensis* shells whereas the larger *C. infraspinatus* occupied mostly *M. occa* and *T. lacera* shells.

13. Shell partitioning between species and sex was apparent and this is possible since different species of gastropod shell differed in terms of size and shape. The extreme bias in shell selection suggests that shell shape, depending on shell species, is the major determinant of shell use by hermit crabs as long as the choice shell is available. The four most used shell of gastropod species differ in their shell morphometrics, particularly aperture length, shell height and shell width as revealed by discriminant analysis (Fig. 3.4.4, pg. 155). *T. malayensis* is more globose, *C. cingulata* is narrow and elongated while *N. cf. olivaceus* has distinctively elongated aperture length. Upon selection of preferred shell dimension, size of shells becomes important in determining optimum shell to wear. This is evidenced by the preference of larger male *D. lopochir* towards larger shell of *T. malayensis* compared to preference of smaller female *D. lopochir* towards smaller shell of *N. jackonianus* whereas *C. infraspinatus* being distinctly larger than both *Diogenes* sp. occupied large shells of *M. occa*, *T. lacera* and *Pugilina* sp.

14. The shell use pattern of these hermit crabs indicates that the occupied shell resource is proportionally dependent on the species and abundance of gastropod populations in the area. Despite intense competition between male *D. moosai* and female *D. lopochir* at shoal station for same shell of *N. jacksonianus,* most of the shells occupied were in good condition indicating shell resource is not in short supply.

15. Based on stable isotope results, microphytobenthos (overall mean proportion = 49.9%±14.6%) is the major contributor on nutrition of hermit crabs followed by

phytoplankton (27.6%±9.3%) and mangroves (22.5%±7.7%) in coastal waters. This affinity was more pronounced for juveniles collected from shoal station which showed high dependency towards microphytobenthos (70.3%) as primary food source. Contribution of mangrove-derived material increased from shoal to mudflat stations. SIAR results showed comparable proportion of mangrove contribution (32.1%) with phytoplankton (29.6%) and microphytobenthos (38.3%) on nutrition of *D. moosai* at mudflat.

16. Results of stomach content analysis showed that *Johnius belangerii* had the highest diogenid prey items in terms of volumetric composition (18.8%). Hermit crabs face the greatest predation at subtidal shoal area (22.9% by volumetric composition of total prey items identified) compared to mudflat (3.7%) and river mouth (1.8%). In the shoal area, predation on *D. lopochir* was greater predation (14.4% of sciaenid fish stomach contents) as compared to *D. moosai* (5.7%). Both stable isotope and stomach content results reflect the trophic role of hermit crabs as intermediary, transferring energy from primary producers to animals of higher trophic level.

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APPENDIX I

Teoh, H.W., & Chong, V.C. (2014a). Reproduction strategies and population dynamics of two *Diogenes* hermit crabs (Superfamily: Paguroidea) in a tropical mangrove estuary. *Hydrobiologia*, 724, 255-265.

APPENDIX II

Teoh, H.W., & Chong, V.C. (2014b). Shell use and partitioning of two sympatric species of hermit crabs on a tropical mudflat. *Journal of Sea Research*, 86, 13-22.

Appendix III. Results of Mann-Whitney significant test on amount of rainfall between seasons and Kruskal-Wallis test on water parameters among stations.

(a) Total rainfall

Mann-Whitney U Test (Rainfall) By variable **Season (northeast, NE and southwest, SW monsoon)** Marked tests are significant at p <.05000

	Rank Sum - SW	**Rank Sum - NE**	**U**	**Z**	**p-level**	**Z - adjusted**	**p-level**	**Valid N - SW**	**Valid N - NE**	**2*1sided - exact p**
Total rainfall (mm)	125.00	253.00	47.00	-2.10	0.035	-2.10	0.035	12	15	0.036531

(b) Temperature

Multiple Comparisons p values (2-tailed); **Temperature** (Water characteristics) Independent (grouping) variable: **Station** Kruskal-Wallis test: H (3, N= 203) =2.169317 p =.5380

	Mid-estuary – R:101.99	**River mouth – R:112.30**	**Mudflat – R:101.91**	**Shoal – R:94.892**
Mid-estuary		1.000000	1.000000	1.000000
River mouth	1.000000		1.000000	0.844930
Mudflat	1.000000	1.000000		1.000000
Shoal	1.000000	0.844930	1.000000	

(c) Salinity

Multiple Comparisons p values (2-tailed); **Sal (ppt)** (Water characteristics) Independent (grouping) variable: **Station** Kruskal-Wallis test: H (3, N= 203) =57.40914 p =.0000

	Mid-estuary – R:54.679	**River mouth – R:82.821**	**Mudflat – R:111.43**	**Shoal – R:139.28**
Mid-estuary		0.168828	0.000010	0.000000
River mouth	0.168828		0.095091	0.000011
Mudflat	0.000010	0.095091		0.058419
Shoal	0.000000	0.000011	0.058419	

(d) Total dissolved solids

Multiple Comparisons p values (2-tailed); **TDS (g/L)** (Water characteristics) Independent (grouping) variable: **Station** Kruskal-Wallis test: H (3, N= 203) =53.00678 p =.0000

	Mid-estuary – R:55.917	**River mouth – R:83.476**	**Mudflat – R:112.59**	**Shoal – R:136.81**
Mid-estuary		0.189401	0.000011	0.000000
River mouth	0.189401		0.084513	0.000038
Mudflat	0.000011	0.084513		0.147366
Shoal	0.000000	0.000038	0.147366	

(e) Dissolved oxygen concentration

Multiple Comparisons p values (2-tailed); **DO (mg/L)** (Water characteristics) Independent (grouping) variable: **Station** Kruskal-Wallis test: H (3, N= 203) =22.14657 p =.0001

	Mid-estuary – R:65.060	**River mouth – R:103.12**	**Mudflat – R:114.07**	**Shoal – R:115.21**
Mid-estuary		0.017930	0.000216	0.000132
River mouth	0.017930		1.000000	1.000000

Mudflat	0.000216	1.000000		1.000000
Shoal	0.000132	1.000000	1.000000	

(f) Disssolved oxygen saturation

Multiple Comparisons p values (2-tailed); **DO% (sat)** (Water characteristics) Independent (grouping) variable: **Station** Kruskal-Wallis test: H (3, N= 203) =23.42865 p =.0000

	Mid-estuary - R:63.976	**River mouth - R:103.35**	**Mudflat - R:113.98**	**Shoal – R:115.89**
Mid-estuary		0.012797	0.000149	0.000067
River mouth	0.012797		1.000000	1.000000
Mudflat	0.000149	1.000000		1.000000
Shoal	0.000067	1.000000	1.000000	

(g) pH

Multiple Comparisons p values (2-tailed); **pH (unit)** (Water characteristics) Independent (grouping) variable: **Station** Kruskal-Wallis test: H (3, N= 203) =23.39583 p =.0000

	Mid-estuary – R:64.286	**River mouth – R:103.69**	**Mudflat – R:118.45**	**Shoal – R:111.04**
Mid-estuary		0.012678	0.000030	0.000457
River mouth	0.012678		1.000000	1.000000
Mudflat	0.000030	1.000000		1.000000
Shoal	0.000457	1.000000	1.000000	

(h) Suspended particulate matter

Multiple Comparisons p values (2-tailed); **Amount of SPM (g/L)** (Water characteriastics) Independent (grouping) variable: **Station** Kruskal-Wallis test: H (3, N= 119) =12.89617 p =.0049

	Mid-estuary – R:43.478	**River mouth – R:49.958**	**Mudflat – R:64.389**	**Shoal – R:72.861**
Mid-estuary		1.000000	0.138947	0.008511
River mouth	1.000000		0.674510	0.070534
Mudflat	0.138947	0.674510		1.000000
Shoal	0.008511	0.070534	1.000000	

(i) Sediment organic content

Multiple Comparisons p values (2-tailed); **arcsine** (Organic content of sediment) Independent (grouping) variable: **Station** Kruskal-Wallis test: H (3, N= 159) =46.84792 p =.0000

	Mid-estuary – R:117.09	**River mouth – R:82.656**	**Mudflat – R:86.830**	**Shoal – R:46.813**
Mid-estuary		0.016644	0.024790	0.000000
River mouth	0.016644		1.000000	0.003882
Mudflat	0.024790	1.000000		0.000137
Shoal	0.000000	0.003882	0.000137	

Appendix IV. Kruskal-Wallis significant test on composition of different sediment particle size categories among stations.

(a) Clay

Multiple Comparisons p values (2-tailed); **Clay**, Independent (grouping) variable: Station Kruskal-Wallis test: H (3, N= 16) =6.860294 p =.0765

	Mid-estuary - R:9.0000	**River mouth - R:8.7500**	**Mudflat - R:12.500**	**Shoal - R:3.7500**
Mid-estuary		1.000000	1.000000	0.713294
River mouth	1.000000		1.000000	0.824911
Mudflat	1.000000	1.000000		0.056075
Shoal	0.713294	0.824911	0.056075	

(b) Fine silt

Multiple Comparisons p values (2-tailed); **Fine silt**, Independent (grouping) variable: Station Kruskal-Wallis test: H (3, N= 16) =9.750000 p =.0208

	Mid-estuary - R:8.2500	**River mouth - R:8.7500**	**Mudflat - R:13.750**	**Shoal - R:3.2500**
Mid-estuary		1.000000	0.613876	0.824911
River mouth	1.000000		0.824911	0.613876
Mudflat	0.613876	0.824911		0.010889
Shoal	0.824911	0.613876	0.010889	

(c) Coarse silt

Multiple Comparisons p values (2-tailed); **Coarse silt**, Independent (grouping) variable: Station Kruskal-Wallis test: H (3, N= 16) =5.536765 p =.1365

	Mid-estuary - R:7.2500	**River mouth - R:7.5000**	**Mudflat - R:6.0000**	**Shoal - R:13.250**
Mid-estuary		1.000000	1.000000	0.448236
River mouth	1.000000		1.000000	0.525813
Mudflat	1.000000	1.000000		0.187643
Shoal	0.448236	0.525813	0.187643	

(d) Very fine sand

Multiple Comparisons p values (2-tailed); **Very fine sand**, Independent (grouping) variable: Station Kruskal-Wallis test: H (3, N= 16) =1.872239 p =.5993

	Mid-estuary - R:7.0000	**River mouth - R:10.125**	**Mudflat - R:6.7500**	**Shoal - R:10.125**
Mid-estuary		1.000000	1.000000	1.000000
River mouth	1.000000		1.000000	1.000000
Mudflat	1.000000	1.000000		1.000000
Shoal	1.000000	1.000000	1.000000	

(e) Fine sand

Multiple Comparisons p values (2-tailed); **Fine sand**, Independent (grouping) variable: Station Kruskal-Wallis test: H (3, N= 16) =1.742869 p =.6274

	Mid-estuary - R:10.000	**River mouth - R:7.5000**	**Mudflat - R:6.6250**	**Shoal - R:9.8750**
Mid-estuary		1.000000	1.000000	1.000000
River mouth	1.000000		1.000000	1.000000
Mudflat	1.000000	1.000000		1.000000
Shoal	1.000000	1.000000	1.000000	

(f) Medium sand

Multiple Comparisons p values (2-tailed); **Medium sand**, Independent (grouping) variable: Station Kruskal-Wallis test: H (3, N= 16) =3.000000 p =.3916

	Mid-estuary - R:10.000	**River mouth - R:8.0000**	**Mudflat - R:8.0000**	**Shoal - R:8.0000**
Mid-estuary		1.000000	1.000000	1.000000
River mouth	1.000000		1.000000	1.000000
Mudflat	1.000000	1.000000		1.000000
Shoal	1.000000	1.000000	1.000000	

(g) Coarse sand

Multiple Comparisons p values (2-tailed); **Coarse sand**, Independent (grouping) variable: Station Kruskal-Wallis test: H (3, N= 16) =3.000000 p =.3916

	Mid-estuary - R:10.000	**River mouth - R:8.0000**	**Mudflat - R:8.0000**	**Shoal - R:8.0000**
Mid-estuary		1.000000	1.000000	1.000000
River mouth	1.000000		1.000000	1.000000
Mudflat	1.000000	1.000000		1.000000
Shoal	1.000000	1.000000	1.000000	

(h) Very coarse sand

Multiple Comparisons p values (2-tailed); **Very coarse sand**, Independent (grouping) variable: Station Kruskal-Wallis test: H (3, N= 16) =0.000000 p =1.000

	Mid-estuary - R:8.5000	**River mouth - R:8.5000**	**Mudflat - R:8.5000**	**Shoal - R:8.5000**
Mid-estuary		1.000000	1.000000	1.000000
River mouth	1.000000		1.000000	1.000000
Mudflat	1.000000	1.000000		1.000000
Shoal	1.000000	1.000000	1.000000	

Appendix V. Results of Mann-Whitney significant tests on water parameters between seasons (northeast and southwest monsoon) at each station.

(a) Mid-estuary

Station2=**Mid-estuary** Mann-Whitney U Test (Water parameters (Season)) By variable **Season** Marked tests are significant at p <.05000

	Rank Sum - SW	**Rank Sum - NE**	**U**	**Z**	**p-level**	**Z - adjusted**	**p-level**	**Valid N - SW**	**Valid N - NE**	**2*1sided - exact p**
Temp	336.00	330.00	120.00	1.27	0.20	1.27	0.20	16	20	0.21
TDS (g/L)	346.50	319.50	109.50	1.61	0.11	1.61	0.11	16	20	0.11
Sal (ppt)	352.00	314.00	104.00	1.78	0.08	1.78	0.08	16	20	0.08
pH (unit)	290.00	376.00	154.00	-0.19	0.85	-0.19	0.85	16	20	0.86

Station2=**Mid-estuary** Mann-Whitney U Test (Water parameters (Season)) By variable Season Marked tests are significant at p <.05000

	Rank Sum - SW	**Rank Sum - NE**	**U**	**Z**	**p-level**	**Z - adjusted**	**p-level**	**Valid N - SW**	**Valid N - NE**	**2*1sided - exact p**
DO% (sat)	345.00	285.00	75.00	2.50	0.01	2.50	0.01	15	20	0.01
DO (mg/L)	339.50	290.50	80.50	2.32	0.02	2.32	0.02	15	20	0.02

Station=**Mid-estuary** Mann-Whitney U Test (Water parameters (Season)) By variable **Season** Marked tests are significant at p <.05000

	Rank Sum - NE	**Rank Sum - SW**	**U**	**Z**	**p-level**	**Z - adjusted**	**p-level**	**Valid N - NE**	**Valid N - SW**	**2*1sided - exact p**
Organic content (%)	274.00	191.00	103.00	-0.21	0.83	-0.21	0.83	18	12	0.85

Station=**Mid-estuary** Mann-Whitney U Test (Water parameters (Season)) By variable **Season** Marked tests are significant at p <.05000

	Rank Sum - NE	**Rank Sum - IN**	**U**	**Z**	**p-level**	**Z - adjusted**	**p-level**	**Valid N - NE**	**Valid N - IN**	**2*1sided - exact p**
Amount of SPM (g/L)	54.00	24.00	14.00	0.34	0.73	0.34	0.73	8	4	0.80

(b) River mouth

Station2=**River mouth** Mann-Whitney U Test (Water parameters (Season)) By variable **Season** Marked tests are significant at p <.05000

	Rank Sum - SW	**Rank Sum - NE**	**U**	**Z**	**p-level**	**Z - adjusted**	**p-level**	**Valid N - SW**	**Valid N - NE**	**2*1sided - exact p**
Temp	319.00	347.00	137.00	0.73	0.46	0.73	0.46	16	20	0.48
TDS (g/L)	350.00	316.00	106.00	1.72	0.09	1.72	0.09	16	20	0.09
Sal (ppt)	354.00	312.00	102.00	1.85	0.06	1.85	0.06	16	20	0.07
pH (unit)	288.50	377.50	152.50	-0.24	0.81	-0.24	0.81	16	20	0.81

Station2=**River mouth** Mann-Whitney U Test (Water parameters (Season)) By variable Season Marked tests are significant at p <.05000

	Rank Sum - SW	**Rank Sum - NE**	**U**	**Z**	**p-level**	**Z - adjusted**	**p-level**	**Valid N - SW**	**Valid N - NE**	**2*1sided - exact p**
DO% (sat)	334.00	261.00	51.00	3.11	0.00	3.11	0.00	14	20	0.00
DO (mg/L)	331.00	264.00	54.00	3.01	0.00	3.01	0.00	14	20	0.00

Station=**River mouth** Mann-Whitney U Test (Water parameters (Season)) By variable **Season** Marked tests are significant at p <.05000

	Rank Sum - NE	**Rank Sum - SW**	**U**	**Z**	**p-level**	**Z - adjusted**	**p-level**	**Valid N - NE**	**Valid N - SW**	**2*1sided - exact p**
Organic content (%)	265.00	200.00	94.00	-0.59	0.55	-0.59	0.55	18	12	0.57

Station=**River mouth** Mann-Whitney U Test (Water parameters (Season)) By variable **Season** Marked tests are significant at p <.05000

	Rank Sum - NE	**Rank Sum - IN**	**U**	**Z**	**p-level**	**Z - adjusted**	**p-level**	**Valid N - NE**	**Valid N - IN**	**2*1sided - exact p**
Amount of SPM (g/L)	60.00	18.00	8.00	1.36	0.17	1.36	0.17	8	4	0.21

(c) Mudflat

Station2=**Mudflat** Mann-Whitney U Test (Water parameters (Season)) By variable **Season** Marked tests are significant at p <.05000

	Rank Sum - SW	**Rank Sum - NE**	**U**	**Z**	**p-level**	**Z - adjusted**	**p-level**	**Valid N - SW**	**Valid N - NE**	**2*1sided - exact p**
Temp	571.50	754.50	318.50	-0.01	0.99	-0.01	0.99	22	29	0.99
TDS (g/L)	610.50	715.50	280.50	0.73	0.46	0.73	0.46	22	29	0.47
Sal (ppt)	620.00	706.00	271.00	0.91	0.36	0.91	0.36	22	29	0.37
pH (unit)	563.50	762.50	310.50	-0.16	0.87	-0.16	0.87	22	29	0.87

Station2=**Mudflat** Mann-Whitney U Test (Water parameters (Season)) By variable Season Marked tests are significant at p <.05000

	Rank Sum - SW	**Rank Sum - NE**	**U**	**Z**	**p-level**	**Z - adjusted**	**p-level**	**Valid N - SW**	**Valid N - NE**	**2*1sided - exact p**
DO% (sat)	501.00	774.00	270.00	-0.68	0.50	-0.68	0.50	21	29	0.51
DO (mg/L)	492.00	783.00	261.00	-0.86	0.39	-0.86	0.39	21	29	0.40

Station=**Mudflat** Mann-Whitney U Test (Water parameters (Season)) By variable **Season** Marked tests are significant at p <.05000

	Rank Sum - NE	**Rank Sum - SW**	**U**	**Z**	**p-level**	**Z - adjusted**	**p-level**	**Valid N - NE**	**Valid N - SW**	**2*1sided - exact p**
Organic content (%)	633.50	356.50	203.50	0.63	0.53	0.63	0.53	27	17	0.54

Station=**Mudflat** Mann-Whitney U Test (Water parameters (Season)) By variable **Season** Marked tests are significant at p <.05000

	Rank Sum - NE	**Rank Sum - IN**	**U**	**Z**	**p-level**	**Z - adjusted**	**p-level**	**Valid N - NE**	**Valid N - IN**	**2*1sided - exact p**
Amount of SPM (g/L)	81.00	90.00	3.00	-3.10	0.00	-3.09	0.00	12	6	0.00

(d) Shoal station

Station2=**Shoal** Mann-Whitney U Test (Water parameters (Season)) By variable **Season** Marked tests are significant at p <.05000

	Rank Sum - SW	Rank Sum - NE	U	Z	p-level	Z - adjusted	p-level	Valid N - SW	Valid N - NE	2*1sided - exact p
Temp	681.50	803.50	338.50	0.37	0.71	0.37	0.71	24	30	0.71
TDS (g/L)	705.50	779.50	314.50	0.79	0.43	0.79	0.43	24	30	0.43
Sal (ppt)	725.50	759.50	294.50	1.14	0.25	1.14	0.25	24	30	0.26
pH (unit)	661.00	824.00	359.00	0.02	0.99	0.02	0.99	24	30	0.99

Station2=**Shoal** Mann-Whitney U Test (Water parameters (Season)) By variable Season Marked tests are significant at p <.05000

	Rank Sum - SW	Rank Sum - NE	U	Z	p-level	Z - adjusted	p-level	Valid N - SW	Valid N - NE	2*1sided - exact p
DO% (sat)	552.00	826.00	299.00	-0.57	0.57	-0.57	0.57	22	30	0.58
DO (mg/L)	545.00	833.00	292.00	-0.70	0.48	-0.70	0.48	22	30	0.49

Station=**Shoal** Mann-Whitney U Test (Water parameters (Season)) By variable **Season** Marked tests are significant at p <.05000

	Rank Sum - NE	Rank Sum - SW	U	Z	p-level	Z - adjusted	p-level	Valid N - NE	Valid N - SW	2*1sided - exact p
Organic content (%)	635.50	399.50	228.50	0.34	0.74	0.34	0.74	27	18	0.74

Station=**Shoal** Mann-Whitney U Test (Water parameters (Season)) By variable **Season** Marked tests are significant at p <.05000

	Rank Sum - NE	Rank Sum - IN	U	Z	p-level	Z - adjusted	p-level	Valid N - NE	Valid N - IN	2*1sided - exact p
Amount of SPM (g/L)	96.00	75.00	18.00	-1.69	0.09	-1.69	0.09	12	6	0.10

Appendix VI. Results of Mann-Whitney significant test on total rainfall between sampling periods (dry and wet periods) and Kruskal-Wallis test on water parameters among moon phases and tidal conditions at each diel sampling period.

(a) Total rainfall

Mann-Whitney U Test (Rainfall) By variable **sampling period** Marked tests are significant at p <.05000

	Rank Sum - Wet	**Rank Sum - Dry**	**U**	**Z**	**p-level**	**Z - adjusted**	**p-level**	**Valid N - NE**	**Valid N - SW**	**2*1sided - exact p**
(mm)	1077.50	875.50	379.50	1.42	0.16	1.43	0.15	31	31	0.16

(b) Temperature

Multiple Comparisons p values (2-tailed); **Temperature (°C)** (YSI - 24 hour) Independent (grouping) variable: **Season** Kruskal-Wallis test: H (1, N= 132) =19.89317 p =.0000

	Wet - R:81.805	**Dry - R:52.096**
Wet		0.000008
Dry	0.000008	

Wet period

Multiple Comparisons p values (2-tailed); **Temperature (°C)**, Independent (grouping) variable: **Moon phases** Kruskal-Wallis test: H (3, N= 64) =32.87128 p =.0000 Exclude condition: Season='Dry'

	Full moon – R:13.094	**Last quarter - R:46.406**	**New moon – R:43.219**	**First quarter - R:27.281**
Full moon		0.000003	0.000028	0.186860
Last quarter	0.000003		1.000000	0.022014
New moon	0.000028	1.000000		0.092847
First quarter	0.186860	0.022014	0.092847	

Wet period (Spring tides)

Multiple Comparisons p values (2-tailed); **Temperature (°C)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 32) =.8879468 p =.3460 Exclude condition: Tide='Neap'

	Ebb - R:18.063	**Flood - R:14.938**
Ebb		0.346079
Flood	0.346079	

Wet period (Neap tides)

Multiple Comparisons p values (2-tailed); **Temperature (°C)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 32) =1.841922 p =.1747 Exclude condition: Tide='Spring'

	Ebb - R:14.250	**Flood - R:18.750**
Ebb		0.174844
Flood	0.174844	

Dry period

Multiple Comparisons p values (2-tailed); **Temperature (°C)**, Independent (grouping) variable: **Moon phases** Kruskal-Wallis test: H (3, N= 68) =25.31044 p =.0000 Exclude condition: Season='Wet'

	Full moon – R:30.618	**New moon - R:43.824**	**First quarter - R:47.029**	**Third quarter - R:16.529**
Full moon		0.309136	0.093179	0.226700
New moon	0.309136		1.000000	0.000343
First quarter	0.093179	1.000000		0.000041
Third quarter	0.226700	0.000343	0.000041	

Dry period (Spring tides)

Multiple Comparisons p values (2-tailed); **Temperature (°C)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 34) =0.000000 p =1.000 Exclude condition: Tide='Neap'

	Ebb - R:17.500	**Flood - R:17.500**
Ebb		1.000000
Flood	1.000000	

Dry period (Neap tides)

Multiple Comparisons p values (2-tailed); **Temperature (°C)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 34) =.3636552 p =.5465 Exclude condition: Tide='Spring'

	Ebb - R:16.471	**Flood - R:18.529**
Ebb		0.546667
Flood	0.546667	

(c) Salinity

Multiple Comparisons p values (2-tailed); **Salinity (ppt)** (YSI - 24 hour) Independent (grouping) variable: **Season** Kruskal-Wallis test: H (1, N= 132) =30.93510 p =.0000

	Wet - R:47.414	**Dry - R:84.463**
Wet		0.000000
Dry	0.000000	

Wet period

Multiple Comparisons p values (2-tailed); **Salinity (ppt)**, Independent (grouping) variable: **Moon phases** Kruskal-Wallis test: H (3, N= 64) =43.84429 p =.0000 Exclude condition: Season='Dry'

	Full moon – R:50.125	**Last quarter - R:41.344**	**New moon – R:29.531**	**First quarter - R:9.0000**
Full moon		1.000000	0.010545	0.000000
Last quarter	1.000000		0.436451	0.000005
New moon	0.010545	0.436451		0.010891
First quarter	0.000000	0.000005	0.010891	

Wet period (Spring tides)

Multiple Comparisons p values (2-tailed); **Salinity (ppt)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 32) =5.910529 p =.0151 Exclude condition: Tide='Neap'

	Ebb - R:20.531	**Flood - R:12.469**
Ebb		0.015060
Flood	0.015060	

Wet period (Neap tides)

Multiple Comparisons p values (2-tailed); **Salinity (ppt)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 32) =.4105114 p =.5217 Exclude condition: Tide='Spring'

	Ebb - R:17.563	**Flood - R:15.438**
Ebb		0.521710
Flood	0.521710	

Dry period

Multiple Comparisons p values (2-tailed); **Salinity (ppt)**, Independent (grouping) variable: **Moon phases** Kruskal-Wallis test: H (3, N= 68) =22.13681 p =.0001 Exclude condition: Season='Wet'

	Full moon – R:19.147	**New moon - R:50.324**	**First quarter - R:30.882**	**Third quarter - R:37.647**
Full moon		0.000026	0.501487	0.038269
New moon	0.000026		0.024907	0.369700
First quarter	0.501487	0.024907		1.000000
Third quarter	0.038269	0.369700	1.000000	

Dry period (Spring tides)

Multiple Comparisons p values (2-tailed); **Salinity (ppt)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 34) =5.406165 p =.0201 Exclude condition: Tide='Neap'

	Ebb - R:21.471	**Flood - R:13.529**
Ebb		0.020075
Flood	0.020075	

Dry period (Neap tides)

Multiple Comparisons p values (2-tailed); **Salinity (ppt)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 34) =.1187264 p =.7304 Exclude condition: Tide='Spring'

	Ebb - R:18.088	**Flood - R:16.912**
Ebb		0.730519
Flood	0.730519	

(d) Total dissolved solids

Multiple Comparisons p values (2-tailed); **Total dissolved solids (g/L)** (YSI - 24 hour) Independent (grouping) variable: **Season** Kruskal-Wallis test: H (1, N= 132) =36.28911 p =.0000

	Wet - R:45.828	**Dry - R:85.956**
Wet		0.000000
Dry	0.000000	

Wet period

Multiple Comparisons p values (2-tailed); **Total dissolved solids (g/L)**, Independent (grouping) variable: **Moon phases** Kruskal-Wallis test: H (3, N= 64) =42.34897 p =.0000 Exclude condition: Season='Dry'

	Full moon – R:49.281	**Last quarter - R:41.000**	**New moon – R:30.906**	**First quarter - R:8.8125**
Full moon		1.000000	0.031492	0.000000
Last quarter	1.000000		0.751137	0.000006
New moon	0.031492	0.751137		0.004740
First quarter	0.000000	0.000006	0.004740	

Wet period (Spring tides)

Multiple Comparisons p values (2-tailed); **Total dissolved solids (g/L)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 32) =8.754801 p =.0031 Exclude condition: Tide='Neap'

	Ebb - R:21.406	**Flood - R:11.594**
Ebb		0.003091
Flood	0.003091	

Wet period (Neap tides)

Multiple Comparisons p values (2-tailed); **Total dissolved solids (g/L)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 32) =.1150568 p =.7345 Exclude condition: Tide='Spring'

	Ebb - R:17.063	**Flood - R:15.938**
Ebb		0.734459
Flood	0.734459	

Dry period

Multiple Comparisons p values (2-tailed); **Total dissolved solids (g/L)**, Independent (grouping) variable: **Moon phases** Kruskal-Wallis test: H (3, N= 68) =22.58677 p =.0000 Exclude condition: Season='Wet'

	Full moon – R:18.735	**New moon - R:50.029**	**First quarter - R:30.765**	**Third quarter - R:38.471**
Full moon		0.000024	0.456736	0.021699
New moon	0.000024		0.027032	0.530000
First quarter	0.456736	0.027032		1.000000
Third quarter	0.021699	0.530000	1.000000	

Dry period (Spring tides)

Multiple Comparisons p values (2-tailed); **Total dissolved solids (g/L)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 34) =5.405339 p =.0201 Exclude condition: Tide='Neap'

	Ebb - R:21.471	**Flood - R:13.529**
Ebb		0.020075
Flood	0.020075	

Dry period (Neap tides)

Multiple Comparisons p values (2-tailed); **Total dissolved solids (g/L)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 34) =.5235033 p =.4694 Exclude condition: Tide='Spring'

	Ebb - R:18.735	**Flood - R:16.265**
Ebb		0.469487
Flood	0.469487	

(e) pH

Multiple Comparisons p values (2-tailed); **pH** (YSI - 24 hour) Independent (grouping) variable: **Season** Kruskal-Wallis test: H (1, N= 132) =.7097093 p =.3995

	Wet - R:69.391	**Dry - R:63.779**
Wet		0.399593
Dry	0.399593	

Wet period

Multiple Comparisons p values (2-tailed); **pH (unit)**, Independent (grouping) variable: **Moon phases** Kruskal-Wallis test: H (3, N= 64) =23.38863 p =.0000 Exclude condition: Season='Dry'

	Full moon – R:22.375	**Last quarter - R:20.531**	**New moon – R:46.438**	**First quarter - R:40.656**
Full moon		1.000000	0.001541	0.032906
Last quarter	1.000000		0.000498	0.013405
New moon	0.001541	0.000498		1.000000
First quarter	0.032906	0.013405	1.000000	

Wet period (Spring tides)

Multiple Comparisons p values (2-tailed); **pH (unit)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 32) =4.617596 p =.0316 Exclude condition: Tide='Neap'

	Ebb - R:20.063	**Flood - R:12.938**
Ebb		0.031692
Flood	0.031692	

Wet period (Neap tides)

Multiple Comparisons p values (2-tailed); **pH (unit)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 32) =.7195007 p =.3963 Exclude condition: Tide='Spring'

	Ebb - R:15.094	**Flood - R:17.906**
Ebb		0.396438
Flood	0.396438	

Dry period

Multiple Comparisons p values (2-tailed); **pH (unit)**, Independent (grouping) variable: **Moon phases** Kruskal-Wallis test: H (3, N= 68) =39.60642 p =.0000 Exclude condition: Season='Wet'

	Full moon – R:46.559	**New moon - R:37.706**	**First quarter - R:44.735**	**Third quarter - R:9.0000**
Full moon		1.000000	1.000000	0.000000
New moon	1.000000		1.000000	0.000139
First quarter	1.000000	1.000000		0.000001
Third quarter	0.000000	0.000139	0.000001	

Dry period (Spring tides)

Multiple Comparisons p values (2-tailed); **pH (unit)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 34) =2.679584 p =.1016 Exclude condition: Tide='Neap'

	Ebb - R:20.294	**Flood - R:14.706**
Ebb		0.101825
Flood	0.101825	

Dry period (Neap tides)

Multiple Comparisons p values (2-tailed); **pH (unit)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 34) =.0074159 p =.9314 Exclude condition: Tide='Spring'

	Ebb - R:17.353	**Flood - R:17.647**
Ebb		0.931380
Flood	0.931380	

(f) Dissolved oxygen concentration

Multiple Comparisons p values (2-tailed); **DO (mg/L)** (YSI - 24 hour) Independent (grouping) variable: **Season** Kruskal-Wallis test: H (1, N= 132) =2.510810 p =.1131

	Wet - R:61.063	**Dry - R:71.618**
Wet		0.113074
Dry	0.113074	

Wet period

Multiple Comparisons p values (2-tailed); **DO (mg/L)**, Independent (grouping) variable: **Moon phases** Kruskal-Wallis test: H (3, N= 64) =34.77327 p =.0000 Exclude condition: Season='Dry'

	Full moon – R:16.156	**Last quarter - R:21.813**	**New moon – R:44.188**	**First quarter - R:47.844**
Full moon		1.000000	0.000124	0.000009
Last quarter	1.000000		0.004058	0.000460
New moon	0.000124	0.004058		1.000000
First quarter	0.000009	0.000460	1.000000	

Wet period (Spring tides)

Multiple Comparisons p values (2-tailed); **DO (mg/L)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 32) =1.409963 p =.2351 Exclude condition: Tide='Neap'

	Ebb - R:18.469	**Flood - R:14.531**
Ebb		0.235148
Flood	0.235148	

Wet period (Neap tides)

Multiple Comparisons p values (2-tailed); **DO (mg/L)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 32) =2.051136 p =.1521 Exclude condition: Tide='Spring'

	Ebb - R:14.125	**Flood - R:18.875**
Ebb		0.152093
Flood	0.152093	

Dry period

Multiple Comparisons p values (2-tailed); **DO (mg/L)**, Independent (grouping) variable: **Moon phases** Kruskal-Wallis test: H (3, N= 68) =46.76788 p =.0000 Exclude condition: Season='Wet'

	Full moon – R:23.588	**New moon - R:13.765**	**First quarter - R:53.912**	**Third quarter - R:46.735**
Full moon		0.885031	0.000047	0.003857
New moon	0.885031		0.000000	0.000007
First quarter	0.000047	0.000000		1.000000
Third quarter	0.003857	0.000007	1.000000	

Dry period (Spring tides)

Multiple Comparisons p values (2-tailed); **DO (mg/L)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 34) =2.734620 p =.0982 Exclude condition: Tide='Neap'

	Ebb - R:20.324	**Flood - R:14.676**
Ebb		0.098272
Flood	0.098272	

Dry period (Neap tides)

Multiple Comparisons p values (2-tailed); **DO (mg/L)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 34) =.2005250 p =.6543 Exclude condition: Tide='Spring'

	Ebb - R:18.265	**Flood - R:16.735**
Ebb		0.654322
Flood	0.654322	

(g) Dissolved oxygen saturation

Multiple Comparisons p values (2-tailed); **DO (%)** (YSI - 24 hour) Independent (grouping) variable: **Season** Kruskal-Wallis test: H (1, N= 132) =2.649745 p =.1036

	Wet - R:60.914	**Dry - R:71.757**
Wet		0.103571
Dry	0.103571	

Wet period

Multiple Comparisons p values (2-tailed); **DO saturation (%)**, Independent (grouping) variable: **Moon phases** Kruskal-Wallis test: H (3, N= 64) =32.87215 p =.0000 Exclude condition: Season='Dry'

	Full moon – R:16.188	**Last quarter - R:22.531**	**New moon – R:44.813**	**First quarter - R:46.469**
Full moon		1.000000	0.000082	0.000025
Last quarter	1.000000		0.004274	0.001659
New moon	0.000082	0.004274		1.000000
First quarter	0.000025	0.001659	1.000000	

Wet period (Spring tides)

Multiple Comparisons p values (2-tailed); **DO saturation (%)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 32) =1.691006 p =.1935 Exclude condition: Tide='Neap'

	Ebb - R:18.656	**Flood - R:14.344**
Ebb		0.193509
Flood	0.193509	

Wet period (Neap tides)

Multiple Comparisons p values (2-tailed); **DO saturation (%)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 32) =1.841247 p =.1748 Exclude condition: Tide='Spring'

	Ebb - R:14.250	**Flood - R:18.750**
Ebb		0.174844
Flood	0.174844	

Dry period

Multiple Comparisons p values (2-tailed); **DO saturation (%),** Independent (grouping) variable: **Moon phases** Kruskal-Wallis test: H (3, N= 68) =46.10065 p =.0000 Exclude condition: Season='Wet'

	Full moon - R:23.529	**New moon - R:14.088**	**First quarter - R:54.118**	**Third quarter - R:46.265**
Full moon		0.983488	0.000039	0.004811
New moon	0.983488		0.000000	0.000013
First quarter	0.000039	0.000000		1.000000
Third quarter	0.004811	0.000013	1.000000	

Dry period (Spring tides)

Multiple Comparisons p values (2-tailed); **DO saturation (%)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 34) =2.456055 p =.1171 Exclude condition: Tide='Neap'

	Ebb - R:20.176	**Flood - R:14.824**
Ebb		0.117072
Flood	0.117072	

Dry period (Neap tides)

Multiple Comparisons p values (2-tailed); **DO saturation (%),** Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 34) =.1308358 p =.7176 Exclude condition: Tide='Spring'

	Ebb - R:18.118	**Flood - R:16.882**
Ebb		0.717608
Flood	0.717608	

(h) Suspended particulate matter

Multiple Comparisons p values (2-tailed); **Amount of suspended particulate matter (g/L)** Independent (grouping) variable: Season Kruskal-Wallis test: H (1, N= 128) =2.503270 p =.1136

	Wet - R:59.313	**Dry - R:69.688**
Wet		0.113610
Dry	0.113610	

Wet period

Multiple Comparisons p values (2-tailed); **Amount of suspended particulate matter (g/L)**, Independent (grouping) variable: Moon phase Kruskal-Wallis test: H (3, N= 64) =8.394952 p =.0385

	First Quarter - R:23.438	**Full Moon – R:40.438**	**Last Quarter - R:28.813**	**New Moon - R:37.313**
First Quarter		0.058855	1.000000	0.210309
Full Moon	0.058855		0.464411	1.000000
Last Quarter	1.000000	0.464411		1.000000
New Moon	0.210309	1.000000	1.000000	

Wet period (Spring tides)

Multiple Comparisons p values (2-tailed); **Amount of suspended particulate matter (g/L)**, Independent (grouping) variable: Tidal conditions Kruskal-Wallis test: H (1, N= 32) =.6875000 p =.4070 Exclude condition: Tide='Neap'

	Ebb - R:15.125	**Flood - R:17.875**
Ebb		0.407016
Flood	0.407016	

Wet period (Neap tides)

Multiple Comparisons p values (2-tailed); **Amount of suspended particulate matter (g/L)**, Independent (grouping) variable: Tidal conditions Kruskal-Wallis test: H (1, N= 32) =.0227273 p =.8802 Exclude condition: Tide='Spring'

	Ebb - R:16.750	**Flood - R:16.250**
Ebb		0.880168
Flood	0.880168	

Dry period

Multiple Comparisons p values (2-tailed); **Amount of suspended particulate matter (g/L)**, Independent (grouping) variable: Moon phase Kruskal-Wallis test: H (3, N= 64) =25.76070 p =.0000

	First Quarter - R:16.563	Full Moon – R:43.063	Last Quarter - R:25.750	New Moon - R:44.625
First Quarter		0.000341	0.976863	0.000121
Full Moon	0.000341		0.051237	1.000000
Last Quarter	0.976863	0.051237		0.024838
New Moon	0.000121	1.000000	0.024838	

Dry period (Spring tides)

Multiple Comparisons p values (2-tailed); **Amount of suspended particulate matter (g/L)**, Independent (grouping) variable: Tidal conditions Kruskal-Wallis test: H (1, N= 32) =1.454545 p =.2278 Exclude condition: Tide='Neap'

	Ebb - R:18.500	Flood - R:14.500
Ebb		0.227800
Flood	0.227800	

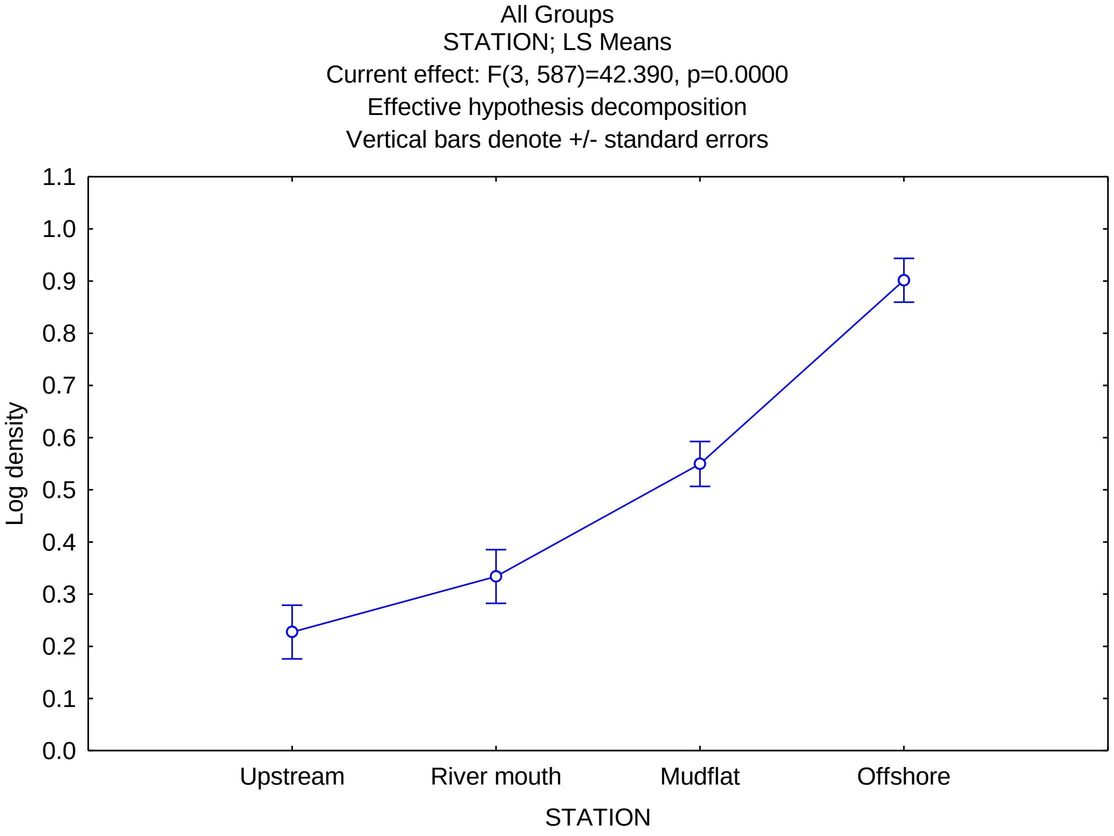
Dry period (Neap tides)

Multiple Comparisons p values (2-tailed); **Amount of suspended particulate matter (g/L)**, Independent (grouping) variable: Tidal conditions Kruskal-Wallis test: H (1, N= 32) =2.750000 p =.0973 Exclude condition: Tide='Spring'

	Ebb - R:13.750	Flood - R:19.250
Ebb		0.097254
Flood	0.097254	

Appendix VII. Results of ANOVA significant tests on density of hermit crabs among stations.

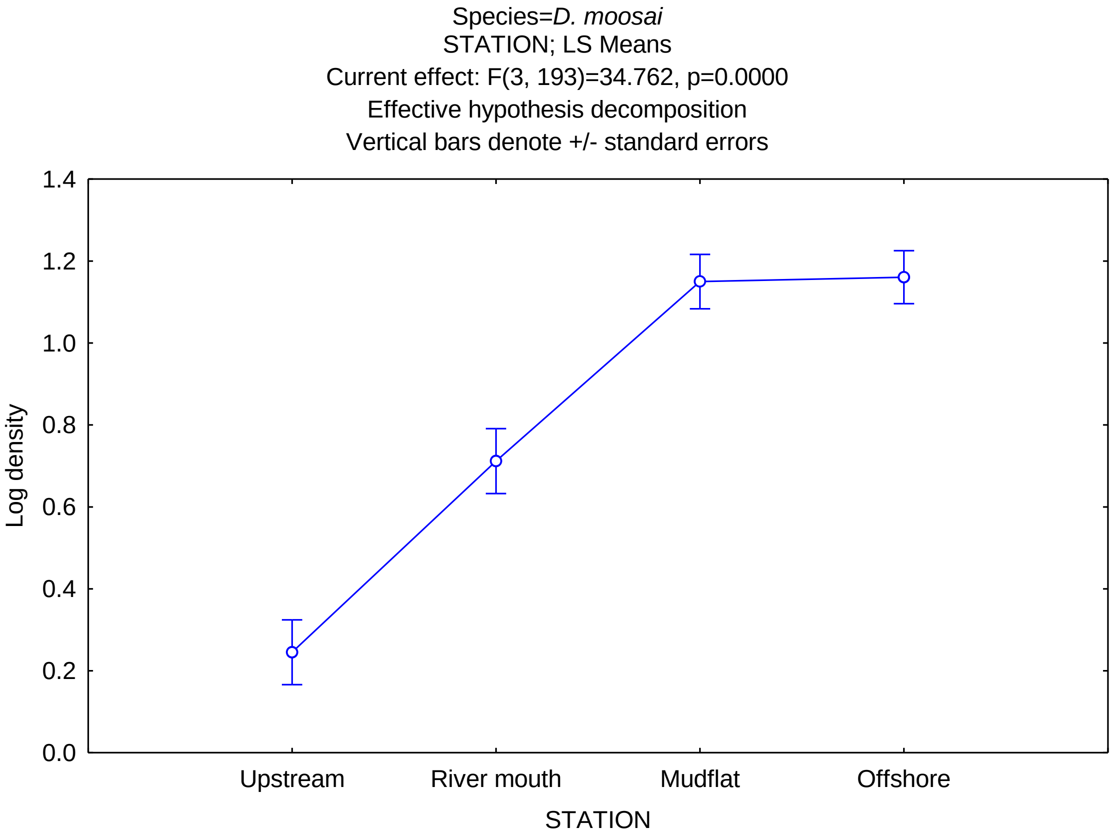
(a) Overall density of hermit crabs among sampling stations irrespective of species



All Groups Tukey HSD test; variable log density Approximate Probabilities for Post Hoc Tests Error: Between MS = .31734, df = 587.00

	STATION	{1} - .22734	{2} - .33382	{3} - .54942	{4} - .90164
1	Mid-estuary (upstream)		0.459336	0.000017	0.000008
2	River mouth	0.459336		0.007173	0.000008
3	Mudflat	0.000017	0.007173		0.000008
4	Shoal (nearshore)	0.000008	0.000008	0.000008	

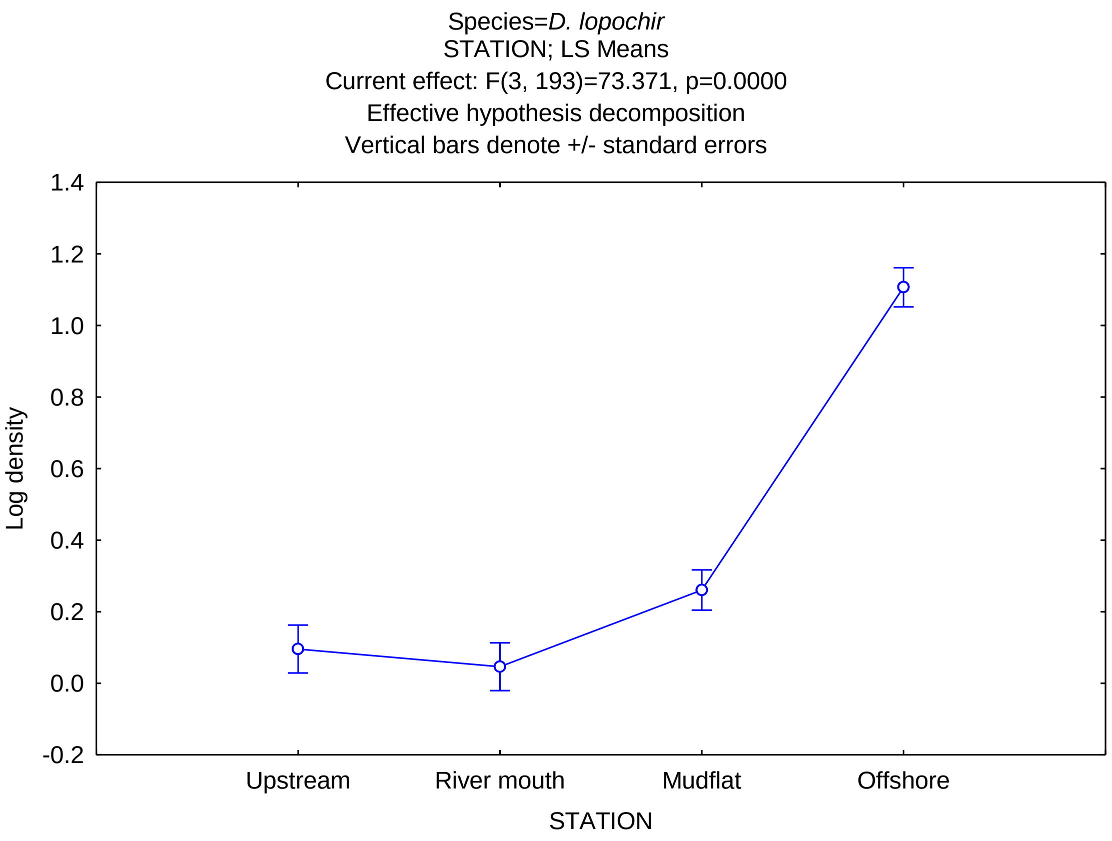
(b) Density of *D. moosai* among sampling stations



Species=*D. moosai* Tukey HSD test; variable log density (ind/ha) Approximate Probabilities for Post Hoc Tests Error: Between MS = .25051, df = 193.00

	STATION	**{1} - .24526**	**{2} - .71173**	**{3} - 1.1499**	**{4} - 1.1606**
1	Mid-estuary (upstream)		0.000185	0.000008	0.000008
2	River mouth	0.000185		0.000134	0.000072
3	Mudflat	0.000008	0.000134		0.999447
4	Shoal (nearshore)	0.000008	0.000072	0.999447	

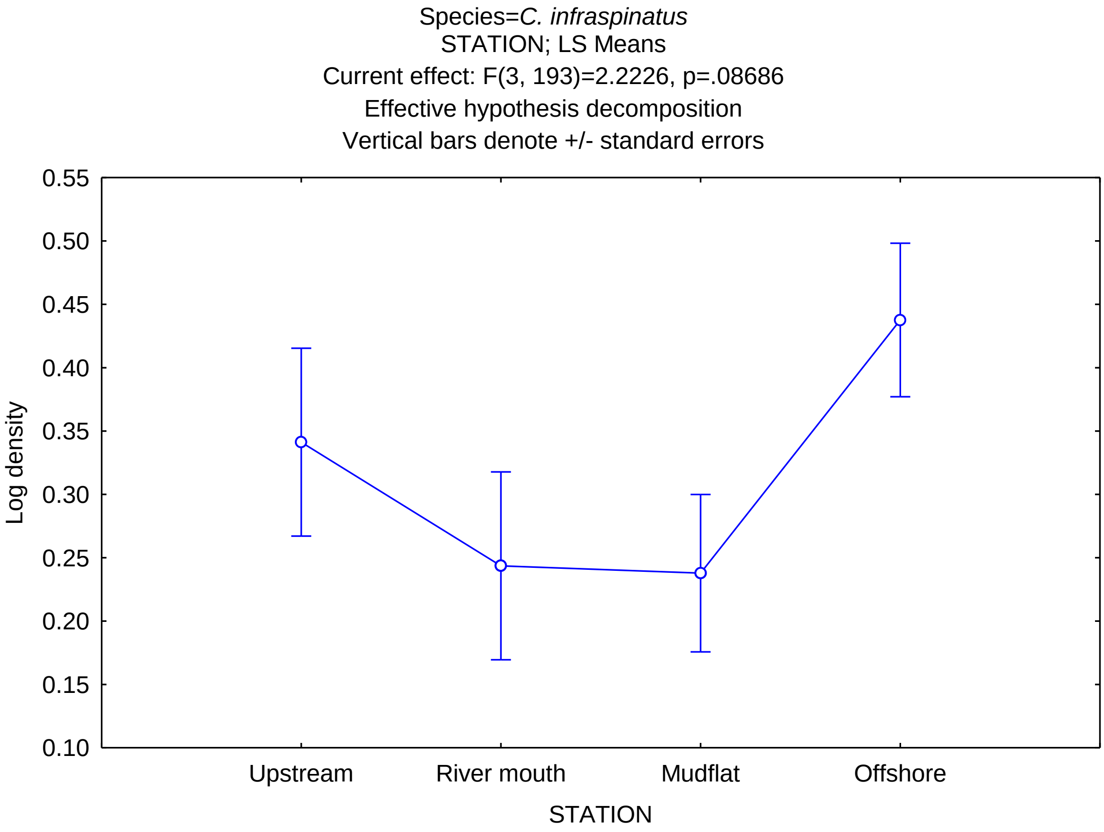
(c) Density of *D. lopochir* among sampling stations



Species=*D. lopochir* Tukey HSD test; variable log density Approximate Probabilities for Post Hoc Tests
Error: Between MS = .17925, df = 193.00

	STATION	**{1} - .09552**	**{2} - .04611**	**{3} - .26049**	**{4} - 1.1067**
1	Mid-estuary (upstream)		0.953867	0.232637	0.000008
2	River mouth	0.953867		0.067199	0.000008
3	Mudflat	0.232637	0.067199		0.000008
4	Shoal (nearshore)	0.000008	0.000008	0.000008	

(d) Density of *C. infraspinatus* among sampling stations



Species=*C. infraspinatus* Tukey HSD test; variable log density Approximate Probabilities for Post Hoc Tests Error: Between MS = .21995, df = 193.00

	STATION	**{1} - .34124**	**{2} - .24361**	**{3} - .23787**	**{4} - .43767**
1	Mid-estuary (upstream)		0.788234	0.708714	0.745130
2	River mouth	0.788234		0.999925	0.177947
3	Mudflat	0.708714	0.999925		0.097224
4	Shoal (nearshore)	0.745130	0.177947	0.097224	

Appendix VIII. Results of Mann-Whitney significant test on density of different species of hermit crabs between seasons (northeast and southwest monsoon) by each station.

(a) Mid-estuary

STATION=Mid-estuary, **SPECIES=*D. moosai***, Mann-Whitney U Test (Density (Season)) By variable **Season** Marked tests are significant at p <.05000

	Rank Sum - SW	**Rank Sum - NE**	**U**	**Z**	**p-level**	**Z - adjusted**	**p-level**	**Valid N - SW**	**Valid N - NE**	**2*1sided - exact p**
Density	234.00	361.00	129.00	-0.39	0.70	-0.50	0.62	14	20	0.72

STATION=Mid-estuary, **SPECIES=*D. lopochir***, Mann-Whitney U Test (Density (Season)) By variable **Season** Marked tests are significant at p <.05000

	Rank Sum - SW	**Rank Sum - NE**	**U**	**Z**	**p-level**	**Z - adjusted**	**p-level**	**Valid N - SW**	**Valid N - NE**	**2*1sided - exact p**
Density	242.00	353.00	137.00	-0.11	0.92	-0.21	0.83	14	20	0.93

STATION=Mid-estuary, **SPECIES=*C. infraspinatus***, Mann-Whitney U Test (Density (Season)) By variable **Season** Marked tests are significant at p <.05000

	Rank Sum - SW	**Rank Sum - NE**	**U**	**Z**	**p-level**	**Z - adjusted**	**p-level**	**Valid N - SW**	**Valid N - NE**	**2*1sided - exact p**
Density	260.00	335.00	125.00	0.52	0.60	0.60	0.55	14	20	0.62

(b) River mouth

STATION=River mouth, **SPECIES=*D. moosai***, Mann-Whitney U Test (Density (Season)) By variable **Season** Marked tests are significant at p <.05000

	Rank Sum - SW	**Rank Sum - NE**	**U**	**Z**	**p-level**	**Z - adjusted**	**p-level**	**Valid N - SW**	**Valid N - NE**	**2*1sided - exact p**
Density	295.00	300.00	90.00	1.75	0.08	1.78	0.08	14	20	0.08

STATION=River mouth, **SPECIES=*D. lopochir***, Mann-Whitney U Test (Density (Season)) By variable **Season** Marked tests are significant at p <.05000

	Rank Sum - SW	**Rank Sum - NE**	**U**	**Z**	**p-level**	**Z - adjusted**	**p-level**	**Valid N - SW**	**Valid N - NE**	**2*1sided - exact p**
Density	238.00	357.00	133.00	-0.25	0.81	-0.84	0.40	14	20	0.82

STATION=River mouth, **SPECIES=*C. infraspinatus***, Mann-Whitney U Test (Density (Season)) By variable **Season** Marked tests are significant at p <.05000

	Rank Sum - SW	**Rank Sum - NE**	**U**	**Z**	**p-level**	**Z - adjusted**	**p-level**	**Valid N - SW**	**Valid N - NE**	**2*1sided - exact p**
Density	316.00	279.00	69.00	2.48	0.01	3.20	0.00	14	20	0.01

(c) Mudflat

STATION=Mudflat, **SPECIES=*D. moosai***, Mann-Whitney U Test (Density (Season)) By variable **Season** Marked tests are significant at p <.05000

	Rank Sum - SW	**Rank Sum - NE**	**U**	**Z**	**p-level**	**Z - adjusted**	**p-level**	**Valid N - SW**	**Valid N - NE**	**2*1sided - exact p**
Density	631.00	594.00	159.00	2.67	0.01	2.67	0.01	20	29	0.01

STATION=Mudflat, **SPECIES=*D. lopochir***, Mann-Whitney U Test (Density (Season)) By variable **Season** Marked tests are significant at p <.05000

	Rank Sum - SW	**Rank Sum - NE**	**U**	**Z**	**p-level**	**Z - adjusted**	**p-level**	**Valid N - SW**	**Valid N - NE**	**2*1sided - exact p**
Density	496.00	729.00	286.00	-0.08	0.94	-0.11	0.91	20	29	0.94

STATION=Mudflat, **SPECIES=*C. infraspinatus***, Mann-Whitney U Test (Density (Season)) By variable **Season** Marked tests are significant at p <.05000

	Rank Sum - SW	**Rank Sum - NE**	**U**	**Z**	**p-level**	**Z - adjusted**	**p-level**	**Valid N - SW**	**Valid N - NE**	**2*1sided - exact p**
Density	541.00	684.00	249.00	0.83	0.40	1.11	0.27	20	29	0.41

(d) Shoal station

STATION=Shoal, **SPECIES=*D. moosai***, Mann-Whitney U Test (Density (Season)) By variable **Season** Marked tests are significant at p <.05000

	Rank Sum - SW	**Rank Sum - NE**	**U**	**Z**	**p-level**	**Z - adjusted**	**p-level**	**Valid N - SW**	**Valid N - NE**	**2*1sided - exact p**
Density	679.00	647.00	182.00	2.55	0.01	2.55	0.01	21	30	0.01

STATION=Shoal, **SPECIES=*D. lopochir***, Mann-Whitney U Test (Density (Season)) By variable **Season** Marked tests are significant at p <.05000

	Rank Sum - SW	**Rank Sum - NE**	**U**	**Z**	**p-level**	**Z - adjusted**	**p-level**	**Valid N - SW**	**Valid N - NE**	**2*1sided - exact p**
Density	701.00	625.00	160.00	2.97	0.00	2.98	0.00	21	30	0.00

STATION=Shoal, **SPECIES=*C. infraspinatus***, Mann-Whitney U Test (Density (Season)) By variable **Season** Marked tests are significant at p <.05000

	Rank Sum - SW	**Rank Sum - NE**	**U**	**Z**	**p-level**	**Z - adjusted**	**p-level**	**Valid N - SW**	**Valid N - NE**	**2*1sided - exact p**
Density	696.50	629.50	164.50	2.88	0.00	3.23	0.00	21	30	0.00

Appendix IX. Non-parametric Kruskal-Wallis and Mann-Whitney significant tests on density (ind/ha) of juvenile hermit crabs among stations and seasons (northeast and southwest monsoon).

(a) Density of juvenile hermit crabs among stations

Multiple Comparisons p values (2-tailed); **Density (ind/ha)** (**Juvenile hermit crab**) Independent (grouping) variable: **Station** Kruskal-Wallis test: H (3, N= 160) =14.26433 p =.0026

	Mid-estuary - R:57.313	**River mouth - R:89.016**	**Mudflat - R:86.552**	**Shoal - R:84.229**
Mid-estuary		0.037198	0.034124	0.065455
River mouth	0.037198		1.000000	1.000000
Mudflat	0.034124	1.000000		1.000000
Shoal	0.065455	1.000000	1.000000	

(b) Density of juvenile hermit crabs between seasons

Station=Mid-estuary Mann-Whitney U Test (Juvenile hermit crab) By variable **Season** Marked tests are significant at p <.05000

	Rank Sum - NE	**Rank Sum - SW**	**U**	**Z**	**p-level**	**Z - adjusted**	**p-level**	**Valid N - NE**	**Valid N - SW**	**2*1sided - exact p**
Density (ind/ha)	230.50	175.50	94.500	-0.07	0.94	-0.16	0.88	16	12	0.95

Station=River mouth Mann-Whitney U Test (Juvenile hermit crab) By variable **Season** Marked tests are significant at p <.05000

	Rank Sum - NE	**Rank Sum - SW**	**U**	**Z**	**p-level**	**Z - adjusted**	**p-level**	**Valid N - NE**	**Valid N - SW**	**2*1sided - exact p**
Density (ind/ha)	269.50	136.50	58.50	1.74	0.08	1.89	0.05	16	12	0.08

Station=Mudflat Mann-Whitney U Test (Juvenile hermit crab) By variable **Season** Marked tests are significant at p <.05000

	Rank Sum - NE	**Rank Sum - SW**	**U**	**Z**	**p-level**	**Z - adjusted**	**p-level**	**Valid N - NE**	**Valid N - SW**	**2*1sided - exact p**
Density (ind/ha)	568.00	335.00	164.00	1.32	0.19	1.47	0.14	24	18	0.19

Station=Shoal Mann-Whitney U Test (Juvenile hermit crab) By variable **Season** Marked tests are significant at p <.05000

	Rank Sum - NE	**Rank Sum - SW**	**U**	**Z**	**p-level**	**Z - adjusted**	**p-level**	**Valid N - NE**	**Valid N - SW**	**2*1sided - exact p**
Density (ind/ha)	535.00	368.00	197.00	0.48	0.63	0.54	0.59	24	18	0.64

Appendix X. Results of Kruskal-Wallis significant tests on density of *D. moosai* between different moon phases and tidal conditions at each diel samplings seasons.

Wet period

Multiple Comparisons p values (2-tailed); **Abundance *D. moosai* (ind/ha)**, Independent (grouping) variable: **Moon phases** Kruskal-Wallis test: H (3, N= 46) =10.66416 p =.0137 Exclude condition: Season='Dry'

	Full moon – R:14.000	**New moon – R:19.923**	**First quarter - R:31.125**	**Last quarter - R:24.750**
Full moon		1.000000	0.013192	0.595855
New moon	1.000000		0.152483	1.000000
First quarter	0.013192	0.152483		1.000000
Last quarter	0.595855	1.000000	1.000000	

Wet period (Spring tides)

Multiple Comparisons p values (2-tailed); **Abundance *D. moosai* (ind/ha)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 22) =1.256522 p =.2623 Exclude condition: Tide='Neap'

	Ebb - R:12.917	**Flood - R:9.8000**
Ebb		0.262311
Flood	0.262311	

Wet period (Neap tides)

Multiple Comparisons p values (2-tailed); **Abundance *D. moosai* (ind/ha)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 24) =3.000000 p =.0833 Exclude condition: Tide='Spring'

	Ebb - R:10.000	**Flood - R:15.000**
Ebb		0.083265
Flood	0.083265	

Dry Period

Multiple Comparisons p values (2-tailed); **Abundance *D. moosai* (ind/ha)**, Independent (grouping) variable: **Moon phases** Kruskal-Wallis test: H (3, N= 64) =3.319984 p =.3449 Exclude condition: Season='Wet'

	Full moon – R:38.313	**New moon - R:34.625**	**First quarter - R:29.563**	**Third Quarter - R:27.500**
Full moon		1.000000	1.000000	0.602873
New moon	1.000000		1.000000	1.000000
First quarter	1.000000	1.000000		1.000000
Third Quarter	0.602873	1.000000	1.000000	

Dry period (Spring tides)

Multiple Comparisons p values (2-tailed); **Abundance *D. moosai* (ind/ha)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 32) =16.57122 p =.0000 Exclude condition: Tide='Neap'

	Ebb - R:23.250	**Flood - R:9.7500**
Ebb		0.000047
Flood	0.000047	

Dry period (Neap tides)

Multiple Comparisons p values (2-tailed); **Abundance *D. moosai* (ind/ha)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 32) =.0174038 p =.8950 Exclude condition: Tide='Spring'

	Ebb - R:16.719	**Flood - R:16.281**
Ebb		0.895055
Flood	0.895055	

Appendix XI. Results of Kruskal-Wallis significant tests on density (ind/ha) of male, non-ovigerous female and ovigerous female *D. moosai* among moon phases and tidal conditions at each diel sampling period.

(a) Male *D. moosai*

Wet period

Multiple Comparisons p values (2-tailed); **Abundance male *D. moosai* (ind/ha)**, Independent (grouping) variable: **Moon phases** Kruskal-Wallis test: H (3, N= 46) =10.70344 p =.0134 Exclude condition: Season='Dry'

	Full moon – R:14.556	**New moon – R:19.000**	**First quarter - R:31.000**	**Last quarter - R:25.875**
Full moon		1.000000	0.019673	0.495892
New moon	1.000000		0.099916	1.000000
First quarter	0.019673	0.099916		1.000000
Last quarter	0.495892	1.000000	1.000000	

Wet period (Spring tides)

Multiple Comparisons p values (2-tailed); **Abundance male *D. moosai* (ind/ha)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 22) =.2130435 p =.6444 Exclude condition: Tide='Neap'

	Ebb - R:12.083	**Flood - R:10.800**
Ebb		0.644392
Flood	0.644392	

Wet period (Neap tides)

Multiple Comparisons p values (2-tailed); **Abundance male *D. moosai* (ind/ha)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 24) =1.763333 p =.1842 Exclude condition: Tide='Spring'

	Ebb - R:10.583	**Flood - R:14.417**
Ebb		0.184209
Flood	0.184209	

Dry period

Multiple Comparisons p values (2-tailed); **Abundance male *D. moosai* (ind/ha)**, Independent (grouping) variable: **Moon phase** Kruskal-Wallis test: H (3, N= 64) =6.170694 p =.1036 Exclude condition: Season='Wet'

	Full moon – R:40.938	**New moon - R:34.563**	**First quarter - R:26.000**	**Third Quarter - R:28.500**
Full moon		1.000000	0.139548	0.353036
New moon	1.000000		1.000000	1.000000
First quarter	0.139548	1.000000		1.000000
Third Quarter	0.353036	1.000000	1.000000	

Dry period (Spring tides)

Multiple Comparisons p values (2-tailed); **Abundance male *D. moosai* (ind/ha)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 24) =1.763333 p =.1842 Exclude condition: Tide='Spring'

	Ebb - R:10.583	**Flood - R:14.417**
Ebb		0.184209
Flood	0.184209	

Dry period (Neap tides)

Multiple Comparisons p values (2-tailed); **Abundance male *D. moosai* (ind/ha),** Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 32) =.0031966 p =.9549 Exclude condition: Tide='Spring'

	Ebb - R:16.594	**Flood - R:16.406**
Ebb		0.954917
Flood	0.954917	

(b) Non-ovigerous female *D. moosai*

Wet period

Multiple Comparisons p values (2-tailed); **Abundance non-ovigerous female *D. moosai* (ind/ha)**, Independent (grouping) variable: **Moon phases** Kruskal-Wallis test: H (3, N= 46) =19.87687 p =.0002 Exclude condition: Season='Dry'

	Full moon – R:13.278	**New moon – R:15.346**	**First quarter - R:30.813**	**Last quarter - R:33.625**
Full moon		1.000000	0.010302	0.010863
New moon	1.000000		0.012176	0.014647
First quarter	0.010302	0.012176		1.000000
Last quarter	0.010863	0.014647	1.000000	

Wet period (Spring tides)

Multiple Comparisons p values (2-tailed); **Abundance non-ovigerous female *D. moosai* (ind/ha)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 22) =.1050708 p =.7458 Exclude condition: Tide='Neap'

	Ebb - R:11.125	**Flood - R:11.950**
Ebb		0.766679
Flood	0.766679	

Wet period (Neap tides)

Multiple Comparisons p values (2-tailed); **Abundance non-ovigerous female *D. moosai* (ind/ha)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 24) =3.308939 p =.0689 Exclude condition: Tide='Spring'

	Ebb - R:9.8750	**Flood - R:15.125**
Ebb		0.068964
Flood	0.068964	

Dry period

Multiple Comparisons p values (2-tailed); **Abundance non-ovigerous female *D. moosai* (ind/ha)**, Independent (grouping) variable: **Moon phases** Kruskal-Wallis test: H (3, N= 64) =17.89918 p =.0005 Exclude condition: Season='Wet'

	Full moon – :20.875	**New moon - R:26.281**	**First quarter - R:45.219**	**Third Quarter - R:37.625**
Full moon		1.000000	0.001303	0.065659
New moon	1.000000		0.024103	0.509072
First quarter	0.001303	0.024103		1.000000
Third Quarter	0.065659	0.509072	1.000000	

Dry period (Spring tides)

Multiple Comparisons p values (2-tailed); **Abundance non-ovigerous female *D. moosai* (ind/ha)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 32) =4.371744 p =.0365 Exclude condition: Tide='Neap'

	Ebb - R:19.438	**Flood - R:13.563**
Ebb		0.076498
Flood	0.076498	

Dry period (Neap tides)

Multiple Comparisons p values (2-tailed); **Abundance non-ovigerous female *D. moosai* (ind/ha)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 32) =1.039321 p =.3080 Exclude condition: Tide='Spring'

	Ebb - R:14.813	**Flood - R:18.188**
Ebb		0.308868
Flood	0.308868	

(c) Ovigerous female *D. moosai*

Wet period

Multiple Comparisons p values (2-tailed); **Abundance ovigerous female *D. moosai* (ind/ha)**, Independent (grouping) variable: **Moon phases** Kruskal-Wallis test: H (3, N= 46) =6.027139 p =.1103 Exclude condition: Season='Dry'

	Full moon – R:20.222	**New moon – R:20.308**	**First quarter - R:30.125**	**Last quarter - R:19.125**
Full moon		1.000000	0.459720	1.000000
New moon	1.000000		0.300824	1.000000
First quarter	0.459720	0.300824		0.350480
Last quarter	1.000000	1.000000	0.350480	

Wet period (Spring tides)

Multiple Comparisons p values (2-tailed); **Abundance ovigerous female *D. moosai* (ind/ha)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 22) =2.972701 p =.0847 Exclude condition: Tide='Neap'

	Ebb - R:13.667	**Flood - R:8.9000**
Ebb		0.086457
Flood	0.086457	

Wet periods (Neap tides)

Multiple Comparisons p values (2-tailed); **Abundance ovigerous female *D. moosai* (ind/ha)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 24) =4.813333 p =.0282 Exclude condition: Tide='Spring'

	Ebb - R:9.3333	**Flood - R:15.667**
Ebb		0.028240
Flood	0.028240	

Dry period

Multiple Comparisons p values (2-tailed); **Abundance ovigerous female *D. moosai* (ind/ha)**, Independent (grouping) variable: **Moon phases** Kruskal-Wallis test: H (3, N= 64) =11.53543 p =.0092 Exclude condition: Season='Wet'

	Full moon - R:39.625	**New moon - R:40.688**	**First quarter - R:27.375**	**Third Quarter - R:22.313**
Full moon		1.000000	0.376543	0.051237
New moon	1.000000		0.258864	0.031492
First quarter	0.376543	0.258864		1.000000
Third Quarter	0.051237	0.031492	1.000000	

Dry period (Spring tides)

Multiple Comparisons p values (2-tailed); **Abundance ovigerous female *D. moosai* (ind/ha)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 32) =15.12505 p =.0001 Exclude condition: Tide='Neap'

	Ebb - R:22.938	**Flood - R:10.063**
Ebb		0.000104
Flood	0.000104	

Dry period (Neap tides)

Multiple Comparisons p values (2-tailed); **Abundance ovigerous female *D. moosai* (ind/ha)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 32) =.1302006 p =.7182 Exclude condition: Tide='Spring'

	Ebb - R:17.094	**Flood - R:15.906**
Ebb		0.720310
Flood	0.720310	

Appendix XII. Results of Kruskal-Wallis significant tests on compositions (%) of male, non-ovigerous female and ovigerous female *D. moosai* among moon phases and tidal conditions at each diel samplings seasons.

(a) Male *D. moosai*

Wet period

Multiple Comparisons p values (2-tailed); **Male *D. moosai* composition (%) (arcsined)**, Independent (grouping) variable: **Moon phases** Kruskal-Wallis test: H (3, N= 45) =.9233219 p =.8198 Exclude condition: Season='Dry'

	First quarter - R:20.719	**Full moon – R:24.278**	**Last quarter - R:25.750**	**New moon – R:23.250**
First quarter		1.000000	1.000000	1.000000
Full moon	1.000000		1.000000	1.000000
Last quarter	1.000000	1.000000		1.000000
New moon	1.000000	1.000000	1.000000	

Wet period (Spring tides)

Multiple Comparisons p values (2-tailed); **Male *D. moosai* composition (%) (arcsined)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 21) =1.043918 p =.3069 Exclude condition: Tide='Neap'

	Ebb - R:9.6818	**Flood - R:12.450**
Ebb		0.307226
Flood	0.307226	

Wet period (Neap tides)

Multiple Comparisons p values (2-tailed); **Male *D. moosai* composition (%) (arcsined)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 24) =2.803333 p =.0941 Exclude condition: Tide='Spring'

	Ebb - R:14.917	**Flood - R:10.083**
Ebb		0.094069
Flood	0.094069	

Dry period

Multiple Comparisons p values (2-tailed); **Male *D. moosai* composition (%) (arcsined)**, Independent (grouping) variable: **Moon phases** Kruskal-Wallis test: H (3, N= 64) =7.763419 p =.0512 Exclude condition: Season='Wet'

	First quarter - R:22.844	**Full moon – R:38.969**	**New moon - R:30.375**	**Third Quarter - R:37.813**
First quarter		0.085818	1.000000	0.137826
Full moon	0.085818		1.000000	1.000000
New moon	1.000000	1.000000		1.000000
Third Quarter	0.137826	1.000000	1.000000	

Dry period (Spring tides)

Multiple Comparisons p values (2-tailed); **Male *D. moosai* composition (%) (arcsined)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 32) =3.083813 p =.0791 Exclude condition: Tide='Neap'

	Ebb - R:13.594	**Flood - R:19.406**
Ebb		0.079682
Flood	0.079682	

Dry period (Neap tides)

Multiple Comparisons p values (2-tailed); **Male *D. moosai* composition (%) (arcsined)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 32) =1.156307 p =.2822 Exclude condition: Tide='Spring'

	Ebb - R:18.281	**Flood - R:14.719**
Ebb		0.282763
Flood	0.282763	

(b) Non-ovigerous female *D. moosai*

Wet period

Multiple Comparisons p values (2-tailed); **Non-ovigerous female composition (%) (arcsined)**, Independent (grouping) variable: **Moon phases** Kruskal-Wallis test: H (3, N= 45) =13.73033 p =.0033 Exclude condition: Season='Dry'

	First quarter - R:26.094	**Full moon – R:14.611**	**Last quarter - R:34.875**	**New moon – R:17.250**
First quarter		0.215295	0.735458	0.467152
Full moon	0.215295		0.008984	1.000000
Last quarter	0.735458	0.008984		0.019689
New moon	0.467152	1.000000	0.019689	

Wet period (Spring tides)

Multiple Comparisons p values (2-tailed); **Non-ovigerous female composition (%) (arcsined)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 21) =1.133884 p =.2869 Exclude condition: Tide='Neap'

	Ebb - R:9.7273	**Flood - R:12.400**
Ebb		0.324207
Flood	0.324207	

Wet period (Neap tides)

Multiple Comparisons p values (2-tailed); **Non-ovigerous female composition (%) (arcsined)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 24) =1.764868 p =.1840 Exclude condition: Tide='Spring'

	Ebb - R:10.583	**Flood - R:14.417**
Ebb		0.184209
Flood	0.184209	

Dry period

Multiple Comparisons p values (2-tailed); **Non-ovigerous female composition (%) (arcsined)**, Independent (grouping) variable: **Moon phases** Kruskal-Wallis test: H (3, N= 64) =31.92877 p =.0000 Exclude condition: Season='Wet'

	First quarter - R:49.688	**Full moon – R:18.375**	**New moon - R:22.438**	**Third Quarter - R:39.500**
First quarter		0.000012	0.000209	0.730323
Full moon	0.000012		1.000000	0.007989
New moon	0.000209	1.000000		0.057255
Third Quarter	0.730323	0.007989	0.057255	

Dry period (Spring tides)

Multiple Comparisons p values (2-tailed); **Non-ovigerous female composition (%) (arcsined)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 32) =3.832439 p =.0503 Exclude condition: Tide='Neap'		
	Ebb - R:19.250	**Flood - R:13.750**
Ebb		0.097254
Flood	0.097254	

Dry period (Neap tides)

Multiple Comparisons p values (2-tailed); **Non-ovigerous female composition (%) (arcsined)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 32) =1.509485 p =.2192 Exclude condition: Tide='Spring'		
	Ebb - R:14.469	**Flood - R:18.531**
Ebb		0.220617
Flood	0.220617	

(c) Ovigerous female *D. moosai*

Wet period

Multiple Comparisons p values (2-tailed); **Ovigerous female *D. moosai* composition (%) (arcsined)**, Independent (grouping) variable: **Moon phases** Kruskal-Wallis test: H (3, N= 45) =7.865763 p =.0489 Exclude condition: Season='Dry'				
	First quarter - R:26.281	**Full moon – R:26.444**	**Last quarter - R:11.438**	**New moon – R:23.750**
First quarter		1.000000	0.054318	1.000000
Full moon	1.000000		0.112196	1.000000
Last quarter	0.054318	0.112196		0.239931
New moon	1.000000	1.000000	0.239931	

Wet period (Spring tides)

Multiple Comparisons p values (2-tailed); **Ovigerous female *D. moosai* composition (%) (arcsined)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 21) =2.526738 p =.1119 Exclude condition: Tide='Neap'		
	Ebb - R:13.045	**Flood - R:8.7500**
Ebb		0.113102
Flood	0.113102	

Wet period (Neap tides)

Multiple Comparisons p values (2-tailed); **Ovigerous female *D. moosai* composition (%) (arcsined)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 24) =1.691176 p =.1934 Exclude condition: Tide='Spring'		
	Ebb - R:10.625	**Flood - R:14.375**
Ebb		0.193931
Flood	0.193931	

Dry period

Multiple Comparisons p values (2-tailed); **Ovigerous female *D. moosai* composition (%) (arcsined)**, Independent (grouping) variable: **Moon phases** Kruskal-Wallis test: H (3, N= 64) =15.13483 p =.0017 Exclude condition: Season='Wet'

	First quarter - R:26.688	**Full moon – R:37.719**	**New moon - R:44.281**	**Third Quarter - R:21.313**
First quarter		0.562703	0.045148	1.000000
Full moon	0.562703		1.000000	0.076154
New moon	0.045148	1.000000		0.002907
Third Quarter	1.000000	0.076154	0.002907	

Dry period (Spring tides)

Multiple Comparisons p values (2-tailed); **Ovigerous female *D. moosai* composition (%) (arcsined)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 32) =2.225237 p =.1358 Exclude condition: Tide='Neap'

	Ebb - R:18.969	**Flood - R:14.031**
Ebb		0.136563
Flood	0.136563	

Dry period (Neap tides)

Multiple Comparisons p values (2-tailed); **Ovigerous female *D. moosai* composition (%) (arcsined)**, Independent (grouping) variable: **Tidal conditions** Kruskal-Wallis test: H (1, N= 32) =.1915413 p =.6616 Exclude condition: Tide='Spring'

	Ebb - R:17.219	**Flood - R:15.781**
Ebb		0.664708
Flood	0.664708	

Appendix XIII. Non-parametric Kruskal-Wallis significant tests on size (shield length) of hermit crabs between species and stations.

(a) Size (shield length) between species

Multiple Comparisons p values (2-tailed); **Shield Length (mm)** (Size) Independent (grouping) variable: **Species**
Kruskal-Wallis test: H (5, N= 2927) =1029.698 p =0.000

	***C. infraspinatus* - R:2775.2**	***C. padavensis* - R:2657.4**	***D. lopochir* - R:1733.9**	***D. moosai* - R:1152.7**	***Diogenes* sp. 2 - R:2522.5**	***Diogenes* sp. 3 - R:2600.0**
C. infraspinatus		1.000000	0.000000	0.000000	1.000000	1.000000
C. padavensis	1.000000		0.439271	0.005621	1.000000	1.000000
D. lopochir	0.000000	0.439271		0.000000	1.000000	1.000000
D. moosai	0.000000	0.005621	0.000000		1.000000	1.000000
***Diogenes* sp. 2**	1.000000	1.000000	1.000000	1.000000		1.000000
***Diogenes* sp. 3**	1.000000	1.000000	1.000000	1.000000	1.000000	

(b) Size (shield length) of hermit crabs by species among stations

Species=***Diogenes moosai*** Multiple Comparisons p values (2-tailed); **Shield Length (mm)** (Size) Independent (grouping) variable: **Stations** Kruskal-Wallis test: H (3, N= 1879) =3.761160 p =.2884

	Mudflat - R:935.10	**Nearshore - R:955.12**	**River mouth - R:936.06**	**Upstream - R:755.22**
Mudflat		1.000000	1.000000	0.534758
Shoal	1.000000		1.000000	0.362067
River mouth	1.000000	1.000000		0.661944
Mid-estuary	0.534758	0.362067	0.661944	

Species=***Diogenes lopochir*** Multiple Comparisons p values (2-tailed); **Shield Length (mm)** (Size) Independent (grouping) variable: **Stations** Kruskal-Wallis test: H (3, N= 757) =5.768374 p =.1234

	Mudflat - R:343.55	**Nearshore - R:379.67**	**River mouth - R:315.67**	**Upstream - R:567.50**
Mudflat		1.000000	1.000000	0.115920
Shoal	1.000000		1.000000	0.216965
River mouth	1.000000	1.000000		0.620282
Mid-estuary	0.115920	0.216965	0.620282	

Species=***Clibanarius infraspinatus*** Multiple Comparisons p values (2-tailed); **Shield Length (mm)** (Size) Independent (grouping) variable: **Stations** Kruskal-Wallis test: H (3, N= 285) =18.72786 p =.0003

	Mudflat - R:182.36	**Nearshore - R:109.29**	**River mouth - R:176.00**	**Upstream - R:146.86**
Mudflat		0.001058	1.000000	0.259864
Shoal	0.001058		0.047307	0.010752
River mouth	1.000000	0.047307		1.000000
Mid-estuary	0.259864	0.010752	1.000000	

(c) Size (shield length) of hermit crabs between sexes of each species.

Species=***Diogenes moosai*** Multiple Comparisons p values (2-tailed); **Shield Length (mm)** (Size) Independent (grouping) variable: **Sex** Kruskal-Wallis test: H (2, N= 1879) =677.9783 p =0.000

	Male - R:1165.5	**Non-ovigerous female - R:305.96**	**Ovigerous female - R:532.45**
Male		0.000000	0.000000
Non-ovigerous female	0.00		0.000046
Ovigerous female	0.00	0.000046	

Species=***Diogenes lopochir*** Multiple Comparisons p values (2-tailed); **Shield Length (mm)** (Size) Independent (grouping) variable: **Sex** Kruskal-Wallis test: H (2, N= 757) =88.92562 p =0.000

	Male - R:429.81	**Non-ovigerous female - R:254.74**	**Ovigerous female - R:326.96**
Male		0.000000	0.000617
Non-ovigerous female	0.000000		0.055880
Ovigerous female	0.000617	0.055880	

Species=***Clibanarius infraspinatus*** Multiple Comparisons p values (2-tailed); **Shield Length (mm)** (Size) Independent (grouping) variable: **Sex** Kruskal-Wallis test: H (2, N= 285) =26.36368 p =.0000

	Male - R:158.76	**Non-ovigerous female - R:102.05**	**Ovigerous female - R:128.58**
Male		0.000001	1.000000
Non-ovigerous female	0.000001		1.000000
Ovigerous female	1.000000	1.000000	

(d) Chelae size relative to body size of male, non-ovigerous female and ovigerous female of *D. moosai* and *D. lopochir*.

Tukey HSD test; variable **Ratio chelae size against crab size (arcsine)** (Combined data) Approximate Probabilities for Post Hoc Tests Error: Between MS = .08761, df = 969.00

	Species	**Sex**	**{1} - 7.1424**	**{2} - 7.1686**	**{3} - 7.5471**	**{4} - 6.7894**	**{5} - 6.7389**	**{6} - 7.3616**
1	*D. moosai*	Non-ovigerous female		0.961701	0.000020	0.000020	0.000020	0.000020
2	*D. moosai*	Ovigerous Female	0.961701		0.000020	0.000020	0.000020	0.000020
3	*D. moosai*	Male	0.000020	0.000020		0.000020	0.000020	0.000020
4	*D. lopochir*	Non-ovigerous female	0.000020	0.000020	0.000020		0.978082	0.000020
5	*D. lopochir*	Ovigerous Female	0.000020	0.000020	0.000020	0.978082		0.000020
6	*D. lopochir*	Male	0.000020	0.000020	0.000020	0.000020	0.000020	

Appendix XIV. Kruskal-Wallis significant test of aperture length, aperture width, shell height, shell width and shell thickness among seven shells used by male and female *Diogenes moosai* and *D. lopochir*. Cc=*Cerithidea cingulata*, No=*Nassarius cf. olivaceus*, Nj=*Nassarius jacksonianus*, Nb=*Nassarius bellulus*, Nt=*Natica tigrina*, Tl=*Thais lacera*, Tm=*Thais malayensis*.

Multiple Comparisons p values (2-tailed); **Aperture Length (mm)** (Raw data (shell use)) Independent (grouping) variable: **Shell code** Kruskal-Wallis test: H (6, N= 964) =686.6935 p =0.000

	Cc - R:214.63	**No - R:522.25**	**Nj - R:633.50**	**Nt - R:937.39**	**Tl - R:904.57**	**Tm - R:850.46**	**Nb - R:498.44**
Cc		0.000000	0.000000	0.000000	0.000000	0.000000	0.090976
No	0.000000		0.001164	0.000000	0.007964	0.000000	1.000000
Nj	0.000000	0.001164		0.000146	0.229094	0.000000	1.000000
Nt	0.000000	0.000000	0.000146		1.000000	1.000000	0.004349
Tl	0.000000	0.007964	0.229094	1.000000		1.000000	0.101347
Tm	0.000000	0.000000	0.000000	1.000000	1.000000		0.011846
Nb	0.090976	1.000000	1.000000	0.004349	0.101347	0.011846	

Multiple Comparisons p values (2-tailed); **Aperture Width (mm)** (Raw data (shell use)) Independent (grouping) variable: **Shell code** Kruskal-Wallis test: H (6, N= 964) =610.6656 p =0.000

	Cc - R:299.69	**No - R:292.44**	**Nj - R:641.54**	**Nt - R:930.39**	**Tl - R:902.50**	**Tm - R:879.20**	**Nb - R:324.75**
Cc		1.000000	0.000000	0.000000	0.000000	0.000000	1.000000
No	1.000000		0.000000	0.000000	0.000000	0.000000	1.000000
Nj	0.000000	0.000000		0.000406	0.299409	0.000000	0.031461
Nt	0.000000	0.000000	0.000406		1.000000	1.000000	0.000006
Tl	0.000000	0.000000	0.299409	1.000000		1.000000	0.001278
Tm	0.000000	0.000000	0.000000	1.000000	1.000000		0.000001
Nb	1.000000	1.000000	0.031461	0.000006	0.001278	0.000001	

Multiple Comparisons p values (2-tailed); **Shell Height (mm)** (Raw data (shell use)) Independent (grouping) variable: **Shell code** Kruskal-Wallis test: H (6, N= 964) =310.6788 p =0.000

	Cc - R:533.00	**No - R:209.91**	**Nj - R:444.24**	**Nt - R:640.42**	**Tl - R:912.43**	**Tm - R:772.71**	**Nb - R:249.31**
Cc		0.000000	0.000902	1.000000	0.007427	0.000000	0.091336
No	0.000000		0.000000	0.000000	0.000000	0.000000	1.000000
Nj	0.000902	0.000000		0.077968	0.000231	0.000000	1.000000
Nt	1.000000	0.000000	0.077968		0.594050	1.000000	0.019889
Tl	0.007427	0.000000	0.000231	0.594050		1.000000	0.000088
Tm	0.000000	0.000000	0.000000	1.000000	1.000000		0.000006
Nb	0.091336	1.000000	1.000000	0.019889	0.000088	0.000006	

Multiple Comparisons p values (2-tailed); **Shell Width (mm)** (Raw data (shell use)) Independent (grouping) variable: **Shell code** Kruskal-Wallis test: H (6, N= 964) =655.1029 p =0.000

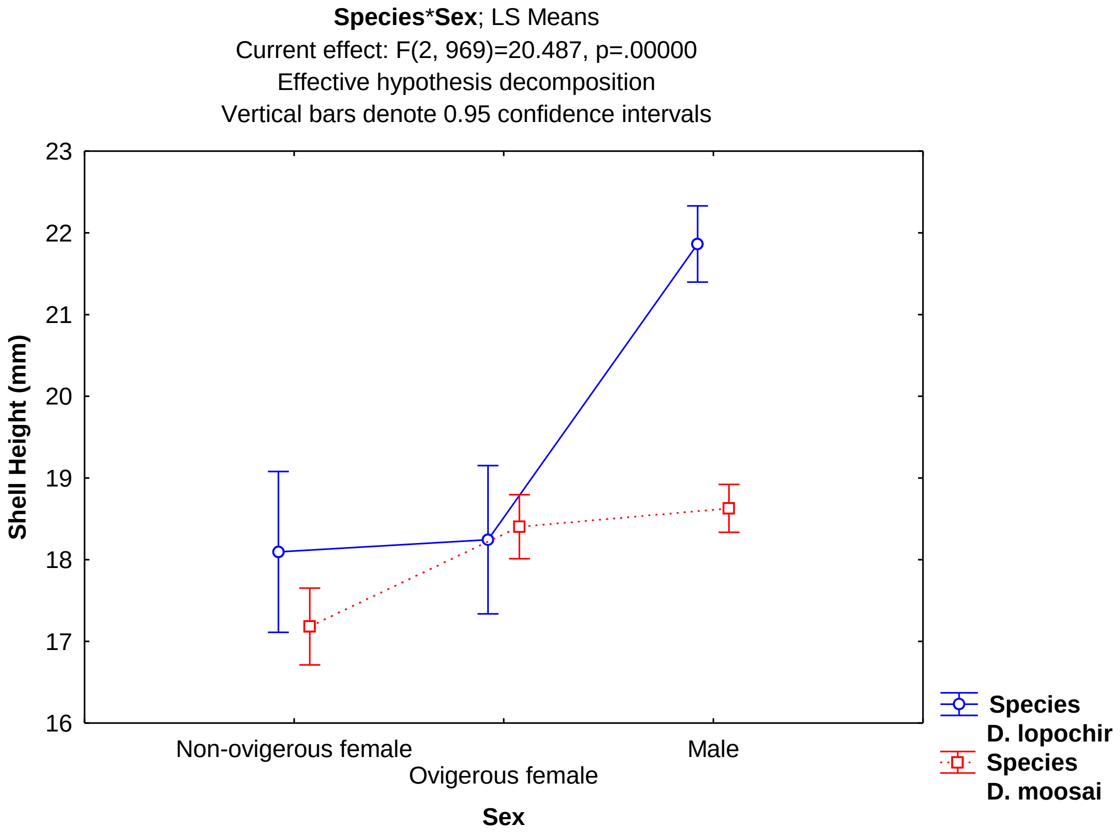
	Cc - R:297.19	**No - R:264.25**	**Nj - R:662.22**	**Nt - R:925.03**	**Tl - R:915.57**	**Tm - R:870.88**	**Nb - R:345.13**
Cc		1.000000	0.000000	0.000000	0.000000	0.000000	1.000000
No	1.000000		0.000000	0.000000	0.000000	0.000000	1.000000
Nj	0.000000	0.000000		0.002131	0.364356	0.000000	0.031125
Nt	0.000000	0.000000	0.002131		1.000000	1.000000	0.000020
Tl	0.000000	0.000000	0.364356	1.000000		1.000000	0.001583
Tm	0.000000	0.000000	0.000000	1.000000	1.000000		0.000005
Nb	1.000000	1.000000	0.031125	0.000020	0.001583	0.000005	

Multiple Comparisons p values (2-tailed); **Thickness index (Shell thickness)** Independent (grouping) variable: Shell code Kruskal-Wallis test: H (6, N= 964) =339.7899 p =0.000

	Cc - R:379.15	**No - R:285.34**	**Nj - R:580.14**	**Nb - R:439.00**	**Nt - R:910.72**	**Tl - R:913.43**	**Tm - R:771.47**
Cc		0.008473	0.000000	1.000000	0.000000	0.000010	0.000000
No	0.008473		0.000000	1.000000	0.000000	0.000000	0.000000
Nj	0.000000	0.000000		1.000000	0.000021	0.036725	0.000000
Nb	1.000000	1.000000	1.000000		0.001404	0.020863	0.023663
Nt	0.000000	0.000000	0.000021	0.001404		1.000000	1.000000
Tl	0.000010	0.000000	0.036725	0.020863	1.000000		1.000000
Tm	0.000000	0.000000	0.000000	0.023663	1.000000	1.000000	

Appendix XV. Factorial (2-way) ANOVA of shell height, shell width, aperture length and aperture width used by different species and sex of hermit crabs.

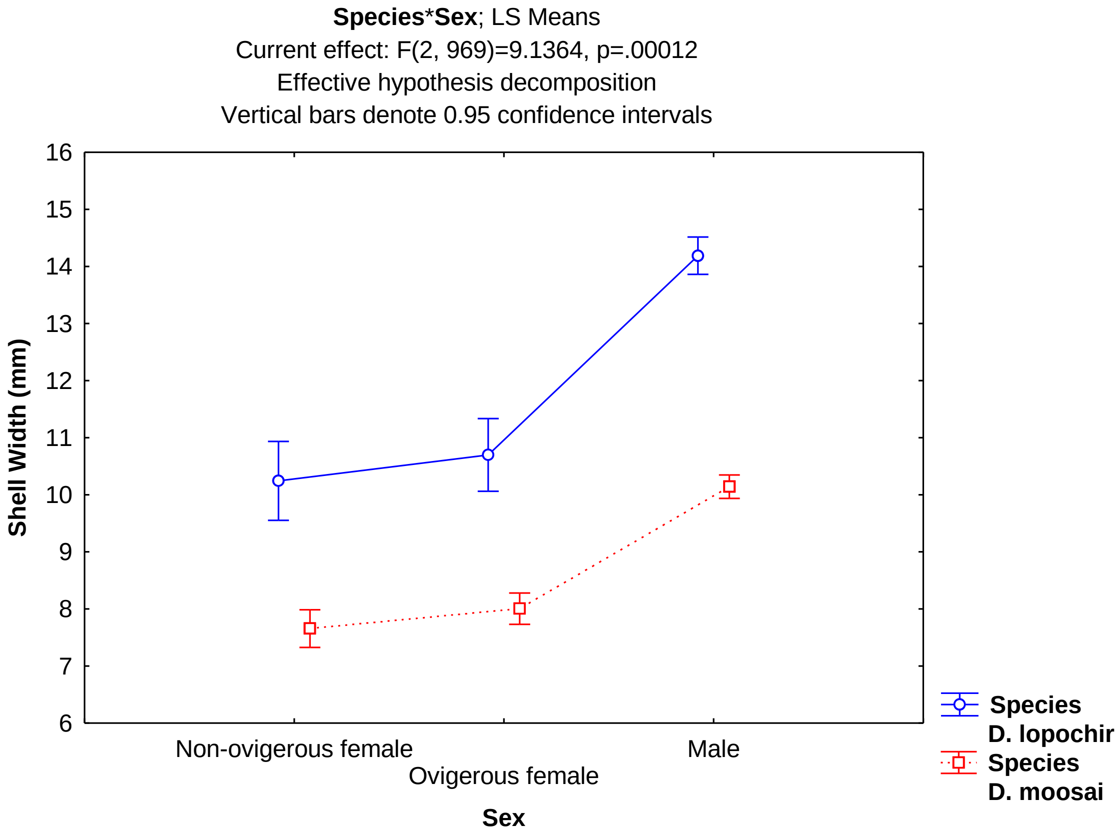
(a) Shell height



Newman-Keuls test; variable **Shell Height (mm)** (Raw data (shell use)) Approximate Probabilities for Post Hoc Tests Error: Between MS = 8.5532, df = 969.00

	Species	**Sex**	**{1} - 18.095**	**{2} - 18.244**	**{3} - 21.864**	**{4} - 17.182**	**{5} - 18.403**	**{6} - 18.629**
1	*D. lopochir*	Non-ovigerous female		0.747626	0.000017	0.048270	0.782935	0.655555
2	*D. lopochir*	Ovigerous female	0.747626		0.000008	0.056241	0.730294	0.682619
3	*D. lopochir*	Male	0.000017	0.000008		0.000020	0.000022	0.000009
4	*D. moosai*	Non-ovigerous female	0.048270	0.056241	0.000020		0.041127	0.015090
5	*D. moosai*	Ovigerous female	0.782935	0.730294	0.000022	0.041127		0.625514
6	*D. moosai*	Male	0.655555	0.682619	0.000009	0.015090	0.625514	

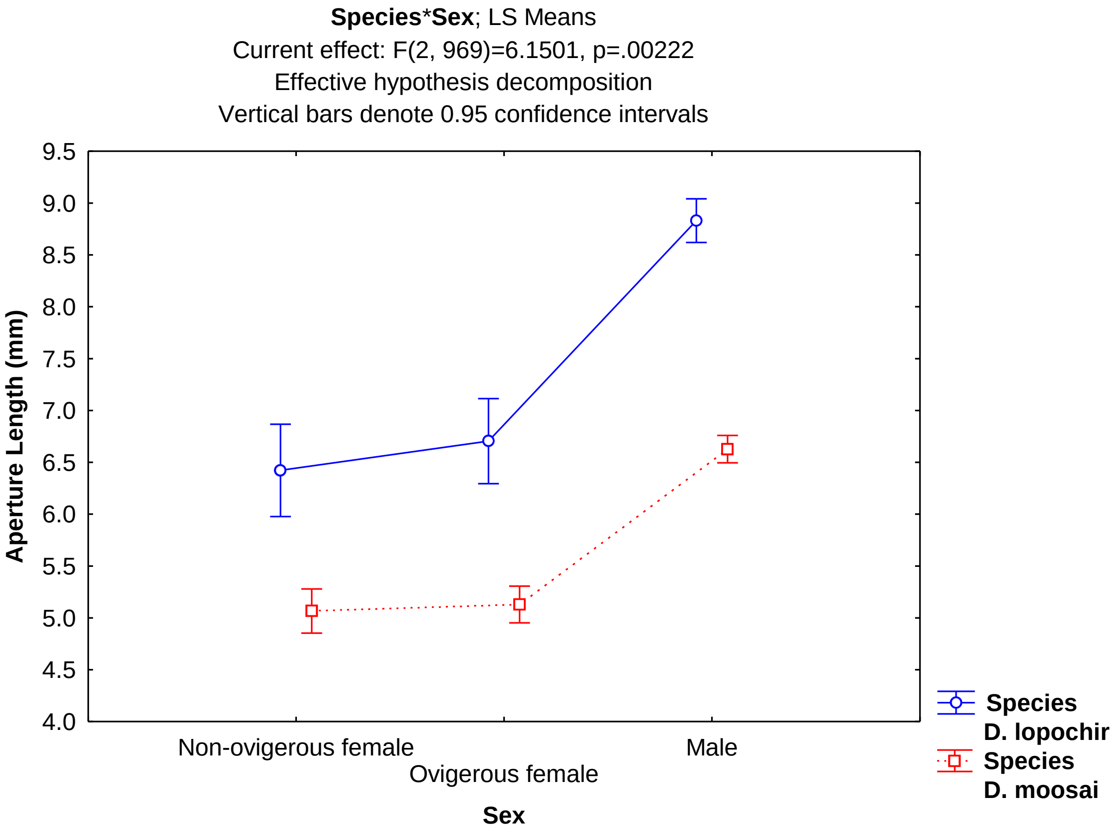
(b) Shell width



Newman-Keuls test; variable **Shell Width (mm)** (Raw data (shell use)) Approximate Probabilities for Post Hoc Tests Error: Between MS = 4.2142, df = 969.00

	Species	**Sex**	**{1} - 10.245**	**{2} - 10.700**	**{3} - 14.189**	**{4} - 7.6560**	**{5} - 8.0056**	**{6} - 10.143**
1	*D. lopochir*	Non-ovigerous female		0.160849	0.000022	0.000008	0.000022	0.753478
2	*D. lopochir*	Ovigerous female	0.160849		0.000009	0.000017	0.000008	0.199027
3	*D. lopochir*	Male	0.000022	0.000009		0.000020	0.000017	0.000008
4	*D. moosai*	Non-ovigerous female	0.000008	0.000017	0.000020		0.281285	0.000022
5	*D. moosai*	Ovigerous female	0.000022	0.000008	0.000017	0.281285		0.000009
6	*D. moosai*	Male	0.753478	0.199027	0.000008	0.000022	0.000009	

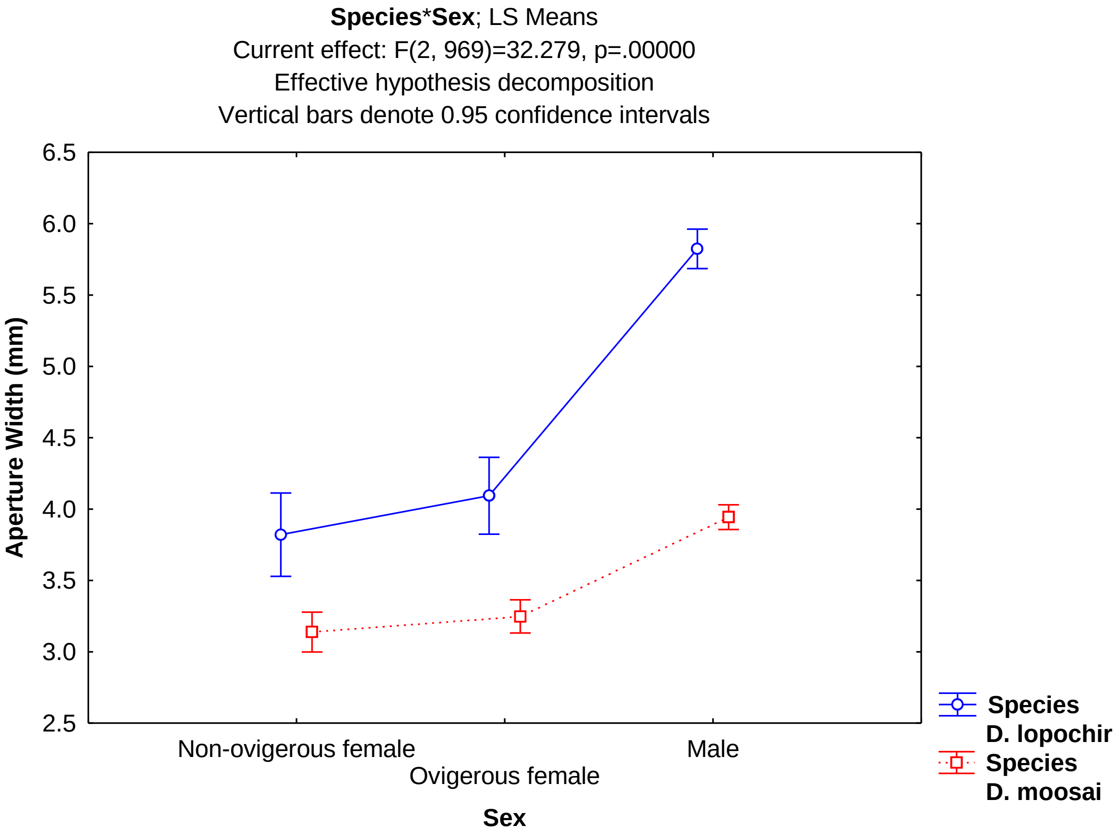
(c) Aperture length



Newman-Keuls test; variable **Aperture Length (mm)** (Raw data (shell use)) Approximate Probabilities for Post Hoc Tests Error: Between MS = 1.7481, df = 969.00

	Species	**Sex**	**{1} - 6.4226**	**{2} - 6.7045**	**{3} - 8.8309**	**{4} - 5.0663**	**{5} - 5.1291**	**{6} - 6.6270**
1	*D. lopochir*	Non-ovigerous female		0.368215	0.000008	0.000022	0.000009	0.328177
2	*D. lopochir*	Ovigerous female	0.368215		0.000009	0.000017	0.000008	0.710717
3	*D. lopochir*	Male	0.000008	0.000009		0.000020	0.000017	0.000022
4	*D. moosai*	Non-ovigerous female	0.000022	0.000017	0.000020		0.763772	0.000008
5	*D. moosai*	Ovigerous female	0.000009	0.000008	0.000017	0.763772		0.000022
6	*D. moosai*	Male	0.328177	0.710717	0.000022	0.000008	0.000022	

(d) Aperture width



Newman-Keuls test; variable **Aperture Width (mm)** (Raw data (shell use)) Approximate Probabilities for Post Hoc Tests Error: Between MS = .75292, df = 969.00

	Species	**Sex**	**{1} - 3.8209**	**{2} - 4.0938**	**{3} - 5.8233**	**{4} - 3.1381**	**{5} - 3.2484**	**{6} - 3.9434**
1	*D. lopochir*	Non-ovigerous female		0.114767	0.000008	0.000023	0.000038	0.371902
2	*D. lopochir*	Ovigerous female	0.114767		0.000009	0.000017	0.000008	0.272824
3	*D. lopochir*	Male	0.000008	0.000009		0.000020	0.000017	0.000022
4	*D. moosai*	Non-ovigerous female	0.000023	0.000017	0.000020		0.421007	0.000008
5	*D. moosai*	Ovigerous female	0.000038	0.000008	0.000017	0.421007		0.000023
6	*D. moosai*	Male	0.371902	0.272824	0.000022	0.000008	0.000023	

Appendix XVI. Kruskal-Wallis significant test on quality of shells categorised as undamaged, slightly damaged, damaged and greatly damaged used by male, non-ovigerous female and ovigerous female of *D. moosai* and *D. lopochir*.

(a) *D. moosai*

Species=Diogenes moosai, Sex=Male Multiple Comparisons p values (2-tailed); **Frequency** (Shell quality) Independent (grouping) variable: **Shell Condition** Kruskal-Wallis test: H (3, N= 84) =59.15738 p =.0000

	Damaged - R:33.833	**Greatly damaged - R:14.714**	**Slightly damaged - R:52.024**	**Undamaged - R:69.429**
Damaged		0.066546	0.094033	0.000014
Greatly damaged	0.066546		0.000004	0.000000
Slightly damaged	0.094033	0.000004		0.124637
Undamaged	0.000014	0.000000	0.124637	

Species=Diogenes moosai, Sex=Female Multiple Comparisons p values (2-tailed); **Frequency** (Shell quality) Independent (grouping) variable: **Shell Condition** Kruskal-Wallis test: H (3, N= 84) =25.86481 p =.0000

	Damaged - R:36.595	**Greatly damaged - R:25.000**	**Slightly damaged - R:51.262**	**Undamaged - R:57.143**
Damaged		0.740869	0.308237	0.038048
Greatly damaged	0.740869		0.002912	0.000117
Slightly damaged	0.308237	0.002912		1.000000
Undamaged	0.038048	0.000117	1.000000	

Species=Diogenes moosai, Sex=Ovigerous female Multiple Comparisons p values (2-tailed); **Frequency** (Shell quality) Independent (grouping) variable: **Shell Condition** Kruskal-Wallis test: H (3, N= 84) =49.49513 p =.0000

	Damaged - R:28.810	**Greatly damaged - R:21.238**	**Slightly damaged - R:56.095**	**Undamaged - R:63.857**
Damaged		1.000000	0.001736	0.000019
Greatly damaged	1.000000		0.000022	0.000000
Slightly damaged	0.001736	0.000022		1.000000
Undamaged	0.000019	0.000000	1.000000	

(b) *D. lopochir*

Species=Diogenes lopochir, Sex=Male Multiple Comparisons p values (2-tailed); **Frequency** (Shell quality) Independent (grouping) variable: **Shell Condition** Kruskal-Wallis test: H (3, N= 84) =16.18130 p =.0010

	Damaged - R:46.405	**Greatly damaged - R:25.143**	**Slightly damaged - R:44.500**	**Undamaged - R:53.952**
Damaged		0.028415	1.000000	1.000000
Greatly damaged	0.028415		0.060765	0.000778
Slightly damaged	1.000000	0.060765		1.000000
Undamaged	1.000000	0.000778	1.000000	

Species=Diogenes lopochir, Sex=Female Multiple Comparisons p values (2-tailed); **Frequency** (Shell quality) Independent (grouping) variable: **Shell Condition** Kruskal-Wallis test: H (3, N= 84) =30.46019 p =.0000

	Damaged - R:45.429	**Greatly damaged - R:21.571**	**Slightly damaged - R:41.881**	**Undamaged - R:61.119**
Damaged		0.009170	1.000000	0.222766
Greatly damaged	0.009170		0.041859	0.000001
Slightly damaged	1.000000	0.041859		0.063597
Undamaged	0.222766	0.000001	0.063597	

Species=Diogenes lopochir, Sex=Ovigerous female Multiple Comparisons p values (2-tailed); **Frequency** (Shell quality) Independent (grouping) variable: **Shell Condition** Kruskal-Wallis test: H (3, N= 84) =16.52973 p =.0009

	Damaged - R:38.024	**Greatly damaged - R:34.000**	**Slightly damaged - R:43.810**	**Undamaged - R:54.167**
Damaged		1.000000	1.000000	0.191980
Greatly damaged	1.000000		1.000000	0.044307
Slightly damaged	1.000000	1.000000		1.000000
Undamaged	0.191980	0.044307	1.000000	

Appendix XVII. Kruskal-Wallis significant test on density (ind/ha) of live gastropods whose shells were most commonly used by hermit crabs (*D. moosai*, *D. lopochir* and *C. infraspinatus*) between sampling stations.

Multiple Comparisons p values (2-tailed); ***Thaisella malayensis***, Independent (grouping) variable: **Station** Kruskal-Wallis test: H (3, N= 189) =65.63551 p =.0000

	Upstream - R:56.077	**River mouth - R:66.789**	**Mudflat - R:102.62**	**Offshore - R:133.09**
Upstream		1.000000	0.000289	0.000000
River mouth	1.000000		0.011421	0.000000
Mudflat	0.000289	0.011421		0.019262
Offshore	0.000000	0.000000	0.019262	

Multiple Comparisons p values (2-tailed); ***Thaisella lacera***, Independent (grouping) variable: **Station** Kruskal-Wallis test: H (3, N= 189) =56.17289 p =.0000

	Upstream - R:79.564	**River mouth - R:79.053**	**Mudflat - R:84.945**	**Offshore - R:125.89**
Upstream		1.000000	1.000000	0.000275
River mouth	1.000000		1.000000	0.000260
Mudflat	1.000000	1.000000		0.000449
Offshore	0.000275	0.000260	0.000449	

Multiple Comparisons p values (2-tailed); ***Nassarius cf. olivaceus***, Independent (grouping) variable: **Station** Kruskal-Wallis test: H (3, N= 189) =72.42207 p =.0000

	Upstream - R:35.846	**River mouth - R:87.000**	**Mudflat - R:128.93**	**Offshore - R:108.07**
Upstream		0.000245	0.000000	0.000000
River mouth	0.000245		0.001678	0.395354
Mudflat	0.000000	0.001678		0.262055
Offshore	0.000000	0.395354	0.262055	

Multiple Comparisons p values (2-tailed); ***Nassarius jacksonianus***, Independent (grouping) variable: **Station** Kruskal-Wallis test: H (3, N= 189) =84.68390 p =.0000

	Upstream - R:43.103	**River mouth - R:69.579**	**Mudflat - R:103.80**	**Offshore - R:138.96**
Upstream		0.202350	0.000001	0.000000
River mouth	0.202350		0.018127	0.000000
Mudflat	0.000001	0.018127		0.004029
Offshore	0.000000	0.000000	0.004029	

Multiple Comparisons p values (2-tailed); ***Natica tigrina***, Independent (grouping) variable: **Station** Kruskal-Wallis test: H (3, N= 189) =34.67977 p =.0000

	Upstream - R:80.795	**River mouth - R:72.355**	**Mudflat - R:95.318**	**Offshore - R:119.51**
Upstream		1.000000	1.000000	0.003962
River mouth	1.000000		0.279580	0.000231
Mudflat	1.000000	0.279580		0.115831
Offshore	0.003962	0.000231	0.115831	

Multiple Comparisons p values (2-tailed); ***Cerithidea cingulata*****,** Independent (grouping) variable: **Station** Kruskal-Wallis test: H (3, N= 189) =24.23392 p =.0000

	Upstream - R:86.500	**River mouth - R:96.118**	**Mudflat - R:109.06**	**Offshore - R:86.500**
Upstream		1.000000	0.292795	1.000000
River mouth	1.000000		1.000000	1.000000
Mudflat	0.292795	1.000000		0.174553
Offshore	1.000000	1.000000	0.174553	

Multiple Comparisons p values (2-tailed); ***Pugilina cochlidium*****,** Independent (grouping) variable: **Station** Kruskal-Wallis test: H (3, N= 189) =32.51124 p =.0000

	Upstream - R:82.846	**River mouth - R:80.500**	**Mudflat - R:92.318**	**Offshore - R:115.57**
Upstream		1.000000	1.000000	0.023965
River mouth	1.000000		1.000000	0.013228
Mudflat	1.000000	1.000000		0.147147
Offshore	0.023965	0.013228	0.147147	

Multiple Comparisons p values (2-tailed); ***Murex occa***, Independent (grouping) variable: **Station** Kruskal-Wallis test: H (3, N= 189) =2.794888 p =.4243

	Upstream - R:94.654	**River mouth - R:89.184**	**Mudflat - R:99.655**	**Offshore - R:94.623**
Upstream		1.000000	1.000000	1.000000
River mouth	1.000000		1.000000	1.000000
Mudflat	1.000000	1.000000		1.000000
Offshore	1.000000	1.000000	1.000000	

Appendix XVIII. Non-parametric Kruskal-Wallis significant tests on density (ind/ha) of ovigerous female among stations.

a) *D. moosai*

Multiple Comparisons p values (2-tailed); **Density of ovigerous female *D. moosai* (ind/ha)** (Sex composition (recompiled)) Independent (grouping) variable: **STATION** Kruskal-Wallis test: H (3, N= 195) =71.50743 p =.0000

	Mid-estuary - R:53.000	**River mouth - R:67.092**	**Mudflat - R:128.89**	**Shoal - R:116.97**
Mid-estuary		1.000000	0.000000	0.000000
River mouth	1.000000		0.000001	0.000121
Mudflat	0.000000	0.000001		1.000000
Shoal	0.000000	0.000121	1.000000	

b) *D. lopochir*

Multiple Comparisons p values (2-tailed); **Density of ovigerous female *D. lopochir* (ind/ha)** (Sex composition (recompiled)) Independent (grouping) variable: **STATION** Kruskal-Wallis test: H (3, N= 195) =29.41150 p =.0000

	Mid-estuary - R:89.500	**River mouth - R:89.500**	**Mudflat - R:92.776**	**Shoal - R:113.96**
Mid-estuary		1.000000	1.000000	0.210711
River mouth	1.000000		1.000000	0.219499
Mudflat	1.000000	1.000000		0.249113
Shoal	0.210711	0.219499	0.249113	

c) *C. infraspinatus*

Multiple Comparisons p values (2-tailed); **Density of ovigerous female *C. infraspinatus* (ind/ha)** (Sex composition (recompiled)) Independent (grouping) variable: **STATION** Kruskal-Wallis test: H (3, N= 195) =4.799137 p =.1871

	Mid-estuary - R:101.50	**River mouth - R:96.500**	**Mudflat - R:96.500**	**Shoal - R:98.125**
Mid-estuary		1.000000	1.000000	1.000000
River mouth	1.000000		1.000000	1.000000
Mudflat	1.000000	1.000000		1.000000
Shoal	1.000000	1.000000	1.000000	

Appendix XIX. Kruskal-Wallis significant test on density (ind/ha) among sampling stations and moon phases at each diel sampling period of sciaenid and ariid fishes.

(a) Among stations

Multiple Comparisons p values (2-tailed); **Sciaenidae density (ind/ha)**, Independent (grouping) variable: **Station** Kruskal-Wallis test: H (3, N= 157) =56.85372 p =.0000

	Mid-estuary - R:109.29	**River mouth - R:63.120**	**Mudflat - R:49.448**	**Shoal - R:107.00**
Mid-estuary		0.007412	0.000011	1.000000
River mouth	0.007412		1.000000	0.000344
Mudflat	0.000011	1.000000		0.000000
Shoal	1.000000	0.000344	0.000000	

Multiple Comparisons p values (2-tailed); **Ariidae (ind/ha)**, Independent (grouping) variable: **Station** Kruskal-Wallis test: H (3, N= 156) =49.38676 p =.0000

	Mid-estuary - R:125.69	**River mouth - R:107.88**	**Mudflat - R:77.086**	**Shoal- R:53.807**
Mid-estuary		1.000000	0.000835	0.000000
River mouth	1.000000		0.026317	0.000004
Mudflat	0.000835	0.026317		0.034385
Shoal	0.000000	0.000004	0.034385	

(b) Among moon phases

Wet period (northeast monsoon)

Multiple Comparisons p values (2-tailed); **Ariidae density (ind/ha)**, Independent (grouping) variable: **Moon phases** Kruskal-Wallis test: H (3, N= 47) =1.316235 p =.7253

	Full Moon - R:19.944	**New Moon - R:24.393**	**First Quarter - R:26.344**	**Third Quarter - R:23.188**
Full Moon		1.000000	1.000000	1.000000
New Moon	1.000000		1.000000	1.000000
First Quarter	1.000000	1.000000		1.000000
Third Quarter	1.000000	1.000000	1.000000	

Multiple Comparisons p values (2-tailed); **Sciaenidae (ind/ha)**, Independent (grouping) variable: **Moon phases** Kruskal-Wallis test: H (3, N= 47) =5.498226 p =.1387

	Full Moon - R:15.056	**New Moon - R:23.786**	**First Quarter - R:27.813**	**Third Quarter - R:26.813**
Full Moon		0.816922	0.153313	0.465741
New Moon	0.816922		1.000000	1.000000
First Quarter	0.153313	1.000000		1.000000
Third Quarter	0.465741	1.000000	1.000000	

Dry period (southwest monsoon)

Multiple Comparisons p values (2-tailed); **Ariidae (ind/ha)** Independent (grouping) variable: **Moon phases**
Kruskal-Wallis test: H (3, N= 64) =3.661622 p =.3004

	Full Moon - R:34.250	**New Moon - R:25.813**	**First Quarter - R:38.063**	**Third Quarter - R:31.875**
Full Moon		1.000000	1.000000	1.000000
New Moon	1.000000		0.376543	1.000000
First Quarter	1.000000	0.376543		1.000000
Third Quarter	1.000000	1.000000	1.000000	

Multiple Comparisons p values (2-tailed); **Sciaenidae (ind/ha)** Independent (grouping) variable: **Moon phases**
Kruskal-Wallis test: H (3, N= 64) =14.40604 p =.0024

	Full Moon - R:37.406	**New Moon - R:17.594**	**First Quarter - R:34.688**	**Third Quarter - R:40.313**
Full Moon		0.015689	1.000000	1.000000
New Moon	0.015689		0.056470	0.003348
First Quarter	1.000000	0.056470		1.000000
Third Quarter	1.000000	0.003348	1.000000	

Appendix XX. Discriminant analysis of shell parameters (AL=aperture length, AW=aperture width, ShH=shell height, ShW=shell length and ShWt=shell weight) of No=*Nassarius cf. olivaceus*, Nj=*N. jacksonianus*, Cc=*Cerithidea cingulata*, Tm=*Thais malayensis*, Tl=*Thais lacera*, Nb=*Nassarius bellulus* and Nt=*Natica tirgrina* whose shells were used by *D. moosai* and *D. lopochir*.

Standardized Coefficients (Book1) for Canonical Variables

	Root 1	**Root 2**	**Root 3**	**Root 4**	**Root 5**
Aperture Length (mm)	0.40069	-1.92655	-0.39375	0.66324	-0.547879
Aperture Width (mm)	0.24674	1.31524	-1.35111	0.03222	1.113286
Shell Height (mm)	-1.21913	0.66211	-0.05658	1.04356	-0.548550
Shell Width (mm)	1.25399	0.67835	2.13332	-0.20984	-0.043002
Shell weight (g)	-0.19820	-0.41710	-0.79993	-1.29415	-0.781237
Eigenval	7.21164	2.36058	0.63643	0.06207	0.008998
Cum.Prop	0.70154	0.93117	0.99309	0.99912	1.000000

Factor Structure Matrix (Book1) Correlations Variables - Canonical Roots (Pooled-within-groups correlations)

	Root 1	**Root 2**	**Root 3**	**Root 4**	**Root 5**
Aperture Length (mm)	0.630969	-0.013007	-0.334234	0.441879	-0.542899
Aperture Width (mm)	0.633524	0.419847	-0.486027	0.270827	-0.335867
Shell Height (mm)	0.126252	0.427282	-0.184188	0.420710	-0.768485
Shell Width (mm)	0.647043	0.382213	-0.028373	0.178310	-0.634547
Shell weight (g)	0.336030	0.286359	-0.327315	-0.229170	-0.803385

Chi-Square Tests with Successive Roots Removed (Book1)

	Eigen- - value	**Canonicl - R**	**Wilks' - Lambda**	**Chi-Sqr.**	**df**	**p-level**
0	7.211636	0.937135	0.020664	3712.552	30	0.000000
1	2.360577	0.838112	0.169685	1697.539	20	0.000000
2	0.636432	0.623630	0.570239	537.547	12	0.000000
3	0.062074	0.241757	0.933157	66.207	6	0.000000
4	0.008998	0.094435	0.991082	8.573	2	0.013755

Classification Matrix (Book1) Rows: Observed classifications Columns: Predicted classifications

	Percent - Correct	**Cc- p=.39004**	**Tm - p=.10996**	**Tl - p=.00726**	**Nb- p=.00830**	**Nj- p=.30394**	**No - p=.16183**	**Nt - p=.01867**
Cc	96.01	361	0	0	0	13	2	0
Tm	70.76	0	75	9	0	19	0	3
Tl	0.00	0	7	0	0	0	0	0
Nb	25.00	0	0	0	2	0	6	0
Nj	94.20	1	0	0	0	276	16	0
No	97.44	3	0	0	0	1	152	0
Nt	88.89	0	2	0	0	0	0	16
Total	91.49	365	84	9	2	309	176	19

Appendix XXI. Length frequency data used for analysis of growth, life span, recruitment and mortality of *D. moosai* and *D. lopochir* (ML=mid shield length in mm) using Fisat II software.

a) *D. moosai*

ML	3/8/2009	5/9/2009	5/10/2009	3/11/2009	1/12/2009	16/1/2010	2/2/2010	1/3/2010	1/4/2010	3/5/2010	1/6/2010	29/6/2010	26/7/2010	25/8/2010	22/9/2010	22/10/2010	22/11/2010	22/12/2010	19/1/2011	17/2/2011	21/3/2011
1.125										1									1		
1.38		1		1	1	1															
1.63	2	8	1		2	1	1	1			1	2		1	1			1	5		3
1.88	1	15	1		9	3		3	8	13	4	11	3	5	1	7	1	3	9	6	3
2.125	4	32	5	3	20	23	9	11	11	35	11	32	14	6	3	16	2	4	19	4	7
2.38	13	38	2	5	32	32	10	16	15	36	9	41	30	23	1	24	4	3	19	2	11
2.63	10	34	4	6	6	32	18	20	14	25	22	43	30	25	9	34	2	2	17	6	3
2.88	10	30	3	6	19	30	9	17	11	35	27	50	24	30	10	28		6	12	3	2
3.125	17	12	4	5	20	21	4	12	17	11	7	20	15	32	9	15	2		13	2	1
3.38	6	6	2	5	9	8	4	4	2	9		4	6	10	2	5		1	7	1	
3.63	3	1		1	3	1				1		6	1		1	6					
3.88	2				1						1				1	3	1				
4.125	1					1			1	1			2			1					
4.38																			1		
4.63																1					
4.88		1														1					

b) *D. lopochir*

ML	3/8/2009	5/9/2009	5/10/2009	3/11/2009	1/12/2009	16/1/2010	2/2/2010	1/3/2010	1/4/2010	3/5/2010	1/6/2010	29/6/2010	26/7/2010	25/8/2010	22/9/2010	22/10/2010	22/11/2010	22/12/2010	19/1/2011	17/2/2011	21/3/2011
0.88																			1		
1.13																			1		
1.38			1																3		
1.63		2												2					4	4	
1.88		1				2					1		3	3	3	1		1	2	1	
2.13	1	3	2			3	1	1	1		1		4	3	2	2			5	5	2
2.38	1	8	1		1	7			4		3		7	3	15	4			5	2	2
2.63	1	4	2		4	13		1	3		3	3	19	5	12	3		2	11		9
2.88		4	1		3	10	4	2	7	1	4	4	24	7	17	9		2	7		8
3.13		3	1		4	23		2	8	2	7	11	22	4	10	9	2		10		4
3.38			1	1	3	15	4		10		9	7	14	8	12	4	2	1	7	3	5
3.63		2		1	3	10	2	1	9	2	8		11	1	4	5		2	6	1	6
3.88					1	6			6		1	1	12	1	1	1			1	1	
4.13						6	1	1	3	2	3	2	1	2		1				1	1
4.38						5					6	1	4	1		4					
4.63	1	1				4			2		1		1						1		
4.88	1					2							2						2	1	
5.13									1				1						3	1	