THE ECOLOGY OF STOMATOPODS IN MATANG WATERS WITH EMPHASIS ON *MIYAKEA NEPA* AND *ORATOSQUILLINA PERPENSA*

NG YING PEI

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ABSTRACT

An ecological study of the adult and larvae of stomatopods was carried out in the estuary of the Matang Mangrove Forest Reserve (Malaysia) and its adjacent coastal waters. The study investigated the spatial and temporal distribution of the adult stomatopod population; estimated the various parameters of stomatopod population dynamics; and elucidated the reproduction biology, larval ecology and feeding habits of stomatopods.

Monthly trawl surveys (from September 2004 to February 2006) of adult stomatopods revealed four stomatopod species of the family Squillidae. *Miyakea nepa* (Latreille, 1828) was the most abundant species (16.36±12.48 ind/ha; 65.41%) followed by *Oratosquillina perpensa* (Kemp. 1911) (6.63±10.74 ind/ha; 26.51%), *Harpiosquilla raphidea* (Fabricius, 1798) (1.77±5.32 ind/ha; 7.08%) and *Cloridopsis scorpio* (Latreille, 1828) (0.25±0.80 ind/ha; 1.00%). In term of adult size, *Harpiosquilla raphidea* and *Cloridopsis scorpio* were the largest and smallest stomatopod collected, respectively. Although all four species shared the same general habitat, they were more abundant at particular sites, suggesting spatial differences and preference for environmental parameters. The spatial distribution of stomatopods juxtaposes with the continuous migration of juvenile shrimps from their estuarine nursery areas (mangroves, mudflats) to offshore grounds where they mature; the smallest species (*Cloridopsis scorpio*) in estuarine areas fed on the juvenile shrimps, the nearshore species (*Miyakea nepa* and *Oratosquillina perpensa*) fed on medium size shrimps, and the offshore species, *Harpiosquilla raphidea* (largest species) fed on adult shrimps.

The four stomatopod species consumed a wide range of prey organisms, with shrimp as the most abundant food (26% to 80% by volume). The study shows the importance of the Matang mangrove estuary as an important source of prey organisms (for stomatopods) that migrate out of their nursery ground to offshore waters. Severe food competition among species is unlikely since shrimp fauna are diverse and occur in high abundance, and secondary diet specialization exists among the stomatopod species. The latter suggests some degree of trophic partitioning. PCA biplot ordination of stomatopod food items showed that *Miyakea nepa* is a generalist while three other species tend to specialize in their prey choice; *Oratosquillina perpensa* on crab, *Harpiosquilla raphidea* on fish and *Cloridopsis scorpio* on shrimp.

Analysis of size frequency distribution of the two most abundant species showed that *Miyakea nepa* has a faster grow rate (growth parameter, K = 0.93 yr^{-1}) and shorter lifespan (3.23 years) than *Oratosquillina perpensa* (K = 0.70 yr^{-1}; lifespan = 4.29 year). Intensive fishing of *Miyakea nepa* and *Oratosquillina perpensa* in Matang due to their popularity as seafood has resulted in their overfishing (exploitation rate, E = 0.47 to 0.59). Therefore, sustainable fishing practices should be implemented.

In general, the stomatopod populations were female-biased except *Cloridopsis scorpio* which was male-biased. Five stages of ovarian development of female *Miyakea nepa*, *Oratosquillina perpensa*, and *Cloridopsis scorpio* are discerned and described. Three stages of maturity of male *Miyakea nepa* and *Oratosquillina perpensa* based on cohorts of different mean penile lengths are described for the first time. *Miyakea nepa* and *Oratosquillina perpensa* breed throughout the year, each with two spawning peaks and one to two recruitment peaks.

Planktonic stomatopod larvae were earlier sampled by bongo nets from the upper estuary to offshore waters from November 2002 to October 2003. The study has successfully identified four middle stages and two late stages of *Cloridopsis scorpio* larvae, whereby only three larval stages had been identified in other study. Collected larvae of *Miyakea nepa* only showed the late developmental stage. Stomatopod larvae distribution and abundance are affected by their environment including the availability of their potential food. Generally, *Cloridopsis scorpio* larvae were found mainly in the mangrove estuary while *Miyakea nepa* and the unidentified larvae were found throughout the coastal areas. Despite the temporal variations in abundance of newly recruited *Cloridopsis scorpio*, the results suggest only one spawning season in a year.

ABSTRAK

Kajian ekologi stomatopod peringkat dewasa dan larva telah dijalankan di sekitar kawasan perairan laut Matang. Kajian tersebut bertujuan untuk mengkaji taburan populasi stomatopod dewasa, menganggar pelbagai parameter populasi dinamik , mengkaji biologi reproduksi, ekologi larva dan tabiat pemakanan stomatopod.

Penyampelan bulanan (dari September 2004 hingga Februari 2006) untuk stomatopod dewasa menunjukkan terdapat empat spesies stomatopod daripada famili Squillidae. *Miyakea nepa* (Latreille, 1828) adalah spesies yang mencatatkan kelimpahan yang tertinggi (16.36±12.48 ind/ha; 65.41%) diikuti dengan *Oratosquillina perpensa* (Kemp, 1911) (6.63±10.74 ind/ha; 26.51%), *Harpiosquilla raphidea* (Fabricius, 1798) (1.77±5.32 ind/ha; 7.08%) dan *Cloridopsis scorpio* (Latreille, 1828) (0.25±0.80 ind/ha; 1.00%). Dari segi saiz, *Harpiosquilla raphidea* adalah spesies yang terbesar manakala *Cloridopsis scorpio* adalah spesies yang terkecil. Walaupun kesemua spesies stomatopod mempunyai taburan yang meluas di kawasan kajian, namun kelimpahan setiap spesies adalah berbeza di setiap lokasi. Ini mencadangkan bahawa taburan mereka adalah disebabkan oleh faktor alam sekitar. Taburan stomatopod didapati selaras dengan corak migrasi kitar hayat udang, di mana udang juvenile akan keluar dari kawasan nurseri (muara sungai bakau) dan matang di kawasan luar persisiran. Spesies terkecil (*Cloridopsis scorpio*) di muara sungai bakau akan memakan udang juvenil, spesies berdekatan pesisir (*Miyakea nepa* and *Oratosquillina perpensa*) akan memakan udang bersaiz sederhana dan spesies di luar persisir *Harpiosquilla raphidea* (spesies terbesar) akan memakan udang dewasa.

Keempat-empat spesies mempunyai diet pemakanan yang luas dan udang merupakan makanan utama (dengan purata isipadu sebanyak 26% hingga 80%). Kajian ini menunjukkan kepentingan paya bakau Matang sebagai sumber makanan utama untuk mangsa stomatopod yang berhijrah dari tempat nursery ke kawansan peraiaran laut. Keempat-empat spesies tidak mengalami persaingan hebat untuk pemakanan udang disebabkan kelimpahan udang yang tinggi dan kesemua spesies stomatopod menunjukan diet sekunder yang khusus. Ordinasi PCA biplot untuk diet stomatopod menunjukkan bahawa *Miyakea nepa* mempunyai pemakanan yang lebih umum manakala ketiga-tiga spesies yang lain mempunyai pemakanan yang lebih khusus; pemakanan *Oratosquillina perpensa*, *Harpiosquilla raphidea* dan *Cloridopsis scorpio* adalah masing-masing lebih khusus kepada ketam, ikan dan udang.

Miyakea nepa didapati mempunyai kadar pertumbuhan (koefisien pertumbuhan, K = 0.93 per tahun) yang lebih cepat dan jangka hayat yang lebih pendek (3.23 tahun) berbanding *Oratosquillina perpensa* (K = 0.70 per tahun; jangka hayat = 4.29 tahun). Penangkapan intensif terhadap *Miyakea nepa* dan *Oratosquillina perpensa* di perairan laut Matang telah menyebabkan penangkapan berlebihan (Kadar eksploitasi, E = 0.47 hingga 0.59). Oleh yang demikian, langkah pemeliharaan dan pemuliharaan sumber tersebut harus dilaksanakan.

Keseluruhannya, jumlah individu stomatopod betina yang ditangkap adalah lebih tinggi daripada stomatopod jantan untuk kesemua spesies kecuali *Cloridopsis scorpio* di mana bilangan individu jantan adalah lebih tinggi. Lima peringkat kematangan ovari untuk betina *Miyakea nepa*, *Oratosquillina perpensa* dan *Cloridopsis scorpio* telah dikenalpasti dan dihuraikan. Dengan pertama kalinya, tiga peringkat kematangan testis untuk *Miyakea nepa* dan *Oratosquillina perpensa* telah dikenalpasti dengan kaedah pengasingan purata kepanjangan zakar. *Miyakea nepa* dan *Oratosquillina perpensa* membiak sepanjang tahun masing-masing dengan dua puncak pembiakan. Kedua-dua spesies tersebut juga didapati mempunyai satu atau dua musim perekrutan dalam setahun.

Penyampelan larva stomatopod dijalankan daripada kawasan hulu sungai hingga ke kawasan perairan laut (dari November 2002 hingga Oktober 2003) dengan menggunakan jaring bongo. Kajian ini telah berjaya mengenal pasti empat peringkat tengah dan dua peringkat akhir pertumbuhan larva *Cloridopsis scorpio* pertama kalinya. Larva *Miyakea nepa* yang disampel merupakan larva di peringkat akhir pertumbuhan. Kajian in menunjukkan bahawa taburan dan kelimpahan larva stomatopods adalah disebabkan oleh faktor alam sekitar termasuk makanan potensi mereka. Secara umumnya, larva *Cloridopsis scorpio* banyak terdapat di kawasan muara sungai bakau manakala larva *Miyakea nepa* dan larva untuk spesies yang tidak dapat dikenalpasti banyak terdapat di kawasan perairan laut Matang. *Cloridopsis scorpio* didapati mempunyai satu puncak pembiakan sahaja dalam setahun.

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CHAPTER 1

INTRODUCTION

1.1 An overview of stomatopods, their distribution and environment

The class Malacostraca contains over half of all the known species of crustaceans, as well as most of the larger forms, such as lobsters, crabs and shrimps (Ruppert & Barnes, 1994). Stomatopoda is the only order of hoplocaridans.

There are at least 450 species of stomatopods grouped into seven superfamilies and 17 families (Ahyong, 2001). The seven superfamilies and 17 families are show as follows:

1) Bathysquilloidea – Bathysquillidae and Indosquillidae
2) Erythrosquilloidea - Erythrosquillidae
3) Eurysquilloidea - Eurysquillidae
4) Gonodactyloidea - Takuidae, Gonodactylidae, Protosquillidae, Odontodactylidae, Pseudosquillidae, Alainosquillidae and Hemisquillidae
5) Lysiosquilloidea – Lysiosquillidae, Coronididae, Nannosquillidae and Tetrasquillidae
6) Parasquiloidea - Parasquillidae
7) Squilloidea – Squillidae

According to Moosa (2000), a total of 116 species of stomatopods belonging to 51 genera of 13 families and four superfamilies have been identified from the South China Sea. In addition, some new species have been described from Indonesia such as *Manningia misool* found in Irian Jaya, Indonesia (Ahyong, 1997). The diversity of stomatopods is the highest in the Indo-West Pacific region (Ahyong, 2001). Based on a 24-hour study conducted by Chong (2007b), two species of stomatopods, *Cloridopsis* *scorpio* and *Miyakea nepa* were recorded in Matang mangrove estuary, Perak, Malaysia. Both species belong to the family of Squillidae.

Squillidae is the most diverse stomatopod and comprises more than 40 genera (Ahyong, 2005). The superfamily of squilloidea can be distinguish from other superfamily as; cornea with 2 rows of hexagonal ommatidia in the midband. Propodi of maxillipeds 3-4 ovate, not ribbed ventrally. Body depressed, compact. Raptorial claw with ischiomeral articulation terminal; dactylus not inflated basally. Telson with distinct median carina; submedian teeth movable or fixed; with 4 or more intermediate denticles. Uropodal protopod with two primary spines; articulation of exopod segments terminal (Ahyong *et al.*, 2008).

Stomatopods are predatory crustaceans found in tropical or subtropical regions, with few species in cool temperate regions (Schram 1986; Reaka & Manning 1987; Ahyong 2001). They are not closely related to shrimps or the other decapod crustaceans, although they are commonly known as "mantis shrimps" due to their raptorial appendages resembling those of the preying mantis. They live in soft sediment burrows or corals which they excavate themselves (Caldwell, 1991). Their short carapace and flexible body enable them to turn around inside the burrow.

Mantis shrimps have elongated bodies that are dorsoventrally flattened with small carapace and a large, broad segmented abdomen. The most distinctive feature is their second pair of appendages developed for raptorial feeding. Mantis shrimps can be divided into two functional groups, the spearers who use their forelimbs with numerous spines to spear soft-bodied preys and smashers who use clublike appendages to crush hard-shelled animals (Caldwell, 1991). Patek *et al.* (2004) reported that *Odontodactylus* *scyllarus* (smasher) perhaps the fastest appendicular striker in the animal kingdom with the dactyl heel reaching peak speeds of 14-23 ms^{-1}, peak angular speeds of 670-990 $rads^{-1}$ and peak acceleration of 65-104 kms^{-2} within an average period of 2.7ms.

Generally, spearers are larger and less aggressive than the smashers (Caldwell, 1991).Most smashers live in natural cavities in coral or rock that are easier to defend than the burrows of the spearers. Cavities could provide protection from predators and is a safe place to brood eggs, protect larvae or when moulting (Caldwell, 1991). Stomatopods have been found to be good pollution bioindicators of coral reefs (Erdmann & Caldwell, 1997).

Stomatopods studies conducted by Abello & Martin (1993) and Lui (2005) indicate the spatial and seasonal changes in their population structure in relation to environment and habitat conditions. Reaka (1980) reported that stomatopod species with exclusively shallow or broad depth distribution have significantly wider geographic distribution and are significantly larger in body size than species that occur exclusively in deep habitats. In India, the macrobenthic community including stomatopods population in Zuari estuary is affected by changes in environmental parameters, which are seasonally influenced by the monsoons (Sivadas *et al.*, 2011). Bottom hypoxia was found affecting the early life history of *Oratosquilla oratoria* in Japan (Kodama *et al.* 2006). According to these authors, the distribution of newly settled juveniles of *Oratosquilla oratoria* was found to be affected by bottom hypoxia.

A study conducted in Klang Strait – Angsa Bank waters showed that macrobenthos including stomatopods varied according to environment and habitat conditions (Zgozi, 2000). Chong (2007b) indicates that the abundance of *Cloridopsis scorpio* was not affected by diel and tidal changes in Matang mangrove estuary.

1.2 Population dynamics of stomatopods

Population dynamics is defined as changes in the size and age composition of a population which are influenced by biological and environmental factors. Stomatopods species of temperate and subtropical countries show different growth patterns, reproduction patterns, recruitment patterns and mortality rates (Abello & Martin, 1993; Dell & Sumpton, 1999; Lui, 2005; Maynou *et al.*, 2005). These authors found that the lifespan of stomatopods ranged from six months to 2.5 years. The stomatopods in Hong Kong waters are found to have fast growth rates, early maturity and short lifespans (Lui, 2005). In India, the lifespan of *Miyakea nepa* is found to be 1.5 years (Sukumaran, 1987) while the lifespan of a Japanese stomatopod, *Oratosquilla oratoria*, is more than four years (Kodama *et al.*, 2005).

In general, growth and reproduction are the two main biological factors that ensure and maintain the survivorship of a population (Stiling, 1999). Therefore, studying the growth pattern and reproduction pattern of the stomatopod population could provide useful information for the purpose of fishery management.

1.3 Feeding ecology of stomatopods

Stomatopods prey on a broad range of marine organisms such as fishes, squids and benthic invertebrates including molluscs, shrimps, snails, clams and polychaetes (Hamano & Matsuura, 1986; Hamano *et al.*, 1996). Hamano and Matsuura (1986) found that *Oratosquilla oratoria* is one of the major predators of commercially important penaeid shrimps in Japan. Thus, it may have a major influence on the benthic community structure in Japan.

A few studies suggested that stomatopods play an important role in structuring the benthic community through the marine benthic food web (Dingle & Caldwell, 1978; Hamano & Matsuura 1986; Hamano *et al.* 1996). They prey on a broad range of benthic organisms (Dingle & Caldwell, 1975; Hamano & Matsuura 1986; Hamano *et al.*, 1996; Lui, 2005) and they also form part of the diet of fishes and crustaceans (Hamano & Matsuura, 1986; Then, 2008; Chew, 2012). Antony *et al.* (2010) indicated that the increase in stomatopod fishing mortality is responsible for the increase in biomass and yield of benthopelagic carnivore fishes in India. This is because the decreased of stomatopod population could have decreased the potential competitor for food as both stomatopod and benthopelagic carnivore fishes compete for prey.

In Matang, Chew (2012) reported that stomatopods were found in the diet of fishes such as *Cryptarius truncates*, *Thryssa kammalensis*, *Pomadasys kaakan* and *Upeneus sulphureus*. Based on stable isotope study, this author also found that stomatopod larvae were the predator of zooplankton in Matang food web.

Food is one of the important factors that could be used to answer how one population differs in its niche from another although both utilize similar resources. Studies associated with niche separation among species are closely tied in with analysis of their diets. Lui (2005) reported that the dietary patterns of the four stomatopods species showed various degrees of dietary separation, suggested that direct competition for food is rare which could be due to food partitioning or the food resources are abundance.

Resource partitioning is important in allowing coexistence of several species. Dingle *et al.* (1973) and Dingle & Caldwell (1975) found that inter-specific agonistic behaviour in stomatopods is important in resource partitioning. According to these authors, the more aggressive species is more abundant than the less aggressive species.

Feeding habits could also be different among sexes and sizes due to different feeding adaptations, sensory capabilities, strategies of prey capture or nutritional requirements for maturation purpose (Dingle & Caldwell, 1978; Hamano *et al.*, 1996). Hamano & Matsuura (1986) found that the different size groups of male and female mantis shrimp (*Oratosquilla oratoria*) consumed different quantities of prey items. In Matang, ontogenetic shift in the diet of stomatopods has not been studied before but this is evident in many species of fish (Then, 2008).

To date, research on the feeding of stomatopods ecology is limited and mainly focused on subtropical and temperate species (Hamano & Matsuura, 1986; Hamano *et al.*, 1996; Lui, 2005).

1.4 Reproduction, larval ecology and life cycle of stomatopods

Stomatopod mating behavior varies between different species. Most species of mantis shrimp live alone, but there are some species that live in pairs for life. Male and female mantis shrimps have paired testes and paired ovaries respectively. The males have a pair of penis located between the last thoracic legs while the females have a pair of oviducts that open on the middle of the sixth thoracic somite. Females do store sperm but they can produce only one fully fertile clutch without re-mating (Christy & Salmon, 1991). During brooding, the cement-gland material from the ventral cement glands holds the egg mass together and the mother will either stick the egg mass to the wall of their burrows or carry it with all her maxillipeds excluding the raptorial claws until hatched (Hamano & Matsuura, 1984; Wortham-Neal, 2002).

The reproductive behavior of stomatopod varied between species. Both sexes of *Gonodactylus bredini* search for mates (Christy & Salmon, 1991). Most commonly, males search for females and females usually allow only larger males to enter her cavity. They copulate repeatedly and the male defends his mate and the cavity until the female extrudes her eggs. The male leave after the female extrudes her eggs. In *Haptosquilla,* only males search for mates and copulation may last up to 30 minutes and the male then leave (Christy & Salmon, 1991). Females mate only with smaller males as the larger males often evict them from cavity. The mating system of *Oratosquilla oratoria* showed that males search for females and copulation is brief (Hamano, 1988). The male leave after copulation and females were found to mate with males of any size.

Various studies have been conducted on the reproductive biology of mantis shrimps such as description of the reproductive behaviour (Reaka and Manning, 1981), reproductive morphology (Deecaraman and Subramoniam, 1980; Wortham-Neal, 2002) and seasonal reproduction pattern (Lui, 2005).

Stomatopods produce planktonic larvae with the initial few stages staying benthic and the subsequent stages becoming pelagic (Hamano & Matsuura, 1987). Propelagic stages, as the initial larval stages of stomatopod larvae, mainly rely on yolk as their food and they start feeding on prey at the pelagic stages (Hamano & Matsuura, 1987). The later stage larvae or post larvae also spent more and more time at the bottom and behave like the adult.

The larval types of mantis shrimps are poorly known. There is no known naupliar stage. Squilloid larvae hatch as a pseudozoea and develop into an alima larva. The Gonodactyloidea larvae hatch as pseudozoea and develop into an erichthus while Lysiosquilloidea larvae hatch as antizoea and develop into the erichthus larva (Ahyong & Lowry, 2001). These four larval forms of development are defined by Giesbrecht (cited in Pyne, 1972) as:

a) Antizoea. Eyes sessile; antennule uniramous; first five thoracic somites provided with biramous appendages; abdomen unsegmented or only partially segmented; abdomen with single pair of appendages or none at all. Develop into a larva of erichthus type.

b) Pseudozoea. Eyes pedunculate; antennule biramous; thoracic somites with uniramous appendages on the first two somites only; abdomen divided into six segments, the first four or five of which have each a pair of biramous pleopods. Develop into either erichthus or alima.

c) Alima. Eye-stalk generally long; antennular somite with median spine; basis and exopod of antenna elongated; posterolateral spine of carapace with accessory spinules; youngest larva with four pairs of pleopods only; first to fifth pleopods without setae on border of proximal part of exopod; exopod of uropod longer than endopod; telson with four or more intermediate denticles.

d) Erichthus. Eye-stalk short; antennular somite without median spine; basis and exopod of antenna generally thick-set; accessory spinules absent on posterolateral carapace spine; youngest larva with five pairs of pleopods; setae present on proximal margin of first to fifth pleopods; telson with one intermediate denticle.

In general, the life cycle of stomatopods can be shown as follows:

Egg stage
↓
Propelagic larval stages (2 – 3 stages)
↓
Pelagic larval stages (7 – 9 stages)
↓
Sub-adult stage
↓
Sexually mature adult stage

To date, very little research has been done on the ecology of stomatopod larvae. Out of at least 450 species of stomatopod reported worldwide, only the larvae of 33 species of stomatopods have so far been positively identified (Alikunhi, 1952; Pyne, 1972, Hamano & Matsuura, 1987). Of these, eight species have been positively identified by hatching from the egg and 25 species by rearing the late pelagic larvae to adult stage.

Recently, Barber and Boyce (2006) applied molecular DNA analysis to explore the biodiversity of gonodactylid stomatopods in both the Coral Triangle (western Pacific Ocean) and the Red Sea by matching the unknown larvae to known adults. However, the authors concluded that its overall success was limited due to the taxonomic limitations of the newly discovered reference sequence database. Molecular analysis has also been used in Hong Kong to identify stomatopod species (Tang, 2009). However, the author mentioned that this technique only worked because of the limited diversity and all the nine species studied belonged to different genera. In addition, this technique is costly.

In order to obtain a complete series of larval developmental stages, the only reliable way is to rear the larvae from eggs of known parentage. However, rearing of larvae could be time consuming because of the long larval life history as some species can undergo a long planktonic period of up to nine months (Pyne, 1972). In addition, rearing of stomatopod larvae from eggs is very difficult due to various reasons such as the larval stages being very fragile and incomplete molting often resulted in death (Alikunhi, 1967). Furthermore, stomatopod species have different food habits and are cannibalistic. Hamano and Matsuura (1987) reported that *Oratosquilla oratoria* die beyond the fifth larval stage if only fed with *Artemia*. These authors also indicated that the water temperature is highly correlated to the duration of egg incubation.

1.5 Commercial fishery of stomatopods

Stomatopods constitute a commercially important fishery in several countries. *Oratosquilla oratoria* and *Squilla mantis* are commercially exploited in Japan (Kodama *et al.*, 2006) and the Mediterranean (Abello and Martin, 1993) respectively.

In Malaysia, mantis shrimps are getting more attraction as a favourite seafood among Malaysian since 1996 (Fariduddin, 1996). However, the fishery of mantis shrimps has never before been recorded in the fisheries statistics. Before the year 2008, catches of stomatopods were grouped in the ‘trash fishes’ category by the Malaysian Fishery Department (MFD), apparently of little commercial value. However, from 2008 onwards, their increasing catch and popularity as table food made it necessary for the MFD to classify mantis shrimps as a separate fish group. Figure 1.1 shows the latest landings of stomatopods (Malaysian Fishery Department, 2008 to 2010). Their market price increased from RM8.62 (USD2.82) per kg in 2008 to RM13.24 (USD4.32) per kg in 2010 (Malaysian Fishery Department). Thus, there is an urgent need to study their ecology as their fishery becomes more intensive and stomatopod stocks, not known to be as abundant as other shrimps, could have been overfished due to high market demand.

In Malaysia, fishermen used several types of fishing gears to catch stomatopods such as trawl nets, drift nets, barrier nets, push nets and bags nets. Table 1.1 shows the landings of stomatopod using different fishing gears in Peninsular Malaysia (2008 to 2010).

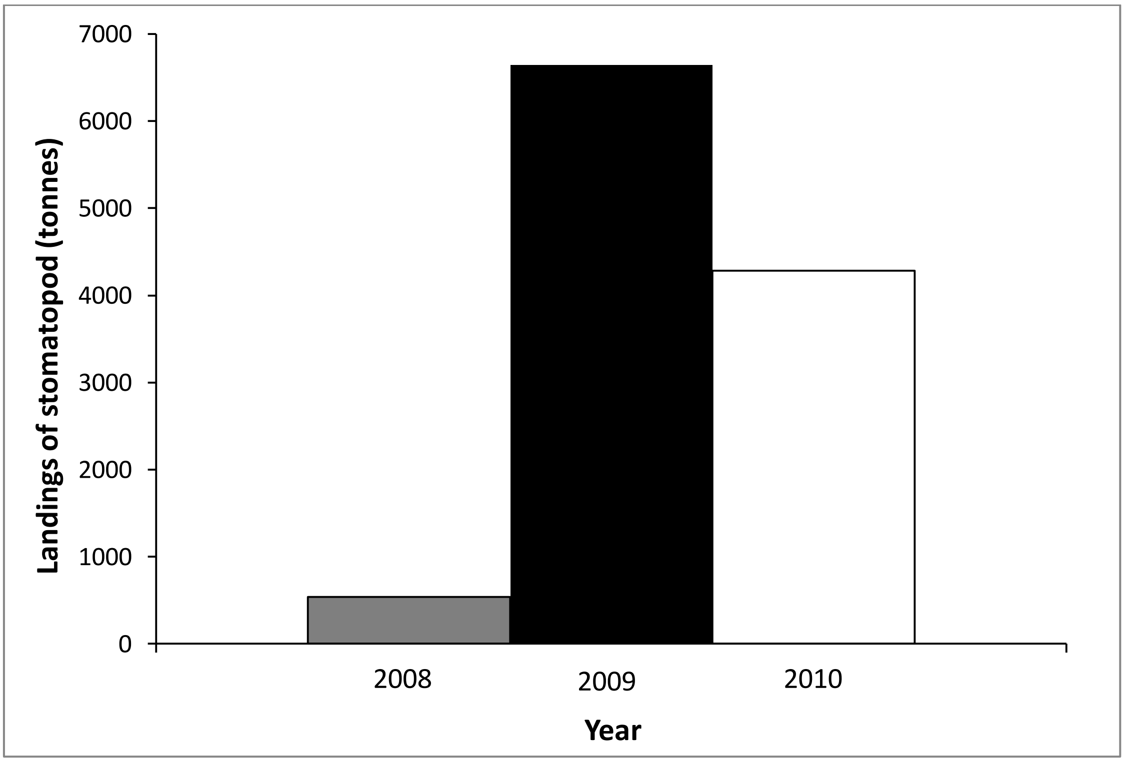


Figure 1.1. Available data from Malaysian Fisheries Department on the landings of stomatopod (tonnes) in Peninsular Malaysia starting from 2008 to 2010.

Table 1.1. Data from Malaysian Fisheries Department on the landings of stomatopod (tonnes) using different fishing gears in Peninsular Malaysia starting from 2008 to 2010.

Year	Trawl nets	Other seines	Drift/grill nets	Barrier nets	Push/scoop nets	Bag nets	Miscellaneous	Total
2008	471	0	68	0	0	0	0	539
2009	6146	217	239	1	7	0	34	6644
2010	3291	335	498	12	31	15	98	4280

1.6 Significance and objectives of study

In Malaysia, although stomatopods are increasingly being harvested as food, studies on their biology and population ecology have not received equal attention. Thus far, there are only two short studies, one conducted in Klang Strait - Angsa Bank waters (Addyhanis, 1995) and another one in Matang mangrove estuary (Chong, 2007b) which focused mainly on their distribution. Another study conducted in Klang Strait – Angsa Bank waters by Zgozi (2000) mainly focused on the distribution and abundance of demersal fishes and macrobenthos including stomatopods. Given the emergence of stomatopods as a valuable fishery commodity, there is a need to further understand its population biology and ecology so as to provide useful information for fisheries management.

Studies on the seasonal reproduction pattern and larval ecology of stomatopods are fairly scarce in tropical waters. There is only one study on the seasonal reproduction pattern of a stomatopod in India; this study indicates two spawning peaks for *Oratosquilla nepa* (Sukumaran, 1987). In Indonesia, larval studies on stomatopod larvae mainly focused on their developmental stages (Alikunhi, 1952; 1967; 1975). These studies are old but useful. Unfortunately, there are no recent work on tropical larval stomatopod distribution and abundance. Thus far, studies on the population dynamics and growth of stomatopods in tropical countries are limited to India (Reddy & Shanbhogue, 1994) and Indonesia (Ali, 2011). Nonetheless, reproduction, larval ecology and growth of stomatopods are key aspects to the survivorship of the population. For this reason, studying these three aspects is necessary.

The Matang Mangrove Forest Reserve serves as an exemplary and one of the best managed mangrove forests in the world (Gan, 1995), supporting the country's highest fisheries yield (Malaysia Annual Fisheries Statistics, 2010). Low *et al.* (1999) found that the production of penaeid prawns in Matang, an area of relatively intact mangroves, is much higher than a disturbed mangrove area in Dinding. As stomatopods are known to be major predators of penaeid prawns (Hamano and Matsuura, 1986) and other crustaceans (Lui, 2005), it is of interest to investigate the feeding habits of stomatopods in Matang and whether these stomatopods are trophically dependent on prawns and thus ecologically dependent on mangroves. .

Mangroves estuaries and mudflats are well known as a feeding and nursery areas for marine juvenile fish, prawns and other invertebrates (Chong *et al.*, 1990; Sasekumar *et al.*, 1992; Chong, 2007a). Prawns and many invertebrates have been shown to enter mangroves at the mysis or postlarval stage, while maturing adults exit mangroves to offshore spawning grounds (Chong, 1979). As stomatopod larvae are predators of zooplankton (Chew, 2012), it is hypothesized that the stomatopod larvae after spawning will move from offshore to inshore waters or estuaries to feed on the rich zooplankton resources. Previous studies have reported that most of the common species of fish found in the Matang mangrove estuaries depend to a large extent on zooplankton as food at the juvenile stage (Chew *et al.*, 2006; Ooi & Chong, 2011). Thus, this study intends to investigate both the dependence of stomatopod larvae on their planktonic food sources, as well as the dependence of stomatopod juveniles/adults in offshore grounds on emigrating prawns and fish as food. Hence, the present study would contribute further knowledge and understanding of the role of these coastal biotopes as sources of trophic energy. Previous study by Morgan (1980) have shown that the larvae of *Squilla empusa* moult more frequently and survive better at the higher temperature (25 ºC) and salinity (35 °/oo). Based on this study, the present study aimed to test this further in the field by investigating the influence of these and other environmental factors on the abundance and distribution of stomatopod larvae. Matang Mangrove Forest Reserve, with its spatial and temporal variation in environmental factors such as salinity, dissolved oxygen, pH and turbidity (Chew & Chong, 2011; Ooi & Chong, 2011) could serve as an ideal area to investigate the community structure and abundance of stomatopods in relation to the environmental conditions.

Research questions:

1) How do stomatopods distribute and adapt to their environment?

2) Given the increasing popularity of stomatopods as table food, are the stomatopod stocks overfished?

3) Are tropical stomatopods continous or annual spawners?

4) What is the contribution of coastal biotopes (mangrove and mudflat) to stomatopod feeding ecology?

The present study thus, aimed:

1) To determine the spatial and temporal distribution of stomatopod species in Matang.

2) To estimate the various parameters of stomatopod population dynamics.

3) To elucidate the reproduction biology and larval ecology of stomatopods.

4) To elucidate the feeding habits of stomatopods.

Two hypotheses were tested in this study as follows:

1) Matang stomatopod (juveniles/adults) species adapt to take advantage of the emigrating shrimp from mangrove nursery areas (Chapter 6).

2) The abundance and distribution of stomatopod larvae are influenced by the environmental factors and their potential zooplankton food (Chapter 5).

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

1) Environment, distribution and abundance of stomatopods in Matang (Chapter 3).

2) Population dynamics of stomatopods in Matang (Chapter 4).

3) Reproduction and Larval Ecology of stomatopods in Matang(Chapter 5).

4) Feeding ecology of stomatopods in Matang (Chapter 6).

CHAPTER 2

MATERIALS AND METHODS

2.1 Study site

The Matang Mangrove Forest Reserve (4° 50’N, 100° 35’E) which covers an area of about 40,711 hectares is located in Perak, west coast of Peninsular. Matang Mangrove Forest Reserve (MMFR) is built on deltaic sediments deposited from three major river basins, namely Sepetang river, Larut river and Terong river (Figure 2.1).

Generally, more than 80% of the production forest in Matang comprises at least 60% *Rhizophora* while the rest are *Bruguiera* and *Ceriops tagal* (Gan, 1995). The major fishing gears used by the fishermen in capture fisheries include trawls, push nets, gill nets and long-lines. Besides capture fisheries, aquaculture also becomes an important economic activity in the Matang area with two forms of brackish water aquaculture activity. These are net cage fin-fish and cockle aquaculture. The numerous rivers and waterways have shown to be important feeding and nursery area for marine juvenile fish, prawns and other invertebrates (Chong *et al.*, 1990; Sasekumar *et al.*, 1992; Chong, 2007). The coastal area (< 30 nautical miles from shore) is a major contributor to the total annual marine production (Malaysian Fishery Department, 2010).

2.2 Field collection

2.2.1 Sampling of adult stomatopods

Three depth strata in coastal waters were chosen for sampling stomatopods based on the stratified sampling method. Three sampling strata, namely stratum 1, stratum 2 and stratum 3 were chosen following the depth contours as shown in Figure

2.1. Table 2.1 shows the summary information of sampling sites, mean depths, mean swept area and sampling period for adult stomatopods.

Two trawls were carried out randomly along each stratum. Prawn trawl net with a stretched cod-end mesh size of 2 cm and head rope length of 48 m was used as the sampling gear during neap tide, from September 2004 to February 2006. The trawling duration for each trawl haul varied between 20 to 30 minutes each. The trawled distance was computed by calculating the ground speed of the towed net using the chipboard method. A chipboard was thrown at the bow and the time taken for the stern to reach the chipboard (or for a known distance) was taken using a stop-watch. This step was repeated three times to get the average estimated ground speed. After the catch was hauled on deck, all the stomatopods were sampled without subsampling and kept on ice in an icebox and taken back to the laboratory where they were kept frozen in a freezer until further analysis. Only one haul was conducted at stratum 3 in July 2005 due to rough sea condition.

At each station, physical parameters (salinity, dissolved oxygen, pH, turbidity and depth) were measured with a Hydrolab 4e sonde (Hach Hydromet, Loveland, Colorado, USA). All water parameters were taken at just above the sea bottom.

The Malaysian Tide Tables (2004, 2005, 2006) published by the Hydrographic Branch of Royal Malaysia Navy was used to choose the neap tide sampling dates for each month, from September 2004 to February 2006.

2.2.2 Sampling of stomatopod larvae

The present study used the plankton samples collected during Japan International Research Center for Agricultural Sciences (JIRCAS) project for studying stomatopod larvae. Five sampling stations were established along Sangga Besar (upper estuary) and Sangga Kecil (mid estuary and lower estuary) rivers within the MMFR, another two stations in adjacent coastal waters (nearshore and offshore stations) (Figure 2.1). Table 2.2 shows the detail information of sampling sites, mean water depth and sampling period for stomatopod larvae.

Zooplankton was sampled monthly by horizontally-towed bongo nets from November 2002 to October 2003 during neap tides. The 45 cm diameter bongo net was equipped with 363 µm mesh size net fitted with calibrated flow-meter. Horizontal surface towing was carried out at approximately 0.5 m depth from the water surface for 10 min durations. Duplicate samples were taken at each station during day time. The volume of water filtered for each tow ranged from 25.0 to 194.3 m3 (appendix I). The collected zooplankton samples were immediately preserved in 10% buffered formaldehyde in 500-ml plastic bottles. Samplings were not conducted at offshore station in July 2003 due to rough sea condition.

At each station, physical parameters (salinity, dissolved oxygen, pH and turbidity) were measured for surface layer of the water column with a Hydrolab 4e sonde (Hach Hydromet, Loveland, Colorado, USA).

The Malaysian Tide Tables (2002, 2003) which was published by the Hydrographic Branch of Royal Malaysia Navy was used to choose the neap tide sampling dates for each month, from November 2002 to October 2003.

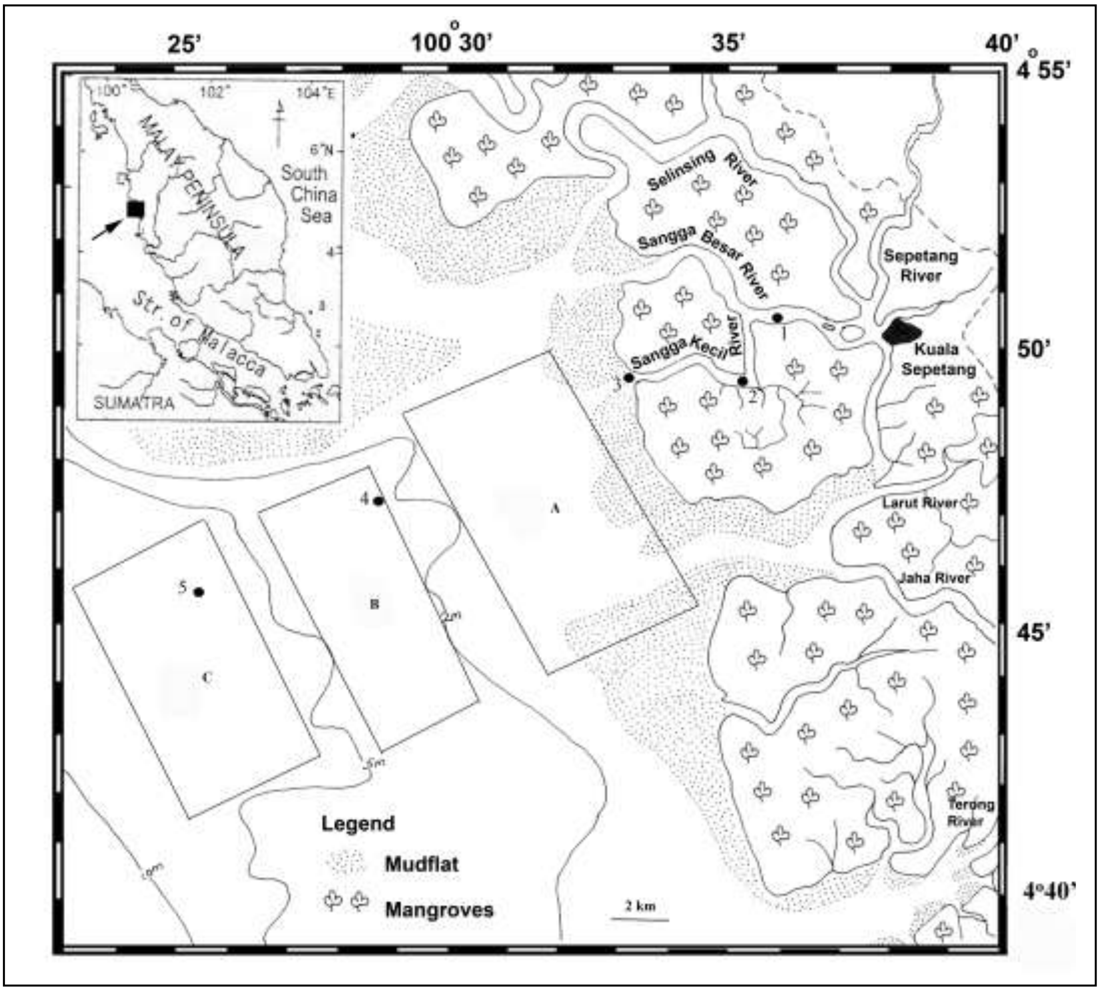


Figure 2.1. Sampling area in mangrove estuaries and adjacent coastal waters in Matang, Perak. ▭ Indicates sampling location for adult stomatopods; A = stratum 1, B = stratum 2, C = stratum 3. ● Indicate sampling sites for stomatopod larvae; 1 = upper estuary, 2 = mid estuary, 3 = lower estuary, 4 = near shore waters, 5 = offshore waters.

Table 2.1. Summary information of sampling sites, mean water depth, mean swept area and sampling period for adult stomatopods. n = number of trawl hauls.

Strata	Distance from Sangga Kecil river mouth (km)	Mean water depth (m)	Mean swept area (ha)	Sampling period	n
1	< 9	2.12	3.47 ± 0.42	September 2004 to February 2006	36
2	9 - 15	4.30	3.54 ± 0.30	September 2004 to February 2006	36
3	> 15 - 20	6.65	3.46 ± 0.42	September 2004 to February 2006	35

Table 2.2. Summary information of sampling sites, mean water depth and sampling period for stomatopod larvae. Negative distance indicates in upstream direction, positive distance indicates in the offshore direction.

Station	Distance from Sangga Kecil river mouth (km)	Mean water depth (m)	Sampling period	n
Upper estuary	-7	3.46	November 2002 to October 2003	24
Mid estuary	-3.5	7.25	November 2002 to October 2003	24
Lower estuary	0	5.75	November 2002 to October 2003	24
Near shore waters	9	3.30	November 2002 to October 2003	24
Offshore waters	16	7.04	November 2002 to October 2003	22

2.3 Laboratory analyses

2.3.1 Identification and quantification of adults stomatopod

Stomatopods were rinsed with freshwater and identified using the available references such as Naiyanetr (1980) and Carpenter & Niem (1998). The following measurements were made from each specimen:

1) Wet weight (g) - using a standard electronic weighing balance to the nearest 0.01 g.

2) Total length (mm) (Plate 2.1) – along the midline from the apex of the rostral plate to the posterior apices of the submedian teeth of the telson, using a digimatic calliper to the nearest 0.01 mm.

3) Carapace length (mm) (Plate2.1) – along the midline from the anterior margin of the carapace to the posterior margin of the carapace, without the rostral plate, using a digimatic calliper to the nearest 0.01 mm.

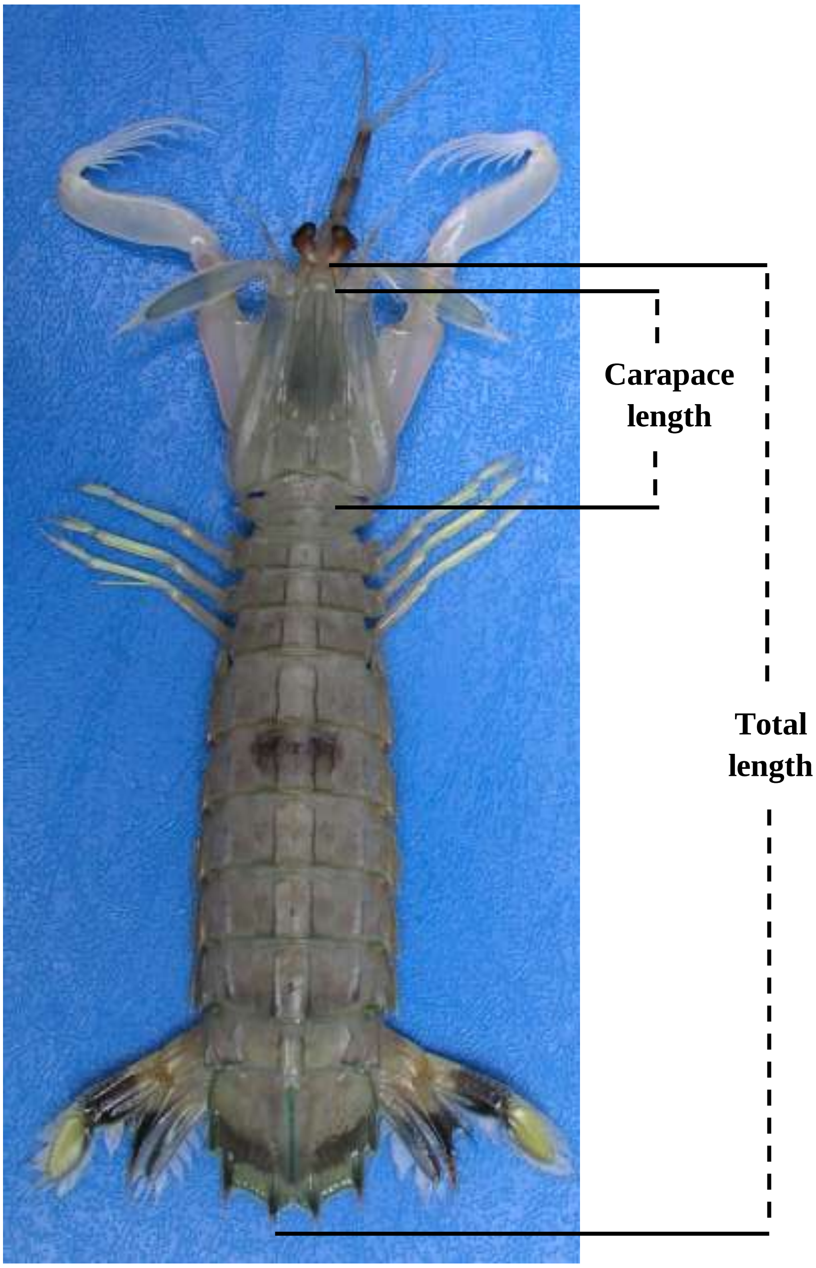


Plate 2.1. Measurements of carapace length and total length of *M. nepa*. Picture of *M. nepa* in dorsal view.

2.3.2 Reproduction

Ovarian development of female *Miyakea nepa*, *Oratosquillina perpensa*, and *Cloridopsis scorpio* were determined and described based on visual assessment of fresh samples of the ovaries. Individuals were staged according to the development of the ovary based on colour and the relative width of ovaries, i.e the width of the ovaries in the cavity of the thoracic or abdominal somite.

The male mantis shrimp was however very difficult to stage based on external morphology of the testes which appeared thin and showed no obvious signs of enlargement or colour changes as they developed. Thus, the length of the penis was used as a general guide to the maturity of the male. The right penis length (Plate 2.2) of all male *Miyakea nepa* and *Oratosquillina perpensa* was measured. Penises of *Harpiosquilla raphidea* and *Cloridopsis scorpio* were not measured due to the small numbers of individuals collected.

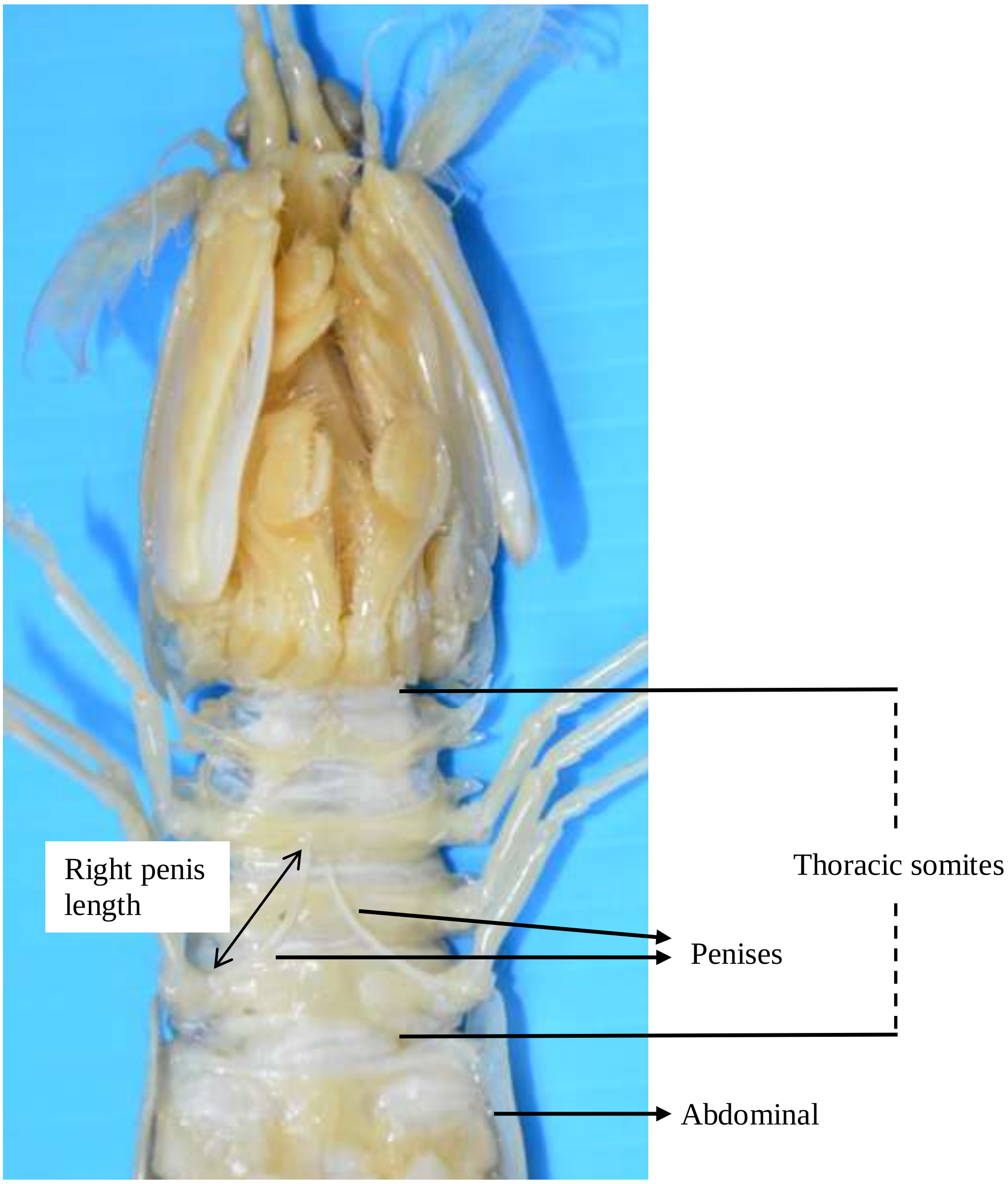


Plate 2.2. Measurement of right penis length of *M. nepa*. Picture of *M. nepa* in ventral view.

Based on the three maturity stages (immature, maturing and mature) of male *Miyakea nepa* which were determined from Bhattacharya method, the testes of male specimens for each maturity stage based on size were prepared for histological study. The purpose of the histological work was to verify the classified three maturity stages. Samples of testis (from between the fourth and fifth abdominal segments) were dissected out and fixed overnight in 10% formosaline before washing in 70% alcohol. The samples were then dehydrated in 95% alcohol and then absolute alcohol. Clearing agents used were terpineol or toluene. Embedding of tissues was done using paraffin wax. The tissues were then sectioned to a thickness of 6-8 µm, deparaffinated by xylene, washed through a series of declining concentrations of ethanol, tap water, before they were stained with haematoxylin-eosin. The sections were finally mounted in Canada Balsam. Prepared sections were examined under a light microscope.

2.3.3 Stomach contents analysis

Ingested food materials were analyzed for their composition and occurrence. The stomach portions of the samples were removed and arbitrarily classified according to their fullness, as follows: 1 - fully with food; 3/4 – full, but not gorged; 1/2 – half full; 1/4 – containing a small but significant amount of food; 0 – empty, but possibly containing bits of debris. The entire stomach content was examined without subsampling. The entire stomach content was washed onto a rafter cell (50 x 10 x 1 mm), or onto a microscopic slide if the content was small. The eye-estimation method (Chong & Sasekumar, 1981) applied here made use of an eyepiece grid (10 x 10 squares) to estimate the area occupied by a particular food item. Area estimates were approximately proportional to volume since height differences among fine food items were small. Hence, the contribution of each food item was expressed in percentage volume. Frequency of occurrence (%) was expressed in term of the number of stomachs containing a particular food item divided by the total number of stomachs examined with food.

2.3.4 Sorting and identification of stomatopod larvae

Zooplankton samples were washed under running tap water and immediately kept in 100 ml screw capped vials containing 80% alcohol. All stomatopods larvae were sorted out using a dissecting microscope (magnification x 10 – 40). The stomatopods larvae were immediately resuspended in 80% alcohol kept in 10 ml screw capped vials. Stomatopod larval abundance of each species and total of all species were estimated as number of individuals per 100 m^{-3} based on the volume of water filtered which was estimated by a flowmeter.

Stomatopods larvae were identified to species level according to previous studies (Alikunhi, 1952, 1975; Tang 2009).

2.3.5 Descriptions and illustrations of larval development stages

Due to the lack of identification keys of stomatopod larvae and the missing of some developmental stages of stomatopods larvae in the samples collected, only the pelagic larvae of *Cloridopsis scorpio* were described with the aid from Alikunhi (1952, 1975) study. Based on the external morphology of the stomatopod larvae, they were initially sorted into three different developmental stages, namely early, mid and late stage according to Tang (2009) with modification as follows:

1) Early stage – The absence of fifth pleopods and uropods. The telson is rectangular in shape instead of being oval or fan shaped and lacks a lateral denticle.

2) Mid stage – Fifth pleopods just developed or present as buds. The uropods are newly developed and become visible on the telson.

3) Late stage – Full development of fifth pleopods and uropods, with the presence of exopods, a forked ventral process and endopods. The telson with a lateral denticle.

Illustrations of each larval morphotype were produced from a camera-lucida attached to a compound microscope (Olympus BX50F-DA). Full description and illustrations of the larval developmental stages of *Cloridopsis scorpio* were made without their second to fourth pleopods, as there are only increment in length and setation. The illustration and description of the larval developmental stages for the other species were focused on the carapace spinulation (number of ventrolateral spinules on anterior + number of ventrolateral spinules on posterior), number of dactylus teeth other than the terminal tooth and telson spinulation (number of lateral, intermediate and submedian denticles). Figure 2.2 shows the terminologies used to describe the stomatopod larvae (summarized from Morgan & Provenzano Jr., 1979; Hamano & Matsuura, 1987).

2.4 Data and statistical analyses

2.4.1 Rainfall

Daily rainfall data from 2004 to 2006 were obtained from Malaysian Meteorological Department and monthly averages were calculated. Sampling months were categorized according to two monsoons seasons, namely Northeast monsoon (November to March), Southwest monsoon (May to September) and two inter-monsoon periods (April and October) in between them.

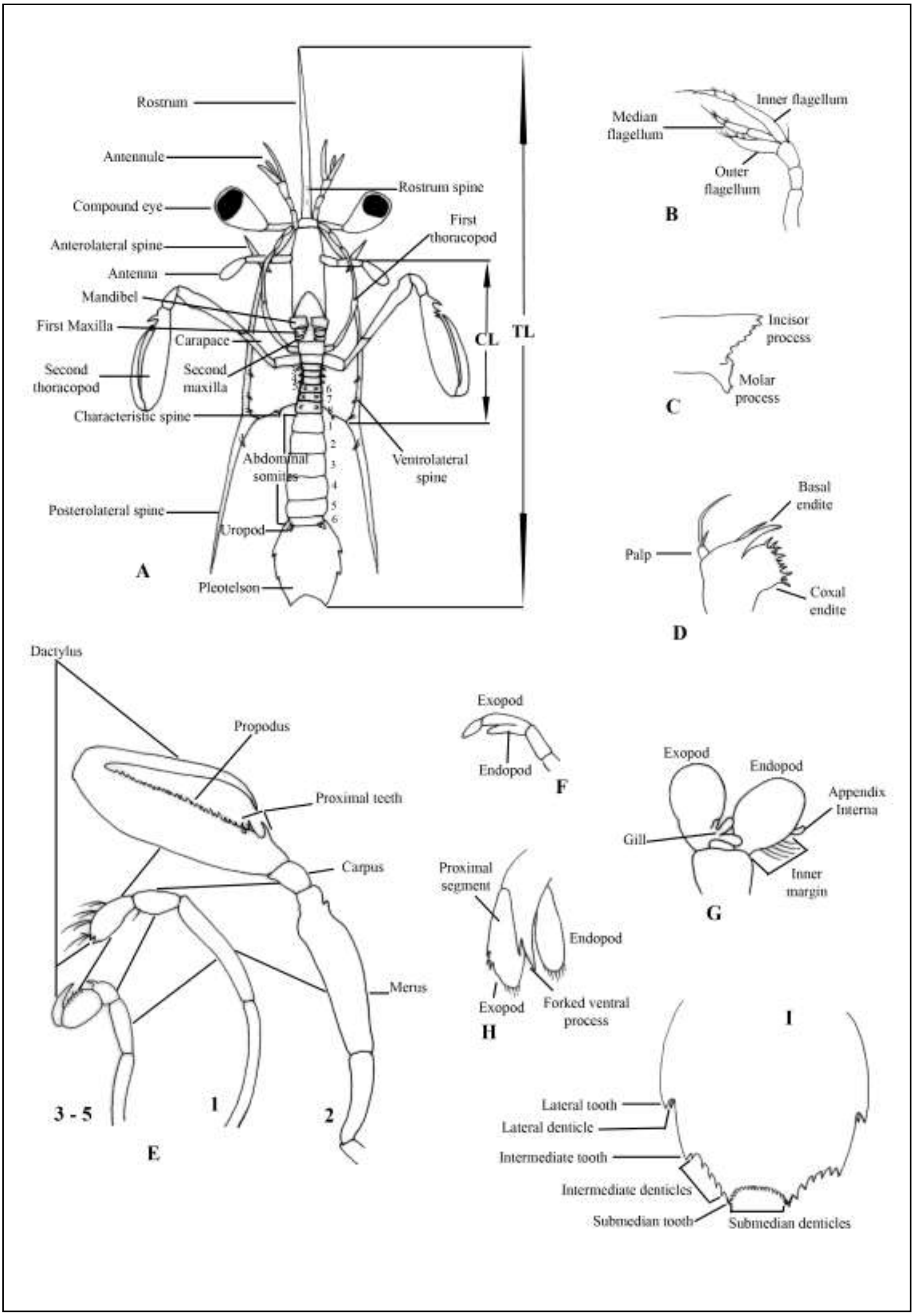


Figure 2.2. Terminologies and size measurements used in descriptions of larvae. A – animal in ventral view; B – antennule; C – mandible; D – first maxilla; E – first to fifth thoracopods (maxillipeds); F – sixth to eight thoracopods (pereopods); G – pleopod; H – uropod; I – pleotelson.

2.4.2 Stomatopods distribution and abundance

The standard procedure of the "swept area method" for estimating demersal fish abundance was adopted (Sparre et al, 1989). Species abundance and biomass were measured in term of number of individuals per hectare (no/ha) and wet weight per hectare (kg/ha), respectively. The swept area (a) was estimated from the following formula;

$$a = D*h*x_2$$

where

D = Distance of tow path (= $v * t$) (m)

v = The velocity of the trawl over the ground when trawling (m/min)

h = The length of the head rope (m)

t = The time spent trawling (min)

x_2 = The fraction of the head rope which is equal to the width of the path swept by the trawl (= 0.5, see Sparre et al, 1989)

Abundance or Density (Di) of each species (i^{th} species) (no./ha) was estimated by the swept area method as

$$Di = \frac{\text{Total number of individuals of } i^{th} \text{ species}}{\text{Area swept (a)} * x_1} \text{ X } 10000$$

Where x_1 = Portion of individuals or fish actually retained by net (assumed to be 0.5, see Sparre *et* al, 1989)

Biomass of the i^{th} species (Bi) (kg/ha) was estimated by the swept area as:

$$B_i = \frac{\underline{\text{Total wet weight of } i^{th} \text{ species (kg)}}}{\text{Area swept (a)} * x_1} \text{ X } 10000$$

2.4.3 Length-frequency analyses

The carapace length (CL) data of *Miyakea nepa* and *Oratosquillina perpensa* were used in these analyses. The data of *Harpiosquilla raphidea* and *Cloridopsis scorpio* were not used due to the small quantity of their catches.

The von Bertalanffy growth function (VBGF) (Von Bertalanffy 1934, cited in Sparre *et al.*, 1989) was used to describe the annual growth rate and maximum length of the stomatopod at oldest age. This equation was expressed as below:

$$L_t = L\infty \, [1 - e^{-K(t-t_0)}]$$

Where, L_t is the predicted length at age t, $L\infty$ is the maximum length or asymptotic length, K is the growth coefficient and t_0 is the theoretical age at zero length. $L\infty$ and K were generated from Electronic Length Frequency Analysis (ELEFAN I). The t_0 value was taken as zero, as commonly practised when the accurate value has not been defined (e.g. Lui, 2005). The 'winter point' value (WP) and the amplitude of growth rate oscillation between seasons (C) were considered as the seasonal effect on growth rate. A zero value was entered for both WP and C because Malaysia does not has winter and the monthly temperature fluctuations were small.

Munro's growth performance index (φ′) (Pauly & Munro, 1984) was used to calculate their growth performance:

$$\varphi' = \log_{10} K + 2 \log_{10} L\infty$$

This index was used to evaluate the growth potential of different species or different sites.

The recruitment pattern was obtained by ELEFAN II which is able to reconstruct the recruitment pulses from a time series of length-frequency data to determine the number of pulses per year and the relative strength of each pulse.

The maximum longevity (lifespan) was calculated from Taylor’s formula (1958):

$$t_{max} = 3 / K$$

Total mortality (Z) was estimated from length-converted catch curves of Pauly (1983):

$$\ln(N_i/dt_i) = a + bt_i$$

where, N_i is the number of fish in length class i, dt_i is the time needed for the fish to grow through length class i, t_i is the age corresponding to the midlength of class i, a is the Y-intercept and b is the slope of the regression of $\ln(N_i/dt_i)$ on t_i. The absolute value of ‘b’ shows instantaneous total mortality rate (Z).

Natural mortality (M) was estimated using Pauly’s empirical formula (cited in Sparre *et al.*, 1989):

$$\log_{10} M = -0.0066 - 0.279 \log_{10}(L\infty) + 0.6543 \log_{10}(K) + 0.4634 \log_{10} (T)$$

where, T is the mean annual environmental temperature in °C, which was taken as 29.7 (mean monthly temperature during the study period) for the present study.

The fishing mortality (F) was calculated by deducting the natural mortality from total mortality. With these, the exploitation rate (E) was calculated as

$$E = F/Z$$

All length-frequency data were analysed using FISAT II software version 1.2.2

2.4.4 Reproduction

Preliminary size frequency analysis of the penis lengths showed that they belonged to several cohorts of different age groups. As a result, the Bhattacharya method for polymodal analysis in ELEFAN (using FISAT II software version 1.2.2) was used to separate out the different male cohorts based on their penis lengths. The estimated mean penis length for each cohort was then generated. These information of penis length for each cohort, were then used to stage the maturity of each male, arbitrarily, as immature, maturing and mature males.

The reproductive period and spawning peaks of *Miyakea nepa* and *Oratosquillina perpensa* were estimated based on the percentage of mature females (stage IV) collected during the study. Since the number of sampled mature females (stage IV) of *Hapiosquilla raphidea* and *Cloridopsis scorpio* were too little during the sampling periods, their reproductive period was not estimated.

2.4.5 Statistical analysis

A one-way ANOVA was used to compare the mean stomatopod density and biomass between the two monsoon seasons. All stomatopods density and biomass data were either fourth-rooted or $\log_{10}(x+1)$ transformed to homogenize the variance as required before using parametric tests (Zar, 1998). Two-way ANOVA was applied to test whether the factors strata and the two monsoon seasons had significant effects on stomatopod population density and biomass. If the test was significant, Tukey HSD test was further applied for multiple comparisons of means.

Non-parametric Kruskal-Wallis test and Mann-Whitney U test were used to test for differences in mean rainfall and the mean of various water parameters among strata and the two monsoon seasons, if the data did not fulfill parametric considerations. The STATISTICA software package version 8 was used for statistical analyses.

For the data obtained from stomach content analysis, principle component analysis (PCA) was used to examine the preferential prey items among the stomatopod species by using the CANOCO 4.5 software. PCA is a linear transformation of data to a new coordinate system to reduce the dimensionality of the data so as to summarize the most importance data and detect structure underlying the relationships between variables. The percentage volumetric compositions of the prey items were aggregated according to the sex and size classes of the stomatopods. Then, the data were arcsine-transformed before they were analyzed using PCA.

Canonical Correspondence Analysis (CCA) was performed to determine the relationships among the abundance of stomatopod larvae, environmental parameters and their potential food items (zooplankton in three size fractions). This was done using the CANOCO for Windows Version 4.5 software (ter Braak & Smilauer, 2002). CCA or non-linear eigenvector ordination technique enables the representation of multidimensional aggregated data in two or three dimensions, and thus the simultaneous analysis and comparison of two data matrices, one containing the species abundance data and the second one containing the environmental variables (Legendre & Legendre, 1998).

Five species of stomatopod larvae (*Cloridopsis scorpio*, *Miyakea nepa,* early sp1, early sp2 and late sp3) were related to five environmental parameters (salinity, dissolved oxygen, temperature, turbidity and pH) and zooplankton density of three size-fractions, ‘>500µm’, ‘>250µm’ and ‘>125µm’. The three size fractions of zooplankton were potentially the food items of stomatopod larvae.

The environmental parameters, density data of stomatopod larvae and zooplankton were obtained from JIRCAS project during the sampling period November 2002 to October 2003.

CHAPTER 3

ENVIRONMENT, DISTRIBUTION AND ABUNDANCE OF STOMATOPODS IN MATANG

3.1 Results

3.1.1 Rainfall

Figure 3.1 gives the monthly total rainfall and number of rainy days from September 2004 to February 2006 at Taiping. There are generally two seasonal monsoons occuring in Matang; the Southwest monsoon (SW) which is comparatively drier prevails from May to September, and the Northeast monsoon (NE), which brings wetter weather condition prevails from November to March. The transition period between these two monsoons, called the inter-monsoon (IN), occurs in April and October.

Monthly total rainfall recorded over the study period ranged from 87.0 to 627.2 mm (appendix II), with the lowest rainfall recorded in July 2005 and the highest rainfall recorded in November 2004 (Figure 3.1). Monthly number of rainy days ranged from 11 (June 2005) to 27 days (November 2004; appendix II). No significant differences in total rainfall between the two monsoon periods during the study (Table 3.1; appendix III). The inter monsoon period (mean total rainfall = 395.8 mm) was relatively wetter that both monsoon seasons.

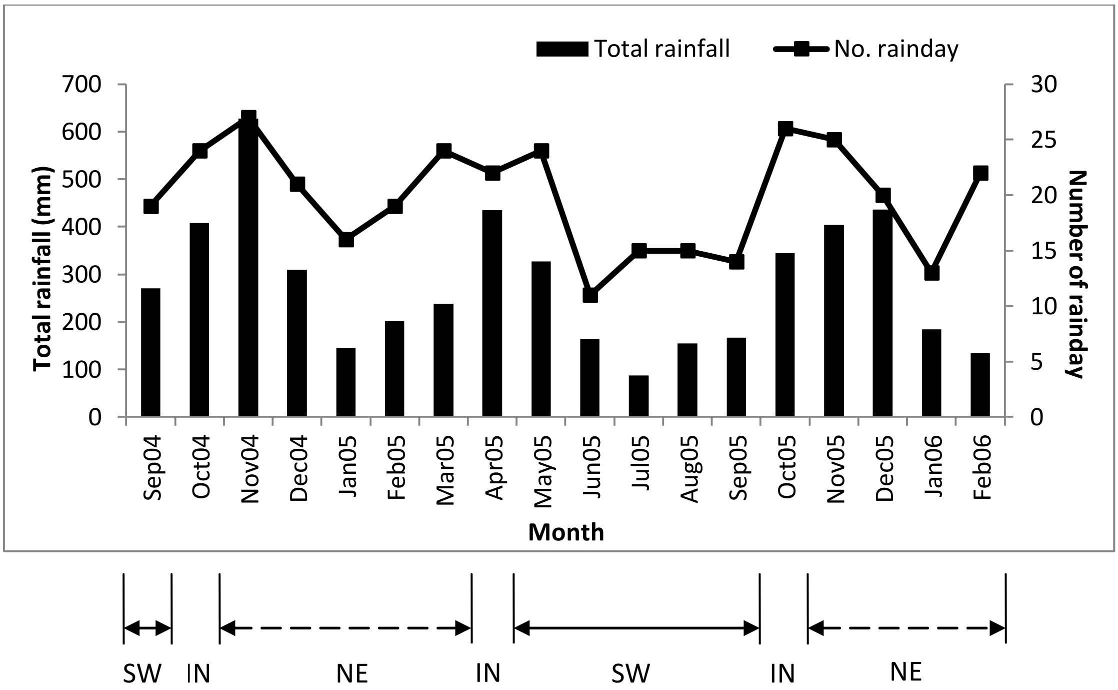


Figure 3.1. Monthly total rainfall and number of rainy days recorded from September 2004 to February 2006 at Taiping (Data obtained from Malaysian Meteorological Department). SW- southwest monsoon, IN- inter-monsoon, NE- northeast monsoon.

Table 3.1. Summary results of Mann-Whitney U test on monthly total rainfall between monsoon periods. No significance at $p > 0.05$.

	Northeast Monsoon (NE)	Southwest Monsoon (SW)	p-level
mean	298.0	195.2	< 0.05
sd	163.75	87.53	
range	135.2-627.2	87.0-327.4	
Sample size (n)	9	6	

3.1.2 Hydrographic conditions

a) Bottom Salinity

The mean bottom salinity ranged from 23.4 to 36.1 ppt (Table 3.2a). Mean salinity increased from stratum 1 to stratum 3, with significant differences ($p < 0.01$) between stratum 1 and stratum 2, and between stratum 1 and stratum 3 (Table 3.2a; appendix IVa). The latter two strata presented nearly similar salinity values ($p > 0.05$), with however slightly lower value at stratum 2. Figure 3.2a showed that the lowest mean salinity was recorded in November 2004 (stratum 1) while the highest mean salinity was recorded in July 2005 (stratum 3). These coincided with the months of highest total rainfall (November 2004) and lowest total rainfall (July 2005), respectively (Figure 3.1). There were differences ($p < 0.01$) in salinity between SW and NE monsoons (Table 3.2b; appendix Va). Salinity was lower during NE while SW recorded higher salinity level.

b) Bottom Dissolved Oxygen

The bottom dissolved oxygen values at all strata ranged from 4.3 to 6.3 mg/L (Table 3.2a). In general, stratum 1 recorded the lowest mean dissolved oxygen values at all strata and in all months while stratum 2 and stratum 3 showed nearly similar mean values in all the months (Table 3.2a; Figure 3.2b). Kruskal-Wallis test revealed significant differences ($p < 0.01$) in dissolved oxygen between stratum 1 and stratum 2, and between stratum 1 and stratum 3 (Table 3.2a; appendix IVb). No significant difference ($p > 0.05$) of dissolved oxygen was found between stratum 2 and stratum 3. There was no obvious temporal pattern observed during the sampling (Figure 3.2b). There were significant differences ($p < 0.05$) between dissolved oxygen recorded in the monsoon periods (Table 3.2b; appendix Vb).

c) Bottom Turbidity

Stratum 1 generally recorded a higher ($p < 0.01$) turbidity as compared to the other two strata over the sampling period (Table 3.2a; appendix IVc). Mean turbidity tended to fluctuate greatly over the sampling period with unclear temporal pattern (Figure 3.2c). There was no significant difference ($p > 0.05$) between the monsoon periods (Table 3.2b; appendix Vc).

d) Bottom Temperature

Mean temperature at all three strata similarly ranged from 30.2 °C to 30.5 °C ($p > 0.05$; Table 3.2a; appendix IVd). Mean monthly temperatures did not show any clear temporal pattern and were rather consistent (Figure 3.2d). Water temperatures among the three strata were not significantly different ($p > 0.05$) among monsoon periods (Table 3.2b; appendix Vd).

e) Bottom pH

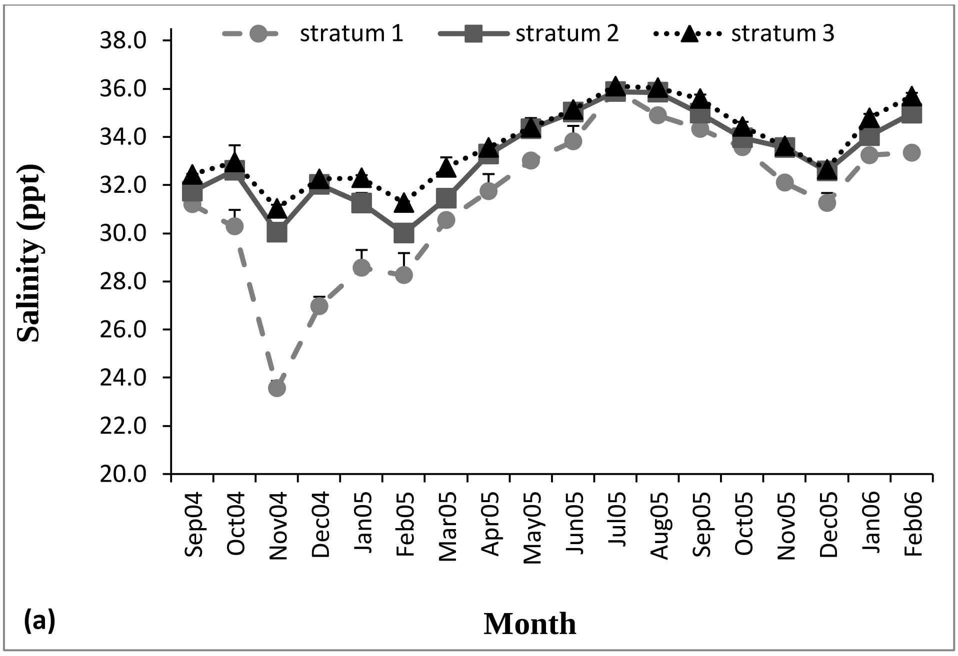
The mean bottom pH ranged from 7.5 to 8.6 (Table3.2a). Kruskal-Wallis test revealed significant differences ($p < 0.01$) in pH between stratum 1 and stratum 2, and between stratum 1 and stratum 3 (Table 3.2a; appendix IVe). Mean monthly pH did not show any clear temporal pattern and were rather consistent (Figure 3.2e). There were significant differences ($p < 0.01$) in dissolved oxygen between the monsoon periods (Table 3.2b; appendix Ve).

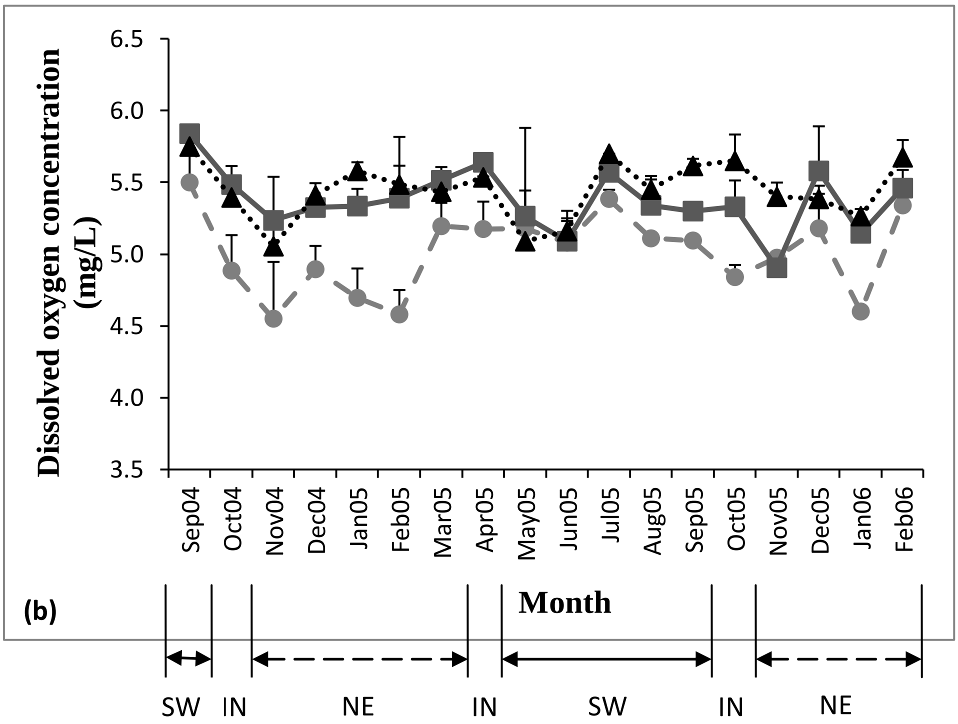
Table 3.2a Mean bottom water parameter readings recorded at three different depth strata over the 18 months of survey. Test of significance by Kruskal-Wallis test. Similar superscripted alphabet indicates homogenous groups. Similar superscripted alphabet indicates homogenous groups.

Water Parameter		Stratum 1	Stratum 2	Stratum 3	p-level
Salinity (ppt)	mean	31.4^a	33.1^b	33.7^b	< 0.01
	sd	3.07	1.82	1.57	
	range	23.4-36.0	30.0-35.9	30.9-36.1	
	n	36	36	35	
Dissolved Oxygen (mg/L)	mean	5.0^a	5.3^b	5.4^b	< 0.01
	sd	0.35	0.33	0.34	
	range	4.3-5.7	4.8-5.8	4.8-6.3	
	n	36	36	35	
Turbidity (NTU)	mean	69.1^a	49.3^b	38.1^b	< 0.01
	sd	20.44	24.57	16.63	
	range	26.4-110.0	11.1-98.2	10.8-88.0	
	n	36	36	35	
Temperature (°C)	mean	30.2^a	30.5^a	30.2^a	> 0.05
	sd	0.59	0.51	0.54	
	range	29.0-31.6	29.6-31.5	29.4-31.6	
	n	36	36	35	
pH	mean	8.0^a	8.1^b	8.1^b	< 0.01
	sd	0.16	0.12	0.10	
	range	7.5-8.3	7.9-8.6	8.0-8.3	
	n	36	36	35	

Table 3.2b Mean water parameter readings recorded at two different monsoon periods over the 18 months of survey. Test of significance by Mann-Whitney U test.

Water parameter		Northeast Monsoon (NE)	Southwest Monsoon (SW)	p-level
Salinity	mean	31.6	34.4	< 0.01
	sd	2.58	1.49	
	range	23.4-35.8	30.8-36.1	
	n	54	35	
Dissolved Oxygen (mg/L)	mean	5.2	5.4	< 0.05
	sd	0.37	0.28	
	range	4.3-6.3	4.8-5.8	
	n	54	35	
Turbidity (NTU)	mean	47.9	56.6	> 0.05
	sd	21.42	24.38	
	range	11.1-88.3	19.8-110.0	
	n	54	35	
Temperature (°C)	mean	30.3	30.2	> 0.05
	sd	0.62	0.32	
	range	29.0-31.6	29.7-31.1	
	n	54	35	
pH	mean	8.0	8.1	< 0.01
	sd	0.13	0.12	
	range	7.5-8.3	7.8-8.3	
	n	54	35	


stratum 1
stratum 2
stratum 3
Salinity (ppt)
38.0
36.0
34.0
32.0
30.0
28.0
26.0
24.0
22.0
20.0
Sep04
Oct04
Nov04
Dec04
Jan05
Feb05
Mar05
Apr05
May05
Jun05
Jul05
Aug05
Sep05
Oct05
Nov05
Dec05
Jan06
Feb06
(a)
Month


Dissolved oxygen concentration (mg/L)
6.5
6.0
5.5
5.0
4.5
4.0
3.5
Sep04
Oct04
Nov04
Dec04
Jan05
Feb05
Mar05
Apr05
May05
Jun05
Jul05
Aug05
Sep05
Oct05
Nov05
Dec05
Jan06
Feb06
(b)
Month
SW
IN
NE
IN
SW
IN
NE

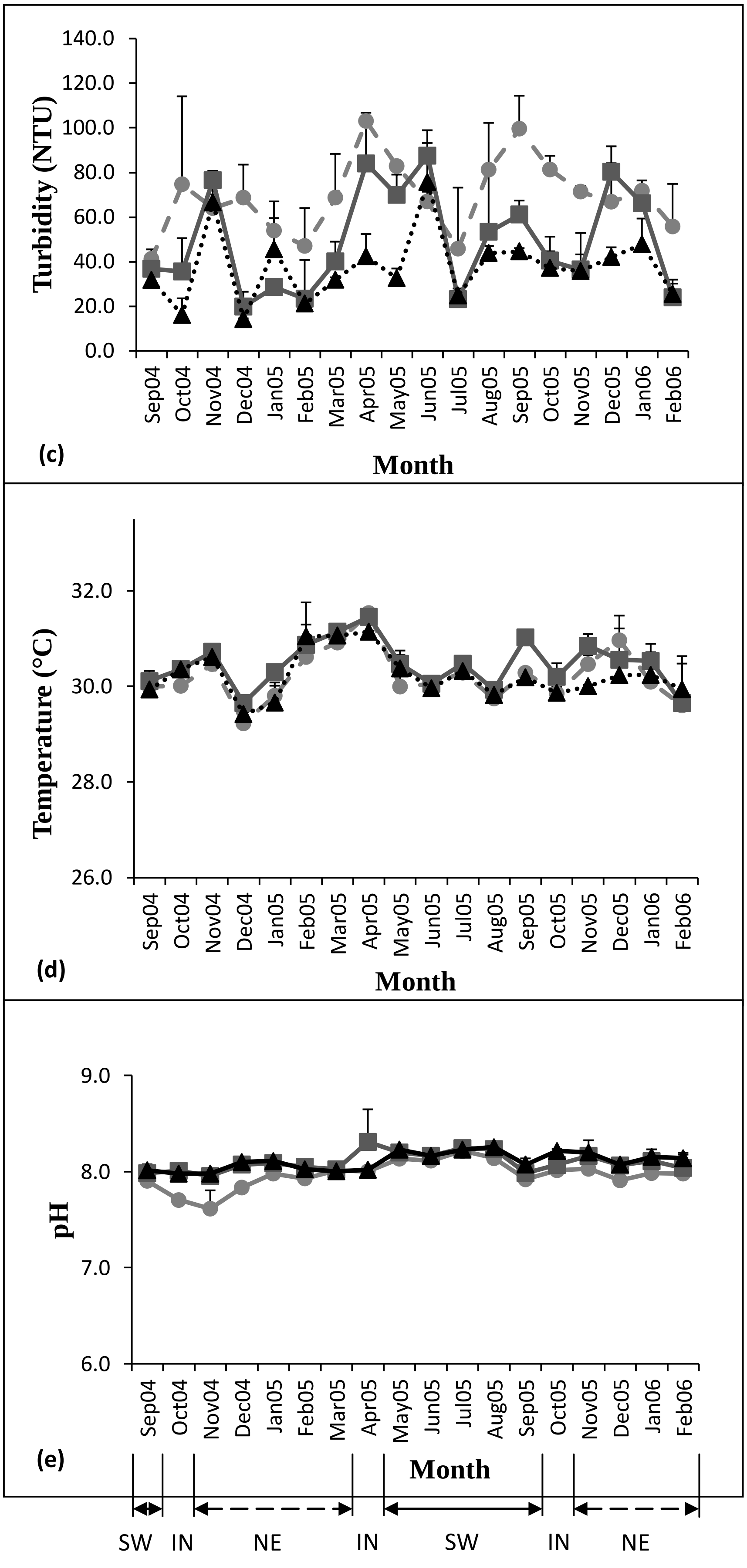


Figure 3.2. Monthly mean of hydrographic conditions at three different depth strata over the 18 months of survey in Matang. (a) Salinity, (b) Dissolved oxygen, (c) Turbidity, (d) Temperature, (e) pH. SW = southwest monsoon, IN = inter-monsoon, NE = northeast monsoon.- -●- - indicates stratum 1,—■— indicates stratum 2, ····▲··· indicates stratum 3.

3.1.3 Distribution and abundance of stomatopod population

3.1.3.1 Percentage abundance of stomatopods

Miyakea nepa (Plate 3.1) was the major species recorded composing 65.52% (total number of specimens, n = 2954) and 68.44% of the total density and biomass of the stomatopod population (Figure 3.3). *Oratosquillina perpensa* (Plate 3.2) contributed 26.48% (n = 1112) and 21.20% of the total stomatopod abundance and biomass, respectively. Low abundance and biomass were recorded for *Harpiosquilla raphidea* (n = 331; Plate 3.3) while the least was *Cloridopsis scorpio* (n = 45; Plate 3.4). The density and biomass of each trawl for the four stomatopod species were shown in appendix VI.

Plate 3.1. Picture of *Miyakea nepa* caught in Matang coastal water.

Plate 3.2. Picture of *Oratosquillina perpensa* caught in Matang coastal water.

Plate 3.3. Picture of *Harpiosquilla raphidea* caught in Matang coastal water.

Plate 3.4. Picture of *Cloridopsis scorpio* caught in Matang coastal water.

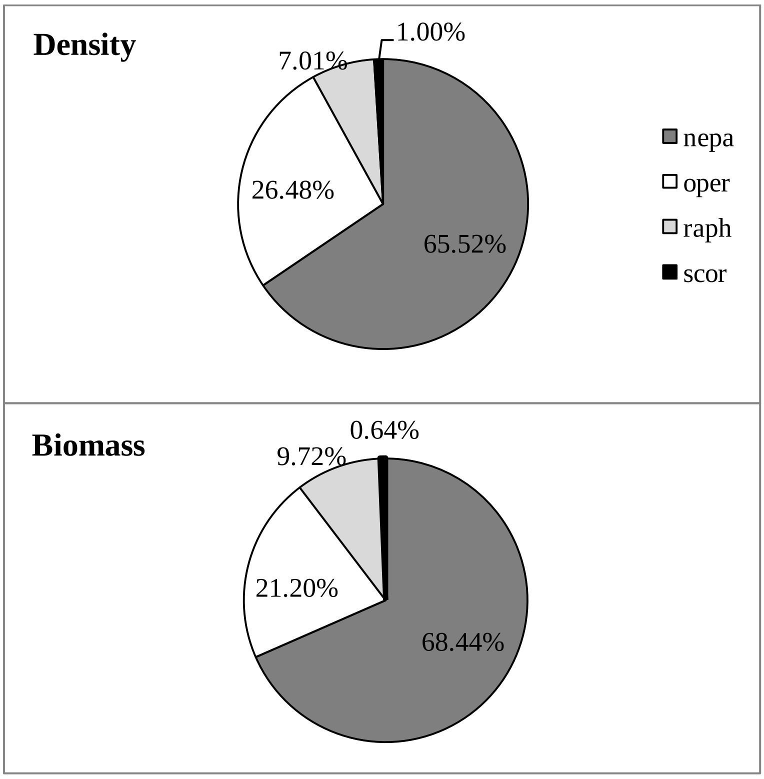


Figure 3.3. Percentage of total density and total biomass of the four stomatopod species over the 18 months of survey in Matang. nepa - *Miyakea nepa*, oper - *Oratosquillina perpensa*, raph - *Harpiosquilla raphidea,* scor - *Cloridopsis scorpio*.

3.1.3.2 Stomatopod size

The largest stomatopod sampled in Matang was *Harpiosquilla raphidea* (mean carapace length = 25.90 mm) followed by *Miyakea nepa* (mean = 24.00 mm), *Oratosquillina perpensa* (mean = 22.30 mm) and *Cloridopsis scorpio* (mean = 20.40 mm). Each of the four stomatopod species showed similar carapace length size among three different strata (Table 3.3).

Table 3.3. Mean and range of carapace length of four stomatopod species at three different depth strata over the 18 months of survey in Matang.

Species	Stratum	Mean (mm)	Range (mm)
Miyakea nepa	1	23.8 ± 4.77	9.6 - 35.6
	2	23.9 ± 4.90	10.2 - 36.0
	3	24.7 ± 4.83	9.5 - 36.9
Oratosquillina perpensa	1	21.2 ± 4.53	12.1 - 35.7
	2	22.7 ± 4.34	10.8 - 32.0
	3	22.4 ± 4.48	10.8 - 32.7
Harpiosquilla raphidea	1	25.3 ± 8.23	14.3 – 51.3
	2	27.0 ± 8.44	13.8 – 61.1
	3	25.5 ± 6.37	13.0 – 58.9
Cloridopsis scorpio	1	20.4 ± 2.42	13.5 – 25.2
	2	20.5 ± 2.46	16.3 – 24.3
	3	18.8 ± 0.18	18.7 – 18.9

3.1.3.3 General distribution and abundance

A total number of 4442 stomatopods with a total weight of 66.64kg were caught from the three stratas during the 18-month sampling period in Matang, Perak. The mean swept area of each haul was 3.5 ± 0.38 ha. Figure 3.4a showed that the total stomatopod population had minimum and maximum monthly mean density of 3.0 ± 2.06 ind/ha (January 2006) and 11.0 ± 8.41 ind/ha (March 2005), respectively. The maximum monthly mean biomass was also recorded in March 2005 (0.18 ± 0.14 kg/ha) and the minimum was recorded in August 2005 (0.04 ± 0.02 kg/ha) and September 2005 (0.04 ± 0.02 kg/ha). Spatially, the mean density and mean biomass (Figure 3.4b) showed that stratum 1 had the lowest mean abundance (4.9 ± 5.08 no/ha) and biomass (0.07 ± 0.07 kg/ha) while the maximum mean density and mean biomass were recorded in stratum 2 (6.9 ± 6.38 ind/ha and 0.11 ± 0.10 kg/ha). Stratum 3 recorded almost similar mean density (6.2 ± 8.40 ind/ha) and mean biomass (0.10 ± 0.12 kg/ha) as stratum 2. Interaction effect from two-way ANOVA test showed that the mean density (Figure 3.5a; appendix VIIa) and mean biomass (Figure 3.5b; appendix VIIb) at stratum 1 were significantly lower ($p < 0.05$) than at the other two strata during northeast monsoon whereas these parameters were not significantly different ($p > 0.05$) among strata during the southwest monsoon.

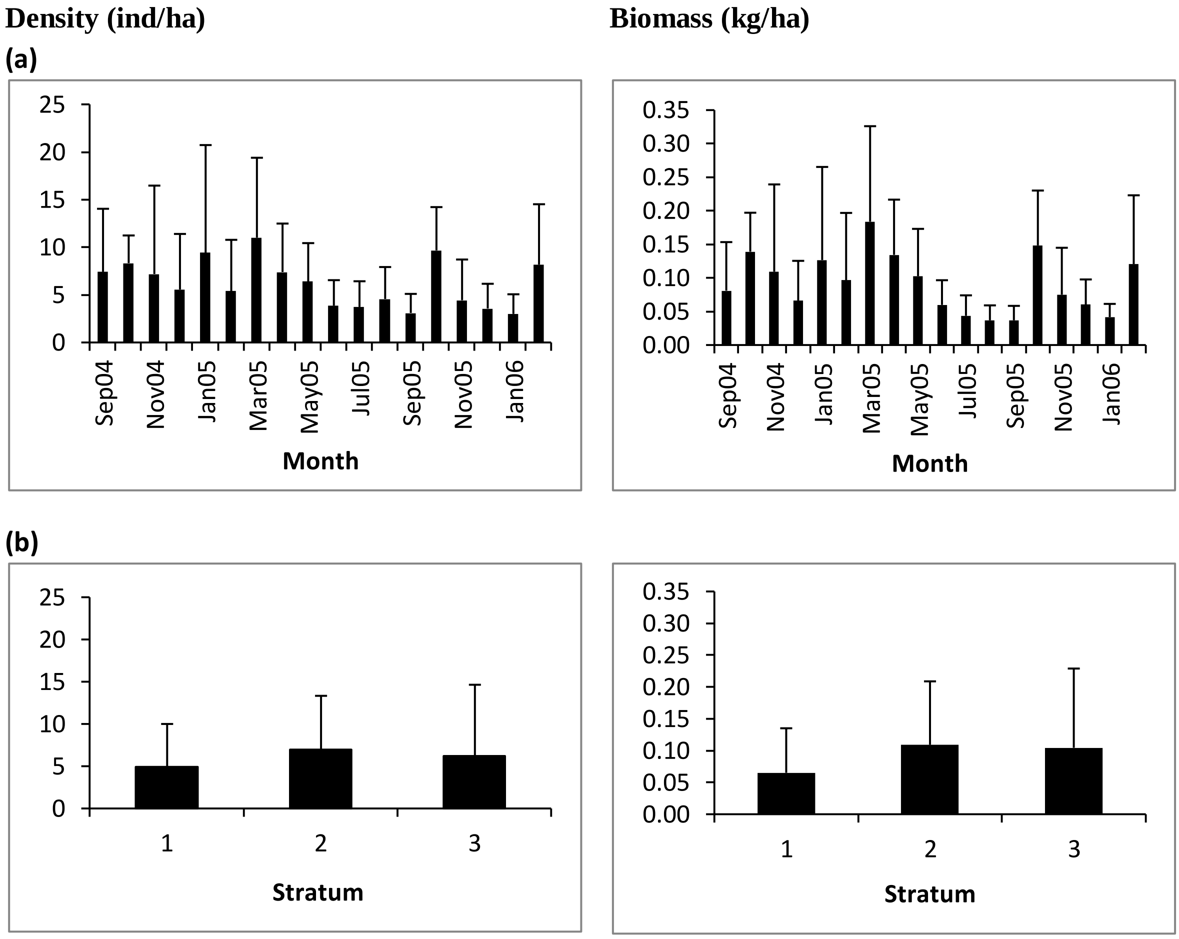


Figure 3.4. Monthly (a) and spatial (b) mean density (right) and mean biomass (left) of the stomatopods sampled at three different depth strata over the 18 months of survey.

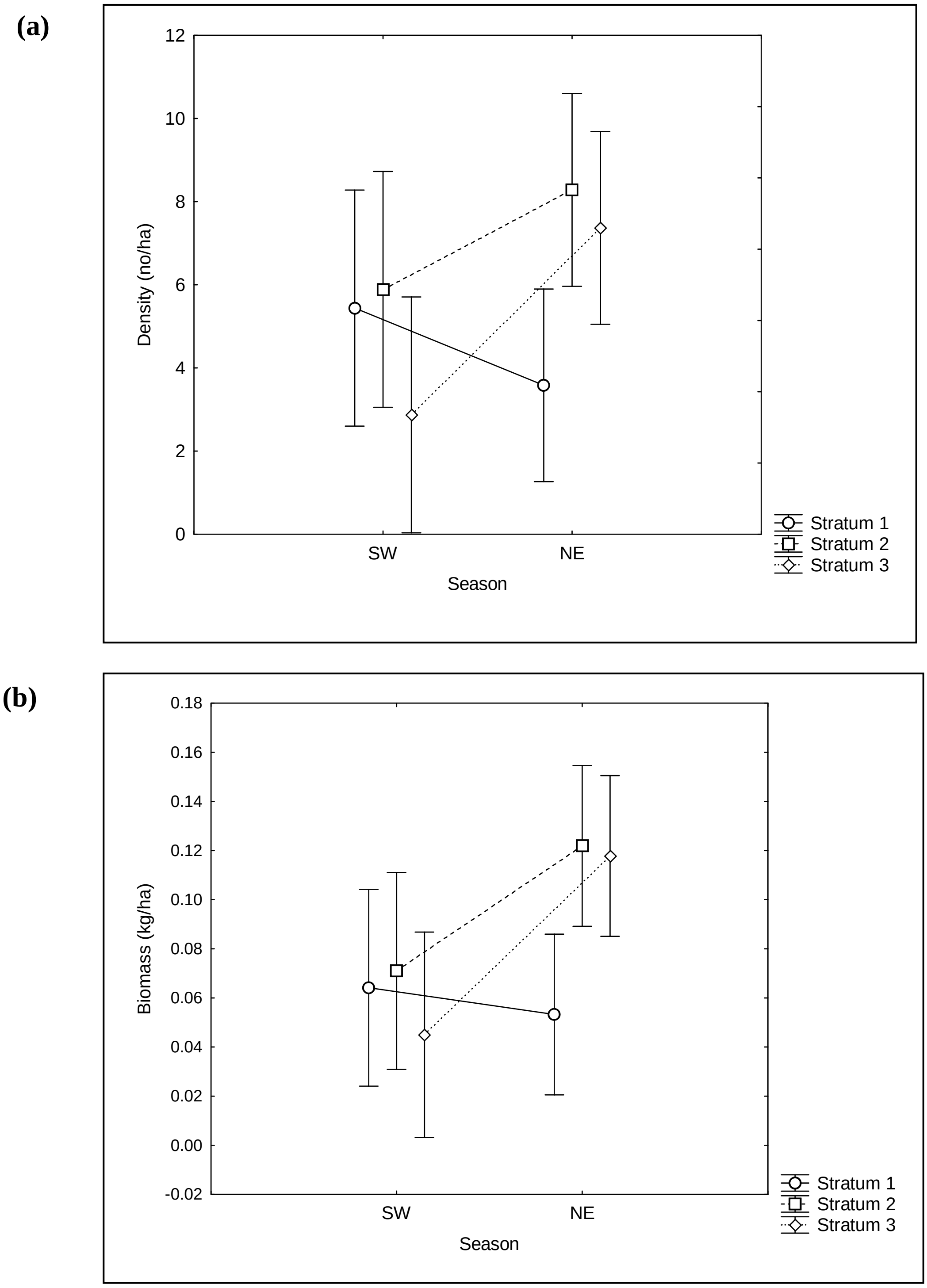


Figure 3.5. Comparison of mean density (a) and mean biomass (b) between monsoon seasons for the stomatopods sampled at three depth strata over the 18 months of survey. SW = southeast monsoon, NE = northeast monsoon.

3.1.3.4 Distribution and abundance of stomatopods by species.

a) *Miyakea nepa*

Miyakea nepa was found abundantly in stratum 2 (Table 3.4). ANOVA test showed statistical difference ($p < 0.05$) in mean density between stratum 1 (15.3 ± 12.39 ind/ha) and stratum 2 (20.9 ± 12.81 ind/ha), and between stratum 2 and stratum 3 (12.9 ± 11.10 ind/ha; Table 3.4; appendix VIIIa). Stratum 1 and stratum 3 recorded nearly similar density values. Figure 3.6a showed that stratum 1 recorded the lowest mean density and mean biomass from November 04 to January 05. Stratum 2 recorded seasonal abundance and biomass changes with several peaks. Stratum 3 showed similar seasonal trend but only one abundance peak occurred in October 05. Figure 3.7 showed that the mean density (appendix VIIId) and mean biomass (appendix IXa) of *Miyakea nepa* were not significantly different ($p > 0.05$) between monsoon periods

b) *Oratosquillina perpensa*

Oratosquillina perpensa was widely distributed at stratum 2 and stratum 3 (Table 3.4). Stratum 1 had the lowest mean density (3.79 ± 6.29 ind/ha) and were significant differences ($p <0.05$) between stratum 2 (7.99 ± 10.62 ind/ha) and stratum 3 (8.15 ± 13.77 ind/ha; Table 3.4; appendix VIIIb). Mean density and mean biomass of *Oratosquillina perpensa* generally showed temporal variation with two or three peaks occurring in each strata (Figure 3.6b). *Oratosquillina perpensa* recorded higher ($p < 0.01$) mean density (appendix VIIIe) and mean biomass (appendix IXb) during northeast monsoon as compared to southwest monsoon (Figure 3.7).

c) *Harpiosquilla raphidea*

Harpiosquilla raphidea was mainly found at stratum 3 with a large peak in March 2005 (32.3 ± 6.70 ind/ha) (Table 3.4; Figure 3.6c). This species was seldom found in stratum 1 (0.09 ± 0.38 ind/ha). It only occurred in three months (January 2005, March 2005 and January 2006) at stratum 1 throughout the 18 months of sampling (Figure 3.6c). Stratum 2 (0.76 ± 1.66 ind/ha) also recorded a low density of *Harpiosquilla raphidea* with zero catches in twelve sampling months. Although stratum 3 (4.35 ± 8.57 ind/ha) recorded the highest density of *Harpiosquilla raphidea*, there were also zero catches in October 2004, April 2005, October 2005, November 2005 and December 2005. Statistical differences ($p < 0.01$) were observed between stratum 1 and stratum 3, and between stratum 2 and stratum 3 (Table 3.4; appendix VIIIc). *Harpiosquilla raphidea* was found abundantly from February 2005 to April 2005 at stratum 2 and from December 2004 to April 2005 at stratum 3 (Figure 3.6c). Figure 3.6c showed that the mean biomass increased in November 2004 at stratum 2 and stratum 3 while the biomass decreased in December 2004 at stratum 3. The increase of biomass was due to one extremely large *Harpiosquilla raphidea* caught at stratum 2 and stratum 3, while the decrease of biomass was due to all catches having small individuals. The mean density (appendix VIIIf) and mean biomass (appendix IXc) of *Harpiosquilla raphidea* were significantly different ($p < 0.05$) between monsoon periods (Figure 3.7).

d) *Cloridopsis scorpio*

Cloridopsis scorpio was caught in ten months out of 18 months of sampling (55.6%) at stratum 1, seven months (38.9%) at stratum 2 and only two months (11.1%) at stratum 3. This indicates that the preferred habitat of *Cloridopsis scorpio* is at or further inside of stratum 1 (Table 3.4; Figure 3.6d). Figure 3.6d showed that most of the months recorded no catches of *Cloridopsis scorpio* in the coastal areas; there were only 45 individuals of *Cloridopsis scorpio* caught during this study. No seasonal changes of the mean density and mean biomass were observed during the sampling periods due to the small amount of catches (Figure 3.7; see also Figure 3.6d).

Table 3.4. The mean density and mean biomass of the four stomatopod species at three different depth strata over the 18 months of survey in Matang. Similar superscripted alphabet indicates homogenous groups.

Species	Stratum 1		Stratum 2		Stratum 3	
	Density (ind/ha)	Biomass (kg/ha)	Density (ind/ha)	Biomass (kg/ha)	Density (ind/ha)	Biomass (kg/ha)
Miyakea nepa	15.25^{a} ±12.39	0.210 ±0.172	20.87^{b} ±12.81	0.311 ±0.208	12.87^{a} ±11.10	0.239 ±0.205
Oratosquillina perpensa	3.79^{a} ±6.29	0.041 ±0.074	7.99^{b} ±10.62	0.104 ±0.139	8.15^{b} ±13.77	0.092 ±0.122
Harpiosquilla raphidea	0.09^{a} ±0.38	0.005 ±0.020	0.76^{a} ±1.66	0.019 ±0.047	4.53^{b} ±8.57	0.086 ±0.170
Cloridopsis scorpio	0.52 ±1.27	0.005 ±0.014	0.19 ±0.42	0.002 ±0.004	0.03 ±0.14	0.0002 ±0.001

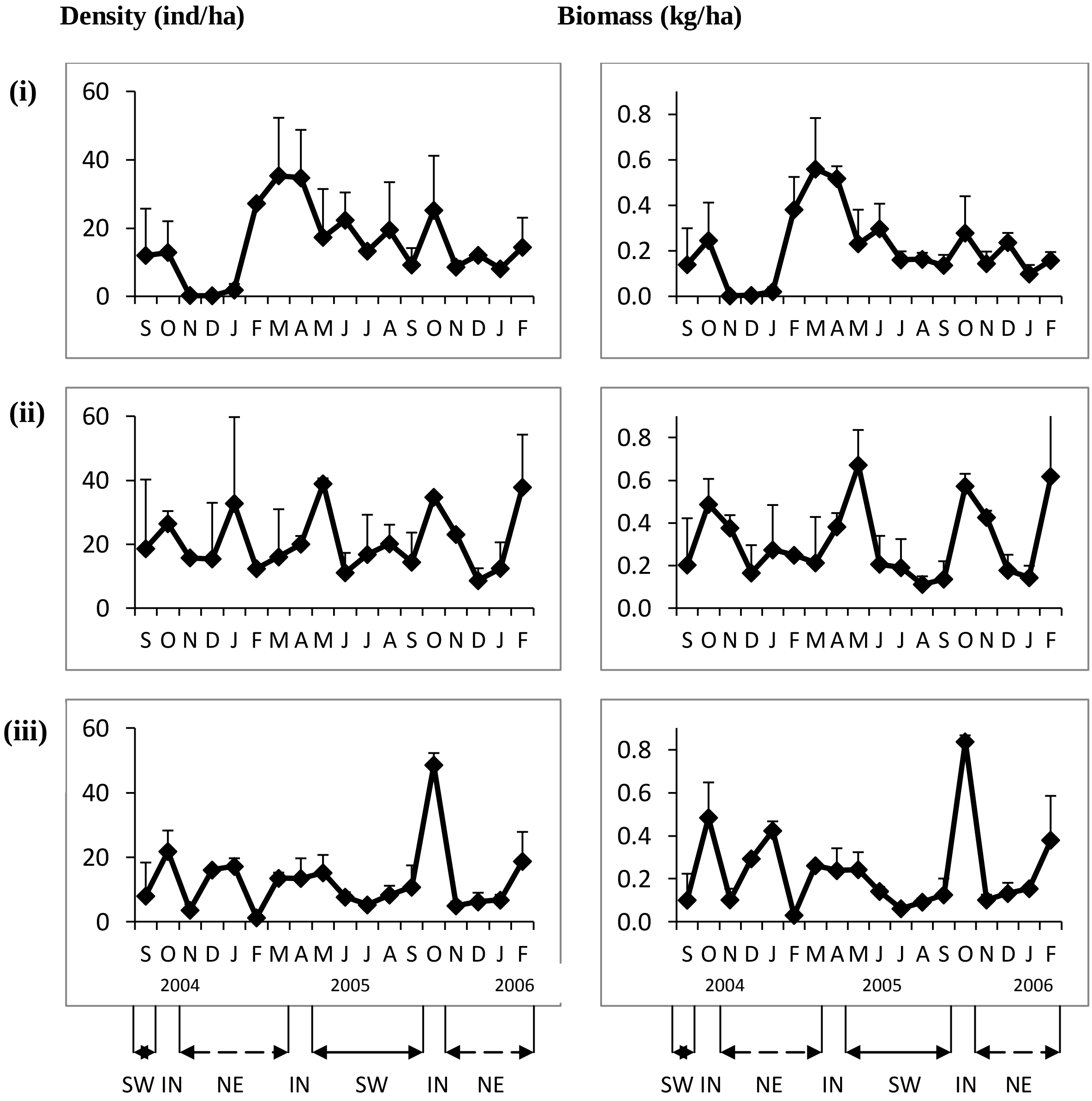


Figure 3.6a. Monthly mean density (right) and mean biomass (left) of the *Miyakea nepa* at three different depth strata over the 18 months of survey in Matang. (i) Stratum 1 (ii) Stratum 2 (iii) Stratum 3.

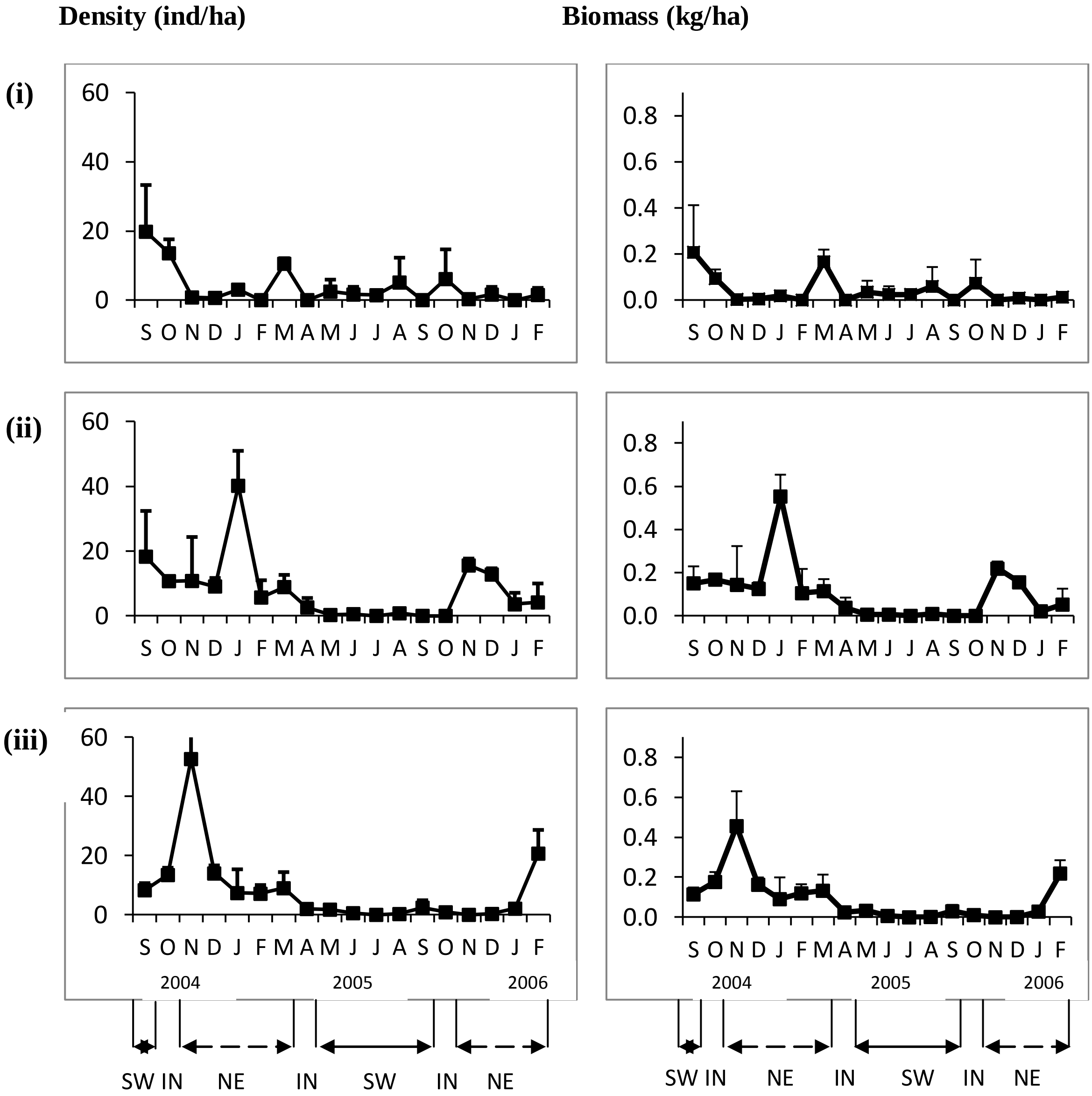


Figure 3.6b. Monthly mean density (right) and mean biomass (left) of *Oratosquillina perpensa* at three different depth strata over the 18 months of survey. (i) Stratum 1 (ii) Stratum 2 (iii) Stratum 3.

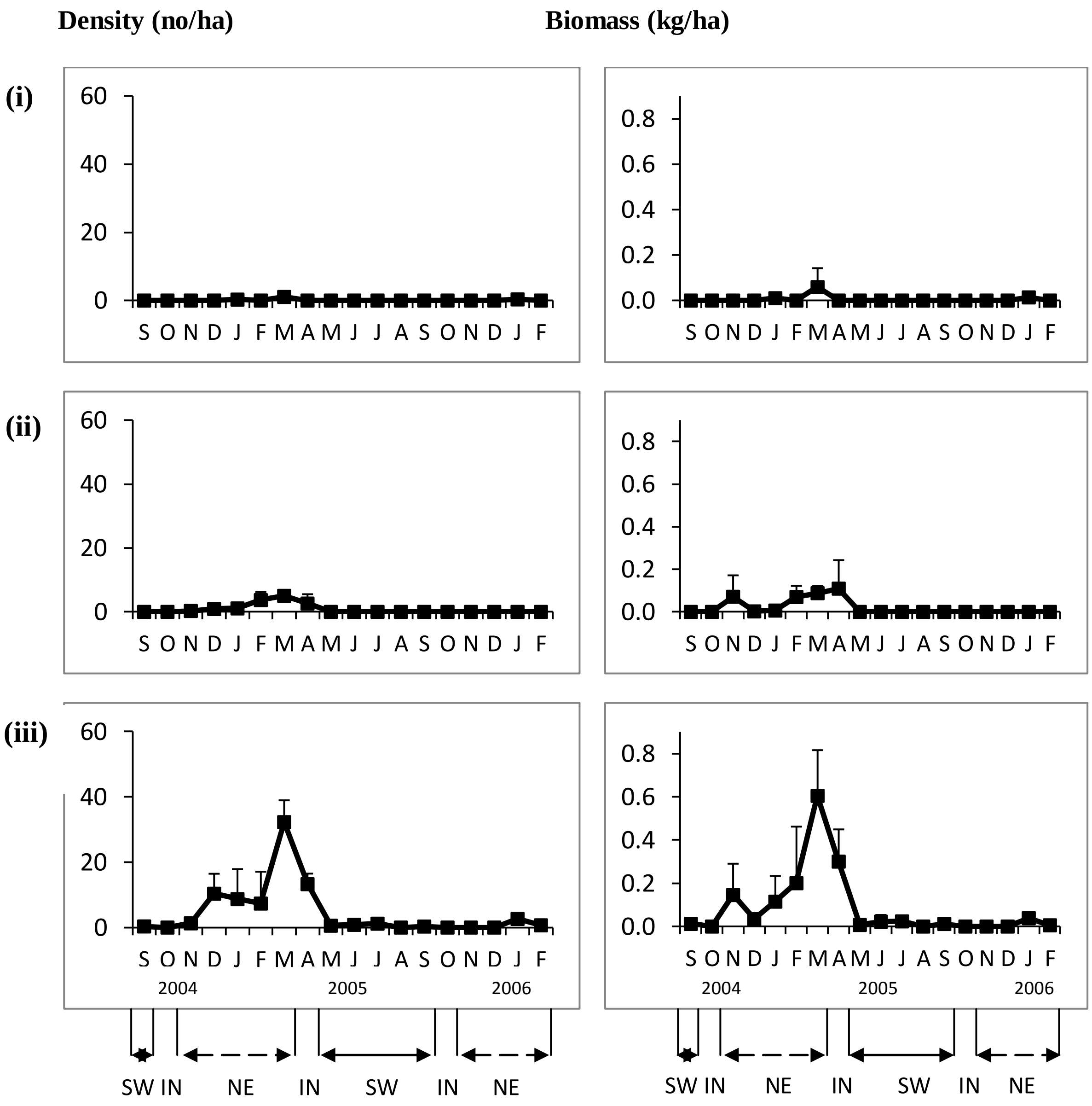


Figure 3.6c. Monthly mean density (right) and mean biomass (left) of *Harpiosquilla harpax* at three different depth strata over the 18 months of survey. (i) Stratum 1 (ii) Stratum 2 (iii) Stratum 3.

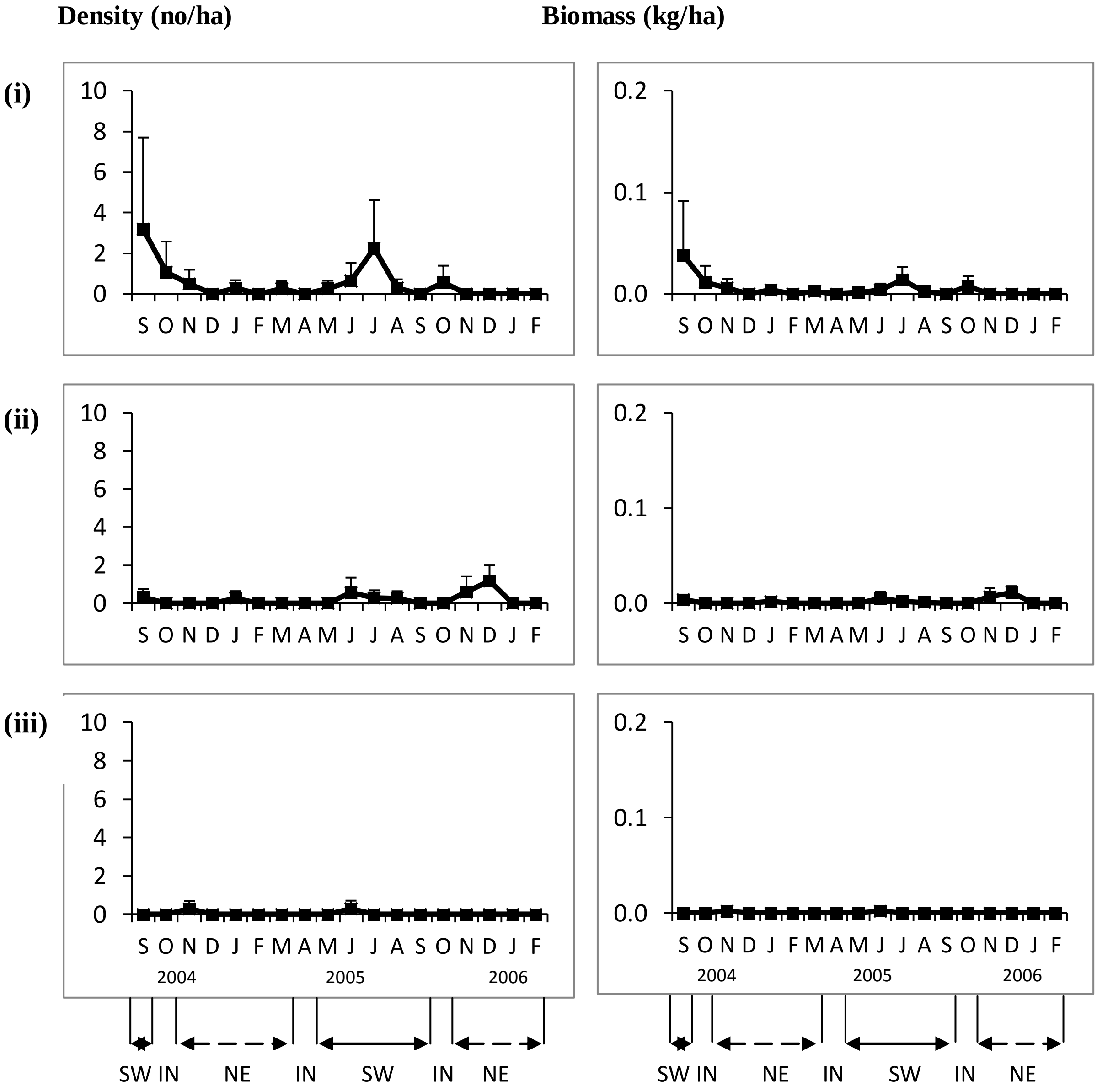
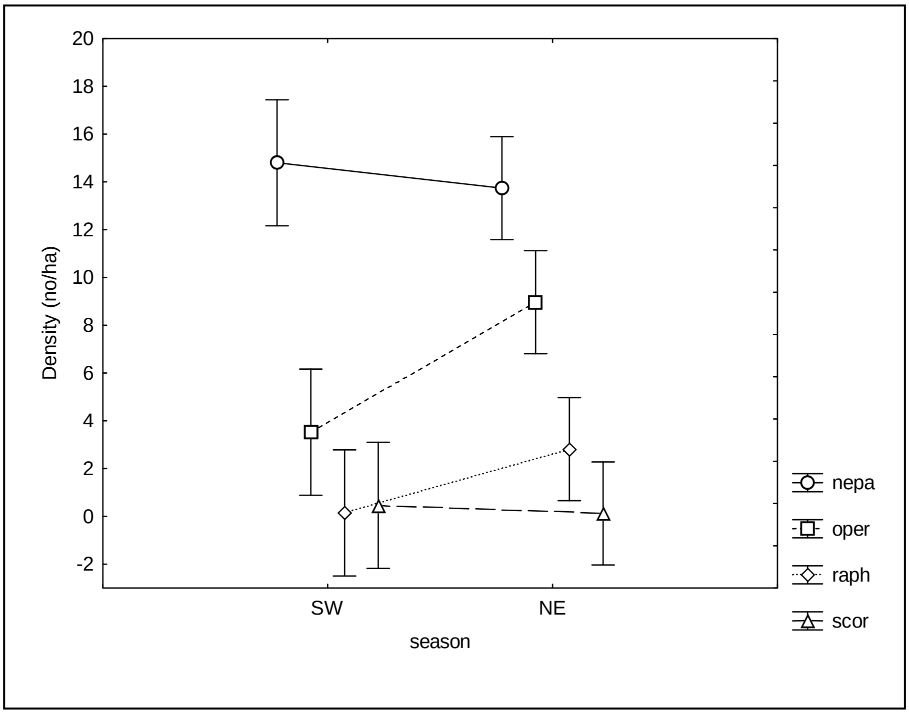


Figure 3.6d. Monthly mean density (right) and mean biomass (left) of *Cloridopsis scorpio* at three different depth strata over the 18 months of survey. (i) Stratum 1 (ii) Stratum 2 (iii) Stratum 3.



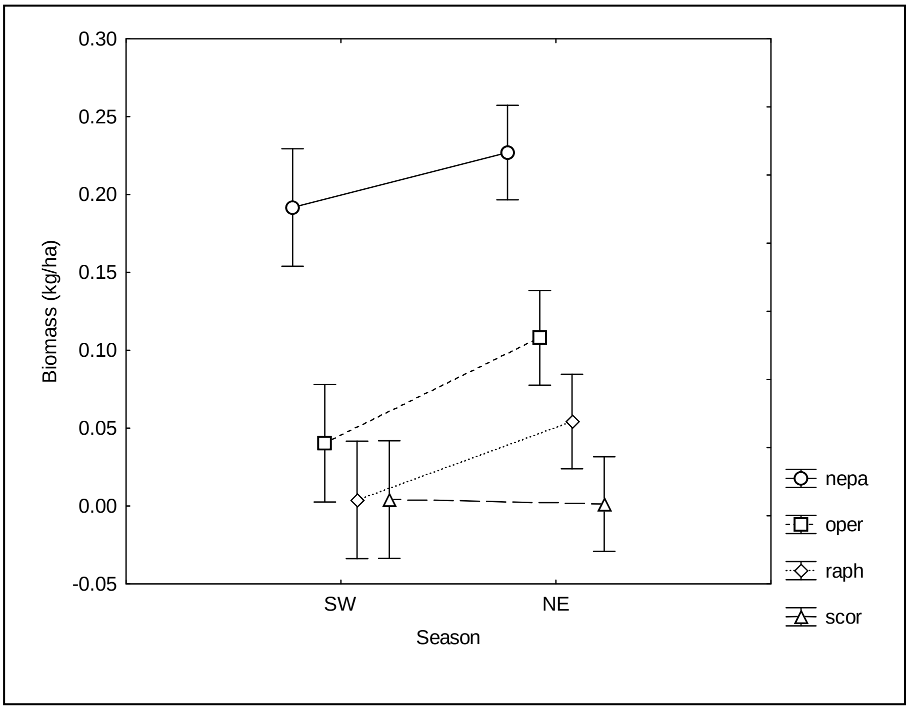


Figure 3.7. Comparison of mean density (top) and mean biomass (bottom) among monsoon seasons for the four stomatopods over the 18 months of survey in Matang. SW – southeast monsoon, NE – northeast monsoon; nepa - *Miyakea nepa*, oper - *Oratosquillina perpensa*, raph - *Harpiosquilla raphidea*, scor - *Cloridopsis scorpio*.

3.2 Discussion

3.1.1 Hydrographic conditions

Various physical and chemical parameters in the offshore of Matang varied according to stratum. Although all three strata have different depths, the readings for salinity, dissolved oxygen, turbidity and pH were similar between stratum 2 and stratum 3, while stratum 1 recorded the lowest salinity, dissolved oxygen and pH, but higher turbidity. This is because stratum 1 was located near to the mouth of Matang estuary. As reported by Harinder (2003) and Chew (2012), Matang estuary system is an open estuary with physical water parameters varying according to climatic factors and tidal movements. During neap tide, a temporary salt wedge is formed (Sasekumar *et al.*, 1994). Chew (2012) noted that dissolved oxygen concentration varied according to water depth, and increased in the offshore direction. Water temperature did not show any spatial or temporal pattern and was rather consistent which is in good agreement with other studies in Matang (Chew, 2012).

Beside the differences between strata, salinity, dissolved oxygen and pH are also influenced by the monsoon seasons. Low salinity, dissolved oxygen and pH were observed during the northeast monsoon while higher salinity, dissolved oxygen and pH occurred during the southwest monsoon. These results are in good agreement with Chew (2012) study. The northeast monsoon normally brings heavy rainfall whereas the southwest monsoon is relatively drier (Malaysian Meteorological Department). Chew (2012) indicated that all severely- and extreme-wet events occurred during the northeast monsoon and inter-monsoon periods, while severely-dry events occurred during the southwest monsoon. Same author reported that heavy rainfall during northeast monsoon has depressive effect on salinity and pH while the low dissolved oxygen concentration was due to the increased of heterotrophic bacteria respiration. However, no changes between monsoon seasons were observed for turbidity and temperature.

3.1.2 Stomatopod size

Present study showed that *Harpiosquilla raphidea* was the largest stomatopod while *Cloridopsis scorpio* was the smallest stomatopod caught in Matang. According to Carpenter and Niem (1998), the family of Harpiosquillidae was grouped as very large mantis shrimps (maximum total length at least 30cm) compared to Squillidae (maximum total length more than 20 cm). According to Manning (1969), *Harpiosquilla raphidea* is the largest known stomatopod. *Cloridopsis scorpio* was grouped as relatively small squillid only occasionally exceeding 10 cm in length (Dingle & Caldwell, 1975). In addition, a longer life-span (6.7 to 8.5 years) of *Harpiosquilla raphidea* (Ali, 2011) as compared to *Miyakea nepa* (3.23 years) and *Oratosquillina perpensa* (4.29 years) in the present study (see Chapter 4) could have led to the larger size of *Harpiosquilla raphidea*. Each of the four stomatopod species showed similar carapace length size among three different strata (Table 3.3) and this showed that stomatopod of different age group did not seemed to occupy certain habitat as seen in shrimps in Matang (Chong & Sasekumar, 1994). These authors reported that most of the penaeid shrimps species spawned their eggs in deep offshore waters, with postlarvae being advected into shallower nursery grounds (mangrove estuary) where they settle into a benthic lifestyle. After a period of growth, the juvenile shrimps migrate to offshore waters to complete the life cycle. Thus, different age groups (different length size) of shrimp are found in different habitat.

3.1.3 Distribution and abundance of stomatopod population

The population of stomatopod caught in Matang were found to comprise four genera namely *Miyakea*, *Oratosquillina*, *Harpiosquilla* and *Cloridopsis* which were grouped in the same family (Squillidea). *Miyakea nepa* was the major spesies followed by *Oratosquillina perpensa*, *Harpiosquilla raphidea* and *Cloridopsis scorpio*. The mean density and mean biomass of the whole stomatopod population were significantly lower at stratum 1 compared to the other two strata during the northeast monsoon. This could be likely due to the environmental factors at stratum 1 because the latter was located near to the mangrove estuary and hence, is subjected to wider variations in environmental conditions. The water parameters (salinity, dissolved oxygen and pH) at stratum 1 were found to vary greatly during northeast monsoon as compared to southwest monsoon while the water parameters at stratum 2 and stratum 3 did not vary much during the monsoon seasons (Figure 3.2). Apart from environmental conditions, seasonal changes of the available prey will directly affect the abundance of stomatopod. Certain prey items could appear abundantly in certain seasons that would attract stomatopods. Ali (2011) noted that the distribution of *Harpiosquilla raphidea* was similar to the distribution of penaeid shrimps, their main prey.

3.1.4 Distribution and abundance of stomatopods according to species

In the present study, overlap of habitat was observed for all the four stomatopod species. Reaka & Manning (1980) reported that stomatopod species were more frequently in association with several others than alone in the same habitat and they concluded that this phenomenon is controlled mainly by general habitat type and abundance than by preferential associations among particular species. Although the four stomatopod species share the same habitat, they were found abundantly at different strata. This could be due to the environmental condition at different habitats. A study in

Klang Strait (southern of Matang) showed that stomatopods were affected by salinity and water depth (Zgozi, 2000). Lui (2005) reported that heterogeneity of the sea bottom influence the stomatopod species composition while Piamthipmanus (1998) found that the density of macrobenthic fauna (including stomatopods) varied according to water depth.

Harpiosquilla raphidea is mainly found further offshore. It probably prefers more deeper and saline waters. According to Manning (1969), *Harpiosquilla raphidea* occurs in shallow water in depths between 1 to 28 fathoms (1 fathoms = 1.8288 meters). In the present study, interview with several fishermen showed that these species are often found further offshore than stratum 3.

The smallest species (*Cloridopsis scorpio*) was found to be rare in the trawl sampled areas (Stratum 1 to Stratum 3). In addition, *Cloridopsis scorpio* was also rare in the estuary and river but the catches here were much higher as compared to the other three stomatopods (Then, 2008). This could be due to the burrowing habit of *Cloridopsis scorpio* which digs deep and complex burrows (Dingle & Caldwell, 1975) and hence, are less vulnerable to capture. Another possibility is they could live farther upstream of the estuary. A short-term study by Chong (2007b) recorded two species of stomatopods in Matang estuary, *Cloridopsis scorpio* and *Miyakea nepa*, with 91 % of the them belong to *Cloridopsis scorpio*. Ahyong (2001) noted that species of *Cloridopsis scorpio* occur in shallow inshore waters with substantial terrigenous influence. In addition, *Cloridopsis scorpio* was found abundantly higher than three other *Oratosquilla* species (including *Oratosquilla nepa* = *Miyakea nepa*) in an intertidal mudflat exposed at the lowest tides (Dingle & Caldwell, 1975). The authors also reported that *Cloridopsis scorpio* became rarer far from shore.

The density and biomass of *Oratosquillina perpensa* and *Harpiosquilla raphidea* varied according to monsoon seasons. Other studies in subtropical (Lui, 2005) and tropical countries (Piamthipmanus, 1998; Sivadas *et al.*, 2011) also indicated temporal variability of density by monsoon. Hylleberg *et al.* (1985) noted that the direction and force of the monsoon wind could influence the current, erosion and sedimentation pattern that might affect the density of stomatopod.

3.3 Conclusion

Four species of stomatopods were found in Matang, namely, *Miyakea nepa*, *Oratosquillina perpensa*, *Harpiosquilla raphidea* and *Cloridopsis scorpio*. *Miyakea nepa* is the most abundant species followed by *Oratosquillina perpensa, Harpiosquilla raphidea* and *Cloridopsis scorpio*. In term of size, *Harpiosquilla raphidea* is the largest stomatopod and *Cloridopsis scorpio* is the smallest stomatopod.

The spatial and temporal variation observed in the distribution and abundance of the four stomatopod species in Matang suggest that the population is affected by environmental factors such as water parameters that are influenced by the monsoon seasons.

CHAPTER 4

POPULATION DYNAMICS OF STOMATOPODS IN MATANG

4.1 Results

4.1.1 Population dynamic parameters

4.1.1.1 Growth parameters,Von Bertalanffy growth curve and Growth Performance Index (φ′)

Von Bertalanffy growth curves of *Miyakea nepa* and *Oratosquillina perpensa* generated from FISAT II, are shown in Figure 4.1a and Figure 4.1b respectively. The growth parameters, K and L∞ for *Miyakea nepa* were estimated at 0.93 yr^{-1} and 40.43 mm (carapace length), respectively. *Oratosquillina perpensa* has a slower growth rate (K = 0.70 yr^{-1}) than *Miyakea nepa*. The maximum size of *Oratosquillina perpensa* (L∞ = 37.28 mm) is also smaller than *Miyakea nepa*. Growth Performance Index (φ′), which is based on the estimated K and L∞, were recorded as 3.18 for *Miyakea nepa* and 2.99 for *Oratosquillina perpensa*.

4.1.1.2 Recruitment pattern

The recruitment events were found throughout the year for both species (Figure 4.2a and Figure 4.2b). However, there were two major peaks in a year for *Miyakea nepa*, while one peak was observed for *Oratosquillina perpensa*.

4.1.1.3 Lifespan

The lifespan for *Miyakea nepa* and *Oratosquillina perpensa* were 3.23 years and 4.29 years respectively.

4.1.1.4 Mortality

The total mortality rates (Z) as calculated from the length-converted catch curve were 3.03 yr^{-1} for *Miyakea nepa* and 3.38 yr^{-1} for *Oratosquillina perpensa*. Natural mortality (M) for *Miyakea nepa* and *Oratosquillina perpensa* were estimated at 1.62 yr^{-1} and 1.37 yr^{-1} respectively. The fishing mortality rate (F) and exploitation rate of *Miyakea nepa* generated from FISAT II were 1.41 yr^{-1} and 0.47 respectively. Based on the fishing mortality rate of 2.01 yr^{-1}, the exploitation rate for *Oratosquillina perpensa* was estimated at 0.59.

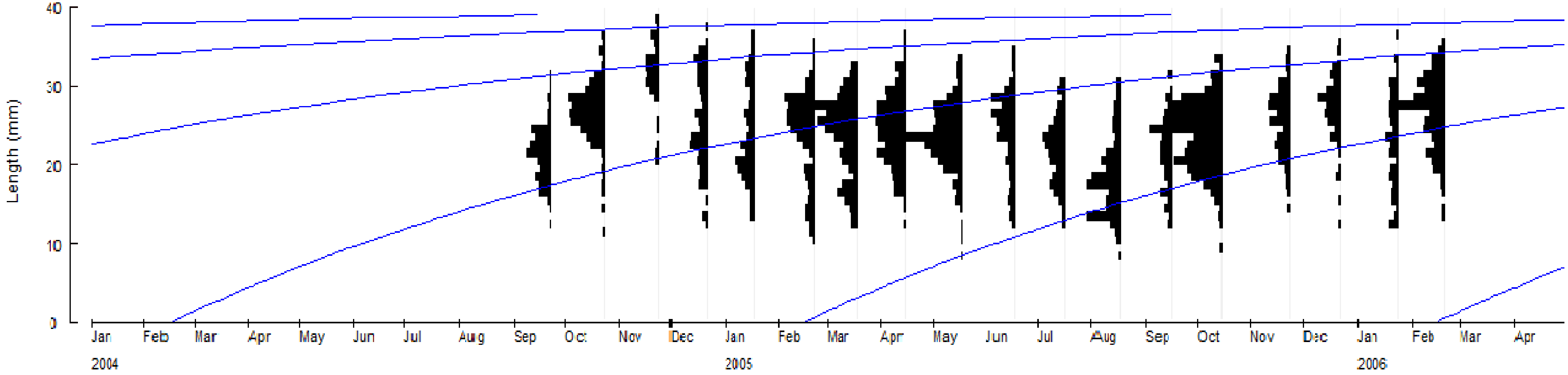


Figure 4.1a. Von Bertalanffy growth curve of *Miyakea nepa* captured monthly from September 2004 to February 2006.

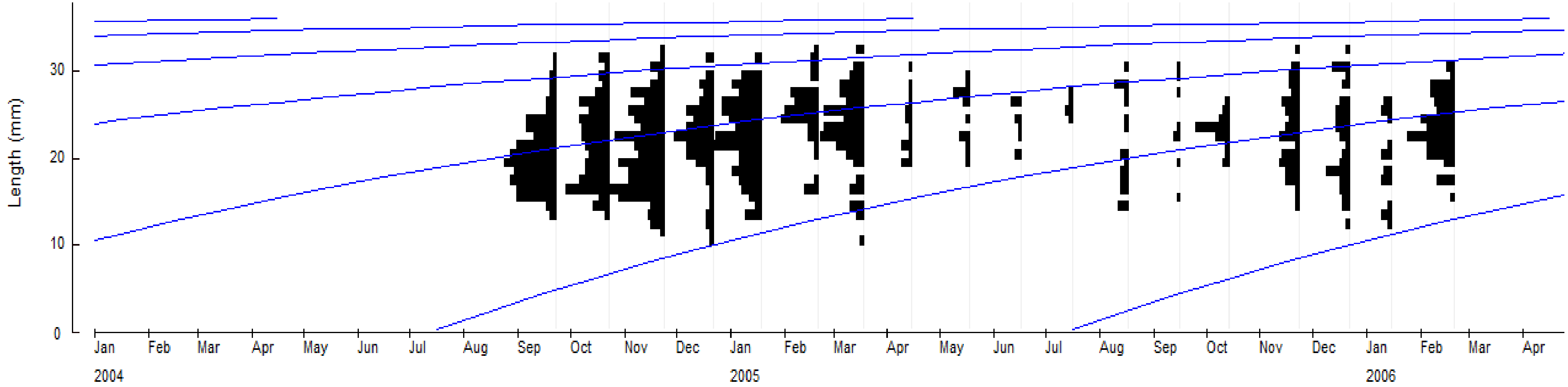


Figure 4.1b. Von Bertalanffy growth curve of *Oratosquillina perpensa* captured monthly from September 2004 to February 2006.

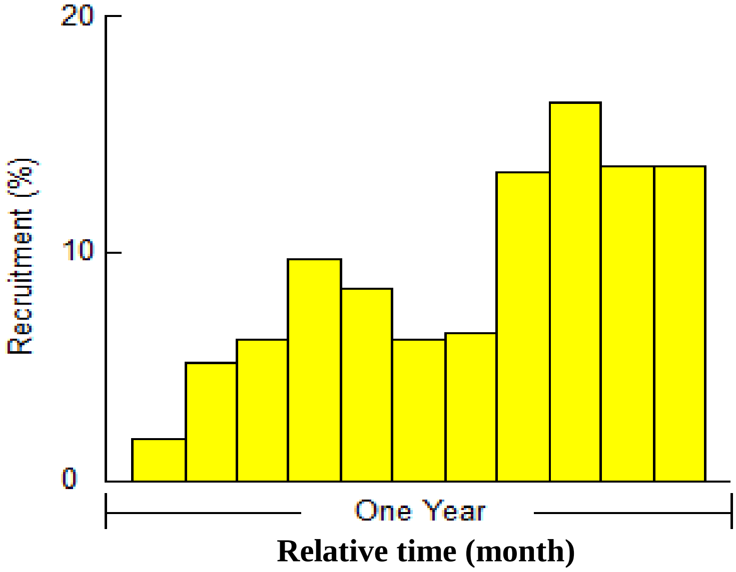


Figure 4.2a. Recruitment pattern of *Miyakea nepa* generated by FISAT II based on length-frequency data.

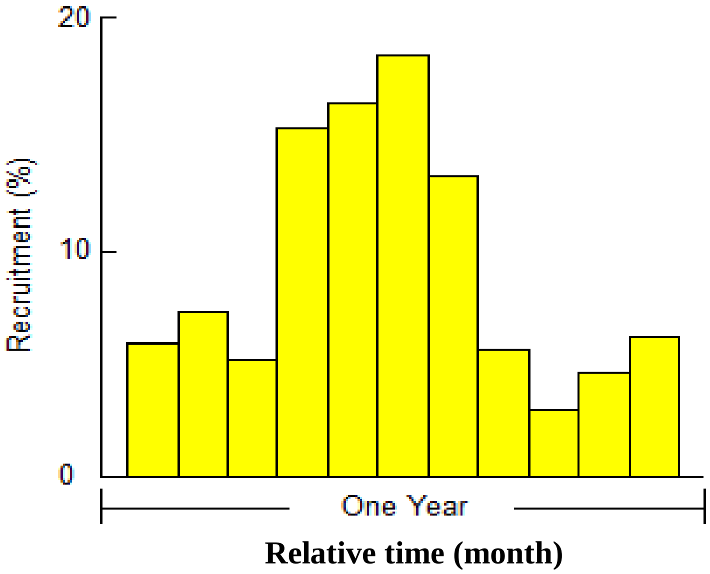


Figure 4.2b. Recruitment pattern of *Oratosquillina perpensa* generated by FISAT II based on length-frequency data.

4.2 Discussion

Present study showed that *Miyakea nepa* (K = 0.93 yr^{-1}) grow slightly faster than *Oratosquillina perpensa* (K = 0.70 yr^{-1}). The VBGF growth coefficient (K) obtained in this study was found to be different from Lui (2005) study (Table 4.1). The growth rate of *Miyakea nepa* recorded by Lui (2005) was smaller as compared to the present study. The variation in growth rate could be due to the differences in water temperature from different geographical areas in the world. Few studies had showed that the growth rate of temperate stomatopods was high during summer and slow down during winter (Ohtomi & Shimizu, 1988; Abello & Martin, 1993). The growth performance index (φ′) of *Miyakea nepa* and *Oratosquillina perpensa* in the present study were different (Table 4.1). Comparison with the growth performance index (φ′) from Lui (2005) showed that present species recorded higher φ′. These variations in growth probably reflect different growth strategies.

Table 4.1. Comparison of population dynamic parameters between present study and Lui's (2005) study.

Species	Study conducted	Study area	K (yr^{-1})	L∞ (mm)	φ′
Miyakea nepa	This study	Matang, Malaysia	0.93	40.43	3.18
Oratosquillina perpensa	This study	Matang, Malaysia	0.70	37.28	2.99
Miyakea nepa	Lui (2005)	Hong Kong (two different sampling areas)	0.31 & 0.59	38.33 & 33.08	2.66 & 2.81
Oratosquilla oratoria	Lui (2005)	Hong Kong (two different sampling areas)	0.73 & 0.53	32.03 & 32.03	2.87 & 2.74
Oratosquilla interrupta	Lui (2005)	Hong Kong (two different sampling areas)	0.19 & 0.78	34.13 & 39.38	2.35 & 3.06
Harpiosquilla harpax	Lui (2005)	Hong Kong (two different sampling areas)	0.14 & 0.10	47.78 & 47.78	2.51 & 2.36

The lifespan of *Miyakea nepa* (3.23 years) estimated from the present study was twice the lifespan (1.5 years) of those in India (Sukumaran, 1987). This could be due to the method use to calculate the lifespan and the maximum size of the population. The largest individuals (maximum total length) captured in India was around 130 mm which was much smaller than in present study (maximum total length = 160 mm). The lifespan of *Oratosquilla stephensoni* (Dell & Sumpton, 1999), *Squilla mantis* (Maynou *et al.*, 2005) and *Oratosquilla oratoria* (Kodama *et al.*, 2005) and were estimated to be 2.5 years, 3 years and >4 years, respectively. However, Kodama *et al.* (2005) pointed out that lipofuscin as an age marker could provide higher accuracy in age estimation than length frequency analysis. Their analysis clearly separated out the population of *Oratosquilla oratoria* into distinct age groups. Kodama *et al.* (2005) also reported that insufficient data collection of larger-sized individuals and the formation of a single broad cohort by older age individuals (due to the growth rate declining as age increases) will lead to difficulty in detecting age groups based on length frequency analysis.

With a fishing mortality rate (F) of 1.41 yr^{-1} and an exploitation rate at 0.47, the present fishing of *Miyakea nepa* in Matang seem to be close to the optimum level of exploitation (E = 0.50) while *Oratosquillina perpensa* appears to be over exploited (E = 0.59). The optimum level of exploitation is based on the assumption that fishing mortality (F) is equal to natural mortality (M). The exploitation rate shows that stomatopods are becoming popular in fishery catches in Matang.

4.3 Conclusion

In Matang, *Miyakea nepa* has a faster grow rate and shorter lifespan than *Oratosquillina perpensa*. With the provided information on the exploitation rate of stomatopods, the fishery of Matang stomatopods is over exploited. Thus, better fishery management and regulation are required for the recovery of the population.

CHAPTER 5

REPRODUCTION AND LARVAL ECOLOGY OF STOMATOPODS IN MATANG

5.1 Results

5.1.1 Reproduction of stomatopods

5.1.1.2 Sex ratio by month and size class

a) *Miyakea nepa*

Throughout the sampling period, the population of *Miyakea nepa* was female-biased in most of the months (Figure 5.1a). Of the total catch (number of specimens, n = 2954), 1561 individuals were females and 1393 individuals were males. The females of *Miyakea nepa* predominated in the smaller carapace length size classes (< 20 mm) and larger size classes (> 28 mm) whereas the males predominated in the middle size classes (20 mm to 28 mm; Figure 5.2a). No male was observed with a carapace length above 36 mm.

b) *Oratosquillina perpensa*

Of the total catch, the number of females (n = 581) of *Oratosquillina perpensa* was higher than males (n = 531). Throughout the sampling period, the number of months dominated by females and males were almost equal (Figure 5.1b). The females of *Oratosquillina perpensa* were found mainly in the smaller size classes (< 20 mm) whereas the number of females and males varied for the other size classes (Figure 5.2b). The largest *Oratosquillina perpensa* was male.

c) *Harpiosquilla raphidea*

The number of females (n = 170) of *Harpiosquilla raphidea* was slightly higher than males (n = 161). The number of months dominanted by either sex was almost similar (Figure 5.1c). The number of females and males varied for each size classes with the largest individual found to be male (Figure 5.2c).

d) *Cloridopsis scorpio*

The catches of *Cloridopsis scorpio* were only 45 individuals. The population of *Cloridopsis scorpio* showed male-biased with 30 individuals of male and 15 individuals of females (Figure 5.1d). The males of *Cloridopsis scorpio* predominated in almost all the size classes due to the higher abundance of males in the population (Figure 5.2d).

5.1.1.3 Female and male maturity stages

a) Female maturity stages

Five stages of ovarian development of female *Miyakea nepa*, *Oratosquillina perpensa* and *Cloridopsis scorpio* have been described based on visual assessment on fresh samples of ovaries based on their colour and relative width (Table 5.1). Since larger immature (stage I) and spent (stage V) females could not be easily distinguished by the naked eye because their ovaries were translucent, only females larger than 29.0 mm (*Miyakea nepa*) and 26.0 mm (*Oratosquillina perpensa*) were taken as spent.

From the 15 individuals of female *Cloridopsis scorpio* collected during the sampling periods, there was only one individual in stage II while the other were immature females. All specimens of *Harpiosquilla raphidea* showed undeveloped ovaries (Stage I). The smallest, early-maturing females (Stage II) in term of carapace

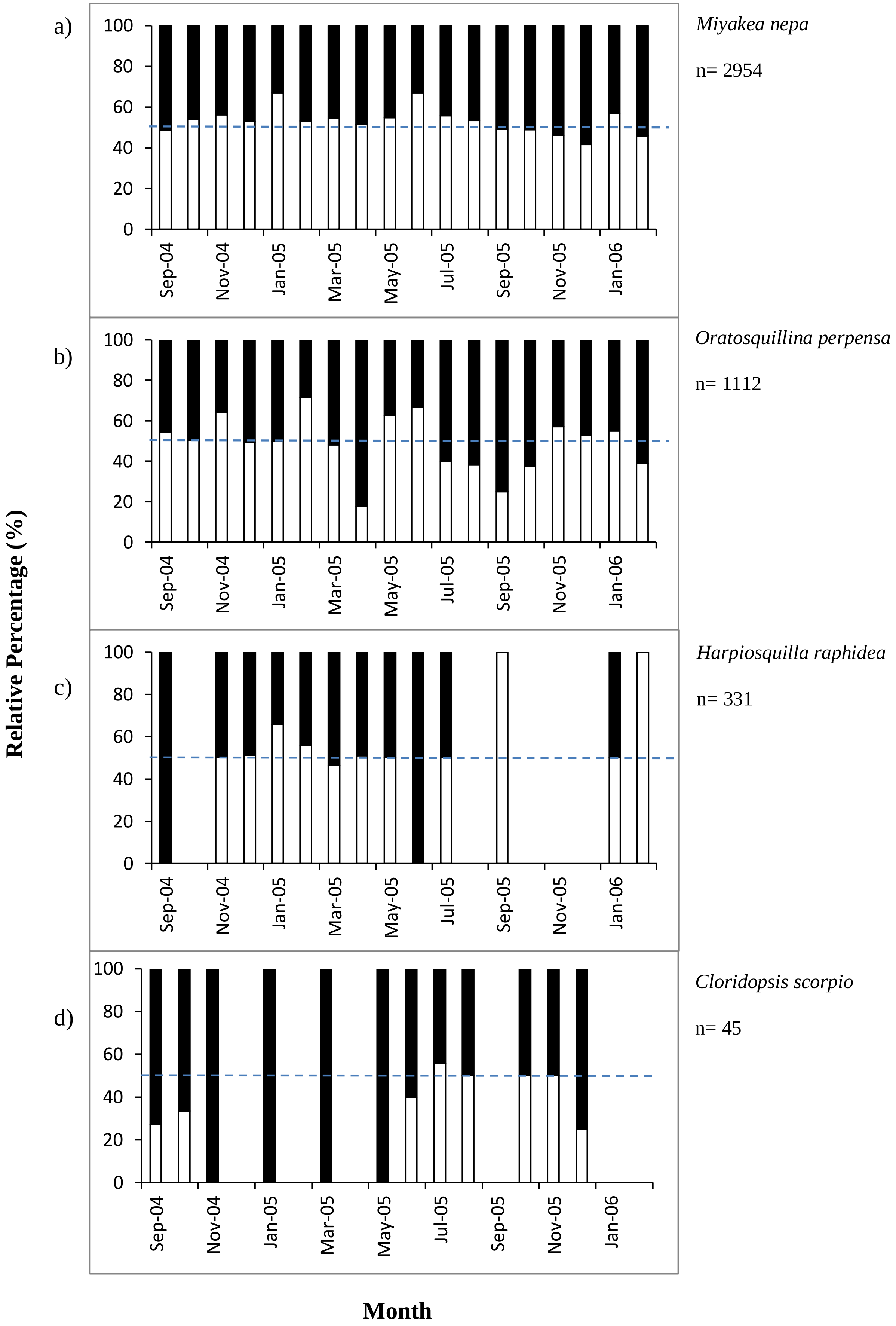


Figure 5.1. Monthly relative sex distribution of four stomatopod species over the 18 months of survey. Open bar: female. Filled bar: male. Dotted lines indicate relative percentage of 50%.

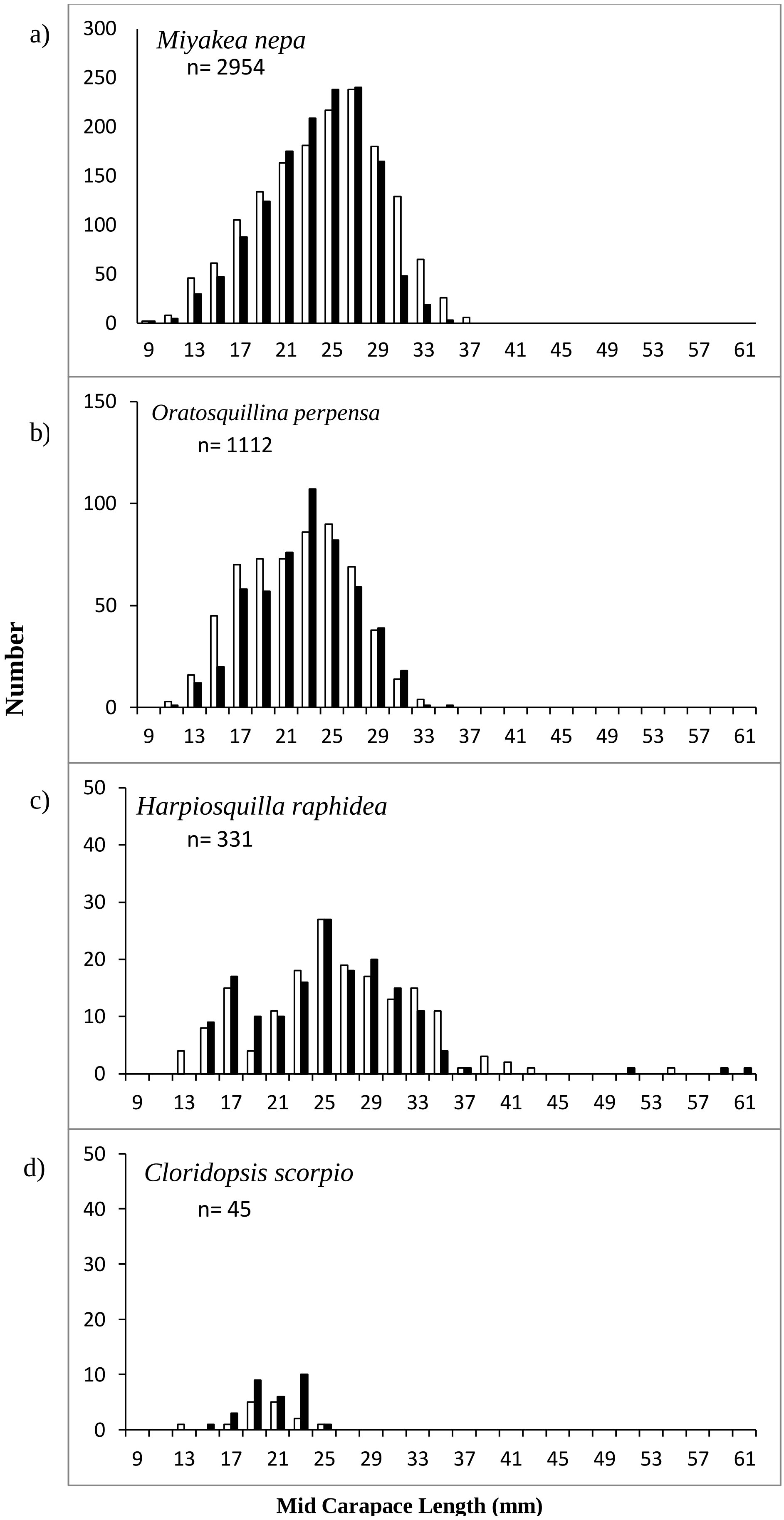


Figure 5.2. Frequency distribution of females and males of the four stomatopod species by size classes (carapace length), pooled from September 2004 to February 2006. Open bar: female. Filled bar: male.

length for *Miyakea nepa*, *Oratosquillina perpensa*, and *Cloridopsis scorpio* were 26.1 mm, 21.77 mm and 22.51 mm, respectively.

Stage II to Stage IV females of *Miyakea nepa* showed similar mean carapace length (Table 5.1). Mean carapace length of immature females (stage I) was significantly ($p < 0.01$) smaller than the carapace length of stage II to stage V females (appendix Xa). The mean carapace length of spent females (stage V) was significantly ($p < 0.01$) larger than the other four maturation groups of females (appendix Xa).

The mean carapace length of immature females (stage I) of *Oratosquillina perpensa* was significantly ($p < 0.01$) smaller than the other four maturation groups of females (Table 5.1; appendix Xb). The mean carapace length of all the stage II to stage V females did not differ much ($p > 0.05$; appendix Xb).

Figure 5.3a shows the monthly changes in the percentage of female *Miyakea nepa* according to maturation stages. In Matang, females with immature ovaries (stage I) occurred throughout the year with peaks in September 04 and July 05 to September 05. Immature females contributed the highest percentage (61.4 %) of the total females. Females in stage II and stage III occurred all year with variable percentages. Mature and gravid females (stage IV) occurred most commonly from October 04 to June 05 and October 05 to February 06 (Figure 5.3a). The percentage of spent females was the lowest (6.0 %) among all the maturation stages.

Immature females of *Oratosquillina perpensa* recorded 64.0 % of the total females (Figure 5.3b). Immature females were found throughout the year except July 05. Stage II females showed a peak percentage in July 05. Late-maturing females (stage III) occurred most commonly in May 05 to June 05 and September 05 to October 05. Stage IV females were found all year except April 05, July 05 and September 05. No spent females were recorded in September 04 and from August 05 to October 05 (Figure 5.3b).

b) Male maturity stages

Males of *Miyakea nepa* and *Oratosquillina perpensa* were grouped into three different maturation stages based on the percentage frequency distribution of male by penis length classes using Bhattacharya method. The three maturation stages correspond to the three cohorts generated by Bhattacharya method for *Miyakea nepa* (Figure 5.4a) and *Oratosquillina perpensa* (Figure 5.4b). The first cohort represents immature male, second cohort maturing and third cohort mature male.

Figure 5.5a shows the monthly distribution of male *Miyakea nepa* according to maturation stages. The mean percentage frequency of immature males (stage I) was the lowest (4.5 %) among the three maturation stages. Immature males only occurred in ten months over the 18 months of sampling, observed from December 04 – May 05, and in July 05 – November 05 (Figure 5.5a). Maturing (stage II) and mature males (stage III) occurred throughout the year with variable numbers. The mean percentage frequency of maturing and mature males was 34.7 % and 60.8 %, respectively.

The mean percentage frequency of immature males of *Oratosquillina perpensa* was 19 %. Immature males were found in ten months over the 18 months of sampling, from September 04 – March 05, August 05 and from December 05-January 06 (Figure 5.5b). 57 % of the males were in stage II (maturing) while 24 % of males were mature (stage III) males. Mature males were found throughout the year except June 05 (Figure 5.5b).

Since it may be useful to know the carapace length at maturity given the penis length, a regression analysis of both variables was carried out. Figure 5.6a shows the carapace length (CL) against penis length (PL) for male *Miyakea nepa* in Matang. Overall, the relationship between two variables is a linear one although individuals with larger carapace tend to have more variable penis lengths. The regression equation CL = 5.053 + 1.969 (PL) was significant at $p < 0.001$, with $r^2 = 0.959$.

Figure 5.6b shows the plots of carapace length against penis length of male *Oratosquillina perpensa* in Matang. The regression equation CL = 4.012 + 2.171 (PL) generated for *Oratosquillina perpensa* was significant at $p < 0.001$ with $r^2 = 0.930$.

Table 5.2 summarizes the predicted carapace lengths at maturity for *Miyakea nepa* and *Oratosquillina perpensa* using the above regression equations. The predicted carapace length of immature, maturing and mature males for *Miyakea nepa* was 12.7 mm, 18.2 mm and 24.8 mm, respectively. For *Oratosquillina perpensa*, the carapace lengths for the same maturity stages were 15.9 mm, 22.3 mm and 27.7 mm, respectively.

5.1.1.4 Histological examinations of testis.

Histological sections of the testis for the three maturation stages (immature, maturing and mature) were examined for *Miyakea nepa*. The types and numbers of germ cells that were contained on the histological section of the testis for immature, maturing and mature male are described as follows:

Stage I (immature; Figure 5.7a): Carapace length = 11.90 mm. The testis shows a thick layer (29-52 µm) of developing spermatogonia beneath the thin germinal layer around the periphery. An empty lumen is found at the centre of the testis.

Table 5.1. Maturity stage of female stomatopod based on colour of ovaries and ovarian development.

Species	Mean carapace length (mm)	n	Stage	Colour of ovaries	Description of ovarian development
Miyakea nepa	21.3 ± 4.18	958	Stage I (Immature)	Translucent	Undeveloped ovaries or if present appear as thin lines, or less than 1/4 width of the thoracic somite and abdominal somite for larger individuals.
	29.0 ± 3.01	103	Stage II (Early-maturing)	Very light orange	Ovaries present along the median thoracic and abdominal body and occupy about 1/4 width of the thoracic somite and abdominal somite.
	28.9 ± 3.04	108	Stage III (Late-maturing)	Light orange	Ovaries present along the median thoracic and abdominal body and occupy about 1/2 width of the thoracic somite and abdominal somite.
	28.4 ± 3.02	292	Stage IV (Mature and gravid)	Dark orange	The paired ovaries were fully developed which cover the whole thoracic somite and abdominal somite and fused at the telson.
	30.7 ± 1.72	100	Stage V (Spent)	Translucent	Ovaries shrunken, present along the median thoracic and abdominal body and occupy about 1/4 width of the thoracic somite and abdominal somite.
Oratosquillina perpensa	19.9 ± 4.09	372	Stage I (Immature)	Translucent	Undeveloped ovaries or if present appear as thin lines, or less than 1/4 width of the thoracic somite and abdominal somite for larger individuals.
	25.4 ± 3.64	31	Stage II (Early-maturing)	Very light yellow	Ovaries present along the median thoracic and abdominal body and occupy about 1/4 width of the thoracic somite and abdominal somite.

Table 5.1, continued

Species	Mean carapace length (mm)	n	Stage	Colour of ovaries	Description of ovarian development
Oratosquillina perpensa	25.5 ± 2.36	27	Stage III (Late-maturing)	Light yellow	Ovaries present along the median thoracic and abdominal body and occupy about 1/2 width of the thoracic somite and abdominal somite.
	25.5 ± 3.18	103	Stage IV (Mature and gravid)	Yellow	The paired ovaries were fully developed which cover the whole thoracic somite and abdominal somite and fused at the telson.
	26.6 ± 0.72	48	Stage V (Spent)	Translucent	Ovaries shrunken, present along the median thoracic and abdominal body and occupy about 1/4 width of the thoracic somite and abdominal somite.
Cloridopsis scorpio	19.9 ± 2.58	14	Stage I (Immature)	Translucent	Undeveloped ovaries or if present appear as thin lines, or less than 1/4 width of the thoracic somite and abdominal somite for larger individuals
	22.5	1	Stage II (Early-maturing)	Very light yellow	Ovaries present along the median thoracic and abdominal body and occupy about 1/4 width of the thoracic somite and abdominal somite.
			Stage III (Late-maturing)	No sample	
			Stage IV (Mature and gravid)	No sample	
			Stage V (Spent)	No sample	

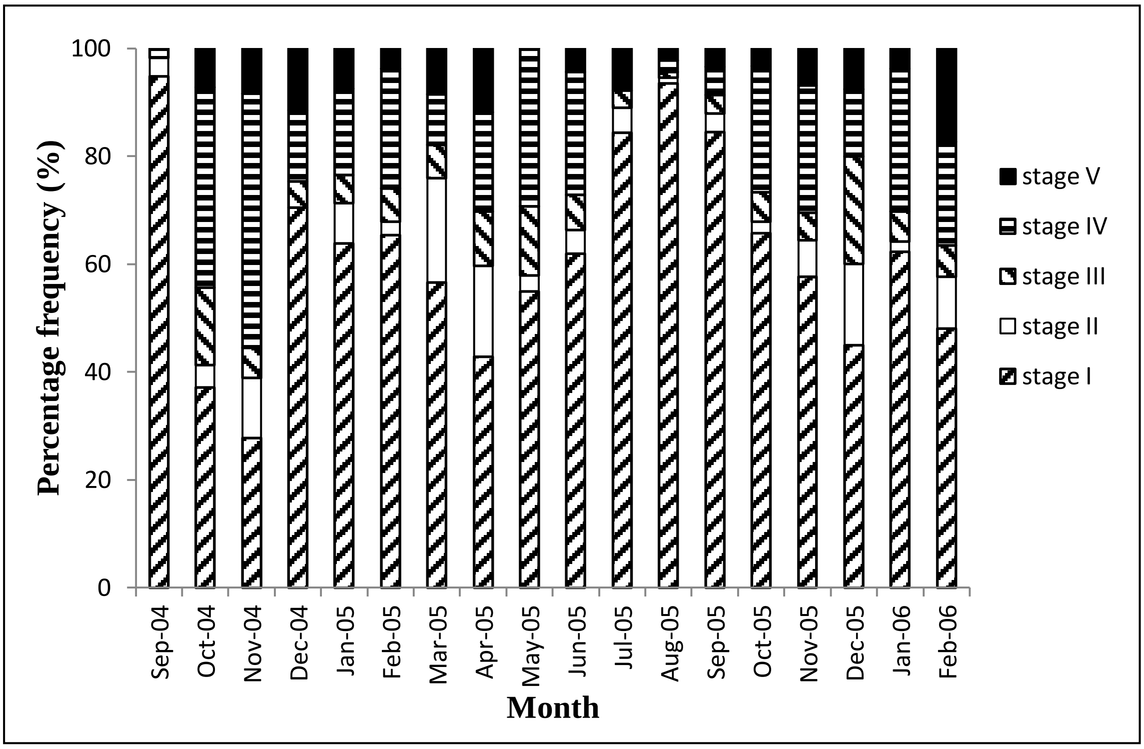


Figure 5.3a Monthly changes in percentage of female *Miyakea nepa* according to five maturation stages in Matang, Perak.

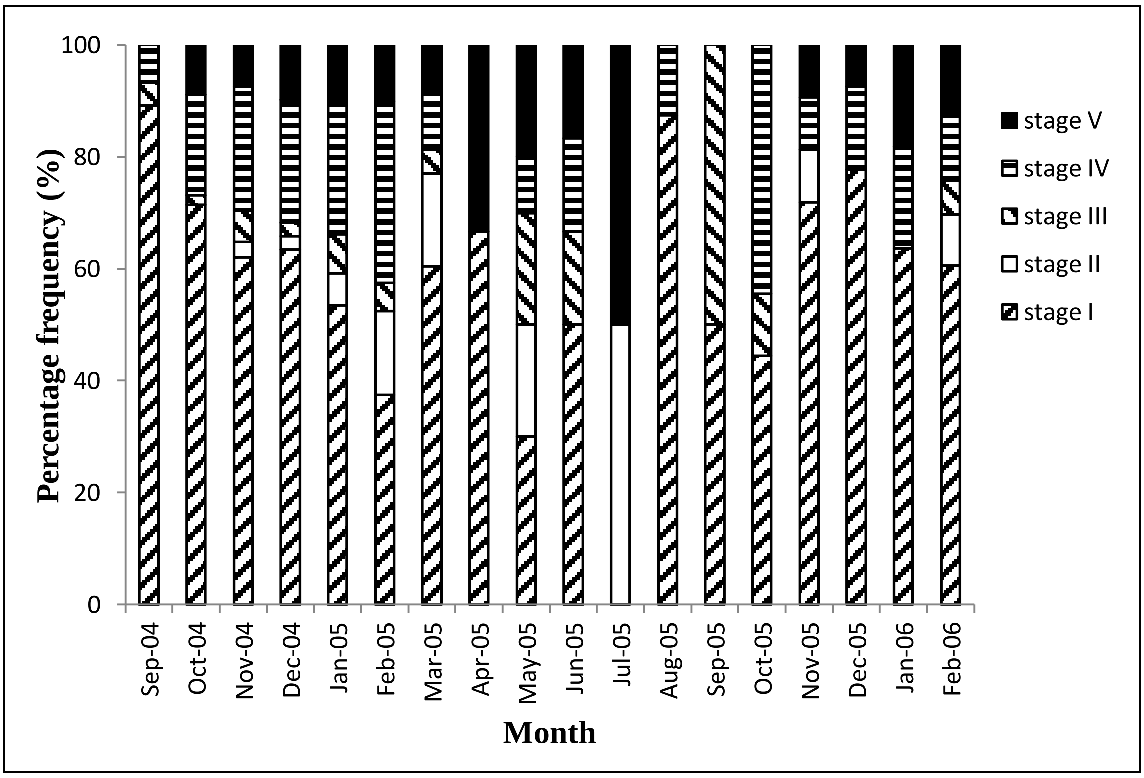


Figure 5.3b Monthly changes in percentage of female *Oratosquillina perpensa* according to five maturation stages in Matang, Perak.

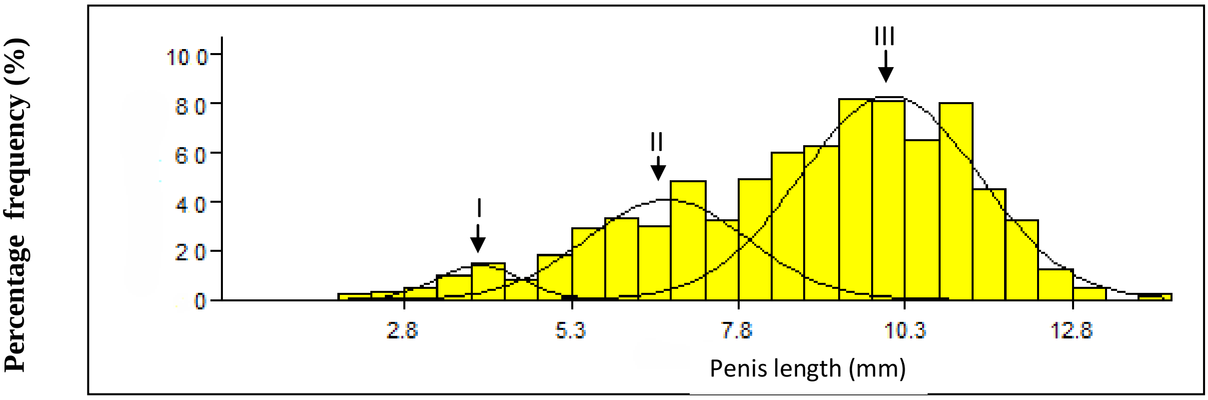


Figure 5.4a. Percentage frequency of male *Miyakea nepa* by penis length classes. Three cohorts were computed using Bhattacharya method. I = first cohort (immature), II = second cohort (maturing), III = third cohort (mature).

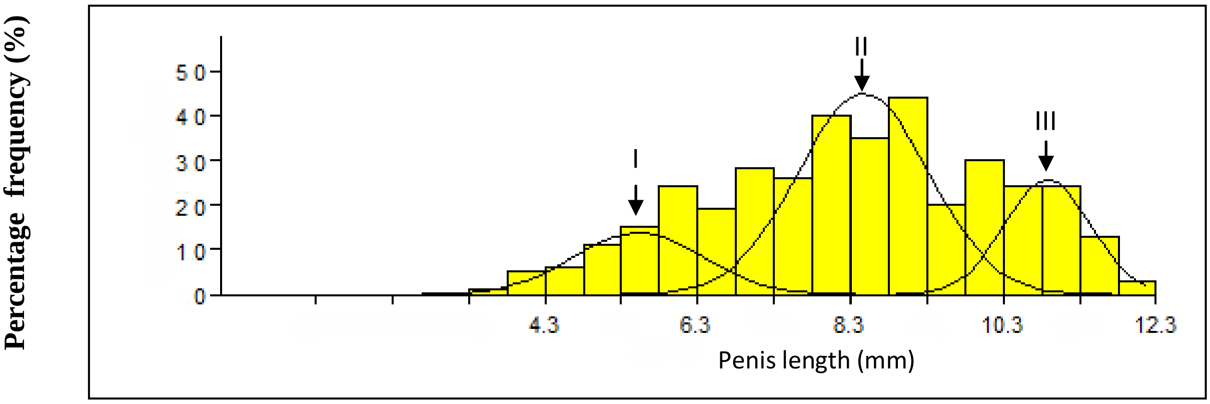


Figure 5.4b. Percentage frequency of male *Oratosquillina perpensa* by penis length classes. Three cohorts were computed using Bhattacharya method. I = first cohort (immature), II = second cohort (maturing), III = third cohort (mature).

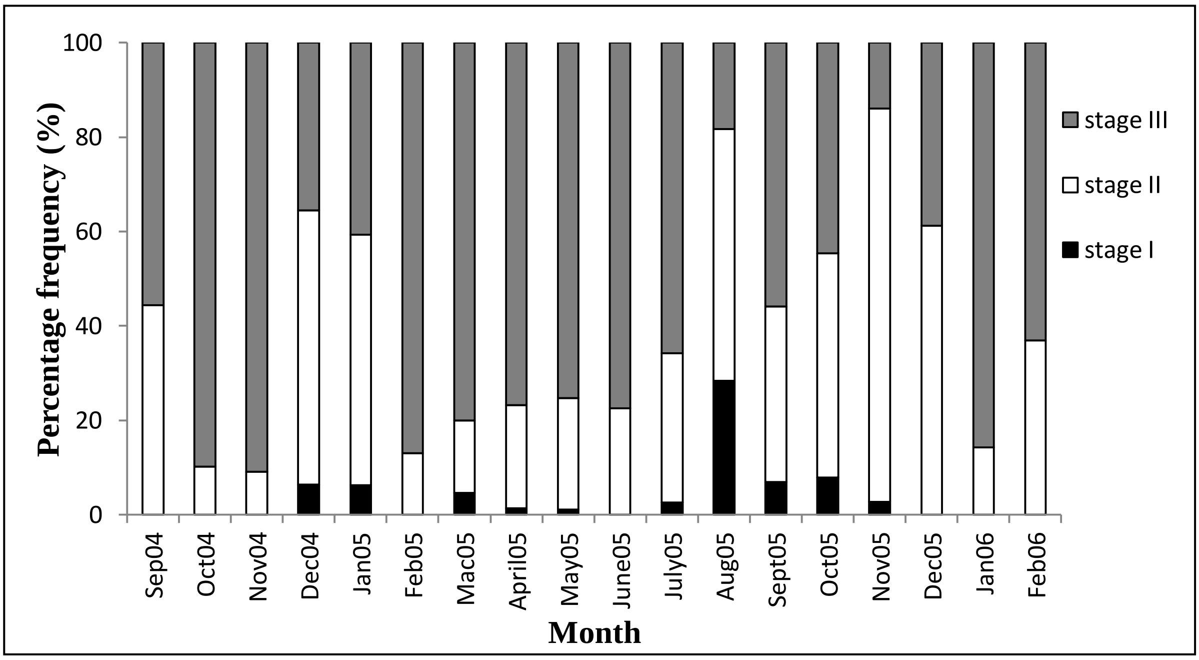


Figure 5.5a Monthly changes in mean percentage of male *Miyakea nepa* according to three maturation stages in Matang, Perak.

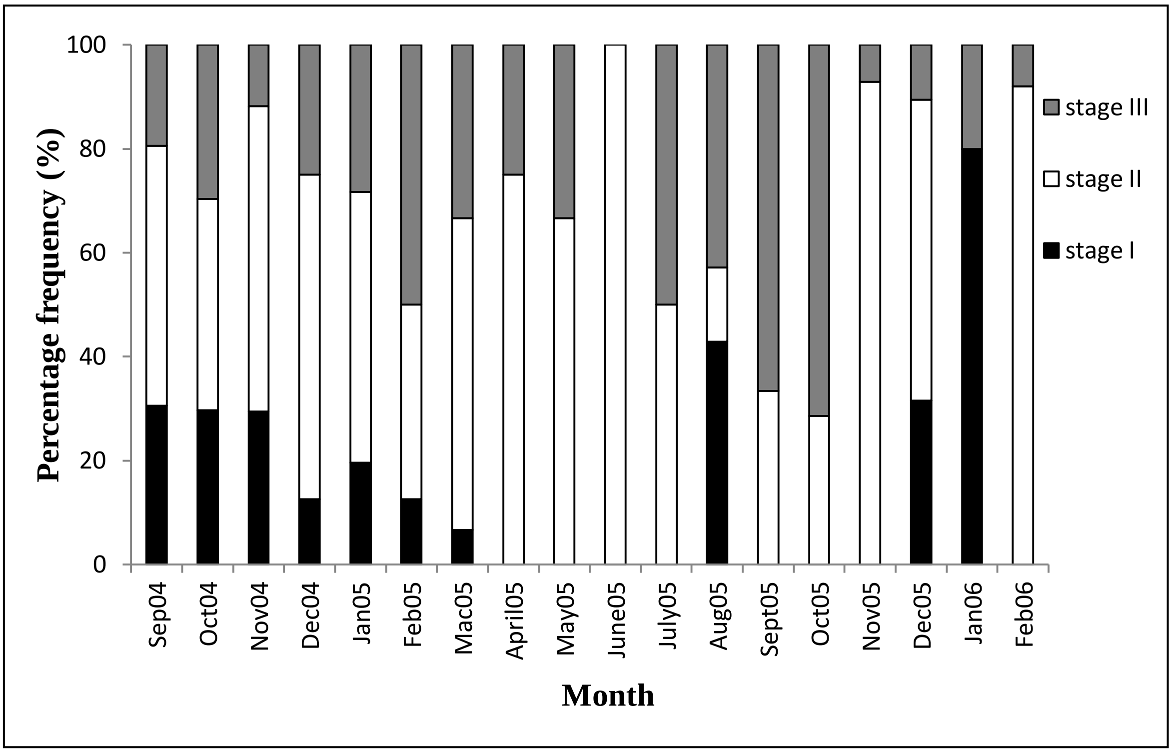


Figure 5.5b Monthly changes in mean percentage of male *Oratosquillina perpensa* according to three maturation stages in Matang, Perak.

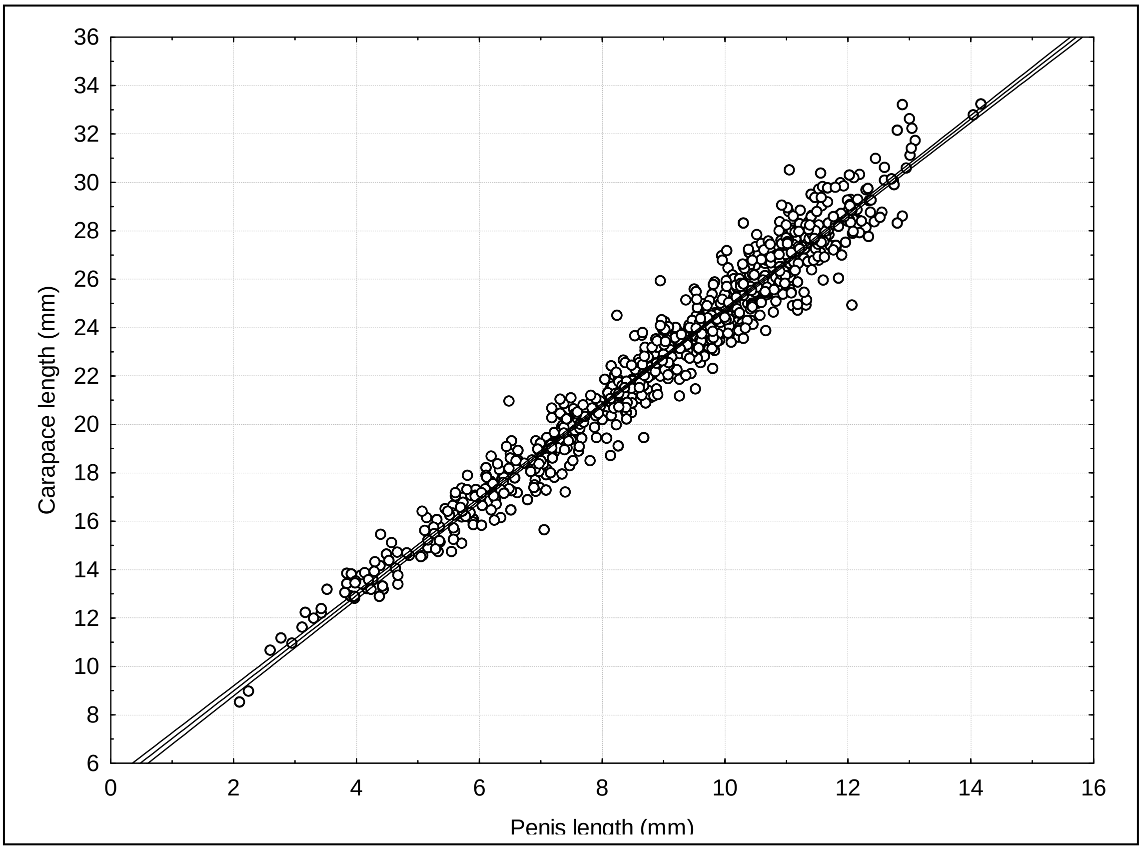


Figure 5.6a. Carapace length (mm) against penis length (mm) of males *Miyakea nepa* in Matang.

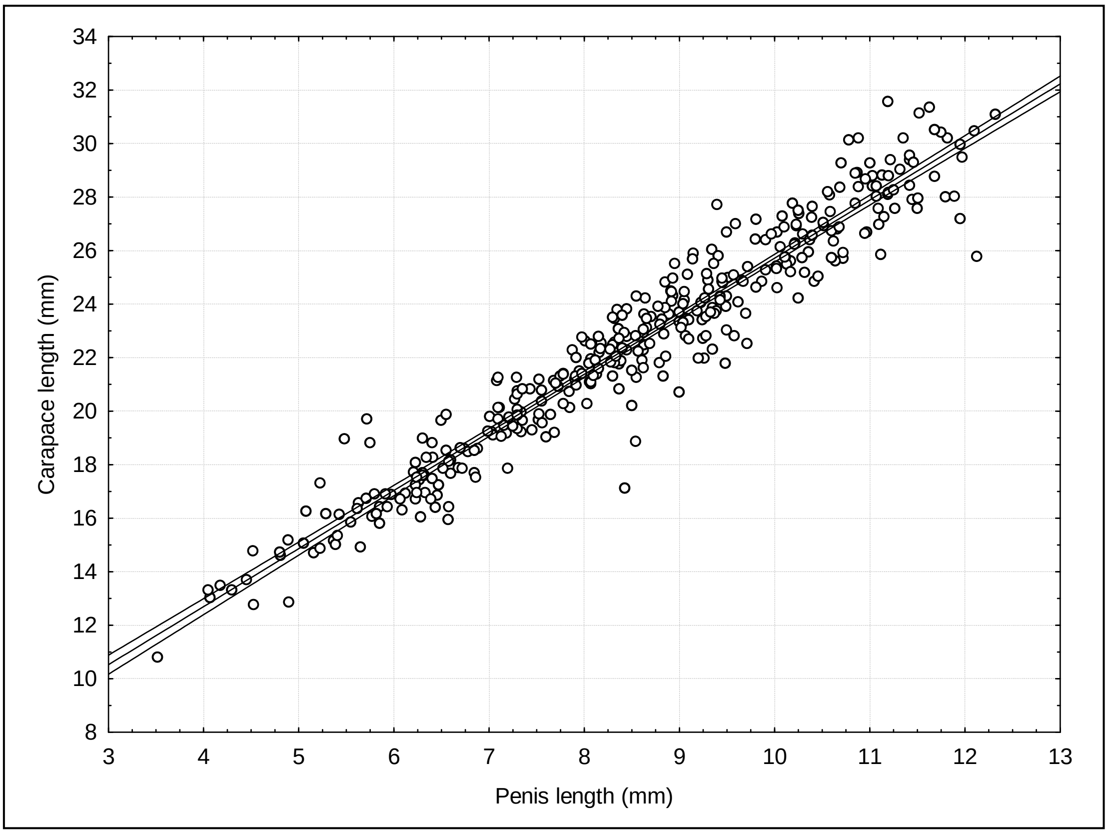


Figure 5.6b. Carapace length (mm) against penis length (mm) of males *Oratosquillina perpensa* in Matang.

Table 5.2. Mean penis length computed by Bhattacharya method, and mean carapace length and range of carapace length predicted by regression equation for male *Miyakea nepa* and *Oratosquillina perpensa* in Matang, Perak.

Species	Cohort	Mean penis length (mm)	Predicted mean carapace length (mm)	Range of carapace length (mm)
Miyakea nepa	1 (Immature)	3.9 ± 0.62	12.7	11.5-14.0
	2 (Maturing)	6.7 ± 1.20	18.2	15.9-20.6
	3 (Mature)	10.02 ±1.34	24.8	22.1-27.4
Oratosquillina perpensa	1 (Immature)	5.5 ± 0.85	15.9	14.1-17.8
	2 (Maturing)	8.4 ± 0.86	22.3	20.4-24.1
	3 (Mature)	10.8 ± 0.57	27.7	26.2-28.7

Stage II (maturing; Figure 5.7b): Carapace length = 17.93 mm. The testis shows development of spermatogonia, spermatocytes and spermatids towards the lumen. Spermatogonia are large cells (5-7 µm) now forming a thinner layer of 2-4 cells thick at the periphery. The number of spermatocytes (with actively dividing nuclei) exceeded that of spermatogonia and spermatids. Spermatocyte cells (3-4 µm) form a layer 2-3 times thicker than the spermatogonia layer. The spermatids (nearest the lumen) contain darker stained nuclei than spermatocytes. They do not form a layer but in nests or patches nearest the lumen. A clear lumen is found at the centre of the testis.

Stage III (mature; Figure 5.7c): Carapace length = 25.30 mm. The testis now contains spermatogonia, spermatocytes, spermatids and spermatozoa. The number of spermatids exceeded that of spermatogonia and spermatocytes. In just mature testes, or testes of older males, the number of spermatozoa may be few in the lumen. However, the lumen contains eosinophilic, clear unknown seminal substance stained light red.

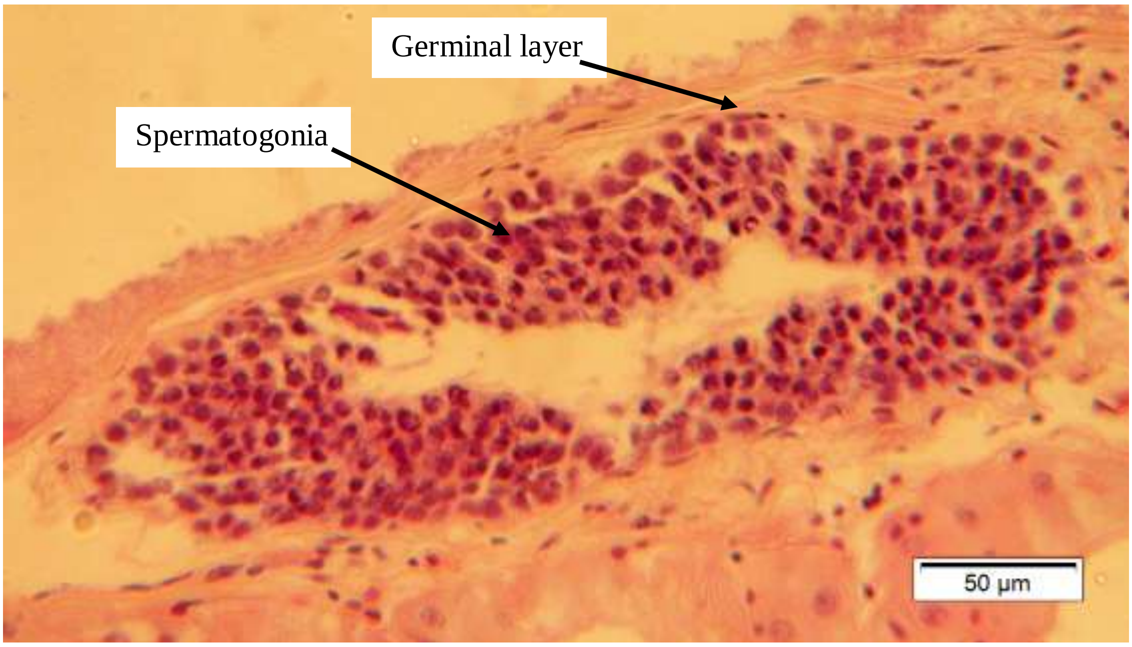


Figure 5.7a. Histological section of the testis of immature *Miyakea nepa*.

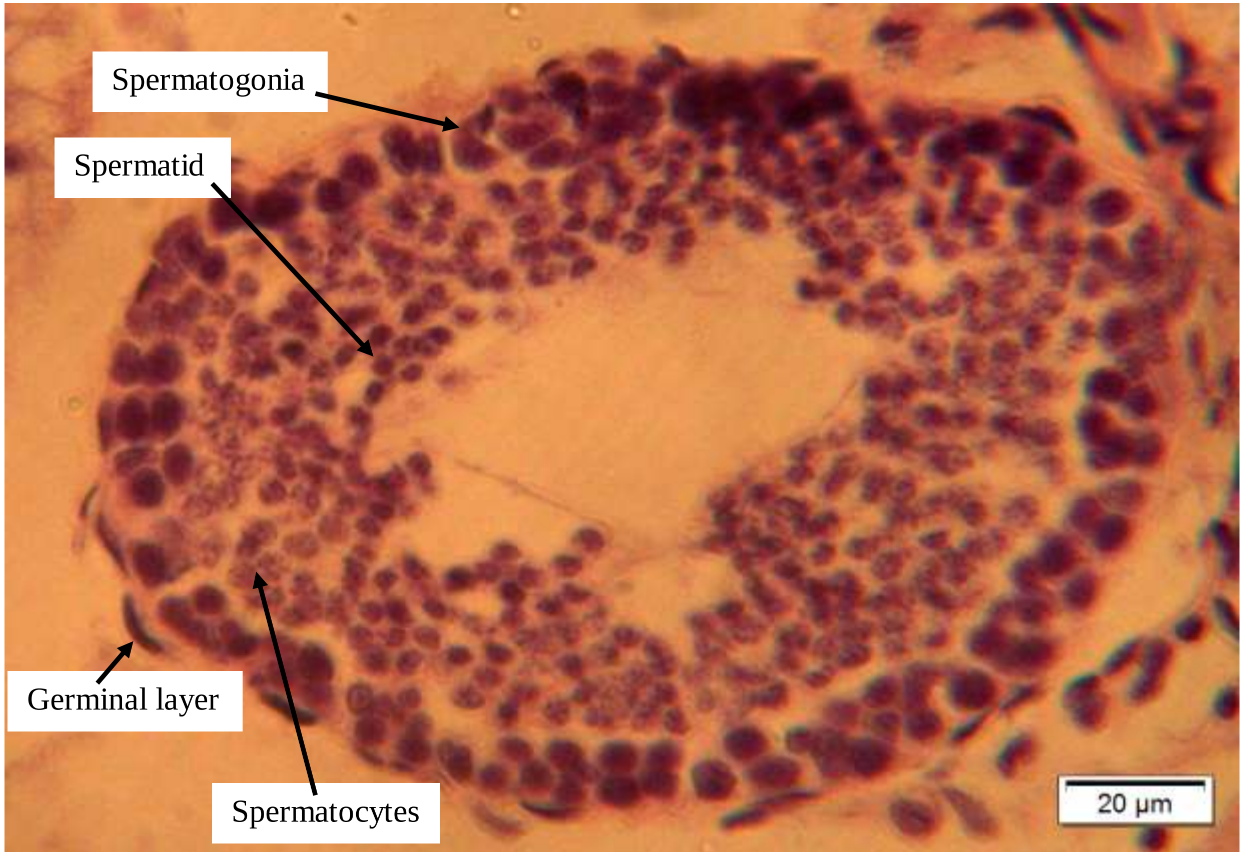


Figure 5.7b. Histological section of the testis of mature *Miyakea*

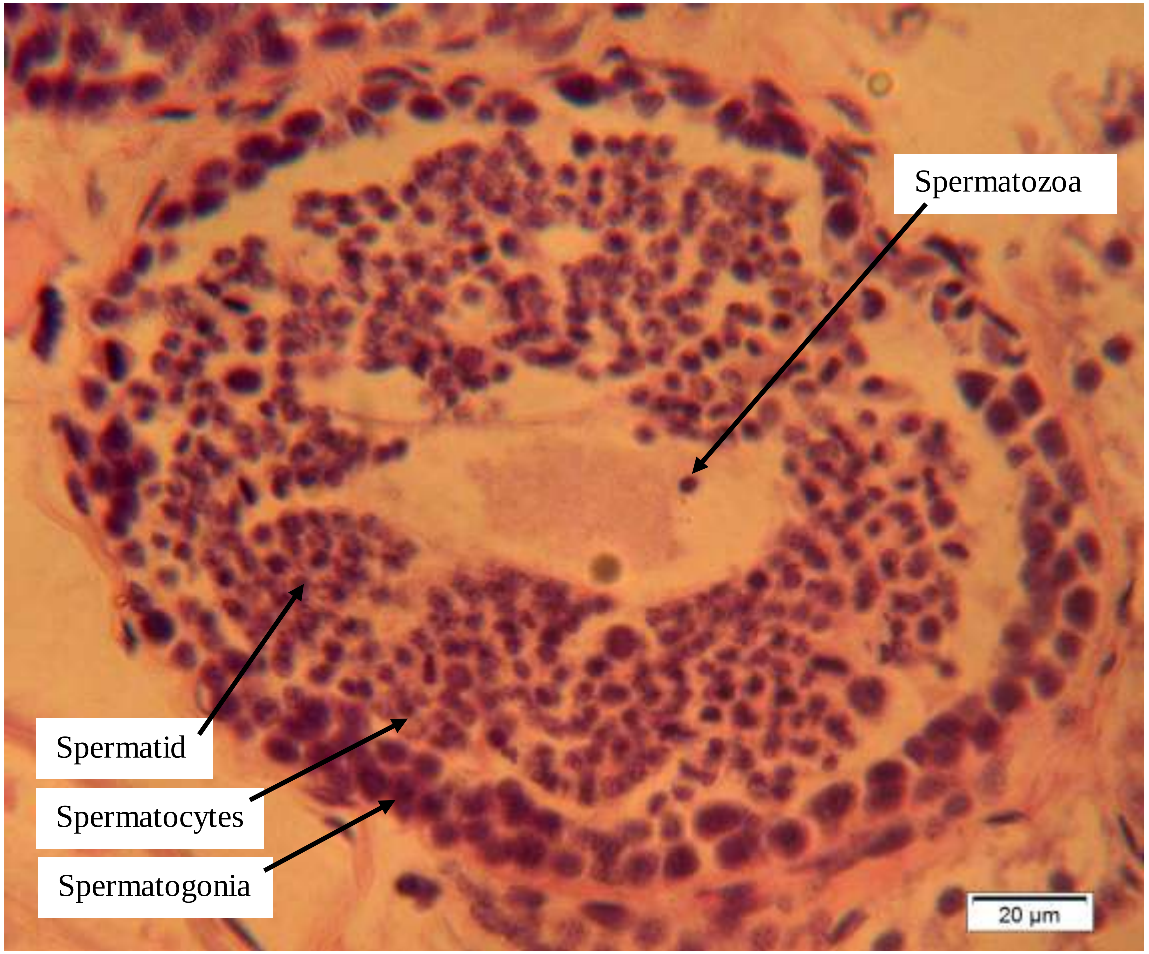


Figure 5.7c. Histological section of the testis of mature *Miyakea nepa*.

5.1.1.5 Spawning season

a) *Miyakea nepa*

Figure 5.8a showed the seasonal changes in the percentage of mature female (stage IV) *Miyakea nepa* recorded at three different depth strata in Matang, Perak. The distribution of mature females at the three study sites showed similar temporal pattern with the highest abundance mainly occurred at stratum 3. The percentage of mature female fluctuated throughout the sampling periods but with a well-defined resting phase lasting from July 05 to September 05. Generally, spawning were year-round but with two spawning peaks; one that was protracted (October to February) during the northeast moosoon, and the other peak (April to June) occurring in the southwest monsoon (Figure 5.8a).

b) *Oratosquillina perpensa*

Oratosquillina perpensa showed different pattern of distribution among the three study areas with most of the mature females (stage IV) occurring mainly at stratum 2 (Figure 5.8b). Generally, *Oratosquillina perpensa* was found to have similar spawning peaks as *Miyakea nepa*. There were also two spawning peaks with a more protracted spawning period (October to February) and another peak around June; both peaks also occurred in the two monsoons (Figure 5.8b).

5.1.2 Stomatopod larval ecology

5.1.2.1 Identification of stomatopod larvae

A total of 501 planktonic stomatopod larvae were earlier sampled by bongo nets from the upper estuary (7 km from Sangga Kecil river mouth) to offshore (16 km from Sangga Kecil river mouth) waters from November 2002 to October 2003. 179 individuals (35.7%) were found to belong to *Cloridopsis scorpio,* 4 individuals (0.80%)

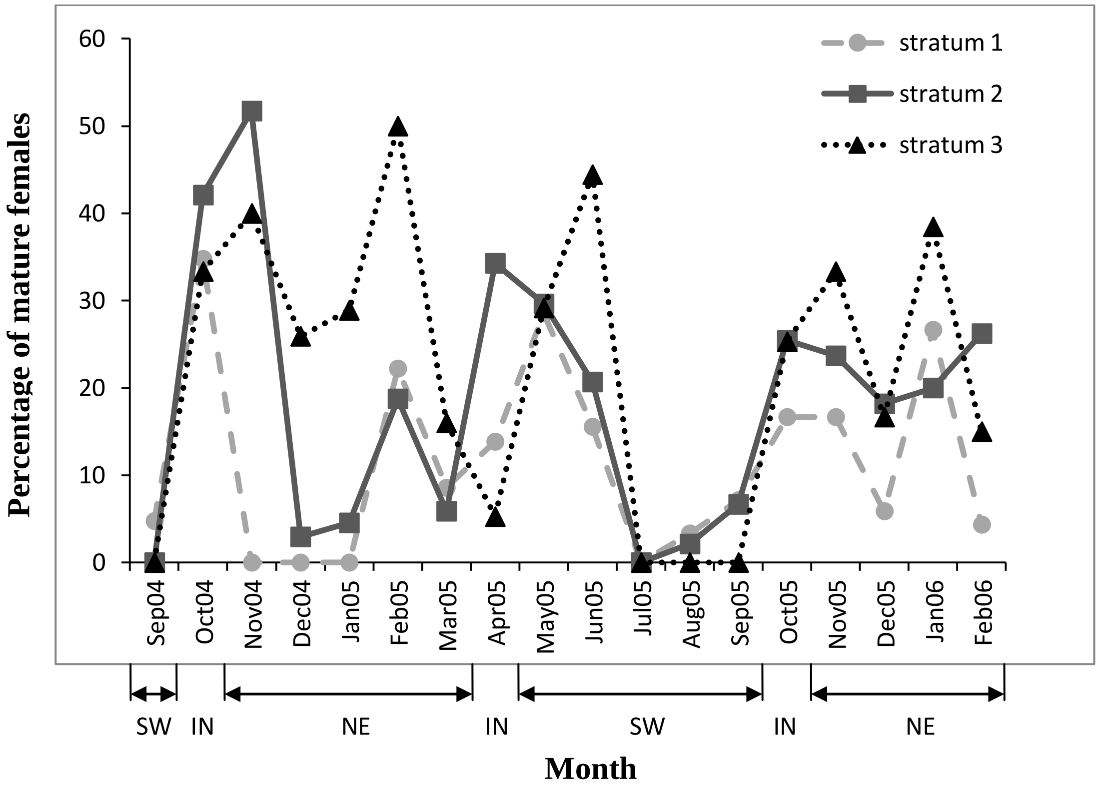


Figure 5.8a. Seasonal changes in the percentage of mature females (stage IV) *Miyakea nepa* recorded at three different depth strata over the 18 months of survey.

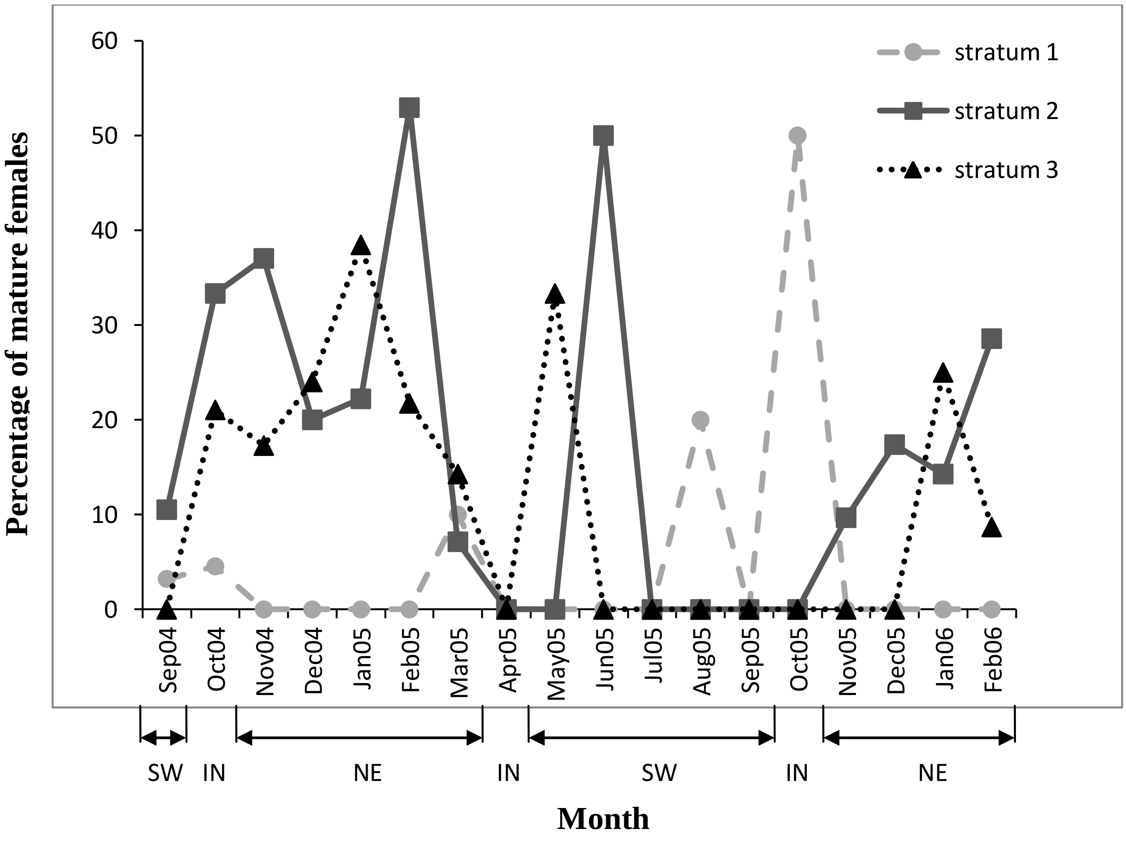


Figure 5.8b. Seasonal changes in the percentage of mature females (stage IV) *Oratosquillina perpensa* recorded at three different depth strata over the 18 months of survey.

belonged to *Miyakea nepa* and the other 318 individuals (63.5%) belonged to unidentified species.

5.1.2.2 Descriptions of different developmental stages of stomatopod larvae according to species.

a) *Cloridopsis scorpio*

Cloridopsis scorpio larvae consisted of four middle stages (first pelagic larval stage to fourth pelagic larval stage) and two late stages (fifth pelagic larval stage and sixth pelagic larval stage) features. Early stage larva was not found in the plankton samples. Descriptions of the six different pelagic developmental stages are presented as follows:

i) First pelagic larval stage (Figure 5.9A & Figure 5.9B)

Measurements (mm): Carapace length, CL = 1.50 mm; Total length, TL = 5.20 mm

Rostrum with 2 ventral spinules. Carapace triangular with 5 ventrolateral spinules in the alignment: 1 on anterior and 4 on posterior. Two characteristic small spinules found at the posterior margin of carapace. Tip of posterolateral spine reaches the level of the submedian tooth of telson.

Antennule (Figure 5.9C): Antennule with two-segmented inner flagellum, apical segment armed with 1 long seta and 1 or 2 short setae. Median flagellum absent. Outer flagellum armed with 1 long and 1 short seta at apex, followed by 2 to 4 aesthetascs arranged in two groups; each group with 1 or 2 aesthetascs.

Antenna (Figure 5.9D): Antenna with 14 plumose setae. Endopod of antennal flagellum present as bud.

Mandible (Figure 5.9E): Incisor process serrate with about 7 teeth, molar process with tiny teeth.

First maxilla (Figure 5.9F): Coxal endites bearing 4 marginal teeth. Basal endite bearing 1 tooth flanked by 2 strong setae. Palp of first maxilla with long setae at apex.

Second maxilla (Figure 5.9G): Armed with 5 setae.

First thoracopod (Figure 5.9H): Inner margin of propodus with 3 groups of setae, each with 2 or 3 setae. Dactylus small and pointed.

Second thoracopod (Figure 5.9I): Propodus with one strong proximal tooth followed by 2 strong teeth in opposition and 15 denticles on inner margin. Dactylus does not have any additional tooth other than the terminal tooth.

Third to fifth thoracopod absent.

Sixth to eighth thoracopod absent.

First pleopod (Figure 5.9J): Endopod bearing 7 setae. Appendix interna present. Exopod bearing 9 setae.

Fifth pleopod (Figure 5.9K): Present as biramous bud without setae.

Uropod (Figure 5.9L): absent.

Pleotelson (Figure 5.9L): Pleotelson with wide submedian space. There were 3 intermediate denticles on each side followed by 16 submedian denticles.

ii) Second pelagic larval stage (Figure 5.10A & Figure 5.10B)

Measurements (mm): CL = 1.66 mm; TL = 5.92 mm

Rostrum and carapace as in first stage. The tip of posterolateral spine reaches the level of the intermediate tooth of telson

Antennule (Figure 5.10C): Antennule with three-segmented inner flagellum. Median flagellum bud present as part of outer flagellum.

Antenna (Figure 5.10D): Antenna with 17 plumose setae. Length of the endopod bud increased.

Mandible (Figure 5.10E): Mandible as in first stage.

First maxilla (Figure 5.10F): Coxal endites bearing 4 marginal teeth and 1 short setae. Basal endite and palp unchanged.

Second maxilla (Figure 5.10G): Armed with 6 setae.

First thoracopod (Figure 5.10H): Carpus with 1 seta distally. Inner margin of propodus with four groups of setae, each group with 2 or 3 setae. Dactylus unchanged.

Second thoracopod (Figure 5.10I): Propodus with one strong proximal tooth followed by 2 strong teeth in opposition and 19 denticles on inner margin. Dactylus unchanged.

Third to fifth thoracopod (Figure 5.10J): present as buds.

Sixth to eighth thoracopod absent.

First pleopod (Figure 5.10K): Endopod bearing 9 setae with 2 of it located at inner margin. Appendix interna unchanged. Exopod bearing 12 setae.

Fifth pleopod (Figure 5.10L): Fifth pleopod small. Endopod bearing 2 setae and appendix interna present. Exopod bearing 4 setae.

Uropod (Figure 5.10M): present as small bud.

Pleotelson (Figure 5.10M): Submedian space became slightly narrow. Number of denticles unchanged.

iii) Third pelagic larval stage (Figure 5.11A & Figure 5.11B)

Measurements (mm): CL = 2.20 mm; TL = 7.60 mm

Rostrum with 3 ventral spinules. Number of ventrolateral spinules unchanged. The tip of posterolateral spine reaches the level of the lateral tooth of telson.

Antennule (Figure 5.11C): Antennule with three-segmented inner flagellum. Median flagellum two segmented with 1 long seta at apex. Outer flagellum bearing 6 to 9 aesthetascs arranged in three groups. Each group with two or three aesthetascs.

Antenna (Figure 5.11D): Antenna with 18 plumose setae. Endopod bud elongated and faintly segmented.

Mandible (Figure 5.11E): Mandible unchanged.

First maxilla (Figure 5.11F): Coxal endite bearing 5 teeth. Basal endite and palp unchanged.

Second maxilla (Figure 5.11G): Second maxilla faintly segmented with 9 setae.

First thoracopod (Figure 5.11H): Carpus with 2 setae distally. Number of setae on the inner margin of propodus unchanged. Dactylus unchanged.

Second thoracopod (Figure 5.11I): Propodus bearing 20 denticles along inner margin.Dactylus unchanged.

Third to fifth thoracopod (Figure 5.11J): Third and fourth thoracopod long and faintly segmented, fifth thoracopod present as long bud.

Sixth to eighth thoracopod (Figure 5.11K): Sixth to eighth thoracopod present as small buds.

First pleopod (Figure 5.11L): Endopod bearing 13 setae with three of it located at inner margin. Appendix interna unchanged. Exopod bearing 14 setae.

Fifth pleopod (Figure 5.11M): Endopod bearing 9 setae with 1 of it located at inner margin. Appendix interna unchanged. Exopod bearing 12 setae.

Uropod (Figure 5.11N): Uropod biramous.

Pleotelson (Figure 5.11O): Submedian space narrow. There were four intermediate denticles on each side followed by 16 submedian denticles.

iv) Fourth pelagic larval stage (Figure 5.12A & Figure 5.12B)

Measurements (mm): CL = 2.42 mm; TL = 8.29 mm

Rostrum and carapace as in third stage.

Antennule (Figure 5.12C): Antennule with three-segmented inner flagellum. Median flagellum three segmented with 1 long seta and 1 or 2 short setae at apex. Outer flagellum as in third stage.

Antenna (Figure 5.12D): Antenna with 20 plumose setae. Three-segmented endopod with length equal to the segment bearing it.

Mandible (Figure 5.12E): Mandible unchanged.

First maxilla (Figure 5.12F): Coxal endites bearing 7 teeth and 2 short setae. Basal endite and palp unchanged.

Second maxilla (Figure 5.12G): Two-segmented with 12 setae.

First thoracopod (Figure 5.12H): Carpus with four setae distally. Inner margin of propodus with five groups of setae, each group with 1 to 3 setae. Dactylus unchanged.

Second thoracopod (Figure 5.12I): Propodus bearing 23 denticles along inner margin. Dactylus unchanged.

Third to fifth thoracopod (Figure 5.12J): Finger-like third and fourth thoracopod with three segments. Fifth thoracopod forming two segments.

Sixth to eighth thoracopod (Figure 5.12K): Buds increased in length, bifurcated.

First pleopod (Figure 5.12L): Endopod bearing 15 setae with 3 of it located at inner margin. Appendix interna unchanged. Exopod bearing 16 setae. Gill present as bud on inner proximal margin of exopod.

Fifth pleopod (Figure 5.12M): Endopod bearing 13 setae with 2 of it located at inner margin. Appendix interna unchanged. Exopod bearing 16 setae. Gill present as bud on inner proximal margin of exopod.

Sixth abdominal somite (Figure 5.12O): Sixth abdominal somite articulated.

Uropod (Figure 5.12N): Endopod and exopod clearly differentiated. Rudimentary forked ventral process of uropod present.

Pleotelson (Figure 5.12O): Five intermediate denticles on each side and 16 submedian denticles.

v) Fifth pelagic larval stage (Figure 5.13A & Figure 5.13B)

Measurements (mm): CL = 2.74 mm; TL = 9.53 mm

Number of rostrum ventral spinules and carapace ventrolateral spinules were same as in fourth stage. The tip of posterolateral spine reaches midway between anterior margin of pleotelson and lateral tooth of telson.

Antennule (Figure 5.13C): Antennule with four-segmented inner flagellum. Median flagellum with three segments. Outer flagellum bearing 8 to 14 aesthetascs arranged in four groups. Each group with 2 to 4 aesthetascs.

Antenna (Figure 5.13D): Antenna with 26 plumose setae. Endopod with three segments.

Mandible (Figure 5.13E): Incisor process serrate with about 8 teeth. Molar process unchanged.

First maxilla (Figure 5.13F): Coxal endite bearing 9 teeth. Basal endite bearing 1 tooth flanked by 1 strong setae. Palp well developed with 1 long and 1 short setae at apex.

Second maxilla (Figure 5.13G): Three-segmented with 15 setae and proximal segment with one endite.

First thoracopod (Figure 5.13H): Carpus with 5 setae distally. Inner margin of propodus consisted of six groups of setae with 2 or 3 setae in each group. Dactylus unchanged.

Second thoracopod (Figure 5.13I): Propodus bearing 27 denticles along inner margin. Dactylus unchanged.

Third to fifth thoracopod (Figure 5.13J): Five segmented third and fourth thoracopod with partially developed dactylus. Fifth thoracopod forming four segments.

Sixth to eighth thoracopod (Figure 5.13K): Endopods and exopods of sixth to eighth thoracopod clearly differentiated with faintly segmented.

First pleopod (Figure 5.13L): Endopod bearing 18 setae with 4 of it located at inner margin. Appendix interna unchanged. Exopod bearing 19 setae with dual-lobed gill present.

Fifth pleopod (Figure 5.13M): Endopod bearing 18 setae with three of it located at inner margin. Appendix interna unchanged. Exopod bearing 20 setae with dual-lobed gill present.

Sixth abdominal somite (Figure 5.13O): partially separated from pleotelson with a pair of sub-median dorsal spines.

Uropod (Figure 5.13N): Forked ventral process elongated to about half length of endopod. Exopod with one spine on outer margin armed with zero to two plumose setae on the distal margin.

Pleotelson (Figure 5.13O): 1 lateral and 5 intermediate denticles on each side followed by 16 submedian denticles.

vi) Sixth pelagic larval stage (Figure 5.14A & Figure 5.14B)

Measurements (mm): CL = 3.52 mm; TL = 10.69 mm

Number of rostrum ventral spinules and carapace ventrolateral spinules unchanged. The tip of posterolateral spine reaches the level of the anterior margin of telson.

Antennule (Figure 5.14C): Seven-segmented inner flagellum. Median flagellum with five segments. Outer flagellum bearing 10 to 19 aesthetascs arranged in five groups, each with 2 to 4 aesthetascs.

Antenna (Figure 5.14D): Antenna with 30 plumose setae. Endopod with five segments.

Mandible (Figure 5.14E): Mandible unchanged.

First maxilla (Figure 5.14F): Coxal endite bearing 11 teeth. Basal endites as in fifth stage. Palp elongated with 1 long and 1 short seta at apex.

Second maxilla (Figure 5.14G): Second maxilla three segmented with 22 setae and proximal segment with 2 endites.

First thoracopod (Figure 5.14H): Carpus with six setae distally. Inner margin of propodus consist seven groups of setae with two or three setae in each group. Dactylus unchanged.

Second thoracopod (Figure 5.14I): Propodus armed with 36 denticles along inner margin. Dactylus unchanged.

Third to fifth thoracopod (Figure 5.14J): A large spine on each carpus, 1 to 3 setae on outer margin of carpus. 3 to 7 setae on outer margin of each propodus Dactylus developed. Spine on carpus and dactylus of fifth thoracopod still not well developed.

Sixth to eighth thoracopod (Figure 5.14K): Sixth to eighth thoracopod with two segmented exopods.

First pleopod (Figure 5.14L): Endopod bearing 19 setae with 5 of it located at inner margin. Appendix interna unchanged. Exopod bearing 23 setae with tri-lobed gill present

Fifth pleopod (Figure 5.14M): Endopod bearing 22 setae with 5 of it located at inner margin. Appendix interna unchanged. Exopod bearing 25 setae with tri-lobed gill present.

Sixth abdominal somite (Figure 5.14O): Sixth abdominal somite separated from pleotelson.

Uropod (Figure 5.14N): Endopod with 3 to 6 setae along distal margin. Forked ventral process with two sharp apices. Exopod with 3 spines on outer margin armed with 3 to 5 plumose setae distally.

Telson (Figure 5.14O): 1 lateral and 5 intermediate denticles on each side followed by 18 submedian denticles.

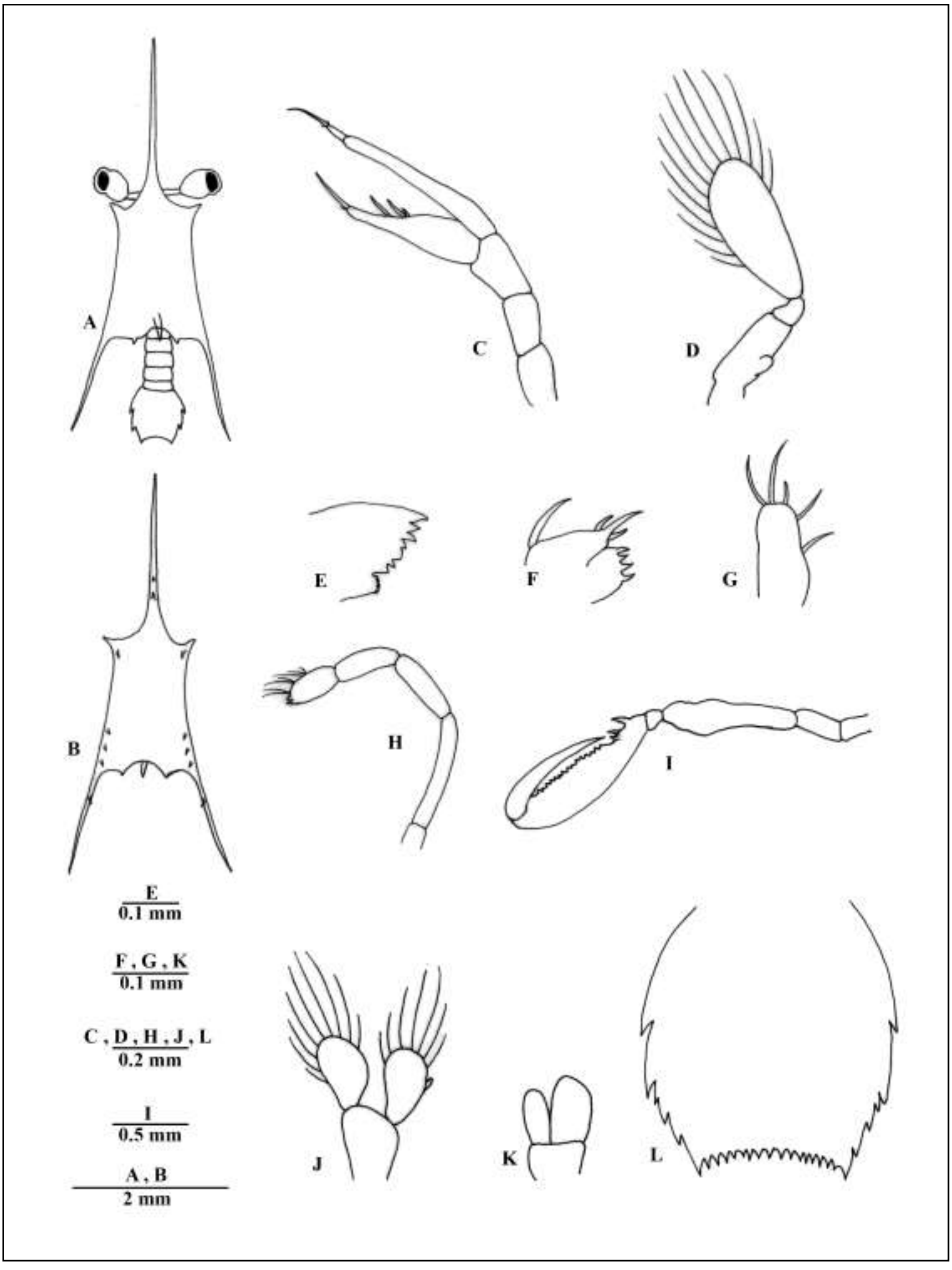


Figure 5.9. First pelagic larval stage of *Cloridopsis scorpio*. A = animal in dorsal view; B = carapace in ventral view; C = antennules; D = antenna; E = mandible; F = first maxilla; G = second maxilla; H = first thoracopod; I = second thoracopod; J = first pleopod; K = fifth pleopod; L = pleotelson. C – K = right parts; C – L = ventral view.

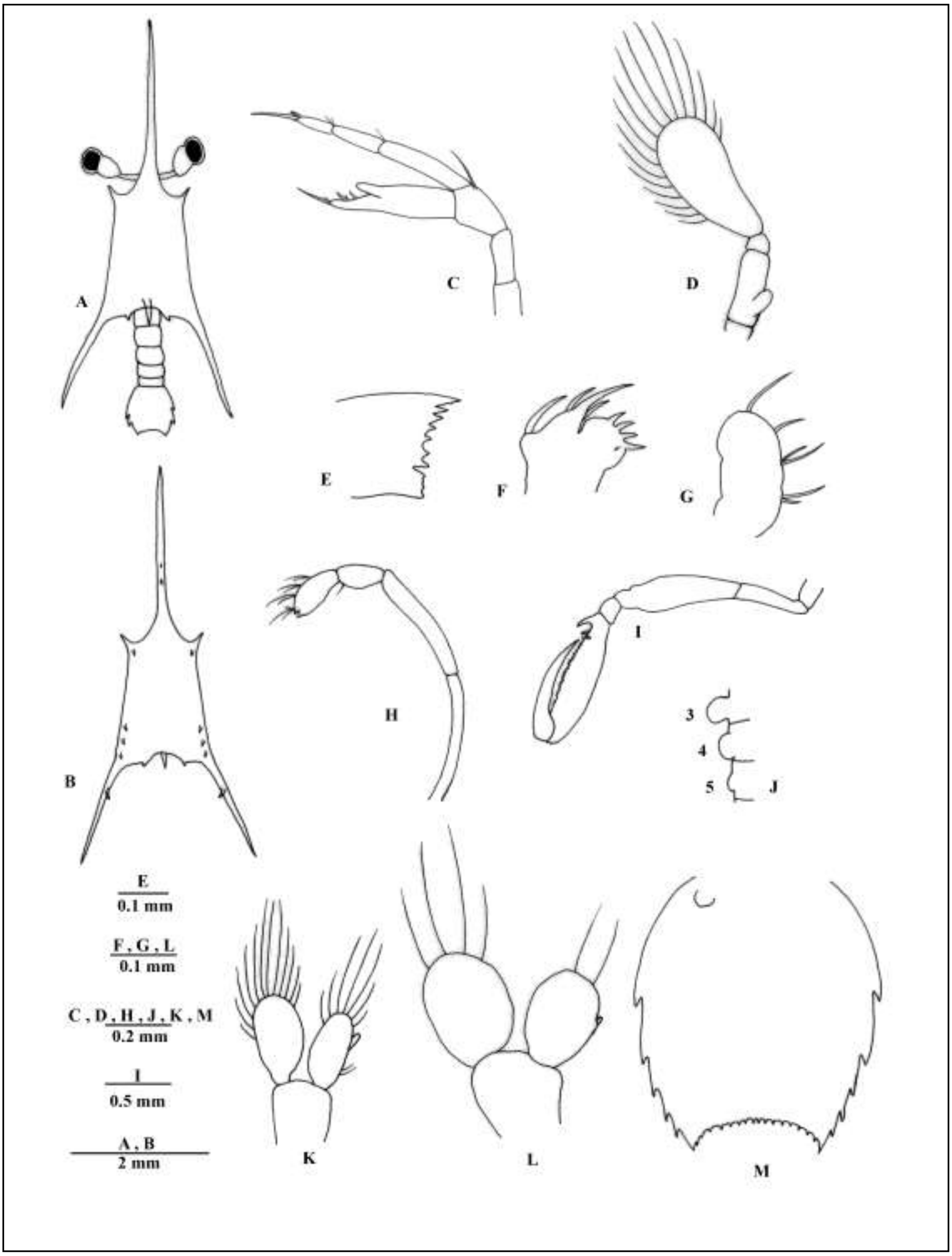


Figure 5.10. Second pelagic larval stage of *Cloridopsis scorpio*. A = animal in dorsal view; B = carapace in ventral view; C = antennules; D = antenna; E = mandible; F = first maxilla; G = second maxilla; H = first thoracopod; I = second thoracopod; J = third to fifth thoracopods; K = first pleopod; L = fifth pleopod; M = pleotelson. C – L = right parts; C – M = ventral view.

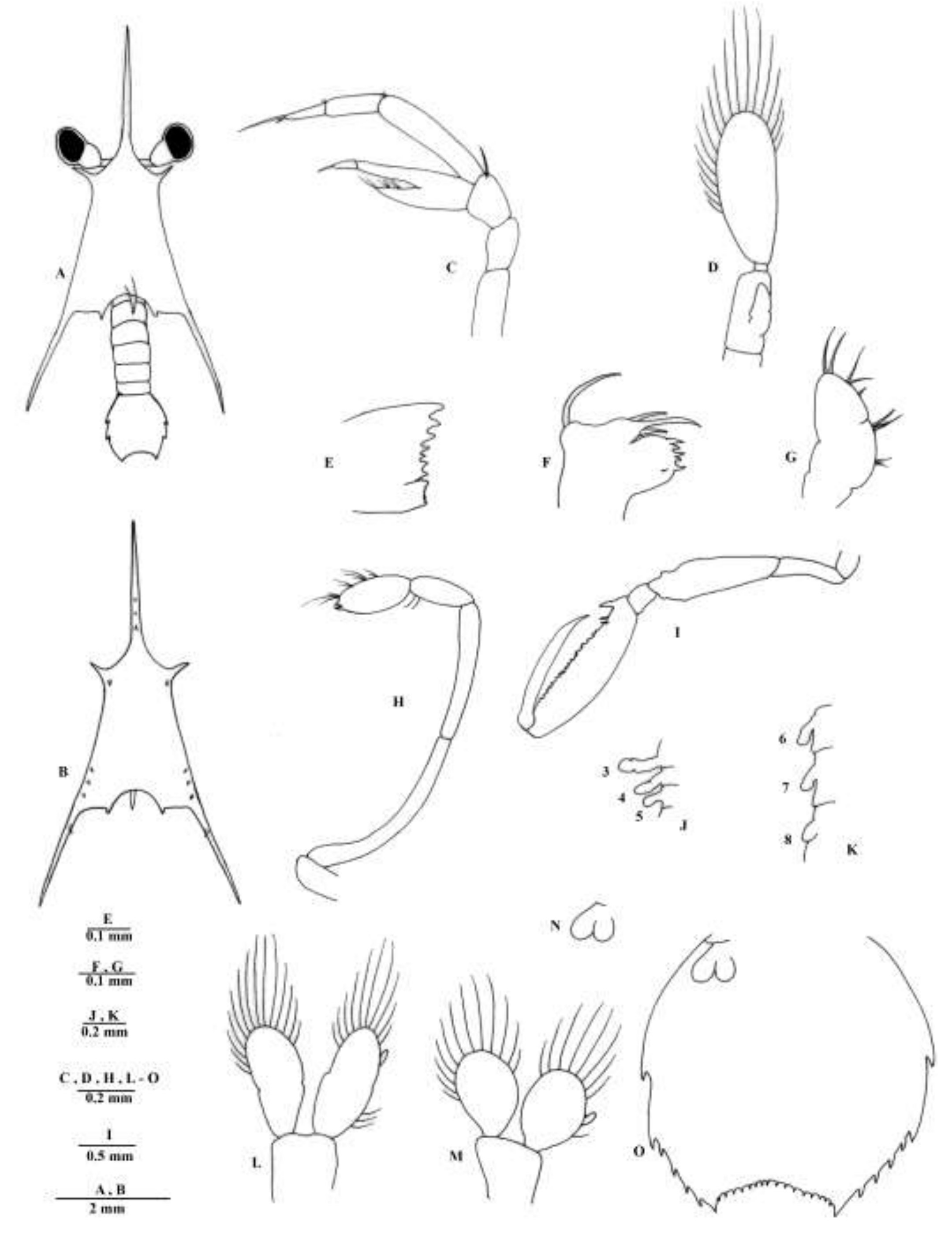


Figure 5.11. Third pelagic larval stage of *Cloridopsis scorpio*. A = animal in dorsal view; B = carapace in ventral view; C = antennules; D = antenna; E = mandible; F = first maxilla; G = second maxilla; H = first thoracopod; I = second thoracopod; J = third to fifth thoracopods; K = sixth to eight thoracopods; L = first pleopod; M = fifth pleopod; N = uropod; O = pleotelson. C – N = right parts; C – O = ventral view.

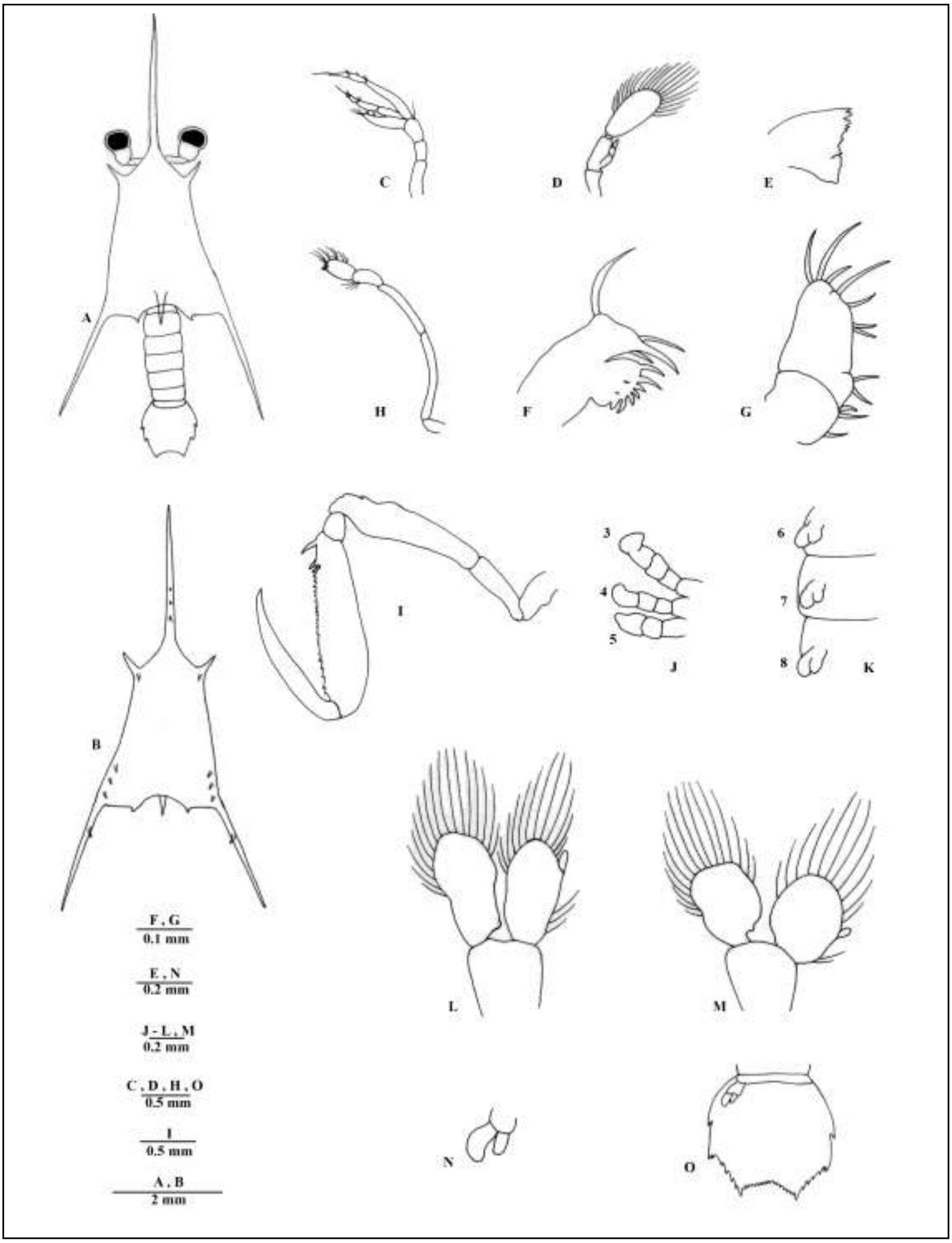


Figure 5.12. Fourth pelagic larval stage of *Cloridopsis scorpio*. A = animal in dorsal view; B = carapace in ventral view; C = antennules; D = antenna; E = mandible; F = first maxilla; G = second maxilla; H = first thoracopod; I = second thoracopod; J = third to fifth thoracopods; K = sixth to eight thoracopods; L = first pleopod; M = fifth pleopod; N = uropod; O = pleotelson. C – N = right parts; C – O = ventral view.

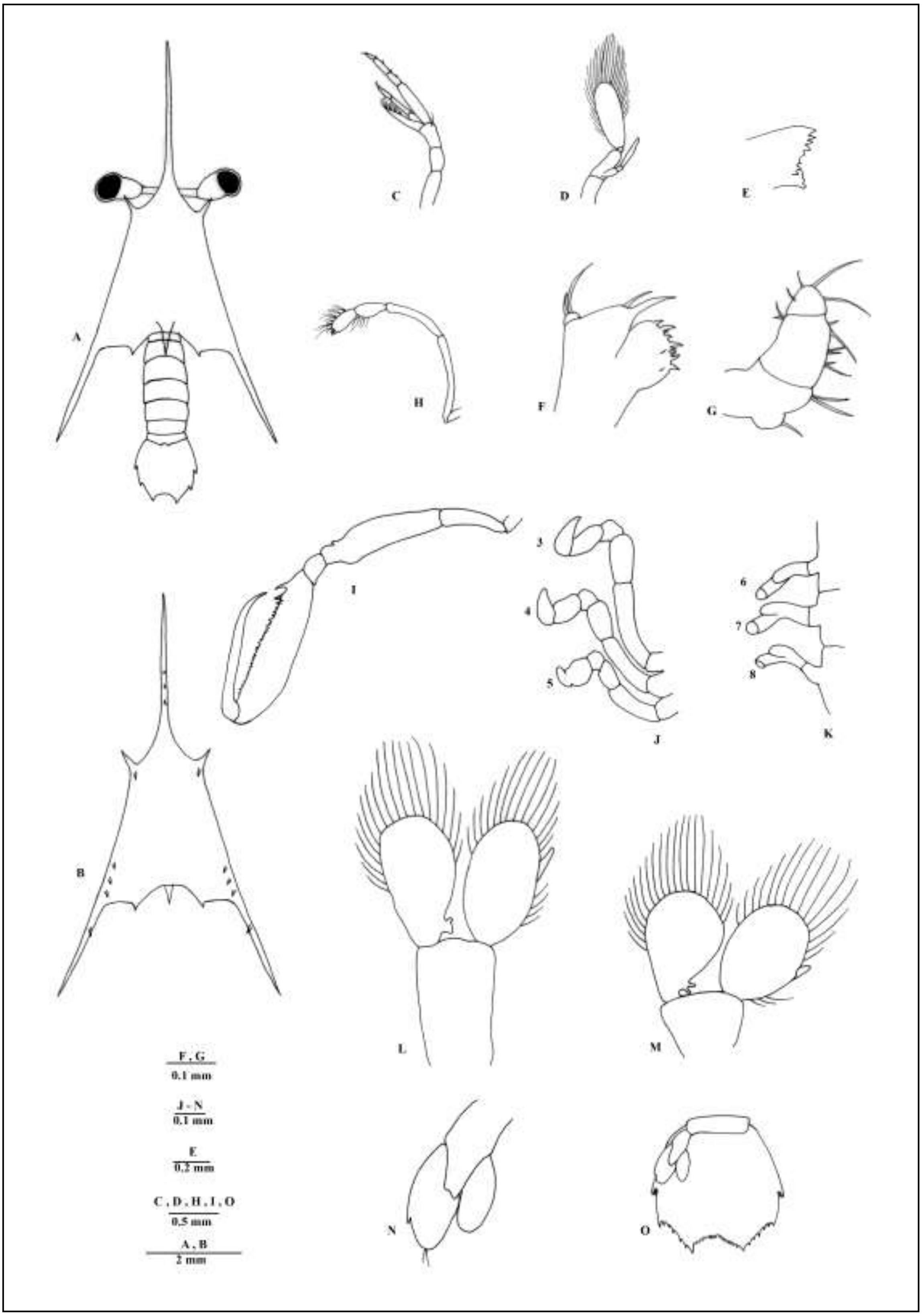


Figure 5.13. Fifth pelagic larval stage of *Cloridopsis scorpio*. A = animal in dorsal view; B = carapace in ventral view; C = antennules; D = antenna; E = mandible; F = first maxilla; G = second maxilla; H = first thoracopod; I = second thoracopod; J = third to fifth thoracopods; K = sixth to eight thoracopods; L = first pleopod; M = fifth pleopod; N = uropod; O = pleotelson. C – N = right parts; C – O = ventral view.

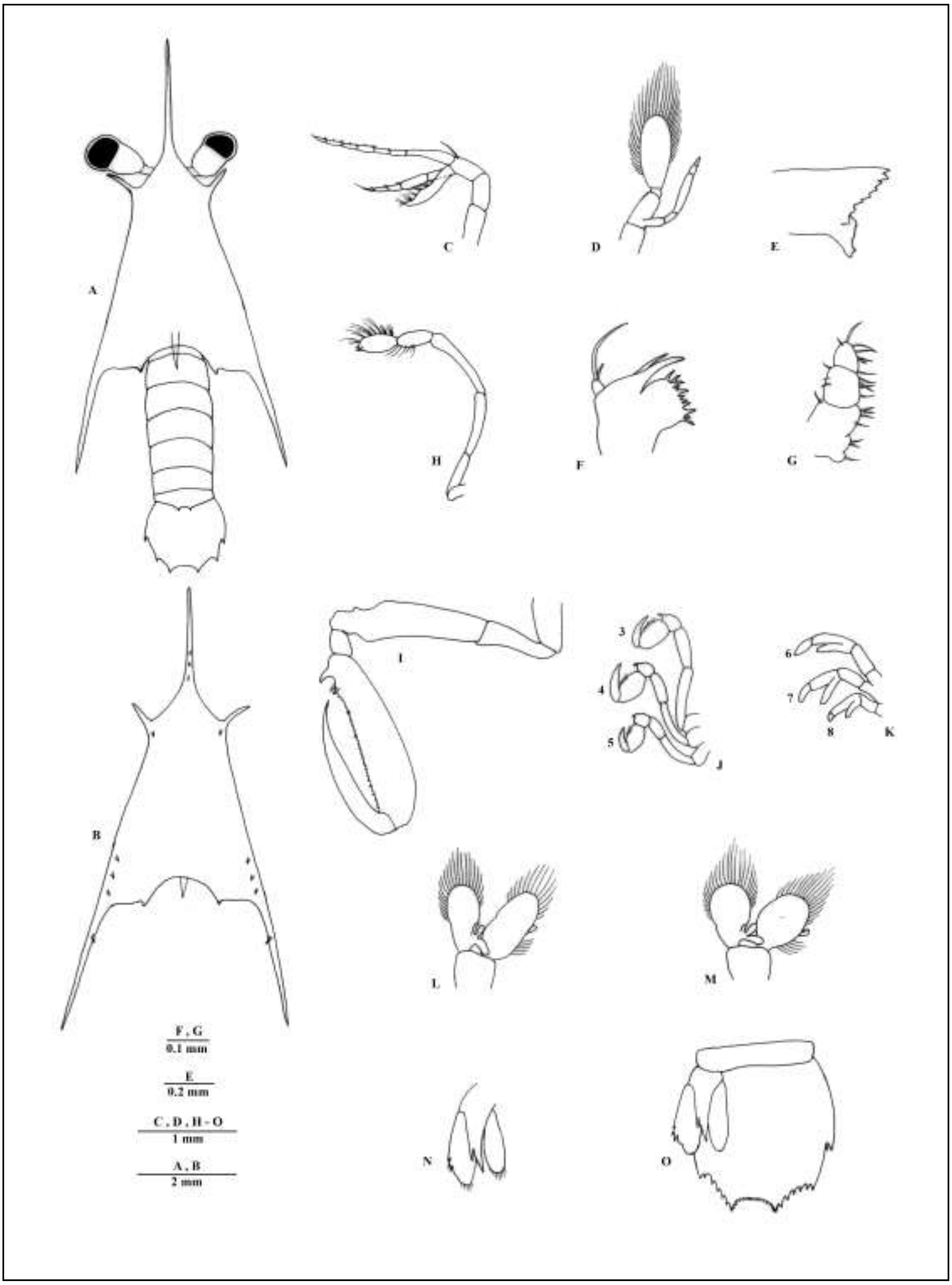


Figure 5.14. Sixth pelagic larval stage of *Cloridopsis scorpio*. A = animal in dorsal view; B = carapace in ventral view; C = antennules; D = antenna; E = mandible; F = first maxilla; G = second maxilla; H = first thoracopod; I = second thoracopod; J = third to fifth thoracopods; K = sixth to eight thoracopods; L = first pleopod; M = fifth pleopod; N = uropod; O = pleotelson. C – N = right parts; C – O = ventral view.

b) *Miyakea nepa*

The four pelagic *Miyakea nepa* larvae captured in Matang were all in late stage (Figure 5.15). Early stage and mid stage larvae were not found in the plankton samples. Figure 5.15A showed the outline of *Miyakea nepa,* CL = 8.85 mm; TL = 23.37 mm. Rostrum without ventral spinules (Figure 5.15B); carapace rectangular in shape with 13 ventrolateral spinules in the alignment: 8 on anterior and 5 on posterior. Propodus of second thoracopod with one strong proximal tooth followed by 2 strong teeth in opposition and 43 denticles on the inner margin (Figure 5.15C); dactylus does not have any additional tooth other than the terminal tooth. Telson with 1 lateral and 9 intermediate denticles on each side followed by 14 submedian denticles (Figure 5.15D).

c) Unidentified species

The unidentified larvae consisted of two different early stage morphotypes (n = 310) and two different late stage morphotypes (n = 8). Since the two late stages morphotype belonged to a larval series of developmental stages, they must belong to one unidentified species. Mid stage larvae were not found in the plankton samples. In conclusion, there were three unidentified species, two species for the two early stages larvae (named as early sp1 and early sp2) and one species with two late larval stages (named as late stage 1, sp3 and late stage 2, sp3).

Figure 5.16A showed the outline of early sp1 (n = 177), CL = 0.74 mm; TL = 2.37 mm. Rostrum without ventral spinules (Figure 5.16B); carapace ovoid in shape with 5 ventrolateral spinules in the alignment: 1 on anterior and 4 on posterior. Telson with 4 intermediate denticles on each side followed by 12 submedian denticles (Figure 5.16C).

Figure 5.17A showed the outline of early sp2 (n = 133), CL = 0.68 mm; TL = 2.34 mm. Rostrum without ventral spinules (Figure 5.17B); carapace ovoid in shape with 6 ventrolateral spinules in the alignment: 1 on anterior and 5 on posterior. Telson with 5 intermediate denticles on each side followed by 14 submedian denticles (Figure 5.17C).

Figure 5.18A showed the outline of late stage 1, sp3 (n = 5), CL = 2.65 mm; TL = 8.14 mm. Rostrum with 2 ventral spinules (Figure 5.18B); carapace triangular in shape with 5 ventrolateral spinules in the alignment: 1 on anterior and 4 on posterior. Propodus of second thoracopod with one strong proximal tooth followed by 2 strong teeth in opposition and 25 denticles on the inner margin (Figure 5.18C); dactylus with 1 tooth other than the terminal tooth. Telson with 1 lateral and 6 intermediate denticles on each side followed by 30 submedian denticles (Figure 5.18D).

Figure 5.19A showed the outline of late stage 2, sp3 (n = 3), CL = 3.16 mm; TL = 10.39 mm. Rostrum with 2 ventral spinules (Figure 5.19B); carapace triangular in shape with 5 ventrolateral spinules in the alignment: 1 on anterior and 4 on posterior. Propodus of second thoracopod with one strong proximal tooth followed by 2 strong teeth in opposition and 27 denticles on the inner margin (Figure 5.19C); dactylus with 2 teeth other than the terminal tooth. Telson with 1 lateral and 6 intermediate denticles on each side followed by 32 submedian denticles (Figure 5.19D).

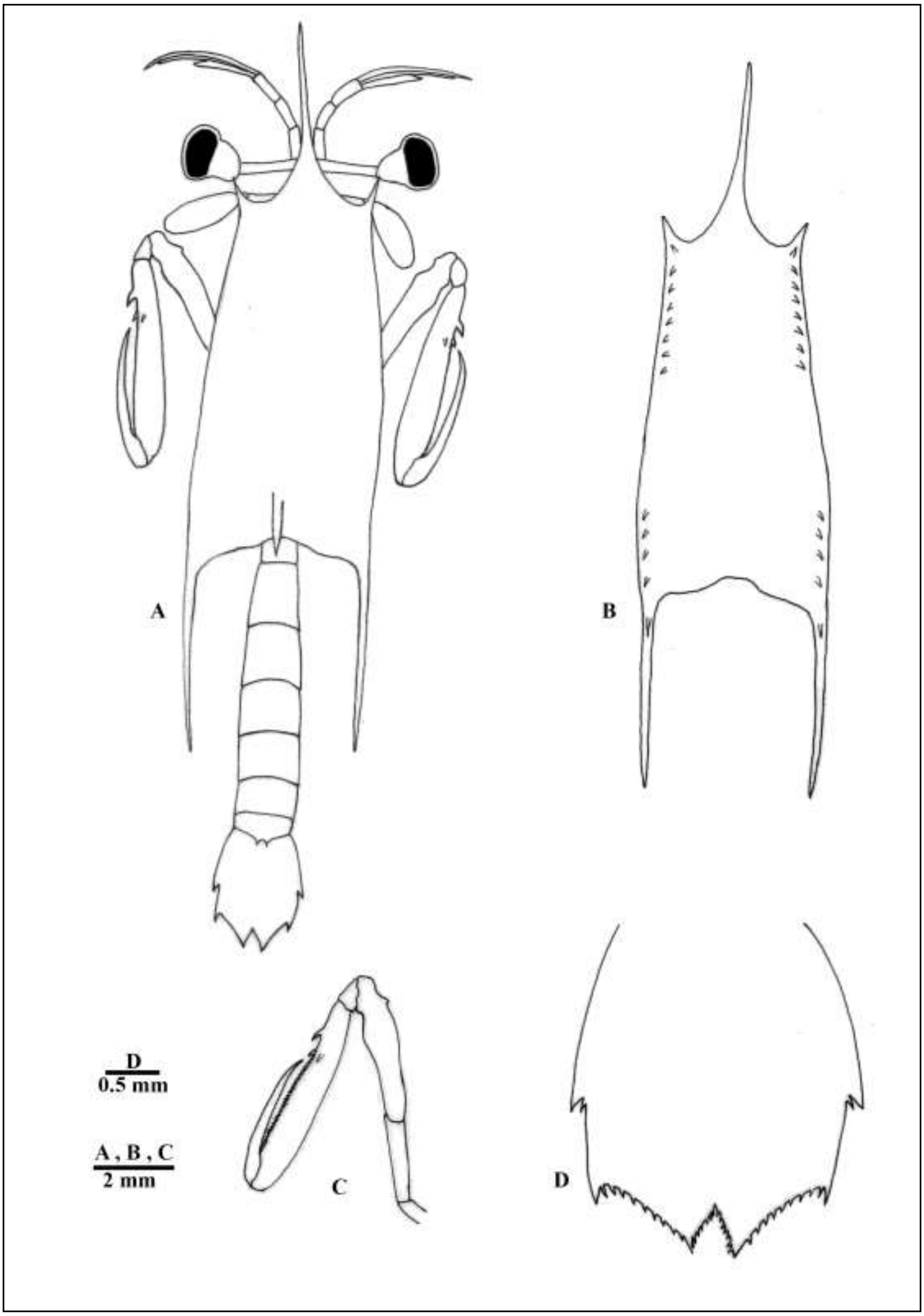


Figure 5.15. Late pelagic larval stage of *Miyakea nepa*. A = animal in dorsal view; B = carapace in ventral view; C = second maxilla (right part); D = telson. C – D = ventral view.

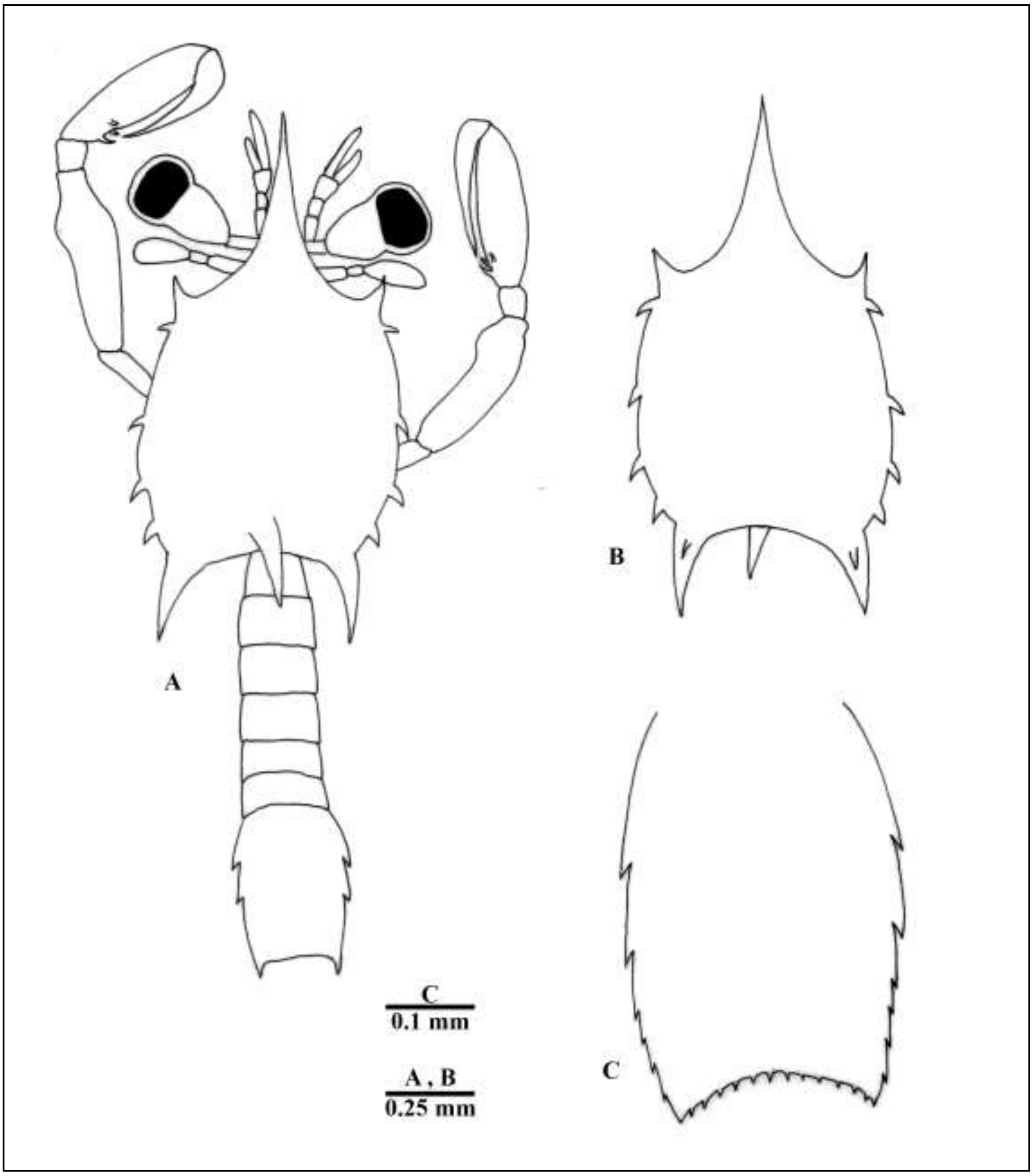


Figure 5.16. Early pelagic larval stage of early sp1. A = animal in dorsal view; B = carapace in ventral view; C = telson, ventral view.

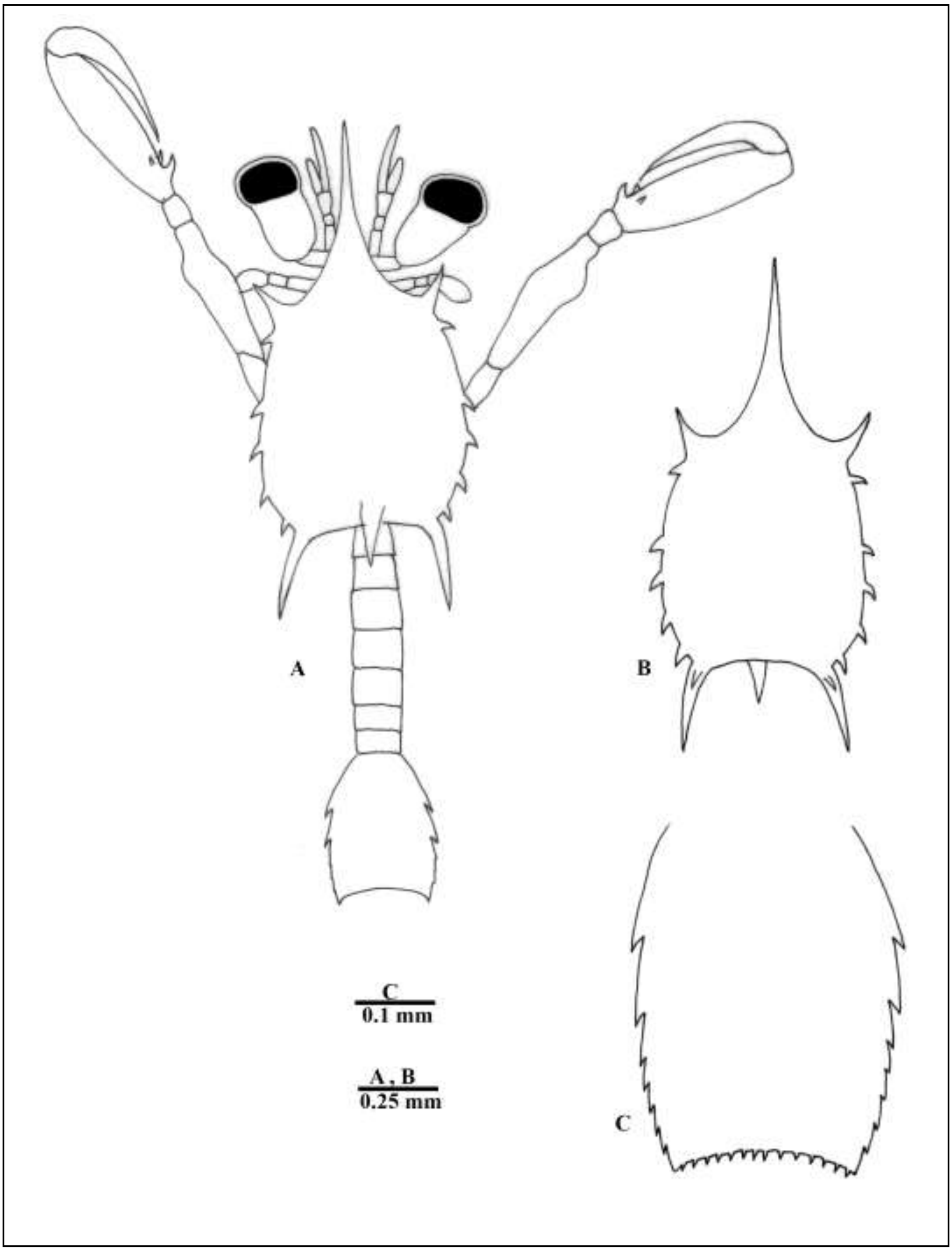


Figure 5.17. Early pelagic larval stage of early sp2. A = animal in dorsal view; B = carapace in ventral view; C = telson, ventral view.

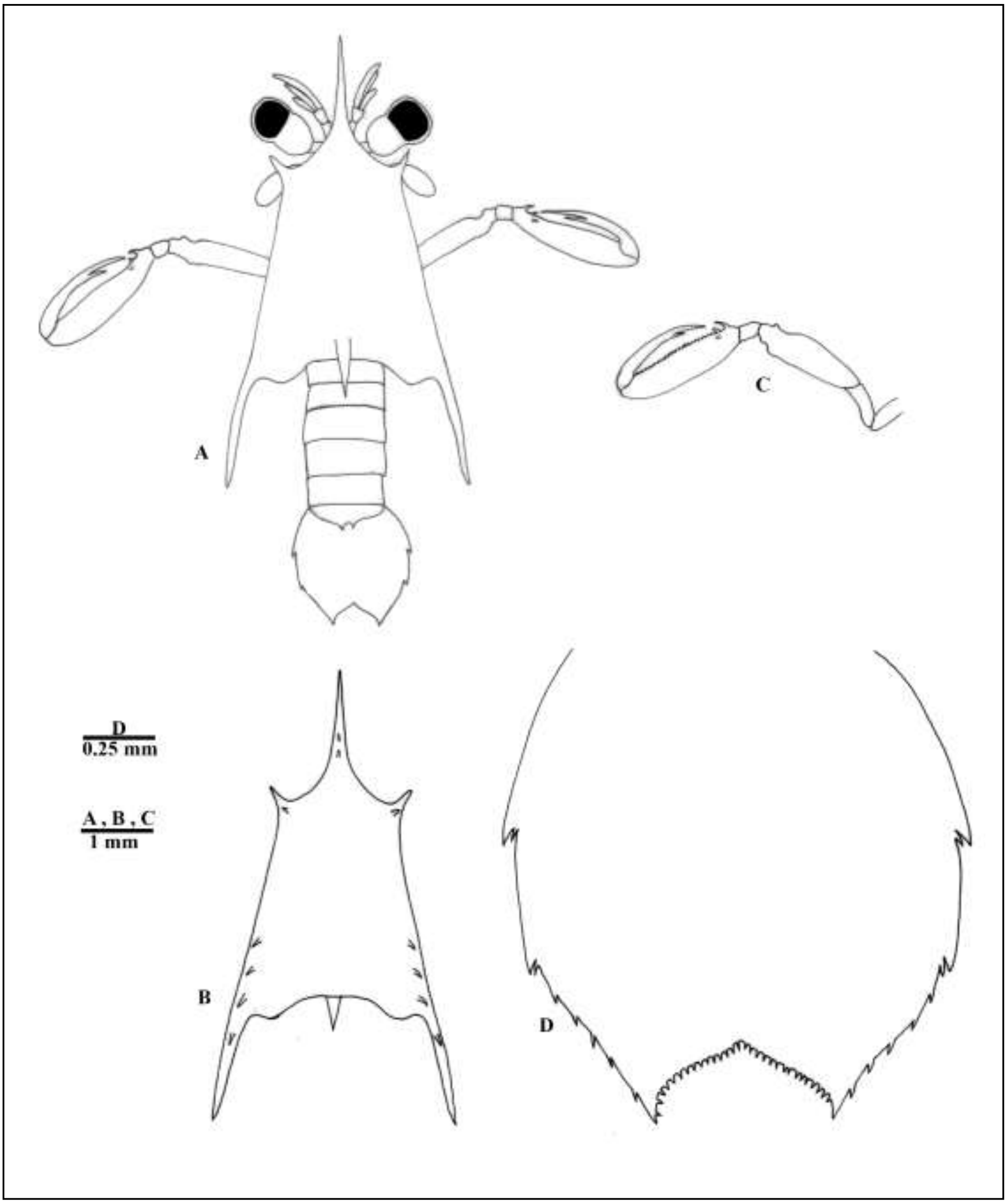


Figure 5.18. Late pelagic larval stage 1, sp3. A = animal in dorsal view; B = carapace in ventral view; C = second maxilla (right part); D = telson. C – D = ventral view.

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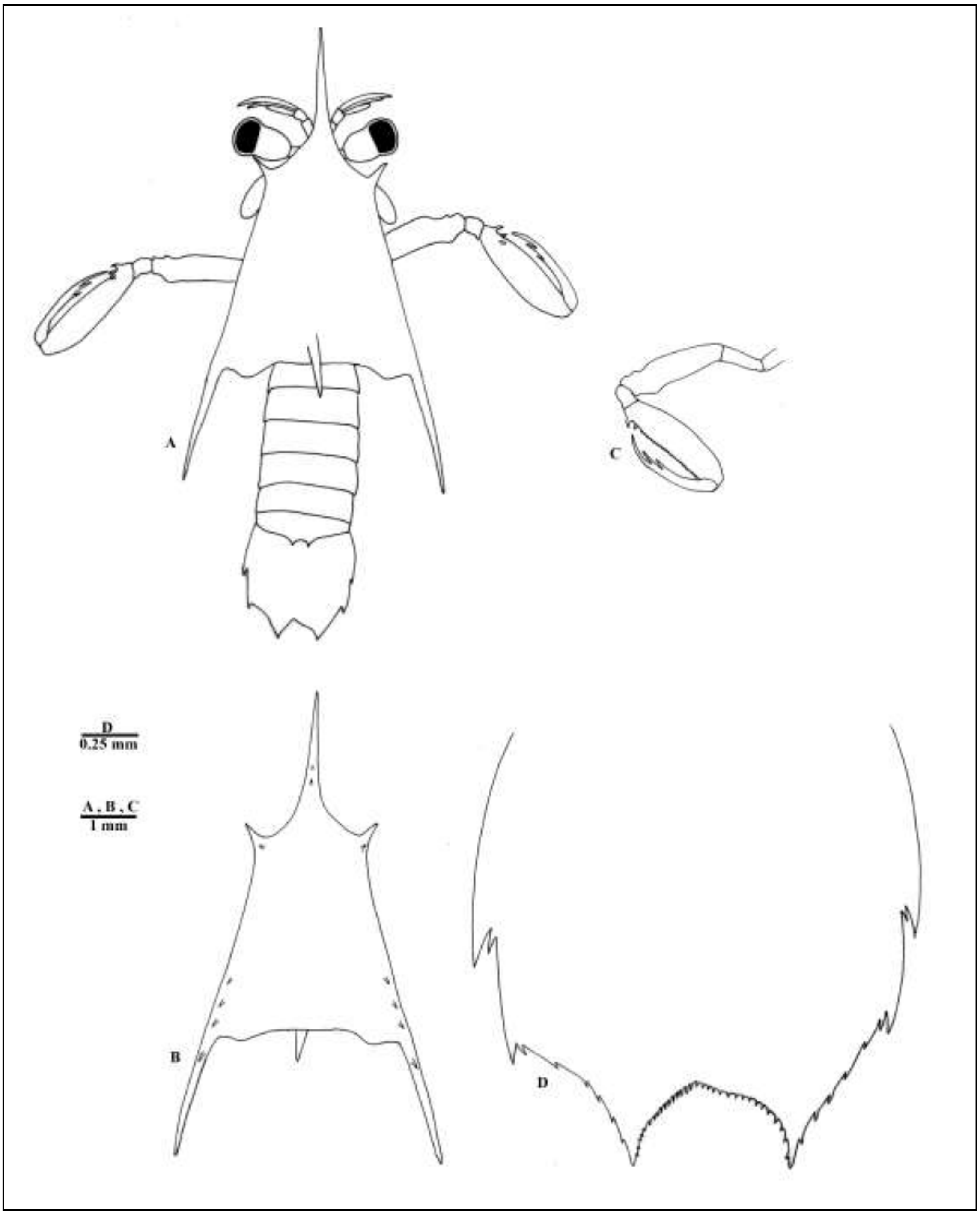

Figure 5.19. Late pelagic larval stage 2, sp3. A = animal in dorsal view; B = carapace in ventral view; C = second maxilla (right part); D = telson. C – D = ventral view.

5.1.2.3 Distribution and abundance of stomatopod larvae

5.1.2.3.1 Spatial and temporal abundance of stomatopods larvae population

Cloridopsis scorpio larvae recorded a mean density of 1.13 ± 3.06 N.100 m^{-3}, *Miyakea nepa* larvae recorded 0.03 ± 0.22 N.100 m^{-3} and the unidentified stomatopod larvae recorded 2.39 ± 4.36 N.100 m^{-3} from November 2002 to October 2003. The mean density fluctuated greatly among stations and months (Figure 5.20). *Cloridopsis scorpio* larvae were generally found inside the mangrove estuary but not found in adjacent coastal waters, whereas *Miyakea nepa* and unidentified stomatopods larvae showed the opposite result. However two individuals of unidentified stomatopods larvae were observed at mid estuary. The lower estuary showed a mixture of *Cloridopsis scorpio* larvae and unidentified stomatopods larvae. However the mean density for both groups of stomatopod larvae at lower estuary was relatively low as compared to the other stations.

Figure 5.20 shows that *Cloridopsis scorpio* larvae were present from February 2003 to September 2003 in the upper, mid and lower estuary. A density peak was observed at the upper and mid-estuary in April 2003 to May 2003 and a second one in July 2003. *Miyakea nepa* larvae only observed in August 2003 in nearshore and offshore waters. The mean density of unidentified stomatopods larvae tended to fluctuate greatly over the sampling period. Three density peaks of these larvae were recorded in December 2002 to January 2003, April 2003 to May 2003 and July 2003 to August 2003. No differences of densities were observed between monsoon seasons for the larvae.

5.1.2.3.2 Spatial and temporal abundance of *Cloridopsis scorpio* larvae according to developmental stages

The total length (TL) of the smallest larvae caught in Matang was 4.94 mm and this was a mid stage larva. No larvae of < 4.94 mm total length were found in the plankton samples. In addition, there were no post-larvae caught in the samples.

Cloridopsis scorpio larvae showed spatial variability in abundance with the highest density observed in the upper estuary followed by mid-estuary while the lower estuary recorded the lowest density (Figure 5.21). All the six described developmental stages of *Cloridopsis scorpio* larvae were found in the upper estuary and mid-estuary whereas the lower estuary had only the mid stage larvae (stage 1 to stage 4).

Cloridopsis scorpio larvae were found from February 2003 to September 2003 (8 months). Stage 1 and stage 2 larvae were only found from February 2003 to July 2003 while stage 5 and stage 6 larvae were collected from April 2003 to September 2003 (Figure 5.21a, b). Generally, the six development stages showed a seasonal pattern with the mid stage larval (stage 1 to stage 4) found abundantly from February 2003 but whose number decreased until September 2003, while the later stage larval (stage 5 and stage 6) appeared starting from April 2003 until September 2003.

5.1.2.3.3 Spatial and temporal abundance of *Miyakea nepa* larvae and unidentified stomatopod larvae according to developmental stages

All the *Miyakea nepa* larvae found in Matang showed late stage characters with the total length ranging from 22.5 mm to 24.7 mm. No early stage larvae, mid stage larvae and post-larvae of *Miyakea nepa* were caught.

The total length of early sp1 larvae and early sp2 larvae caught in Matang were ranged from 2.21 mm to 3.09 mm and 2.26 mm to 2.98 mm, respectively. All the unidentified sp3 larvae showed late stage characters with the total length ranging from 7.92 mm to 10.51 mm. No mid stage larvae and post-larvae were caught for these unidentified species.

Figure 5.22 showed that nearshore and offshore stations recorded the highest density of the two early stage unidentified larval groups (early sp1 and early sp2). Two individuals of early sp1 larvae were found in mid estuary in February 2003. Small numbers of late stage larvae which consisted of *Miyakea nepa* larvae (n = 4) and unidentified sp3 larvae (n = 8) were found at nearshore and offshore stations.

The monthly mean density of early sp1 showed three peaks which occurred in December 2002 to January 2003, July 2003 to August 2003 and October 2003 (Figure 5.22). The mean density of early sp1 was relatively low during February 2003 to June 2003. Two peaks of abundance of early sp2 were observed in December 2002 and May 2003. Late stage larvae of *Miyakea nepa* was found in August 2003 while late stage larvae of unidentified sp3 were found in January 2003, April 2003 and May 2003.

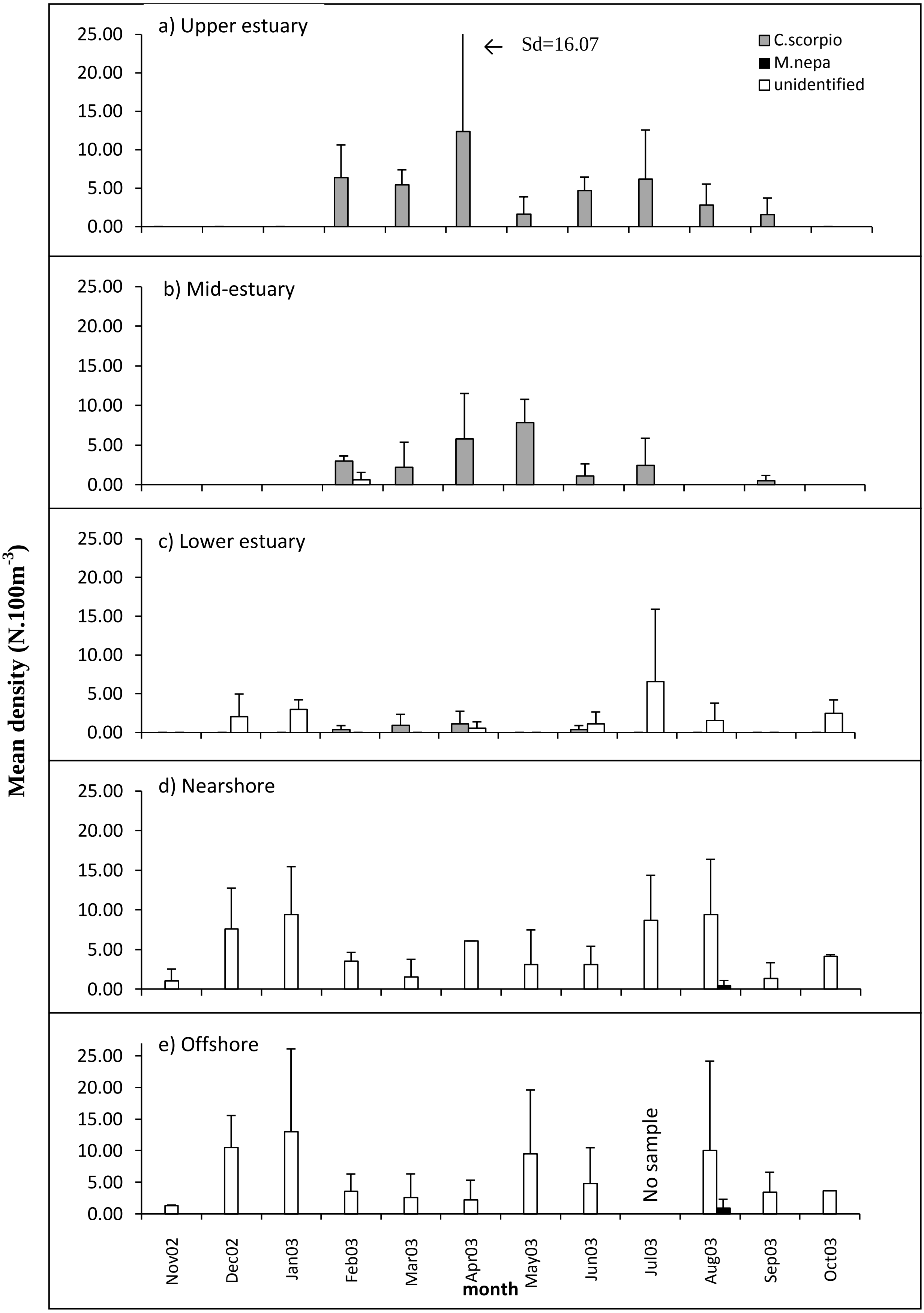

Figure 5.20. Monthly mean density of *Cloridopsis scorpio* larvae, *Miyakea nepa* larvae and unidentified stomatopods larvae in mangrove estuary; a) upper estuary, b) mid-estuary, c) lower estuary and adjacent coastal waters; d) nearshore, e) offshore from November 2002 to October 2003.

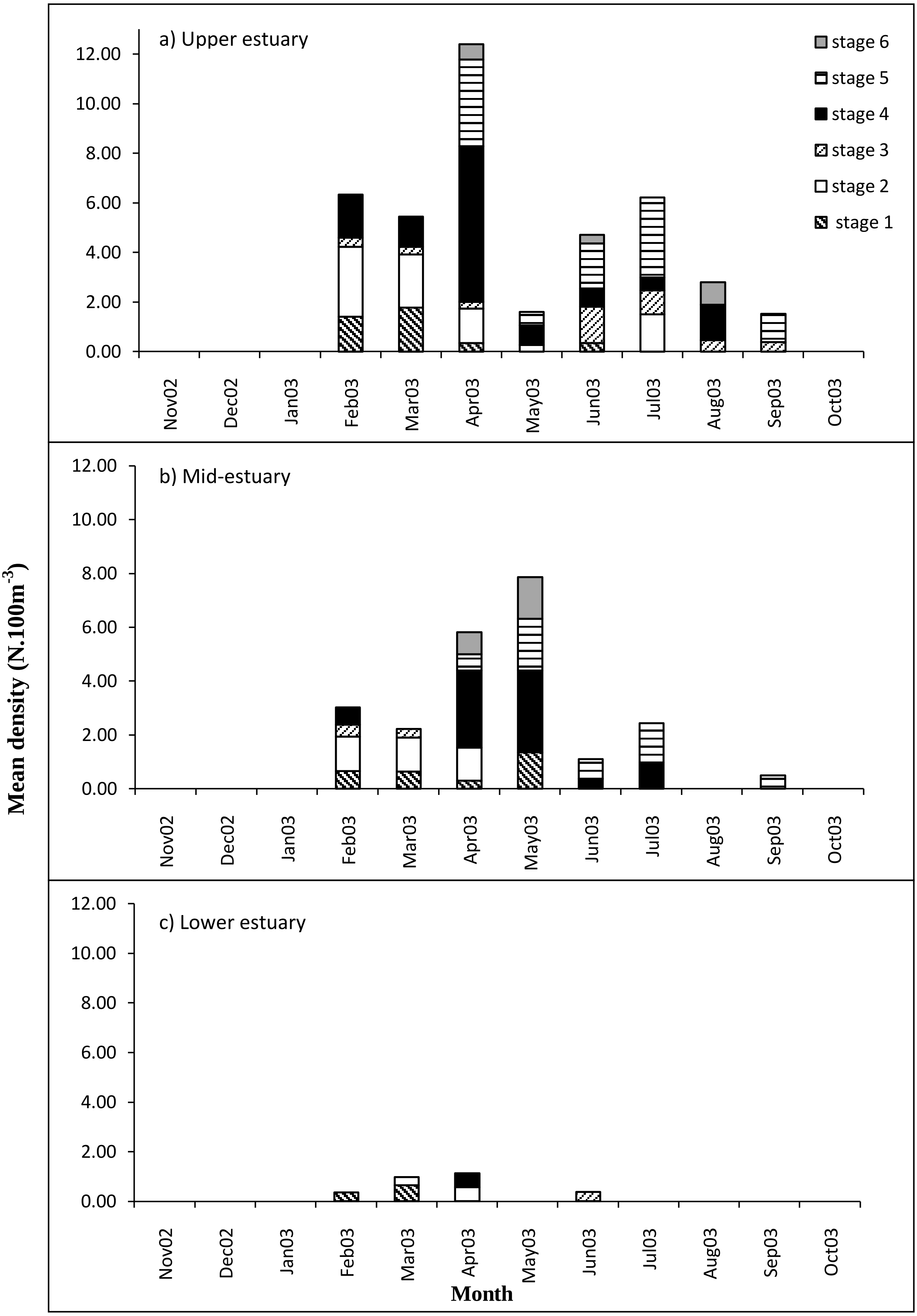

Figure 5.21. Monthly mean density of the *Cloridopsis scorpio* larvae according to six developmental stages (mid stage = stage 1 to stage 4; late stage = stage 5 to stage 6) in mangrove estuary; a) upper estuary, b) mid-estuary, c) lower estuary from November 2002 to October 2003.

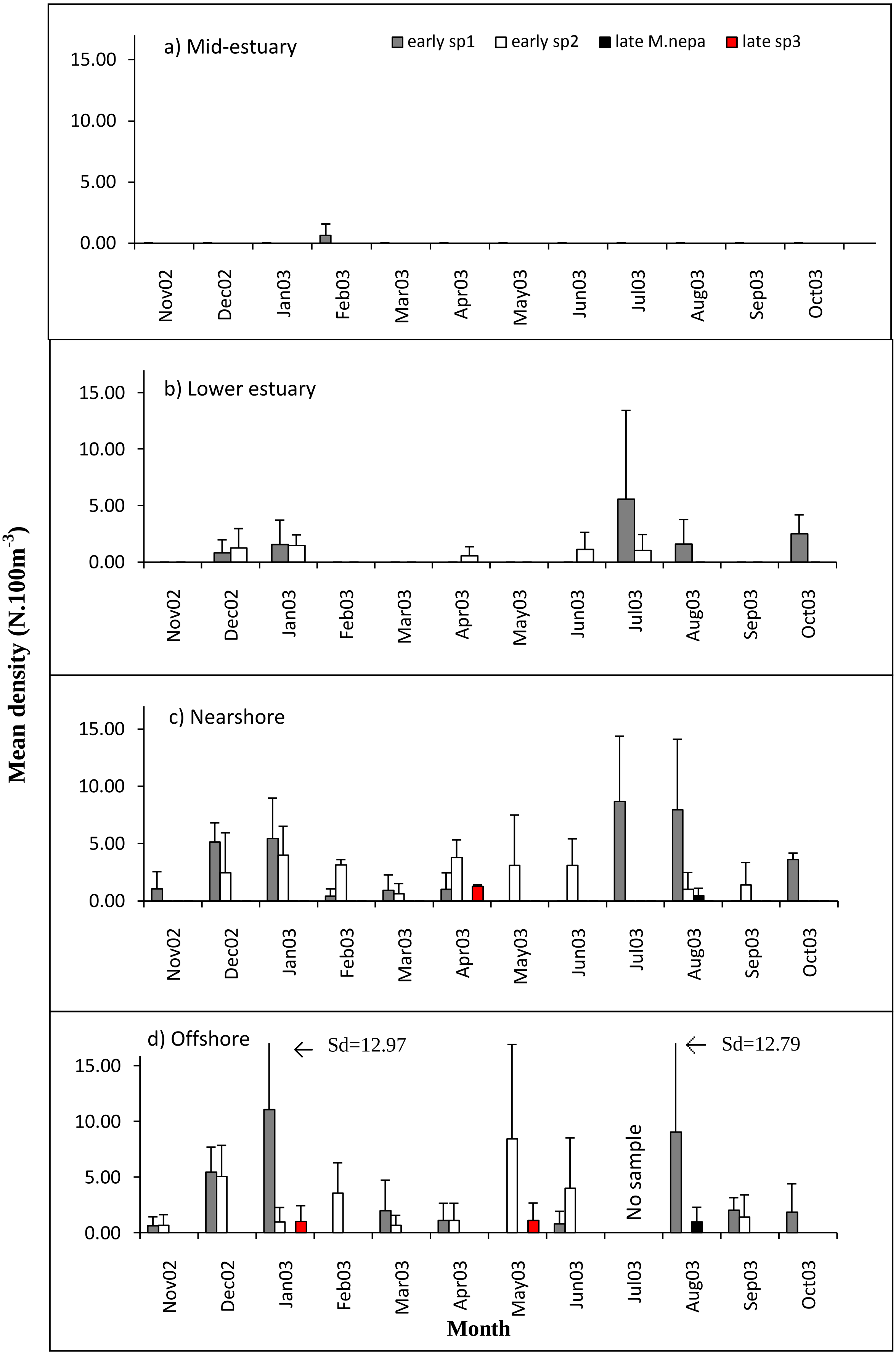

Figure 5.22 Monthly mean density of *Miyakea nepa* (late M.nepa), unidentified early stage larval groups (early sp1 and early sp2) and late stage sp3 in mangrove estuary; a) mid-estuary, b) lower estuary and adjacent coastal waters; c) nearshore, d) offshore from November 2002 to October 2003.

5.1.2.4 Relationship between stomatopod larvae abundance, food items (zooplankton in three size fractions) and environmental parameters.

Canonical correspondence analysis (CCA) was used to test the correlation between stomatopod larvae abundance, food items (zooplankton in three size fractions) and environmental parameters.

The Monte Carlo permutation test of the sum of all canonical axes showed significance of the species-environment, food items correlation at $p = 0.014$ (Table 5.3). The first two axes explained 82.4% of the variance in the stomatopod larval abundance data and 98.3% of the variance in the correlation of stomatopod larval abundance and environmental parameters and food items. The interpretation of the results derived from CCA is illustrated by the ordination triplots (Figure 5.23). The canonical coefficients or eigen vectors of the first four axes was given in appendix XI.

The first canonical axis (axis 1) was primarily a descriptor of salinity, dissolved oxygen, turbidity and zooplankton density with size of '> 250µm' (arrows) in the negative direction (left) and zooplankton density with size of '> 125µm' in the positive direction (right). Temperature and zooplankton density with size of '> 500µm' were positively associated with the second canonical axis (axis 2) on the positive side as opposed to pH on the negative side. Figure 5.23 shows that the stations (open circles) inside the mangrove estuary (station 1 and 2) were generally positively correlated to higher turbidity, temperature and zooplankton with size of '> 500µm' and '> 125µm'. The waters of the coastal stations (4 and 5) had higher salinity, pH and dissolved oxygen, but lower temperature and turbidity, with higher abundance of intermediate size zooplankton of '> 250µm'.

The five species of stomatopods larvae displayed in the CCA plot can be generally classified into mangrove species (*Cloridopsis scorpio*) and coastal species (late *Miyakea nepa*, early sp1, early sp2 and late sp3) based on their abundance along the five sampling stations (1-5). Station 1 and 2 generally had more *Cloridopsis scorpio* larvae while station 4 and 5 had more late *Miyakea nepa*, early sp1, early sp2 and late sp3. The distribution of the estuarine species and coastal species of stomatopod larvae appeared spatially distinct and did not seem to be affected by the two monsoons (northeast and southwest monsoons) (Figure 5.23, open circles).

Based on Figure 5.23, *Cloridopsis scorpio* larvae showed higher association with small size zooplankton ('>125 µm') and large size zooplankton ('>500 µm') in turbid, warmer and less saline water, while larvae of sp1 and sp2 were more dependent on intermediate size zooplankton ('>250 µm') in less turbid water. The larvae of *M. nepa* and sp. 3 preferred cooler, more saline water and small sized zooplankton.

Table 5.3. Summary results of CCA for five species of stomatopod larvae assemblages from upper estuary to offshore waters at different monsoon periods in relation to environmental parameters and food items (zooplankton in three size fractions) from November 2002 to October 2003.

Axes	1	2	3	4	Total inertia
Eigenvalues :	0.562	0.047	0.009	0.002	0.738
Species-environment, food items correlations :	0.935	0.834	0.643	0.499	
Cumulative percentage variance					
of species data :	76.1	82.4	83.7	83.9	
of species-environment, food items relation:	90.7	98.3	99.7	100.0	
Sum of all eigenvalues					0.738
Sum of all canonical eigenvalues					0.619

**** Summary of Monte Carlo test ****

Test of significance of all canonical axes :
F-ratio = 3.900
P-value = 0.0140
(499 permutations under reduced model)

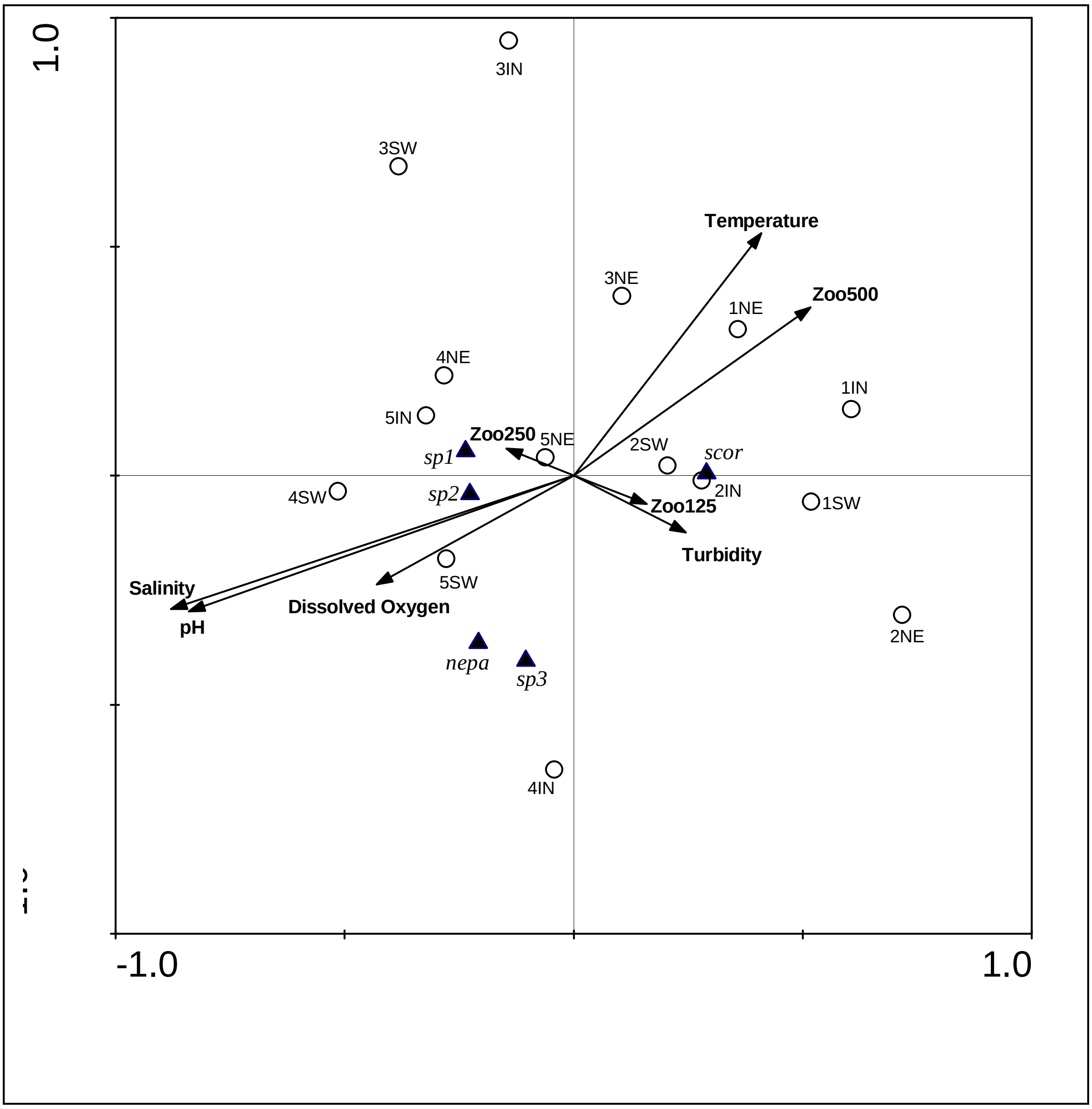

Figure 5.23. CCA triplot diagram shows the five species of stomatopod larvae assemblages from upper estuary to offshore waters at different monsoon periods in relation to environmental parameters and food items (zooplankton in three size fractions) from November 2002 to October 2003. Arrow denote environmental parameters and food items (zooplankton with different fractions); Zoo 500 - density of '> 500µm' zooplankton, Zoo 250 - density of '> 250µm' zooplankton, Zoo 125 - density of '> 125µm'. Symbol ▲ denote stomatopod larvae species; sp1 – early sp1, sp2 – early sp2, nepa - late *Miyakea nepa*, sp3 – late sp3, scor - *Cloridopsis scorpio*. Symbol ○ denote station samples (1-5) at different monsoon period (NE,IN,SW); 1 – upper estuary, 2 – mid-estuary, 3 – lower estuary, 4 – nearshore, 5 – offshore; NE – northeast monsoon, IN – inter-monsoon, SW – southwest monsoon.

5.2 Discussion

5.2.1 Sex ratio by month and size class

Miyakea nepa and *Oratosquillina perpensa* showed a female-biased ratio and these results agree with several studies on stomatopods (Sukumaran, 1987; Dittel, 1991; Hamano *et al.*, 1996; Lui, 2005; Wardiatno & Mashar, 2010). These could be due to the mortality rate of male being higher. Christy & Salmon (1991) noted that males suffer greater mortality than females in searching for a new burrow every time they breed. Dittel (1991) reported that females spend more time in their burrows brooding their eggs during the breeding season and this may reduce their risk of being captured. However, male-biased population has been reported for *Erugosquilla massavensis* (Sallam, 2005).

The present study shows that males of *Miyakea nepa* predominated the middle size classes and females predominated the smaller and larger size classes, as was also shown in another study (Reddy & Shanbhogue, 1994). Female *Miyakea nepa* had the largest size compared to the male and this was opposite to *Oratosquillina perpensa* and *Harpiosquilla raphidea*. Generally, stomatopods are observed to be smaller in female than in male because more energy is used for gonadal maturation and reproduction in female (Dittel, 1991; Ali, 2011). However, it is possible that female *Miyakea nepa* appears larger than male because of sampling error. The largest size class of females only contains four individuals which are small, and this is not enough to represent the population of this size class.

5.2.2 Female and male maturity stages

The differences in ovarian development between immature or spent individuals could not be distinguished by the naked eye because the ovaries of these two stages showed no colour differences and could be of the same width. Apparently, these stages could only be distinguished using histological techniques (Kodama *et al.*, 2004). In this study, the gonadal development of males could not be followed morphologically. Similarly, histological examination is necessary as was used in the Japanese stomatopod, *Oratosquilla oratoria* (Kodama, 2009). Nevertheless, polymodal analysis of male penis lengths as by Bhattacharya method could be used to assign males to one of three arbitrary maturation stages (immature, maturing and mature), based on the premise that the youngest males (short penis) and the oldest males (long penis) are immature and mature respectively. This classification has been independently verified by histological examinations of the testes. Histological examination of the testes of immature (*Miyakea nepa*, carapace length = 11.90 mm) showed only spermatogonia in the seminal tubules, while in the maturing (carapace length = 17.93 mm) male no production of spermatozoa are observed, but consisted of spermatogonia, spermatocytes and spermatids. In the mature (carapace length = 25.30 mm) male, spermatozoa are observed (Figure 5.7a, b, c).

The immature females of *Miyakea nepa* and *Oratosquillina perpensa* were the most abundant among all the maturation stages. Higher proportion of immature females were also found in *Erugosquilla massavensis* (Sallam, 2005). The mean carapace length of stage II (29.0 ± 3.01 mm), stage III (28.9 ± 3.04 mm) and stage IV (28.4 ± 3.02 mm) females of *Miyakea nepa* were similar, suggesting that 28.0 mm is likely close to the size at first maturity for this species. Stage II (25.4 ± 3.64 mm), stage III (25.5 ± 2.36 mm) and stage IV (25.5 ± 3.18 mm) of female *Oratosquillina perpensa* also show similar mean carapace length; the likely size at first maturity is likely 25.0 mm. Males of *Miyakea nepa* (24.8 mm) are found to mature earlier than females (28.0 mm). On the other hand, male *Oratosquillina perpensa* may mature later (27.5mm) than the females (25.0 mm).

5.2.3 Spawning season

Generally, *Miyakea nepa* and *Oratosquillina perpensa* showed year-round breeding and were not specifically affected by the wet or dry periods of the two monsoons. Sukumaran (1987) and Lui (2005) also reported similar results for *Miyakea nepa*. In the present study, *Miyakea nepa* and *Oratosquillina perpensa* showed two spawning peaks and one of the spawning periods is found to have more protracted spawning activity. A prolonged spawning period is also found in *Squilla empusa* (Rockett *et al.*, 1984) and *Oratosquillina nepa* (Sukumaran, 1987). Rockett *et al.* (1984) also reported that *Squilla empusa* spend an extended time in egg mass, propelagic and pelagic stages of development. The prolonged spawning period could also be due to the same female being able to spawn several times during the spawning period (Kodama *et al.*, 2004). Lui (2005) indicated breeding peaks in summer for three studied stomatopods while Kodama *et al.* (2004) found that Japanese mantis shrimp, *Oratosquilla oratoria* had their spawning peaks once in summer and once in winter. These seasonal breeding peaks may exist due to various factors such as environmental parameter, food availability or lunar and tidal changes. Hamano & Matsuura (1987) found that the incubation time of the eggs of *Oratosquilla oratoria* became short at higher water temperature. Reaka (1976) noted that different species deposit eggs at different lunar and tidal rhythms.

5.2.4 Identification of stomatopod larvae

The only member of the genus *Cloridopsis* inhibiting the waters of Matang mangrove was *Cloridopsis scorpio*. *Cloridopsis scorpio* larvae were easily distinguished from the other species in the study area based on the characteristic long rostrum and posterolateral spines, two characteristic small spinules at the posterior margin of carapace and the absence of laterally directed spines on the carapace margin (Alikunhi, 1952). In addition, the early stage larvae (total length = 4.92 mm) are found to have only three intermediate denticles on either side of the telson and this is considered as a regular feature of early larvae of *Cloridopsis scorpio* (Alikunhi, 1975). The two characteristic small spinules at the posterior margin of carapace is a specific character for the genus *Cloridopsis* (Alikunhi 1952, 1975; Morgan & Provenzano, 1979).

The late stage larva of *Miyakea nepa* was found to be similar to the final pelagic *Miyakea nepa* larvae as described by Alikunhi (1952). Apart from *Cloridopsis scorpio* and *Miyakea nepa* larvae, the other three species of larvae caught during the study cannot be identified to species or generic level due to the lack of identification keys. Alikunhi (1952) and Tang (2009) only described the larval stages of *Miyakea nepa* from the mid stage (total length = 6.5mm) while only one final pelagic stage (total length = 18.1 mm) of *Harpiosquilla raphidea* had been described by Alikunhi (1952). No study was conducted for *Oratosquillina perpensa* larvae.

5.2.5 Larval developmental stages of *Cloridopsis scorpio*

From the planktonic samples, it is difficult to determine the number of larval stages as the complete sequence of larval developmental stages may not be collected or there are intermediate molts. Several studies have indicated that not all the developmental stages can be obtained in plankton surveys (Alikunhi, 1952; Michel & Manning, 1972; Morgan, 1980; Tang, 2009). However, according to Hamano &

Matsuura (1987), a small number of inter-molt larval stages may occur due to inadequate environments during rearing.

In present study, new features are incremental with each successive larval stage suggesting that each larval stage results from only a single moult. Larval descriptions by Alikunhi (1952, 1975) lent useful help to the construction of the larval series. Alikunhi (1952) described three pelagic larvae of *Cloridopsis scorpio* collected from plankton samples (Table 5.4). The present study showed that the second larval stage is similar to the early stage larvae while the fifth larval stage is similar to the middle stage larvae as described by Alikunhi (1952). The sixth larval stage looks similar to the final pelagic stage as described by Alikunhi (1952), but with slight differences in the raptorial dactylus and uropod. The author indicated five teeth were beneath the skin of the dactylus, but this feature was not observed in the sixth stage larval in the present study. This may be because the final pelagic larval of Alikunhi (1952) is one molt after the sixth larval stage if the total length of the two individual are taken into consideration. The total length excluding rostrum of the larval mentioned by the author was 9.2 mm while present study larval only measured 7.73 mm.

Table 5.4. Number of *Cloridopsis scorpio* larval developmental stages described in present study and Alikunhi (1952).

Present study	Total length (mm)	Alikunhi (1952)	Total length (mm)
First pelagic larval stage	5.20		
Second pelagic larval stage	5.92	Early stage	5.10
Third pelagic larval stage	7.60		
Fourth pelagic larval stage	8.29		
Fifth pelagic larval stage	9.53	Middle stage	9.80
Sixth pelagic larval stage	10.69	Final stage	9.20 (total length excluding rostrum)

5.2.6 Larval developmental stages of *Miyakea nepa* and unidentified species

Two groups of early stage larvae (early sp1 and early sp2) were caught in Matang mangrove waters. Based on the adult stomatopods found in Matang (*Miyakea nepa*, *Oratosquillina perpensa*, *Harpiosquilla raphidea* and *Cloridopsis scorpio*), these two groups of larvae are suspected to belong to *Miyakea nepa* and *Oratosquillina perpensa*, respectively because both species likely spawn in stratum 2 (ie. nearshore station in present larval study) and stratum 3 (ie. offshore station in present larval study) (see 5.1.1.5). However, the adult stomatopod study and the larval study were conducted in different years.

Since *Miyakea nepa* larvae can be identified based on Alikunhi (1952) study, the late stage 1, sp3 and late stage 2, sp3 could be those of *Oratosquillina perpensa*, the next most abundant species. The most obvious feature observed in sp3 larvae, different from *Miyakea nepa* and *Harpiosquilla raphidea,* is the present of one or two teeth other than the terminal tooth on the dactylus of the second maxilliped (Table 5.5; see also Figure 5.18 & Figure 5.19). This feature was not reported in the final pelagic larvae of the latter two stomatopod species (Alikunhi, 1952). In addition, Morgan & Provenzano (1979) reported that the presence or absence of the teeth (other than the terminal tooth) on the dactylus of the second maxilliped could be used to define generic association. This sp3 species with one or two dactylus teeth was relatively much smaller (total length ranged from 7.92 mm to 10.51 mm) than the final pelagic larvae of *Miyakea nepa* and *Harpiosquilla raphidea* (Table 5.5). The total length of the final pelagic larvae for *Miyakea nepa* and *Harpiosquilla raphidea* were 22.8 mm and 18.1 mm, respectively (Alikunhi, 1952). This sp3 species also showed different carapace spinulation and telson spinulation when compared to *Miyakea nepa* and *Harpiosquilla raphidea* (Table 5.5).

Table 5.5. Total length, carapace spinulation (number of ventrolateral spinules on anterior + number of ventrolateral spinules on posterior), number of dactylus teeth and telson spinulation (number of lateral denticles on each side + number of intermediate denticles on each side + total number of submedian denticles) of the late stage larval among three species in present study and Alikunhi (1952).

Species	Total length (mm)	Carapace spinulation	Number of dactylus teeth	Telson spinulation
Late stage 1, sp3 (present study)	8.14	1 + 4	1	1+6+30
Late stage 2, sp3 (present study)	10.39	1 + 4	2	1+6+32
Late stage *Miyakea nepa* (present study)	23.37	8 + 5	0	1+9+14
Final pelagic stage of *Miyakea nepa* (Alikunhi, 1952)	22.80	8 + 5	0	1+9 +(14-15)
Final pelagic stage of *Harpiosquilla raphidea* (Alikunhi, 1952)	18.10	4 + 4	0	1+(13-14)+(19-20)

5.2.7 Distribution and abundance of stomatopod larvae population

The average larval density in present study ranged from 0.04 ± 0.03 ind.m^{-3} to 0.07 ± 0.07 ind.m^{-3} per sampling station (November 2002 to October 2003). Studies in Vietnamese waters (April 1999 to June 1999) and Hong Kong waters (February 2007 to January 2008) recorded an average density of 0 to 5 ind.m^{-3} (Jivaluk, 2000) and 0.64 ind.m^{-3} (Tang, 2009), respectively. The density of larvae in Matang was relatively low as compared to the two studies. This was due to the differences in sampling methodologies and the diversity and abundance of stomatopod between different regions. In addition, the larvae caught did not form a complete series of developmental stages in Matang waters. Several studies also could not capture the whole series of developmental stages (Alikunhi, 1952; Morgan, 1980; Tang, 2009).

In the present study, the earlier stage larvae (pro-pelagic stage) and the later stage larvae (post-larvae) were not found in the plankton samples. This is because the earlier stage larvae of different species may consist two or three pro-pelagic stages which remained in the burrow of the mother shrimp or on the bottom, with less or without swimming activity (Manning & Provenzano, 1963; Pyne, 1972; Hamano & Matsuura, 1987). The later stage larvae also spent more and more time at the bottom and behave like the adult. This is the reason why these pro-pelagic and later stages of larvae were not found in our samples, as the samples were from surface towing. The missing mid stage larvae of sp1, sp2 and sp3 in the plankton samples could be due to further migration offshore.

Generally, stomatopods larvae showed spatial and temporal variations in Matang waters. *Cloridopsis scorpio* larvae were only found in mangrove estuary while the stomatopod larvae of other species were mainly found in adjacent coastal waters. Based on the spatial distribution and abundance of adult stomatopods (see Chapter 3), although not in the same year, the spatial distributions of the larvae were in good agreement of *Cloridopsis scorpio* (mainly found at stratum 1, near to mangrove estuary), *Miyakea nepa* and *Oratosquillina perpensa* (mainly found at stratum 2 and stratum 3, adjacent coastal waters).

Based on the temporal variability in abundance of the six developmental stages of *Cloridopsis scorpio* larvae (see Figure 5.21), this species is believed to spawn once in a year. Therefore, this could be another reason why the catches of adult *Cloridopsis scorpio* were less (see 3.1.3.4d).

Temporal variability in abundance of early sp1 showed three peaks while early sp2 indicated two peaks (see Figure 5.22). These peaks could represent three spawning seasons for sp1 and two spawning seasons for sp2.

5.2.8 Relationship between stomatopod larvae abundance, food items (zooplankton with three different size fractions) and environmental parameters.

CCA triplot diagram (see Figure 5.23) shows that *Cloridopsis scorpio* appears to be more tolerant of warmer, turbid and less saline water, as found inside the estuary, while the other four species preferred cooler and more saline water, as found in coastal waters.

Thus, the occurrence of *Cloridopsis scorpio* larvae just like the adults inside the estuary, indicate that this species is an estuarine species. In contrast, the coastal species including the larvae of *Miyakea nepa* and the three unidentified species could be either euryhaline or stenohaline species. Several studies on stomatopod larvae also show spatial variability which was affected by environmental factors such as salinity and temperature (Pyne, 1972; Morgan, 1980; Kodama *et al.*, 2003). Chew & Chong (2011) and Ooi & Chong (2011) indicated that environmental factors greatly influence the zooplankton and fish larvae communities in Matang mangrove estuary.

Despite the rich zooplankton food resources inside Matang mangrove as reported by Chew & Chong (2011), stomatopod larvae do not display any inshore migration behavior into the estuary to feed on the rich zooplankton resources as seen in shrimps (Low *et al.*, 1999) and euryhaline fishes (Ooi & Chong, 2011). This is likely due to their intolerance to low salinity except a few species like *Cloridopsis scorpio*. However, Chew (2012) reported that stomatopod larvae only represented < 0.1% of the total zooplankton abundance in Matang waters. Hence, their naturally low numbers do not impose particular pressure of adequate food supply and the need to nurse in rich feeding grounds.

5.3 Conclusion

In general, the populations of stomatopod are female-biased except *Cloridopsis scorpio*. Female *Miyakea nepa* had the largest size compared to the male and this was opposite to *Oratosquillina perpensa* and *Harpiosquilla raphidea*. Five stages of ovarian development of female *Miyakea nepa*, *Oratosquillina perpensa*, and *Cloridopsis scorpio* are discerned and described. Three stages of maturity of male *Miyakea nepa* and *Oratosquillina perpensa* based on cohorts of different mean penile lengths are described. Males of *Miyakea nepa* are found to mature earlier than females while male *Oratosquillina perpensa* may mature later than the females. *Miyakea nepa* and *Oratosquillina perpensa* spawn throughout the year with two peaks and one of the spawning periods is found to have more protracted spawning activity.

Cloridopsis scorpio and the late stage larvae of *Miyakea nepa* have been positively identified whereby two other early stage larvae (early sp1 and early sp2) were suspected to belong to *Miyakea nepa* and *Oratosquillina perpensa*. The late stage larvae of sp3 likely belong to *Oratosquillina perpensa*. The pro-pelagic larvae and post-larvae of all the species were not found in the plankton samples possibly due to their benthic behaviour, as the samples were from surface towing. The missing mid stage larvae of sp1, sp2 and sp3 in the plankton samples could be due to further migration offshore. In order to identify the larvae and to obtain the complete series of developmetal stages, rearing of stomatopod from egg to juvenile is necessary.

Stomatopod larvae were spatially distinct in terms of utilizing the mangrove estuary and adjacent coastal waters. *Cloridopsis scorpio* larvae was found to inhibit the mangrove estuary while *Miyakea nepa* and likely *Oratosquillina perpensa* inhibit the adjacent coastal waters. *Cloridopsis scorpio* adults are believed to stay and spawn in the mangrove estuary while *Miyakea nepa* and *Oratosquillina perpensa* spawn in the adjacent coastal waters. The abundance of stomatopod larvae were not duly affected by monsoon seasons, but rather than environmental factors and food source (zooplankton). Larvae of *Miyakea nepa* and *Oratosquillina perpensa* migrate to farther offshore after hatching for unknown reason but returned back at the final pelagic stage. Larvae of *Harpiosquilla raphidea* were not found from the plankton samples because it is likely that this species spawned farther offshore since their mature female also not found in the sampling areas.

Cloridopsis scorpio was found to spawn once a year in mangrove estuary while the other stomatopods spawn two to three times a year in adjacent coastal water.

CHAPTER 6

FEEDING ECOLOGY OF STOMATOPODS IN MATANG

6.1 Results

6.1.1 Diet analysis

6.1.1.1 Percentage of stomach fullness

1982 (45% of total catch) individuals were examined for their stomach contents (Table 6.1). Table 6.1 showed that all the four stomatopod species had relatively high percent of empty stomachs (>30%) and 1/4 filled stomachs (16% - 31%) whereas percentage of stomachs with nearly full food (3/4 filled) and full stomachs were low (6 – 21%).

Table 6.1. Percentage stomach fullness of the four stomatopod species at three different depth strata over the 18 months of survey.

Species	Sex	Number of examined individuals	Percentage stomach fullness				
			empty	1/4 full	1/2 full	3/4 full	full
Miyakea nepa	Female	584	30.8	18.5	18.0	11.5	21.2
	Male	489	31.7	17.8	20.5	10.6	19.4
Oratosquillina perpensa	Female	339	38.6	18.9	15.6	9.5	17.4
	Male	283	36.7	19.8	17.3	11.0	15.2
Harpiosquilla raphidea	Female	127	32.3	28.3	16.5	7.9	15.0
	Male	114	33.3	23.7	21.9	8.8	12.3
Cloridopsis scorpio	Female	16	31.3	31.3	0	18.7	18.7
	Male	30	53.3	16.7	13.3	6.7	10.0

6.1.1.2 Dietary composition

The food items found in the stomatopod stomachs were fragments of appendages of shrimp and crab, pieces of shells and pincers of crab, scales and otoliths of fish, clubs of squid tentacles, pieces of shells and operculum of gastropod and bivalve, and fragments of brittle star. There were small amount of sediment and unidentified materials found in the stomachs of stomatopod.

6.1.1.3 Dietary pattern

a) *Miyakea nepa*

Table 6.2a and 6.2b showed the percentage frequency of occurrence and mean volumetric composition of three size classes of female and male *Miyakea nepa.* All three size classes for both sexes relied heavily on shrimp with frequency of occurrence and mean volumetric composition of almost 60% and 50%, respectively (Tables 6.2a, b). Gastropod and bivalve was the second major food item in term of frequency of occurrence and volumetric composition. Female and male mantis shrimp showed similar dietary pattern with smaller individuals preferring gastropod, bivalve and brittle star whereas larger individuals preferred squid and fish. However, the mean volumetric composition of squid, fish and brital star were little (< 18%) (Table 6.2b). Sediment and unidentified materials were found in small volume in the stomachs of *Miyakea nepa* (Tables 6.2b).

b) *Oratosquillina perpensa*

Shrimp constituted a major proportion of stomach contents across all sizes for female and male *Oratosquillina perpensa* with the frequency of occurrence and mean volumetric almost 50% and 40%, respectively (Table 6.3a, b). Crabs, gastropod and bivalve were the second major food items of *Oratosquillina perpensa* for all size groups and sexes with the occurrence of gastropod and bivalve slightly more than crab but the mean volumetric composition for both food items were almost similar. The frequency of occurrence and mean volumetric composition of squid showed an increase with size class for female. The mean percentage volume of squid, fish and brittle star were very little (<13%) (Table 6.3b). Sediment and unidentified materials remained the minor food items found in the stomachs of *Oratosquillina perpensa* (Table 6.3a, b).

c) *Harpiosquilla raphidea*

Both frequency of occurrence and mean volumetric composition of *Harpiosquilla raphidea* showed strong preference to fish followed by shrimp and squid (Table 6.4a, b). Gastropod, bivalve and brittle star were not found in the stomach of *Harpiosquilla raphidea*. In term of volumetric composition, the diet of male showed a decrease in consumption of crab and squid as size increased (Table 6.4b). *Harpiosquilla raphidea* had very little amount of sediment (< 0.01%) in their diet (Table 6.4b).

d) *Cloridopsis scorpio*

Shrimp was the dominant food items observed in female and male *Cloridopsis scorpio* with the frequency of occurrence and mean volumetric composition of more than 85% and 75% respectively (Table 6.5a, b). Crab, squid and fish were not observed in this species.

6.1.2 Multivariate analysis and food specialization

Figure 6.1 showed the PCA biplot based on the dietary composition of the four stomatopod species according to sex and size class over the 18 months of survey in matang. The first two axes derived from PCA explained 95% of the cumulative variation (Table 6.6). The eigen vectors showed that the consumption of shrimp, gastropod and bivalve, brittle star and sediment increased in the negative (left) direction while fish increased in the positive (right) direction of axis 1. For the second axis, the consumption of crab and squid increased in the negative direction. Details of PCA analysis on the dietary composition of the four stomatopod species according to sex and size class was given in appendix XII.

PCA biplot ordinations showed that there were four groups of food specialization (Figure 6.1). Each group comprised of a species of stomatopods that showed preference for particular food items. The diet of *Miyakea nepa* indicates that this species is more a generalist, while *Oratosquillina perpensa* had relatively higher proportion of crab in its diet. *Harpiosquilla raphidea* showed a strong preference on fish while *Cloridopsis scorpio* mostly fed on shrimp. Figure 6.1 showed that the dietary composition do not differ much among different size group and sexes of each species, but rather greatly differ among species.

Table 6.2a. Frequency of occurrence (%) of food items according to sex and size class for *Miyakea nepa*.

Sex	Carapace length (mm)	No. examined individuals	No. individuals with stomach contents	Frequency of occurrence (%)							
				Shrimp	Crab	Gastropod & bivalve	Squid	Fish	Brittle Star	Sediment	Unidentified
Female	<18	93	67	59.7% (40)	9.0% (6)	40.3% (27)	13.4% (9)	4.5% (3)	9.0% (6)	7.5% (5)	4.5% (3)
	18≤ - <28	310	207	58.5 (121)	9.0 (18)	41.1 (85)	11.1 (23)	9.7 (20)	7.7 (16)	10.1 (21)	6.3 (13)
	28≤ - <38	181	130	60.8 (79)	10 (13)	27.7 (36)	21.5 (28)	12.3 (16)	2.3 (3)	6.9 (9)	2.3 (3)
Male	<18	78	54	57.4% (31)	9.3% (5)	42.6% (23)	11.1% (6)	5.6% (3)	7.4% (4)	13.0% (7)	1.9% (1)
	18≤ - <28	320	214	58.9 (126)	9.8 (21)	39.3 (84)	12.1 (26)	10.7 (23)	8.4 (18)	9.8 (21)	7.0 (15)
	28≤ - <38	91	66	59.1 (39)	9.1 (6)	24.2 (16)	24.2 (16)	13.6 (9)	3.0 (2)	6.1 (4)	3.0 (2)

Table 6.2b. Mean volumetric composition (%) of food items according to sex and size class for *Miyakea nepa*.

Sex	Carapace length (mm)	Mean volumetric composition (%)							
		Shrimp	Crab	Gastropod & bivalve	Squid	Fish	Brittle Star	Sediment	Unidentified
Female	<18	51.2	8.4	24.7	6.0	2.4	6.0	1.0	0.3
	18≤ - <28	46.6	7.8	26.0	5.9	7.5	3.8	1.2	1.2
	28≤ - <38	51.7	8.7	16.4	11.2	9.7	0.8	0.7	0.8
Male	<18	49.3	9.1	25.9	4.8	3.3	4.0	3.4	0.2
	18≤ - <28	49.5	8.4	21.7	6.5	6.3	4.8	1.0	1.8
	28≤ - <38	50.6	6.9	11.8	17.6	11.2	0.9	0.5	0.4

Table 6.3a. Frequency of occurrence (%) of food items according to sex and size class for *Oratosquillina perpensa*.

Sex	Carapace length (mm)	No. examined individuals	No. individuals with stomach contents	Frequency of occurrence (%)							
				Shrimp	Crab	Gastropod & bivalve	Squid	Fish	Brittle Star	Sediment	Unidentified
Female	<18	81	54	46.3% (25)	31.5%(17)	35.2% (19)	14.8% (8)	7.4% (4)	7.4% (4)	11.1% (6)	1.9% (1)
	18≤ - <26	176	108	47.2 (51)	22.2(25)	30.6 (33)	17.6 (19)	16.7 (18)	12.0 (13)	7.4 (8)	0.9 (1)
	26≤ - <34	82	46	50.0 (23)	28.3(13)	32.6 (15)	23.9 (11)	15.2 (7)	4.3 (2)	8.7 (4)	4.3 (2)
Male	<18	50	34	50.0% (17)	26.5% (9)	38.2% (13)	14.7% (5)	11.8% (4)	11.8% (4)	5.9% (2)	2.9% (1)
	18≤ - <26	168	109	56.0 (61)	19.3 (21)	32.1 (35)	20.2 (22)	12.8 (14)	6.4 (7)	9.2 (10)	2.8 (3)
	26≤ - <34	65	36	52.8 (19)	19.4 (7)	36.1 (13)	22.2 (8)	16.7 (6)	8.3 (3)	11.1 (4)	8.3 (3)

Table 6.3b. Mean volumetric composition (%) of food items according to sex and size class for *Oratosquillina perpensa*.

Sex	Carapace length (mm)	Mean volumetric composition (%)							
		Shrimp	Crab	Gastropod & bivalve	Squid	Fish	Brittle Star	Sediment	Unidentified
Female	<18	40.1	24.2	20.7	9.1	1.8	2.3	1.6	0.2
	18≤ - <26	39.4	18.6	20.0	6.5	11.4	3.0	1.0	0.1
	26≤ - <34	41.5	20.8	17.9	12.6	7.2	0.4	0.7	0.6
Male	<18	42.5	20.8	19.7	9.4	4.1	2.6	0.6	0.3
	18≤ - <26	45.5	16.5	18.9	9.3	6.3	1.4	1.6	0.5
	26≤ - <34	38.4	15.9	20.1	8.7	12.9	1.5	1.3	1.2

Table 6.4a. Frequency of occurrence (%) of food items according to sex and size class for *Harpiosquilla raphidea*.

Sex	Carapace length (mm)	No. examined individuals	No. individuals with stomach contents	Frequency of occurrence (%)					
				Shrimp	Crab	Squid	Fish	Sediment	Unidentified
Female	<23	39	23	43.5% (10)	8.7% (2)	26.1% (6)	56.5% (13)	4.3% (1)	0%
	23≤ - <33	67	48	39.6 (19)	8.3 (4)	29.2 (14)	64.6 (31)	6.3 (3)	4.2 (2)
	33≤ - <43	21	15	46.7 (7)	6.7 (1)	26.7 (4)	60.0 (9)	0	0
Male	<23	37	26	38.5% (10)	11.5% (3)	30.8% (8)	50.0% (13)	0%	0%
	23≤ - <33	69	43	41.9 (18)	4.7 (2)	23.3 (10)	72.1 (31)	2.3 (1)	2.3 (1)
	33≤ - <43	8	7	57.1 (4)	0	28.6 (2)	57.1 (4)	0	0

Table 6.4b. Mean volumetric composition (%) of food items according to sex and size class for *Harpiosquilla raphidea.*

Sex	Carapace length (mm)	Mean volumetric composition (%)					
		Shrimp	Crab	Squid	Fish	Sediment	Unidentified
Female	<23	34.3	8.3	11.7	45.7	0.01	0
	23≤ - <33	25.5	4.8	16.1	51.8	0.01	1.8
	33≤ - <43	27.0	6.7	13.2	53.1	0	0
Male	<23	27.2	6.2	20.6	46.0	0	0
	23≤ - <33	26.9	1.5	11.5	59.1	0.01	1.0
	33≤ - <43	38.7	0	4.7	56.6	0	0

Table 6.5a. Frequency of occurrence (%) of food items according to sex for *Cloridopsis scorpio*.

			Frequency of occurrence (%)				
Sex	No. examined individuals	No. individuals with stomach contents	Shrimp	Gastropod & bivalve	Brittle star	Sediment	Unidentified
Female	15	10	90.0% (9)	30.0% (3)	10.0% (1)	20.0% (2)	10.0% (1)
Male	30	14	85.7 (12)	57.1 (8)	7.1 (1)	21.4 (3)	7.1 (1)

Table 6.5b. Mean volumetric composition (%) of food items according to sex for *Cloridopsis scorpio*.

	Mean volumetric composition (%)				
Sex	Shrimp	Gastropod & bivalve	Brittle star	Sediment	Unidentified
Female	79.5	13.7	2.4	3.4	1.0
Male	77.2	17.2	2.5	2.4	0.7

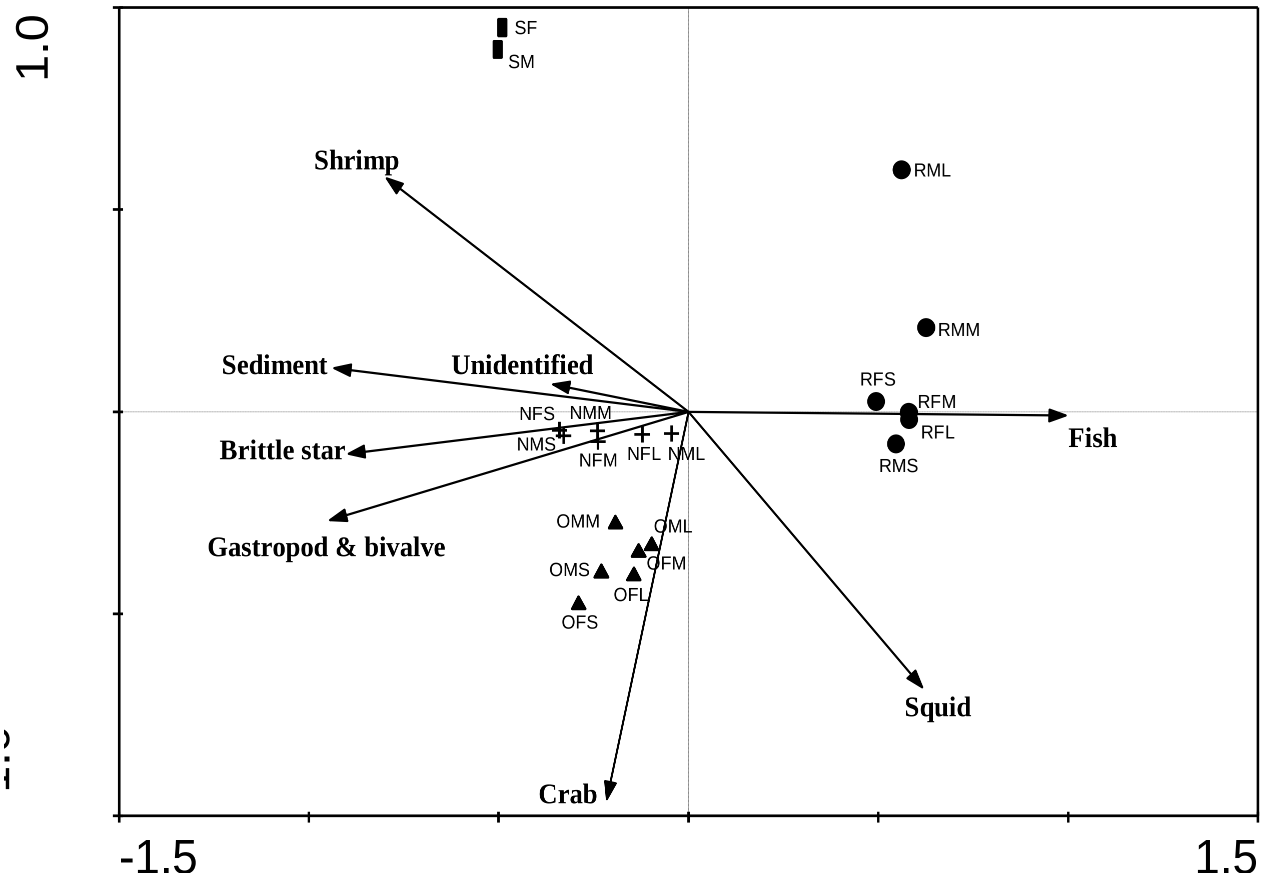

Figure 6.1 PCA biplot based on the dietary composition of the four stomatopod species according to sex and size class over the 18 months of survey in matang. Arrow denote food items, symbols denote stomatopod species by sex and size class. ┼ - *Miyakea nepa*, ▲- *Oratosquillina perpensa*, ● – *Harpiosquilla raphidea*, ▌ - *Cloridopsis scorpio*. First word of the code represents species name: N - *Miyakea nepa*, O - *Oratosquillina perpensa*, R - *Harpiosquilla raphidea*, S - *Cloridopsis scorpio*. Second word of the code represents sex: F – female, M – male. Third word of the code represents size class: S – smaller size class, M – medium size class, L – larger size class (Size class of the four stomatopod species are given in Table 6.2, Table 6.3 and Table 6.4. *Cloridopsis scorpio* was not classified into size class.

Table 6.6. Eigenvalues and eigen vectors of the first four axes computed from PCA, based on the dietary composition of the four stomatopod species according to sex and size class over the 18 months of survey in matang.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.758	0.193	0.021	0.014
Cumulative variance (%)	75.8	95.1	97.2	98.5
Dietary composition				
Shrimp	-0.7953	0.5771	-0.1274	0.0633
Crab	-0.2153	-0.9586	-0.1093	-0.1332
Gastropod & bivalve	-0.9440	-0.2679	0.1728	0.0496
Squid	0.6157	-0.6822	-0.1689	0.3434
Fish	0.9937	-0.0096	0.1031	-0.0029
Brittle star	-0.8958	-0.1037	0.3099	-0.0088
Sediment	-0.9333	0.1074	0.0509	-0.0742
Unidentified	-0.3571	0.0680	0.3090	0.5082

6.2 Discussion

6.2.1 Dietary composition and percentage of stomach fullness

Present study confirms that all four species of stomatopod are predators and consumed a broad range of prey items such as crustaceans (shrimp and crab), gastropod, bivalve, squid, fish and brittle star. Similar prey items were reported by other authors (Hamano & Matsuura, 1986; Hamano *et al.*, 1996; Lui 2005). In addition, Polychaeta and plant materials were observed in some of these studies (Hamano & Matsuura, 1986; Lui, 2005). However, the plant material was reported as accidental ingestion. The Polychaeta that were identified by Hamano & Matsuura (1986) were *Nephtys polybranchia*, *Paraprionospio* sp., *Glycinde* sp. and *Sthenolepis japonica*.

The relatively high percent of empty stomachs for all the four species indicates that they might be largely nocturnal feeders as observed in S*quilla mantis* in the Mediterranean (Maynou *et al.*, 2005).

6.2.2 Dietary pattern and food specialization

All the four species of stomatopods showed secondary food specialization. All four species fed on shrimp to a large extant. However, the second major food item for *Miyakea nepa* was gastropod and bivalve while *Oratosquillina perpensa* recorded similar volume of gastropod and bivalve, and crab as their next important food items. *Harpiosquilla raphidea* showed strong preference for fish.

The preferential predation of all the four species on shrimp could be attributed to their higher content of calcium since calcium is the major component of exoskeleton. Calcium is an important component for crustacean. Davis & Lawrence (1993) found that calcium and phosphorus concentration significantly affected the growth and survival of *Penaeus vannamei*. The squid found in the diet of stomatopod were mainly tentacle parts. Hamano *et al.* (1996) suggested that the squid tentacles were cut off when attacking stomatopod at the entrance of its burrow. The sediment that was found in the stomach was very little suggesting incidental ingestion by stomatopod during predation of gastropod and bivalve which are deposit feeders. This is true as *Harpiosquilla raphidea* which did not consume gastropod and bivalve showed very little amount of sediment (< 0.01%).

Harpiosquilla raphidea had very little amount of sediment (< 0.01%) suggesting feeding above the sea bottom. The diet composition of *Harpiosquilla raphidea* showed strong preference for fish due to their morphological adaptation enhances piscivory. A previous study on *Harpiosquilla harpax* showed that the greater length of its raptorial appendage and larger eyes provide greater efficiency in capturing fish (Dingle & Caldwell, 1978). Same study also reported that *Oratosquilla nepa* (= *Miyakea nepa*), *Oratosquilla inornata* and *Cloridopsis scorpio* with similar raptorial appendages however have difficulty in capturing and holding fish. Dingle & Caldwell (1978) also reported that although *Oratosquilla nepa* managed to capture fish, the fish escaped easily while *Cloridopsis scorpio* did not succeed in capturing fish. This explains why the fish consumption in *Miyakea nepa* and *Oratosquillina perpensa* was infrequent, while it was not observed in *Cloridopsis scorpio*. In addition, Dingle & Caldwell (1978) reported that differences in body size and sensory structures of stomatopod species could also explain the difference in feeding habits.

Based on the structure of their raptorial claws and foraging behaviour, stomatopods can be divided into two groups, spearers and smashers (Caldwell, 1991). The present diet analysis indicated that *Miyakea* nepa, *Oratosquillina perpensa* and

Cloridopsis scorpio can be grouped between spearer and smasher. This is because they use both attacks, by spearing on crustacean, fish and squid while smashing on gastropod and bivalve. Hamano & Matsuura (1986) reported that *Oratosquilla oratoria* also showed the behaviour of spearer and smasher. Larger *O. oratoria* tend to smash the short-necked clam, *Ruditapes philippinarum*, and ate the soft body only, while thin-shelled Pelecypoda, *T.lubrica* and *R. rostralia* were crunched up and ate together with the shell. Based on the prey items (mollusc shell, crustacean cuticle and annelid setae) of *Cloridopsis scorpio* and *Oratosquilla inornata*, Dingle & Caldwell (1975) concluded that they typically kill prey by spearing and smashing them.

There was no differentiation in the feeding habit between sexes for all the four stomatopod species. A similar pattern was found in Lui's study (2005). However, differences in feeding behaviour between sexes were observed in *O. oratoria* in Japan (Hamano & Matsuura, 1986). The authors suggested that these differences may be caused by different strategies of prey capture or nutritional requirements during maturation.

In the present study, the smaller individual of *Miyakea nepa* consumed more gastropod, bivalve and brittle star while larger individuals preferred squid and fish, suggesting that the smaller individual tends to capture slow-moving prey (gastropod, bivalve and brittle star). Female *Oratosquillina perpensa* tend to feed more on squid when their size increased. Squid seems to be an important source of nutrition in their diet. The importance of squid as diet for crustacean was also shown in *Penaeus monodon*. Coman *et al.* (2007) indicated that partial replacement of squid and bivalves with sexually mature shrimp in the maturation diet of *P. monodon* had a negative effect on egg fertility and hatching. Thus, further studies on the diet between different maturity stages of *Oratosquillina perpensa* are required in order to examine whether different maturity stages exhibit different food habit for maturation purpose.

Present study showed overlap of prey items in all the four species especially shrimp which contributed a very high proportion of their diet. This could be due to their living habitat rich in shrimps. This is true because the study area is an active fishing ground for shrimps. In addition, the Matang mangrove estuary is an important feeding and nursery areas for shrimps (Low *et al.*, 1999).

6.3 Conclusion

Based on the stomach fullness analysis, the four species of stomatopods tend to be nocturnal feeders because they had relatively high percent of empty stomachs (>30%) and 1/4 filled stomachs (16% - 31%). The abundant shrimp resource in mangrove and mudflat (nursery areas) (Low *et al.*, 1999) allows food overlap, but severe food competition is unlikely since secondary diet specialization is observed among them. Generally, stomatopods exhibit diet differences among species rather than size group and sexes.

CHAPTER 7

GENERAL DISCUSSION AND CONCLUSION

7.1 Habitat and food utilization among four species of stomatopods in Matang

Generally, competing species do show different patterns of resource use therefore, allowing coexistence of species. Such coexistence of stomatopods species in Matang begs the questions of how these animals utilize their available space and food resources thus, maintaining the survival of their populations. In order to answer this, two aspects will be further discussed in this section, habitat and food utilization.

Based on the previous studies conducted by Chong (2007b) and Chong (unpublished) in Matang in the sampling areas as shown in Figure 7.1, three species of stomatopods were recorded with a high mean density of *Cloridopsis scorpio* distributed along the mangrove estuary to river mouth, while a low mean density of *Miyakea nepa* was recorded from the river mouth to nearshore area (Table 7.1). *Oratosquillina perpensa* only found at nearshore area.

By using the mean density data of *Cloridopsis scorpio* in the estuary of Sangga Besar river from Chong (unpublished) together with the mean density of stomatopods from the present study, the distribution of the four stomatopods species along the mangrove estuary to coastal waters is diagrammed as shown in Figure 7.2. *Cloridopsis scorpio* and *Harpiosquilla raphidea* are spatially distinct with *Cloridopsis scorpio* mainly present in the estuary while the latter is distributed further offshore. Although *Miyakea nepa* and *Oratosquillina perpensa* occur in the same habitat, *Miyakea nepa* is more widely distributed as compared to *Oratosquillina perpensa*.

Based on stomatopod distribution and abundance along the salinity gradient of Matang mangrove estuary and coastal waters, *Cloridopsis scorpio* is an estuarine species which is less tolerant to salinity changes, as the salinity in the estuary is much lower than coastal areas (Chew & Chong, 2011; Ooi & Chong, 2011). *Miyakea nepa* and *Oratosquillina perpensa* are likely euryhaline species while *Harpiosquilla raphidea* a stenohaline species.

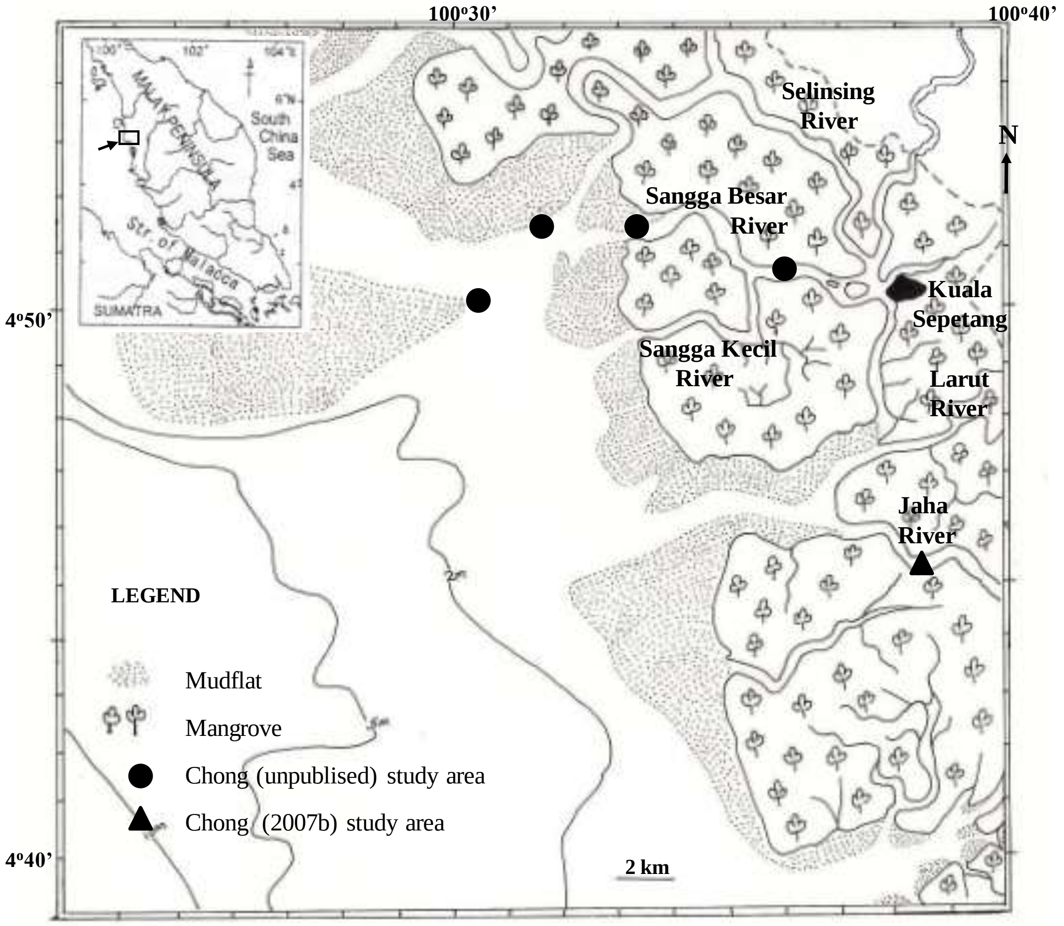

Figure 7.1. Sampling areas of previous studies by Chong (2007b) (filled triangles) and Chong (unpublished, filled circles).

Table 7.1. Detailed information of mean density of stomatopods conducted by Chong (2007b) and Chong (unpublished).

Study conducted by	Study details	Sampling period	Sampling gear	Location	Density (ind/ha)		
					Species		
					Cloridopsis scorpio	*Miyakea nepa*	*Oratosquillina perpensa*
Chong (2007b)	24-hour sampling at 3-hour intervals	8 September 2006 and 15 September	Otter trawl	Estuary of Jaha river	16.45 ± 25.55	0	0
Chong (unpublished)	Monthly sampling (once a month)	October 2009 to September 2010	Otter trawl	Estuary of Sangga Besar river	3.69 ± 10.43	0	0
				River mouth of Sangga Besar river	0.68 ± 3.27	1.12 ± 5.38	0
				Mudflat	0	0.23 ± 1.41	0
				Nearshore	0	0.95 ± 3.39	0.85 ± 3.13

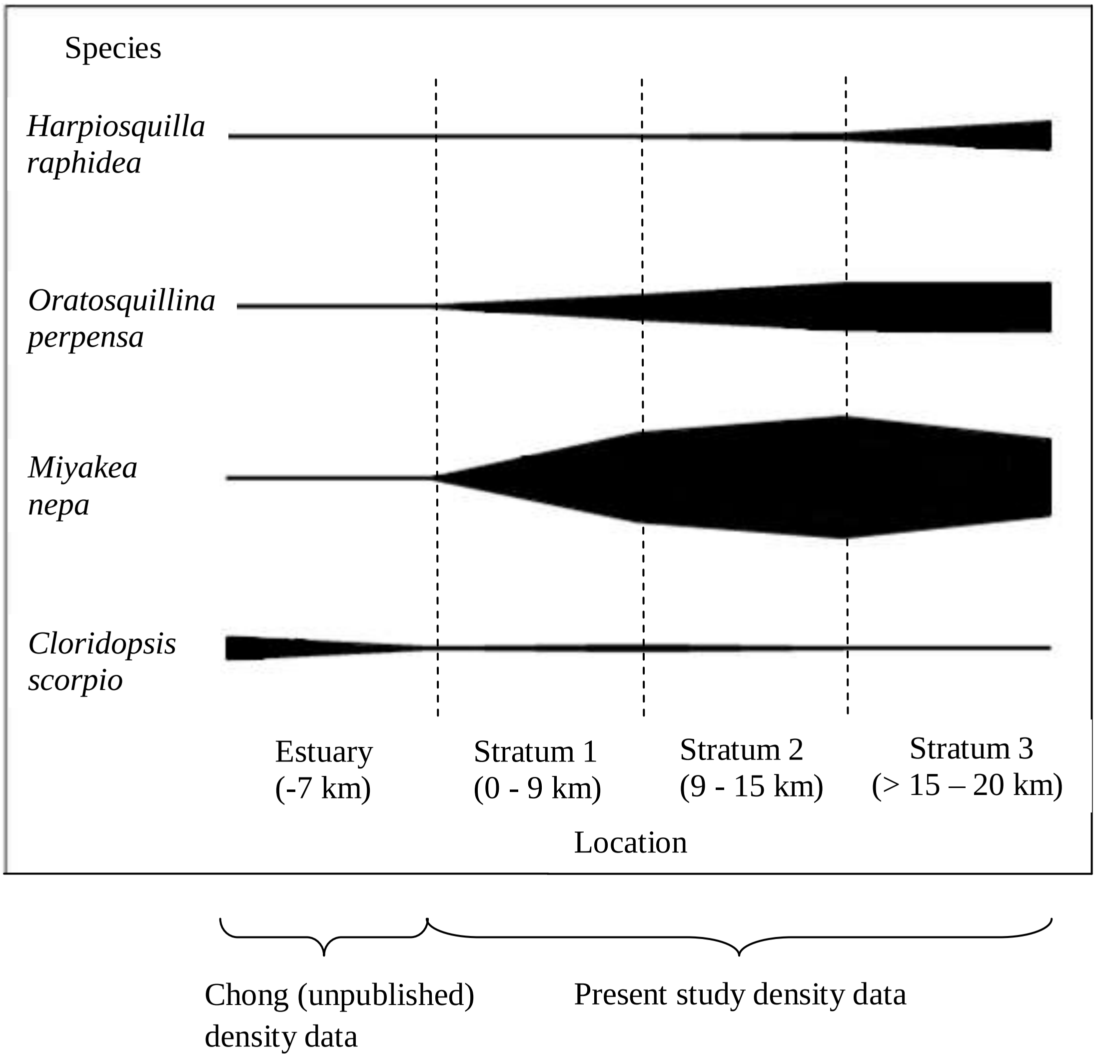

Figure 7.2. Distribution of stomatopods from estuary to coastal areas. Distance from the river mouth of Sangga Kecil river were presented in bracket. Negative indicate distance from river mouth towards estuary, positive indicate distance from river mouth towards offshore.

Based on their feeding habits, all the four stomatopods species showed a good separation based on prey selectivity (see Chapter 6). They show certain degree of trophic partitioning. However, this point should be view with caution because all the four stomatopod species show high percentage of empty stomachs (30% to 53%; Table 6.1). *Cloridopsis scorpio* is a shrimp eater while *Harpiosquilla raphidea* has a strong preference for fish. The large proportion of shrimp in the diet of the *Cloridopsis scorpio* not only indicates its preferred food but also its ability to exploits the large shrimp resource residing inside the mangrove estuary, their nursery area (Low *et al.*, 1999). The larger squillid, *Harpiosquilla raphidea* which resides in deeper more saline waters has a longer raptorial appendage and larger eyes, an adapatation that allows them to prey more efficiently on larger and fast moving prey, such as fish.

The diet of *Miyakea nepa* and *Oratosquillina perpensa* are more similar to each other, than either one to the other two species. This could be the result of their wider distribution from stratum 1 to stratum 3. However *Oratosquillina perpensa* displays secondary diet specialization on crabs. Since preying on crab could expose the predator to risk of injurious encounter due to counter defence, crab prey is not a good food choice. Hamano & Matsuura (1986) reported that stomatopods prey on easily captured organisms to minimize the energy expenditure due to capturing and handling the prey. But in this case, there is probably a trade off for *Oratosquillina perpensa* since this would avoid agonistic encounters with *Miyakea nepa*. *Miyakea nepa* could be the more aggressive of the two. According to Dingle *et al.* (1973) and Dingle and Caldwell (1975), when two or more stomatopod species occupy the same habitat, the more aggressive species is more abundant because it competes more successfully via agonistic behavior. In addition, the authors also noted that the less aggressive species are found in different microhabitats or, if any of them stay in the same habitat with the more aggressive species, their size must be larger. In Matang, a strong overlap of habitat was observed between *Miyakea nepa* and *Oratosquillina perpensa*, but the abundance of *Miyakea nepa* was more than twice the abundance of *Oratosquillina perpensa* (Table 3.4). Preliminary study shows that the abundance of both species was not significantly different between day and night (Table 7.2; appendix XIII). Thus, *Miyakea nepa* is likely to be more aggressive than *Oratosquillina perpensa* in Matang waters.

Oratosquillina perpensa being the less aggressive species fed more on crab and less on shrimp than *Miyakea nepa*, a feeding habit that reduces competition for similar food.

Table 7.2. Mean density of *Miyakea nepa* and *Oratosquillina perpensa* recorded at stratum 3 during the preliminary study (from 22:00 pm to 14:00 pm; every 2-hours interval) in August 2004.

	Miyakea nepa	*Oratosquillina perpensa*
Time	Density (ind/ha)	Density (ind/ha)
Day	5.0 ± 2.56[a]	4.7 ± 2.81[a]
Night	4.9 ± 3.38[a]	4.0 ± 2.79[a]

Since all the stomatopods species in Matang waters are found to feed on a very high proportion of shrimp, it is important to understand the life-cycle of shrimps and their ontogenetic migration path in Matang (Chong, 1996). Such information would substantiate the idea of how stomatopods utilise the shrimp resources. Based on Chong & Sasekumar (1994), the general life-cycle of most penaeid shrimps species (e.g. *Penaeus merguiensis*) according to their preferred habitat is depicted in Figure 7.3.

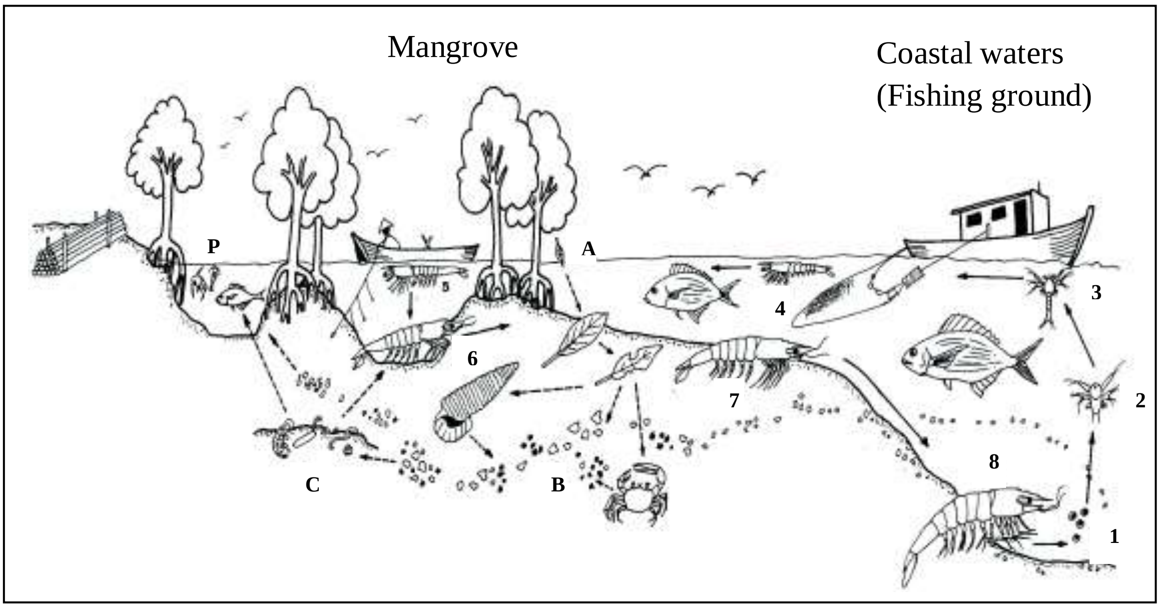

Figure 7.3. Composite picture of the ecology and benefits of mangroves. Mangrove leaf fall (A) contributes to a pool of leaf litter which is broken down into fragments (consumed) by macrofauna like crabs and snails. These plant fragments and the faeces (B) of the macrofauna are further broken down by microorganisms, or are consumed by fish, shrimps, shellfishes and very small benthic animals (C). These animals are themselves consumed by larger fish. The larvae of breeding crabs and other shellfishes which form part of the zooplankton (P) are also important food sources for young fish in

the mangroves. The general life-cycle of most penaeid shrimps species (e.g. *Penaeus merguiensis*) is illustrated; 1) eggs, spawned in deep offshore waters, 2) hatched nauplii larvae, 3) protozoeal larvae, 4) mysis larvae, 5) postlarvae in mangrove waterways, 5) postlarvae just before settling down on mud substrates, 6) juvenile shrimps, 7) maturing, subadult shrimps migrating offshore, and 8) adult shrimps. (Chong & Sasekumar, 1994).

Based on the distribution of stomatopods from estuary to coastal areas (Figure 7.2), the stomatopods appear to take advantage of the abundant resource of shrimps by residing along their migration path from nursery areas to offshore grounds. Thus, the smallest species, *Cloridopsis scorpio* utilize the smallest shrimps (small juveniles) inside the mangrove estuary while the largest stomatopod, *Harpiosquilla raphidea* feed on the largest adult shrimps. Both *Miyakea nepa* and *Oratosquillina perpensa* feed on large juvenile shrimps of intermediate sizes.

Although penaeid shrimps are abundant in Matang nonetheless, their abundance showed temporal variability whereby most of the shrimp species recorded highest abundance in the post-high rainfall month (Low *et al.*, 1999). As such, the secondary diet specialization of stomatopods also reflects their adaptation for alternative food when the shrimp abundance is low in certain months.

7.2 The impact of intensive fishing of stomatopods

In Matang, both *Miyakea nepa* (exploitation rate = 0.47) and *Oratosquillina perpensa* (exploitation rate = 0.59) are heavily exploited by trawling boats. Anthony *et al.* (2010) reported that the increase of trawling efforts had resulted in declining biomass of marine organisms such as stomatopods, crabs, lobsters, shrimps, cephalopods, mackerel and elasmobranchs in India. Kodama *et al.* (2004) found that the depletion of larger, more fecund stomatopod (*Oratosquilla oratoria*) by intensive fishing pressure in turn decreased larval abundance that contributes to the first recruitment event (from the first spawning peak).

Stomatopods may play an important role in the shrimp community as stomatopods are known to prey heavily on shrimps (this study). Dell & Sumpton (1999) found that the catches of stomatopods in Moreton Bay, Australia, show similar seasonal trend as penaeid catches.

As the ecosystems are "balanced by nature" and each component has a role in the sustenance of other components, overfishing of stomatopods in Matang may influence not only the shrimp community but may also disrupt the balance of the ecosystem food chain. According to Anthony *et al.* (2010), the increase in stomatopods fishing mortality had caused the increase of benthopelagic carnivore fishes which might be attributed to the absence of potential competitors for food. The authors also indicated that as all the different groups of organisms are linked through feeding interaction, the abundance of stomatopods would affect their prey (top-down control) and predators (bottom-up control) and vice versa.

Commercial fisheries should ensure sustainability of catch while optimizing benefits. Thus, the exploitation of stomatopods as a fishery commodity should be managed based on scientific information. The problem with managing the stomatopod fishery is that it is really a general problem of multispecies fisheries as occurring in all tropical Southeast Asian countries. In Malaysia, the demersal prawn resource is the major target of the trawl fishery. Stomatopods form a substantial portion of the incidental catches that resulted from the shrimp fishery. Therefore, sustainable management of the stomatopod resource will influence the prawn catches which contributed the highest commercial value of the demersal resources. Thus, it would not be feasible to implement a closed area or season strategy to protect the stomatopod resources without reducing the prawn catch. However, the present fisheries regulation requires that all trawl fishing by small boats (<5 tons gross tonnage) be operated at least five nautical miles offshore, while larger boats have to fish farther offshore. Therefore, *Cloridopsis scorpio* in the estuary and stomatopods within 5 nautical miles inshore are at least protected from trawl fishing; unfortunately, this zone is not the richest in term of stomatopod resources.

In view of the problem of multispecies fisheries, the most pragmatic approach will be either the release of captured gravid females or institute a maximum legal size of capture during spawning peaks to prevent recruitment overfishing. In Matang or Perak waters, the closed seasons will be from October to February and in April to June when most of the stomatopod breed. This release strategy is to protect the brooding females and ensure recruitment to the population. This method is feasible since stomatopods do not die so easily even in the trawl catches.

The first approach based on gravid female will require fishermen to learn how to identify ready-to-reproduce females which will be impractical. The second approach based on size limit is therefore recommended. Based on the length at first maturity of *Miyakea nepa* (carapace length = 28.0 mm) and *Oratosquillina perpensa* (carapace length = 25.0 mm; Table 5.1), the length of stomatopods captured should not exceed 25 mm carapace length to ensure that the females have a chance to spawn at least once. The study seems to suggest that growth overfishing may not be that serious since the proportion of captured juvenile stomatopods was not large. Implementation of minimum size of capture may however be instituted in the future if growth overfishing occurs in the future. If this is to be instituted, the recommended minimum size will be 13.5 mm (total length = 58.2 mm), based on the smallest captured stomatopods (Table 3.3). The legal maximum (or minimum) size of capture of stomatopods could simply be implemented by inspection of captured stomatopods at key landing sites.

7.3 Reproduction and recruitment of stomatopods in Matang

In Matang waters, *Miyakea nepa* shows a faster grow rate and shorter lifespan than *Oratosquillina perpensa*. The two spawning peaks (Figure 5.5a) of *Miyakea nepa* match its two recruitment events (Figure 4.2a). However, for *Oratosquillina perpensa* there was only one recruitment event (Figure 4.2b) from two spawning peaks (Figure 5.5b). This could be due to recruitment failure from high larval mortality. Multiple recruitment events of stomatopods have also been observed in Lui's (2005) study, where recruitment peaks do not coincide with the occurrence of brooding females. Lui (2005) however suggested that this could happen if some large females have two successive clutches in the same spawning season. Mature female of *Harpiosquilla raphidea* and their larvae were not found in the sampling areas suggesting that this species spawned further offshore.

7.4 Conclusion

The present study can be considered as the first comprehensive ecological study on mangrove and coastal waters stomatopods assemblages in Malaysia. One of the main findings of the present study is that the adult distributions of different stomatopod species are spatially distinct; *Cloridopsis scorpio* is estuarine and largely confined inside mangrove estuaries, in contrast to *H. rhaphidea* which is stenohaline and largely found in offshore waters. Another two species, *Miyakea nepa* and *Oratosquillina perpensa* tend to be euryhaline, being found in nearshore waters but not inside the estuary. The second important finding is that the feeding habit of the four species of stomatopods showed some degree of food partitioning. Nevertheless, in Matang waters, the large shrimp resource reduces the competitive pressure for stomatopods to occupy ‘perfect’ niches, although their secondary diet specialization clearly reflects partitioning. This appears to be an adaptation for alternative food in lieu of the temporal variability in shrimp abundance. The study supports the first hypothesis that stomatopod fauna adapt to exploit the most abundant food - shrimps. The spatial distribution of stomatopods, from the smallest to the largest species in the offshore direction, juxtaposes nicely with the continuous migration of juvenile shrimps from their estuarine nursery areas (mangroves, mudlats) to offshore grounds where they mature. Thus, both spatial separation and food differences reinforce the idea of niche partitioning among coexisting stomatopod species in tropical waters. Another finding of the study is that the tropical stomatopods are continuous spawners although one or two spawning peaks are evident, followed by one or two recruitment pulses.

The distribution of stomatopod larvae also appears to be spatially confined but their abundance is not duly affected by the wet and dry monsoon periods. The results support the second hypothesis that stomatopod larvae are affected by their environment including the availability of their potential food. Stomatopod larval abundance and distribution are most affected by salinity, although the abundance of zooplankton or their potential food exerts a smaller influence. In particular, the numbers of *C. scorpio* larvae appears to be related to the higher abundance of larger zooplankton inside the estuary where salinity decreases. In contrast, larvae of other stomatopods are confined to higher salinity coastal waters where smaller zooplankton are more available. The present study has successfully described the complete pelagic larval series (six stages) for *Cloridopsis scorpio*. Previously, only three stages were identified by Alikunhi (1952).

The population dynamics study has shown that the fishery of Matang's two main species of stomatopods is over-exploited and there is an urgent need to implement fishing limits in order that the populations could recover. Ironically, the stomatopod fishery is a result of the prawn fishery, the most valuable fishery commodity targeted by both commercial and traditional fishing gears. However, unlike prawns, stomatopod stocks are very much smaller and more vulnerable to collapse under intensive fishing.

Limitations of the present study:

1) There is possibility that the density of stomatopods estimated in this study was an underestimation. This is related to the efficiency of the sampling gear (otter trawl) in capturing stomatopods since stomatopods are known to be burrowers therefore some of these individuals may have avoided the trawl net.

2) *Cloridopsis scorpio* and *Harpiosquilla raphidea* were rarely taken during the study. This is because the present samplings of stomatopods were carried out at the three established strata from nearshore to about 20 km offshore, and did not include estuarine waters where *Cloridopsis scorpio* resides and far offshore waters where *Harpiosquilla raphidea* mainly resides. The mangrove-lined estuary presents a difficult place to sample using the trawl net. As a result, their numbers were underestimated and their population dynamics could not be studied in the present study.

3) It is not practical to perform histological examination of the testes for each and every male individual; this is the best way to determine male maturity. Nevertheless, the testis histology of *Miyakea nepa* has shown matching results with that of its penile development. Hence, the classification of male maturity stages using Bhattacharya's polymodal method serves as a practical method for assigning male maturity.

4) The larval samples examined in the present study were collected earlier by surface-towed plankton nets in another project. Ideally, for stomatopod larval study, bottom tows should also be taken, or better, oblique tows of the entire water column, in order to account for possible vertical stratification. This may explain why the early stage and late stage larvae which adopted a benthic behavior were absent in the larval catches. For this reason too, the complete series of larval development could not be described. In addition, the present study could not match the abundance of adults with that of the larvae collected at different times, in order to elucidate the spawning and recruitment pattern.

5) Due to lack of larval identification keys for stomatopods, the unidentified species could not be positively identified. In the present study, although rearings of the larvae of *Miyakea nepa*, *Oratosquillina perpensa* and *Cloridopsis scorpio* were carried out, these were not successful. Although eggs of *Miyakea nepa* successfully hatched out, all larvae died within three days without moulting. In addition, the proportion of eggs that hatched was very low. Most of the brooding females were observed to either disposed or ate the eggs for unknown reasons.

6) While the trawl samples were taken during the day, the relatively high percentage of empty stomachs in all four species indicates that the stomatopods tend to be nocturnal feeders. Hence, a 24-hour sampling and analysis of stomach contents should be carried out in the future to confirm their feeding habit.

Future studies:

1) As stomatopods are known to prey heavily on shrimps, a more detailed study on predator – prey (especially shrimps) relationships will be beneficial to any explanation regarding possible co-evolutionary relationships. In this connection, it would be useful

to test such a hypothesis by first relating the stomatopod species to shrimp diversity and abundance.

2) Since it is difficult to successfully culture stomatopod larvae, molecular analysis is suggested in future studies to match the molecular profile of unidentified larvae to that of known adults in order to confirm larval identity. DNA barcoding could probably be a good taxonomic method as it uses a short genetic marker in an organism's DNA to identify it as belonging to a particular species. A good taxonomic key is however required to advance the study of stomatopod larval ecology. Study of stomatopod population genetics is also useful to distinguish genetically-isolated populations, and to elucidate gene flow and thus their migration patterns.

REFERENCES

Abello, P., & Martin, P. (1993). Fishery dynamics of the mantis shrimp *Squilla mantis* (Crustacea: Stomatopoda) population off the Ebro delta (northwestern Mediterranean). *Fisheries Research*, 16, 131-145.

Addyhanis, A. (1995). Kajian taburan dan pemakanan stomatopoda di selat Kelang-Angsa Bank. Unpublished Degree's thesis, University of Malaya, Kuala Lumpur.

Ahyong, S.T. (1997). A new species of *Manningia* (Crustacea: Stomatopoda) from Irian Jaya, Indonesia, with remarks on the Genus. *Raffles Bulletin of Zoology, Supplement* 45(2), 327-333.

Ahyong, S.T. (2001). Revision of the Australian Stomatopod Crustacea. *Records of the Australian Museum, Supplement* 26, 1-326.

Ahyong, S.T. (2005). Phylogenetic analysis of the Squilloidea (Crustacea:Stomatopoda). *Invertebrate Systematics*, 19, 189–208.

Ahyong, S.T., Chan,T.Y., & Liao,Y.C. (2008). A catolog of the mantis shrimps (Stomatopoda) of Taiwan. National Taiwan Ocean University. Keelung, Taiwan.

Ahyong, S.T., & Lowry, J.K. (2001). Stomatopoda: Families. Version 1: 1 September 2001. http://www.crustacea.net.

Ali, M. (2011). Pengelolaan sumberdaya udang mantis (*Harpiosquilla raphidea* Fabricius, 1798) berdasarkan informasi biologi di Kuala Tungkal, Kabupaten Tanjung Jabung Barat, Jambi. Unpublished M.Sc's thesis, Institut Pertanian Bogor, Bogor.

Alikunhi, K. H. (1952). An account of the stomatopod larvae of the Madras plankton. *Records of the Indian Museum*, 49, 239-319.

Alikunhi, K.H. (1967). An account of the post-larval development, moulting and growth of the common stomatopods of the Madras coast. In: *Proceeding symposium on Crustacea II* (pp. 824-939). Marine Biological Association of India, India.

Alikunhi, K.H. (1975). Studies on Indonesia stomatopods: Notes on pelagic larvae and post-larval growth of *Cloridopsis scorpio* Latreille. Bulletin shrimp Culture Research Centre, 1(2), 69-78.

Annual Fisheries Statistics (2008 to 2010). *Annual Fisheries Statistics*. Department of Fisheries, Malaysia. Kuala Lumpur, Malaysia.

Antony, P.J., Dhanya, S., Lyla, P.S., Kurup, B.M., & Ajmal Khan, S. (2010). Ecological role of stomatopods (mantis shrimps) and potential impacts of trawling in a marine ecosystem of the southeast coast of India *Ecological Modelling*, 221(21), 2604–2614.

Barber, P., & Boyce, S. L. (2006). Estimating diversity of Indo-Pacific coral reef stomatopods through DNA barcoding of stomatopod larvae. In: *Proceedings of the Royal Society of London. Series B, Biological sciences* (pp. 2053-2061). London.

Caldwell, R.L. (1991).Stomatopods: The better to see you with my dear. *Australian Natural History* , 23, 696-705.

Carpenter, K.E., & Niem, V.H. (1998). FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific (vol. 2). Cephalopods, crustaceans, holothurians and sharks. Rome. 1396pp.

Chew, L.L. (2012). Dynamics and trophic role of zooplankton community in the Matang mangrove estuaries and adjacent coastal waters (Peninsular Malaysia), with special emphasis on copepods. Unpublished Ph.D.'s thesis, University of Malaya, Kuala Lumpur.

Chew, L.L., & Chong, V.C. (2011). Copepod community structure and abundance in a tropical mangrove estuary, with comparisons to coastal waters. Hydrobiologia, 666, 127-143

Chew, L.L., Chong V.C.& Hanamura, Y. (2007). How important are zooplankton for juvenile fish nutrition in mangrove ecosystems? *JIRCAS Working Report*, 56, 7-18.

Chong, V.C. (1979). The biology of the white prawn *Penaeus merguiensis* demand in the Pulau Angsa. Unpublished master's thesis, University of Malaya, Kuala Lumpur.

Chong, V.C. (1996). The prawn-mangrove connection - fact or fallacy? In: *Sustainable Utilization of Coastal Ecosystems* (pp. 3-20). JIRCAS, Japan.

Chong, V.C. (2007a). Mangroves-fisheries linkages- the Malaysian perspective. Bulletin of Marine Science, 80, 755-772.

Chong, V.C., & Sasekumar, A. (1981). Food and feeding habits of the white prawn *Penaeus merguieneis*. *Marine Ecology Progress Series*, 5, 185-191.

Chong, V.C., & Sasekumar, A. (1994). Status of mangroves fisheries in the ASEAN region. In: Third *ASEAN-Australia Symposium on Living Coastal Resources*: *Living coastal resources of South-east Asia: status and management* (pp. 56-61). Bangkok, Thailand.

Chong, V.C., Sasekumar, A., Leh, M.U.C., & D'Cruz, R. (1990): The fish and prawn communities of a Malaysian coastal mangrove system, with comparisons to adjacent mudflats and inshore waters. *Estuarine, Coastal and Shelf Science*, 31, 703-722.

Chong, Z.Y. (2007b). Tidal and diel abundance of invertebrate fauna of the Matang forest reserve. Unpublished B.Sc's thesis, University of Malaya, Kuala Lumpur.

Christy, J.H., & Salmon, M. (1991). Comparative studies of reproductive behaviour in mantis shrimps and fiddler crabs. *American Zoologist*, 31, 329-337.

Coman, G.J., Arnold, S.J., Callaghan, T.R., & Preston, N.P. (2007). Effect of two maturation diet combinations on reproductive performance of domesticated *Penaeus monodon*. *Aquaculture*, 263, 75–83.

Davis, D.A., & Lawrence,A.L. (1993). Response of *Penaeus vannamei* to dietary calcium, phosphorus and calcium: phosphorus ratio. *Journal of The World Aquaculture Society*, 24(4), 504-515.

Deecaraman, M., & Subramoniam, T. (1980). Male reproductive tract and accessory glands of a stomatopod, Squilla holoschista. *International Journal of Invertebrate Reproduction*, 2, 175-188.

Dell, Q., & Sumpton, W. (1999). Stomatopod by-catch from prawn trawling in Moreton Bay, Australia. *Asian Fisheries Science*, 12, 133-144.

Dingle H., & Caldwell R.L. (1975). Distribution, abundance, and interspecific agonistic behaviour of two mudflat stomatopods. *Oecologia*, 20, 167-178.

Dingle H.,& Caldwell R.L. (1978). Ecology and morphology of feeding and agonistic behaviour in mudflat stomatopods (Squillidae). *Biological Bulletin*, 155, 134-149.

Dingle, H., Highsmith, R.C., Evans, K.E., & Caldwell, R.L. (1973). Interspecific Aggressive Behavior in Tropical Reef Stomatopods and Its Possible Ecological Significance. *Oecologia*, 13(1), 55-64.

Dittel, A.I. (1991). Distribution, abundance, and sexual composition of stomatopods in the Gulf of Nicoya, Costa Rica. *Journal of Crustacean Biology*, 11(2), 269-276.

Erdmann, M.V., & Caldwell, R.L. (1997). Stomatopod Crustaceans as bioindicators of marine pollution stress on coral reefs. *Proceedings of the 8th International Coral Reef Symposium* 2 (pp. 1521–1526).

Fariduddin, O. (1996). Udang Lipan ke pasaran luar negara. *Berita Perikanan*, 7.

Gan, B.K. (1995). *A working plan for the Matang Mangrove Forest Reserve, Perak, 1990-1999*. Peninsular Malaysia: State Forestry Department of Perak.

Hamano, T. (1988). Mating behaviour of *Oratosquilla oratoria*. *Journal of Crustacean Biology*, 8(2), 239-244.

Hamano, T., Hayashi, K., Kubota, K., Matsushita, H., & Tabuchi, K. (1996). Population structure and feeding behaviour of the stomatopod crustacean *Kempina mikado* (Kemp & Chopra, 1921) in the East China Sea. *Fisheries Science*, 62(3), 397-399.

Hamano, T., & Matsuura, S. (1984). Egg laying and egg mass nursing behaviour in the Japanese mantis shrimp. *Bulletin of the Japanese Society of Scientific Fisheries*, 50(12), 1969-1973.

Hamano, T., & Matsuura, S. (1986). Food habits of the Japanese mantis shrimp in the benthic community of Hakata Bay. *Bulletin of the Japanese Society of Scientific Fisheries*, 52 (5), 787-794.

Hamano, T., & Matsuura, S. (1987). Egg size, duration of incubation, and larval development of the Japanese mantis shrimp in the laboratory. *Bulletin of the Japanese Society of Scientific Fisheries*, 53(1), 23-39.

Hylleberg, J., Nateewathana, A., & Chatananthawej, B. (1985). Temporal changes in the macrobenthos on the west coast of Phuket Island, with emphasis on the effects of offshore tin mining. *Phuket Marine Biological Center Research Bulletin*, 38, 32 pp.
Jivaluk, J. (2000). Composition, Abundance and Distribution of Zooplankton in the South China Sea, Area IV: Vietnamese Waters. In: *Proceedings of the SEAFDEC Seminar on Fishery Resources in the South China Sea, Area IV : Vietnamese Waters* (pp. 77-93).

Kodama, K., Horiguch, T., Kume, G., Nagayama, S., Shimizu, T., Shiraishi, H., Morita, M., & Shimizu, M. (2006) Effects of hypoxia on early life history of the stomatopod *Oratosquilla oratoria* in a coastal sea. Marine Ecology Progress Series, 324, 197-206.

Kodama, K., Shimizu, T., & Aoki, I. (2003). Possible factors causing the fluctuation of the recruitment of Japanese mantis shrimp *Oratosquilla oratoria* in Tokyo Bay. *Bulletin of the Kanagawa Prefectural Fisheries Research Institute*, 8, 71-76. (in Japanese, with English abstract)

Kodama, K., Shimizu, T., Yamakawa, T., Aoki, I. (2004). Reproductive biology of the female Japanese mantis shrimp *Oratosquilla oratoria* (Stomatopoda) in relation to changes in the seasonal pattern of larval occurrence in Tokyo Bay, Japan. *Fisheries Science*, 70, 734-745

Kodama, K., Shiraishi, H., Morita, M., & Horiguchi, T. (2009). Reproductive biology of the Japanese mantis shrimp *Oratosquilla oratoria* (Crustacea Stomatopoda): Annual cycle of gonadal development and copulation. *Marine Biology Research*, 5, 415-426.

Kodama, K., Yamakawa, T., Shimizu, T., & Aoki, I. (2005). Age estimation of the wild population of Japanese mantis shrimp *Oratosquilla oratoria* (Crustacea: Stomatopoda) in Tokyo Bay, Japan, using lipofuscin as an age marker. *Fisheries Science*, 71, 141-150

Legendre, P., & Legendre, L. (1998). *Numerical ecology* (2nd ed.). Elsevier Science BV, Amsterdam.

Low, C.B., Chong, V.C., Lim, L.H.S. and S. Hayase (1999). Prawn production of Matang and Dinding River mangroves: Species distribution and seasonal recruitment", In: *Proceedings of Fourth JIRCAS Seminar on Productivity and Sustainable Utilization of Brackish Water Mangrove Ecosystems* (pp. 89-101). Penang, Malaysia.

Lui, K.K.Y. (2005). Ecology of commercially important stomatopods in Hong Kong. Unpublished master's thesis, University of Hong Kong, Hong Kong.

Manning, R.B. (1969). A Review of the Genus *Harpiosquill*a (Crustacea, Stomatopoda), with Descriptions of Three New Species. *Smithsonian Contributions to Zoology*, 36:, 41pp.

Manning, R.B., & Provenzano Jr., A.J. (1963). Studies on development of stomatopod crustacea I. Early larval stages of *Gonodactylus oerstedii* Hansen. *Bulletin of Marine Science of the Gulf of Caribbean*, 13(3), 467-487.

Maynou F.M., Abello P., & Sartor P. (2005). A review of the fisheries biology of the mantis shrimp, *Squilla mantis* (L. 1785) (Stomatopoda, Squillidae) in the Mediterranean. *Crustaceana*, 77 (9), 1081-1099.

Michel, A. and Manning, R. B. (1972). The pelagic larvae of *Chorisquilla tuberculata* (Borradaile, 1907) (Stomatopoda). *Crustaceana*, 22(2), 113-126.

Morgan, S.G. (1980). Aspects of larval ecology of *Squilla empusa* (Crustacea, Stomatopoda) in Chesapeake Bay. *Fishery Bulletin*, 78(3), 693-700.

Morgan, S.G., & Provenzano Jr., A.J. (1979). Development of pelagic larvae and postlarva of *Squilla empusa* (Crustacea, Stomatopoda), with an assessment of larval characters within the Squllidae. *Fishery Bulletin*, 77(1), 61-90.

Moosa, M.K. (2000). Marine biodiversity of the South China Sea: a checklist of stomatopod Crustacea. *The Raffles Bulletin of Zoology*, *Supplement* 8, 405-457.

Naiyatner, P. (1980). "*Stomatopoda of Thailand*". Department of Biology, Chulalongkorn University, Thailand.

Ohtomi, J., Shimizu, M. (1988). Growth after recruitment completion and life span of the Japanese mantis shrimp *Oratosquilla oratoria* in Tokyo Bay. Nippon Suisan Gakkaishi, 54(11), 1935-1940.

Ooi, A.L., & Chong, V.C. (2011). Larval fish assemblages in a tropical mangrove estuary and adjacent coastal waters: Offshore–inshore flux of marine and estuarine species. *Continental Shelf Research*, 31, 1599-1610.

Patek, S.N., Korff, W.L., & Caldwell, R.L. (2004). Deadly strike mechanism of a mantis shrimp. *Nature*, 428, 819-820.

Pauly, D. (1983). Some simple methods for the assessment of tropical fish stocks. *FAO fisheries technical paper*, 234, 1-52.

Pauly, D., & Munro, J.L. (1984). Once more on the comparison of growth in fish and invertebrates. *ICLARM Fishbyte*, 2(1), 21.

Piamthipmanus, M. (1998). Temporal changes in the abundance of macrobenthos in the South China Sea, Area 1: Gulf of Thailand and East Coast of Peninsular Malaysia. In: SEAFDEC. 1998**.** *Proceedings of the first technical seminar on marine fishery resources survey in the South China Sea, Area 1: Gulf of Thailand and East Coast of Peninsular Malaysia* (pp.156-171). SEAFDEC Training Department, Samutprakarn.

Pyne, R.R. (1972). Larval development and behaviour of the mantis shrimp, *Squilla armata* Milne Edwards (Crustacea: Stomatopoda). *Journal of Royal Society of New Zealand*, 2(2), 121-146.

Reaka, M.L. (1976). Lunar and tidal periodicity of molting and reproduction in stomatopod Crustacea: a selfish herd hypothesis. *Biological Bulletin*, 150, 468-490.

Reaka M.L. (1980). Geographic range, life history patterns, and body size in a guild of coral-dwelling mantis shrimps. *Evolution*, 34 (5), 1019-1030.

Reaka, M.L., & Manning, R.B. (1980). The distribution ecology and zoogeographical relationships of stomatopod Crustacea from Pacific Costa Rica. *Smithosonian Contributions to the Marine Science*, 7, 1-29.
Reaka, M.L., & Manning, R.B. (1981). The behaviour of stomatopod crustaceans and its relationship to rates of evolution. *Journal of Crustacean Biology*,. 1, 309-327.

Reaka, M.L., & Manning R.B. (1987). The significance of body size, dispersal potential, and habitat for rates of morphological evolution in stomatopod Crustacea. *Smithsonian Contributions to Zoology*, 448, 1-41.

Reddy, H.R.V., & Shanbhogue, S.L. (1994). Population dynamics of the mantis shrimp, *Oratosquilla nepa* (Latreille) of Mangalore coast. *Mahasagar*, 27(2), 125-130.

Rockett, M.D., Standard, G.W., & Chittenden, M.E. Jr. (1984). Bathymetric distribution, spawning periodicity, sex ratios, and size compositions of the mantis shrimp, *Squilla empusa,* in the northwestern Gulf of Mexico. *Fishery Bulletin*, 82(2), 418-426.

Ruppert, E.E., & Barnes, R.D. (1994). *Invertebrate zoology* (6th ed.). Saunders College. United States of America.

Sallam, W.S. (2005). Reproductive biology of the mantis shrimp *Erugosquilla massavensis* from Port Said, Egypt. *Egyptian Journal of Aquatic Biology and Fisheries*, 9(1), 171-183.

Sasekumar, A., Chong, V.C., Leh, M.U., & D'Cruz, R. (1992). Mangroves as a habitat for fish and prawns. Hydrobiologia, 247, 195-207.

Sasekumar, A., Chong, V.C., & Singh, H.R. (1994). The physical and chemical characteristics of Matang mangrove waters. *Proceedings of the third ASEAN-Australia Symposium on Living Coastal Resources* (pp. 446-454). Chulalongkorn University, Bangkok.

Schram, F.R. (1986). *Crustacea*. Oxford University Press, New York. 606 pp.

Sivadas, S., Ingole, B., & Nanajkar, M. (2011). Temporal variability of macrofauna from a disturbed habitat in Zuari estuary, west coast of India. *Environmental Monitoring and Assessment,* 173(1-4), 65-78.

Sparre, P.E., Ursin, & Venema, S.C. (1989). *Introduction to tropical fish stock assessment-Part 1-Manual*. FAO Fisheries Technical Paper 306/1.

Stiling, P. (1999). *Ecology: Theories and Applications* (3rd ed.). Prentice Hall. Upper Saddle River, New Jersey.

Sukumaran, K.K. (1987). Study on the fishery and biology of the mantis shrimp *Oratosquilla nepa* of South Kanara coast. *Indian Journal of fisheries,* 32, 293-305.

Tang, W.K. (2009). Distribution, seasonality and species identification of larval stomatopoda in Hong Kong waters. Unpublished master's thesis, University of Hong Kong, Hong Kong.

Taylor, C. C. (1958). Cod growth and temperature. *ICES Journal of Marine Science*, 23, 366–370.

ter Braak, C.J.F., & Smilauer, P. (2002). CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination. Version 4.5. Microcomputer Power. Ithaca, New York.

Then, A.Y.H. (2008). The structure and trophodynamics of the fish community in estuaries of Matang mangrove forest reserve, Peninsular Malaysia. Unpublished master's thesis, University of Malaya, Kuala Lumpur.

Wardiatno, Y., & Mashar, A. (2010). Biological information on the mantis shrimp, harpiosquilla raphidea (Fabricius 1798) (Stomatopoda, Crustacea) in Indonesia with a highlight of its reproductive aspects. *Journal of Tropical Biology and Conservation*, 7, 65-73.

Wortham-Neal, J. (2002). Reproductive morphology and biology of male and female mantis shrimp (Stomatopoda: Squillidae). *Journal of Crustacean Biology*, 22(4), 728-741.

Zar, J.H. (1998). *Biostatistical analysis* (4th ed.). Prentice Hall International. New Jersey.

Zgozi, S.W. (2000). The distribution and abundance of fish and macrobenthic communities in relation to environmental factors in Klang Strait (Malaysia). Unpublished master's thesis, University of Malaya, Kuala Lumpur.

Appendix I. Total volume (m^3) of water filtered during the routine monthly sampling.

Month	**Station**									
	1A	**1B**	**2A**	**2B**	**3A**	**3B**	**4A**	**4B**	**5A**	**5B**
Nov02	181.95	143.53	153.31	164.29	152.09	159.48	142.64	137.04	166.91	147.95
Dec02	176.72	140.56	124.60	116.35	177.12	122.03	142.40	125.75	129.60	142.20
Jan03	116.16	131.56	93.21	119.31	140.46	129.88	138.83	136.00	98.83	105.90
Feb03	138.82	150.58	115.73	154.86	138.49	131.55	115.59	142.47	127.57	123.65
Mar03	171.45	161.49	157.59	162.69	141.31	155.80	160.60	144.04	156.67	153.17
Apr03	194.33	143.09	168.68	121.98	165.66	177.53	148.13	164.43	136.47	149.27
May03	187.59	110.56	131.12	86.32	108.61	86.13	80.67	92.03	90.17	83.11
Jun03	143.04	135.16	120.68	137.36	137.69	148.42	137.75	147.97	124.99	124.99
Jul03	93.52	115.89	103.25	102.94	109.88	98.78	85.82	94.54	no sample	no sample
Aug03	105.82	113.76	105.21	102.48	111.47	96.10	97.62	110.65	104.99	60.21
Sep03	130.48	104.21	102.59	108.60	109.71	115.66	108.50	97.62	106.19	83.32
Oct03	85.30	66.23	96.67	83.41	79.81	81.43	25.01	93.35	82.21	93.0

Appendix II. Total rainfall and number of rainy days during the routine monthly sampling.

Month	Total rainfall	No. of rainy days
Sep-04	270.80	19.0
Oct-04	407.60	24.0
Nov-04	627.20	27.0
Dec-04	309.60	21.0
Jan-05	145.00	16.0
Feb-05	202.60	19.0
Mar-05	238.00	24.0
Apr-05	435.60	22.0
May-05	327.40	24.0
Jun-05	164.20	11.0
Jul-05	87.00	15.0
Aug-05	154.40	15.0
Sep-05	167.20	14.0
Oct-05	344.20	26.0
Nov-05	404.40	25.0
Dec-05	436.40	20.0
Jan-06	184.40	13.0
Feb-06	135.20	22.0

Appendix III. Results of Mann-Whitney U test for significant test on amount of total rainfall between monsoon seasons.

	Rank Sum	Rank Sum	U	Z	p-level	Valid N	Valid N	2*1sided
Total rainfall	43.00000	93.00000	22.00000	-0.867722	0.385547	6	10	0.427822

Appendix IV. Results of non-parametric Kruskal-Wallis for significant test on water parameters among strata (stratum 1, stratum 2 and stratum 3). Shaded area indicates significance at $p < 0.01$.

a. Salinity

	1 - R:40.208	2 - R:57.722
1 Stratum 1		
2 Stratum 2	0.009936	
3 Stratum 3	0.003134	1

b. Dissolved oxygen

	1 - R:32.528	2 - R:62.111
1 Stratum 1		
2 Stratum 2	0.000157	
3 Stratum 3	0.000005	1

c. Turbidity

	1 - R:75.319	2 - R:50.097
1 Stratum 1		
2 Stratum 2	0.001692	
3 Stratum 3	0.000000	0.171484

d. Temperature

	1 - R:49.194	2 - R:63.569
1 Stratum 1		
2 Stratum 2	0.148135	
3 Stratum 3	1	0.148506

e. pH

	1 - R:37.306	2 - R:60.694
1 Stratum 1		
2 Stratum 2	0.004156	
3 Stratum 3	0.000749	1

Appendix V. Results of Mann-Whitney U test for significant test on water parameters between monsoon seasons (southwest and northeast monsoons). Shaded area indicates significance at $p < 0.05$.

a. Salinity

	Rank Sum	Rank Sum	U	Z	p-level	Valid N	Valid N	2*1sided
Sal	2230.500	1774.500	289.5000	5.505682	0.000000	35	54	0.000000

b. Dissolved oxygen

	Rank Sum	Rank Sum	U	Z	p-level	Valid N	Valid N	2*1sided
DO	1841.000	2164.000	679.0000	2.234190	0.025471	35	54	0.025209

c. Turbidity

	Rank Sum	Rank Sum	U	Z	p-level	Valid N	Valid N	2*1sided
Turb	1763.500	2241.500	756.5000	1.583251	0.113365	35	54	0.113691

d. Temperature

	Rank Sum	Rank Sum	U	Z	p-level	Valid N	Valid N	2*1sided
temp	1369.000	2636.000	739.0000	-1.73024	0.083589	35	54	0.084353

e. pH

	Rank Sum	Rank Sum	U	Z	p-level	Valid N	Valid N	2*1sided
pH	2024.000	1981.000	496.0000	3.771246	0.000162	35	54	0.000118

Appendix VI. Density and biomass of the four stomatopod species during the routine monthly sampling.

Month	**Stratum**	**Trawl**	**Density (ind/ha)**				**Biomass (kg/ha)**			
			M. nepa	***O. perpensa***	***H. raphidea***	***C. scorpio***	***M. nepa***	***O. perpensa***	***H. raphidea***	***C. scorpio***
Sep04	1	1	2.317	29.356	0	0	0.026	0.352	0	0
Sep04	1	2	21.702	10.213	0	6.383	0.252	0.063	0	0.075
Sep04	2	3	33.938	28.282	0	0.628	0.358	0.206	0	0.007
Sep04	2	4	3.3192	8.298	0	0	0.047	0.094	0	0
Sep04	3	5	15.397	6.599	0	0	0.188	0.089	0	0
Sep04	3	6	0.667	10.016	0.667	0	0.014	0.139	0.023	0
Oct04	1	1	6.422	16.412	0	2.140	0.127	0.121	0	0.023
Oct04	1	2	19.365	10.684	0	0	0.363	0.064	0	0
Oct04	2	3	29.257	11.417	0	0	0.572	0.147	0	0
Oct04	2	4	23.656	10.036	0	0	0.402	0.188	0	0
Oct04	3	5	17.231	11.692	0	0	0.368	0.141	0	0
Oct04	3	6	26.449	15.208	0	0	0.600	0.212	0	0
Nov04	1	1	0	0.995	0	0.995	0	0.005	0	0.012
Nov04	1	2	0.5401	0.540	0	0	0.004	0.001	0	0
Nov04	2	3	15.820	1.171	0	0	0.419	0.016	0	0
Nov04	2	4	15.732	20.393	0.582	0	0.333	0.270	0.142	0
Nov04	3	5	4.975	73.638	1.990	0	0.139	0.579	0.248	0
Nov04	3	6	2.304	31.686	0.576	0.576	0.065	0.332	0.043	0.004
Dec04	1	1	0	0.461	0	0	0	0.003	0	0
Dec04	1	2	0.412	0.824	0	0	0.009	0.007	0	0
Dec04	2	3	27.863	10.946	0	0	0.258	0.146	0	0
Dec04	2	4	3.011	7.227	1.806	0	0.072	0.102	0.004	0

Dec04	3	5	15.659	12.046	6.023	0	0.300	0.136	0.024	0
Dec04	3	6	16.527	15.915	14.691	0	0.286	0.188	0.043	0
Jan05	1	1	0.560	3.941	0.563	0.563	0.006	0.021	0.020	0.007
Jan05	1	2	3.142	2.094	0	0	0.034	0.015	0	0
Jan05	2	3	10.137	32.547	0	0.533	0.124	0.481	0	0.003
Jan05	2	4	55.425	47.818	2.173	0	0.422	0.624	0.012	0
Jan05	3	5	15.398	1.649	2.199	0	0.392	0.013	0.031	0
Jan05	3	6	19.018	13.041	15.214	0	0.455	0.167	0.199	0
Feb05	1	1	27.651	0	0	0	0.279	0	0	0
Feb05	1	2	26.769	0	0	0	0.483	0	0	0
Feb05	2	3	12.815	1.898	1.898	0	0.237	0.025	0.033	0
Feb05	2	4	11.940	9.453	5.4721	0	0.260	0.184	0.106	0
Feb05	3	5	1.675	9.217	14.245	0	0.043	0.152	0.385	0
Feb05	3	6	0.910	5.005	0.455	0	0.018	0.087	0.0152	0
Mar05	1	1	47.363	9.368	0	0	0.718	0.128	0	0
Mar05	1	2	23.332	11.666	2.121	0.530	0.400	0.203	0.118	0.005
Mar05	2	3	26.616	6.229	3.964	0	0.365	0.075	0.064	0
Mar05	2	4	5.479	11.568	6.088	0	0.060	0.154	0.111	0
Mar05	3	5	14.808	5.126	37.022	0	0.259	0.075	0.754	0
Mar05	3	6	12.242	12.854	27.545	0	0.263	0.190	0.455	0
Apr05	1	1	44.682	0	0	0	0.556	0	0	0
Apr05	1	2	24.773	0	0	0	0.479	0	0	0
Apr05	2	3	21.876	0.533	0.533	0	0.427	0.004	0.014	0
Apr05	2	4	18.216	4.684	4.684	0	0.335	0.071	0.204	0
Apr05	3	5	9.080	2.389	10.992	0	0.165	0.026	0.195	0
Apr05	3	6	17.918	1.558	15.581	0	0.312	0.023	0.406	0
May05	1	1	27.333	4.919	0	0.546	0.337	0.069	0	0.002
May05	1	2	7.276	0	0	0	0.125	0	0	0

May05	2	3	40.145	0.549	0	0	0.788	0.011	0	0
May05	2	4	37.722	0	0	0	0.555	0	0	0
May05	3	5	19.168	1.797	0	0	0.300	0.033	0	0
May05	3	6	11.293	1.693	1.129	0	0.185	0.032	0.014	0
Jun05	1	1	16.571	0	0	0	0.218	0	0	0
Jun05	1	2	28.086	3.191	0	1.276	0.375	0.049	0	0.008
Jun05	2	3	15.520	1.070	0	0	0.300	0.011	0	0
Jun05	2	4	6.717	0	0	1.119	0.112	0	0	0.010
Jun05	3	5	6.589	0	0	0.599	0.126	0	0	0.004
Jun05	3	6	8.798	1.099	1.649	0	0.157	0.013	0.044	0
Jul05	1	1	13.669	1.139	0	0.569	0.187	0.018	0	0.004
Jul05	1	2	12.874	1.679	0	3.918	0.133	0.030	0	0.023
Jul05	2	3	8.019	0	0	0	0.095	0	0	0
Jul05	2	4	25.630	0	0	0.569	0.285	0	0	0.004
Jul05	3	5	5.302	0	1.178	0	0.061	0	0.023	0
Jul05	3	6								
Aug05	1	1	29.382	0	0	0	0.183	0	0	0
Aug05	1	2	9.584	10.183	0	0.599	0.142	0.119	0	0.004
Aug05	2	3	24.393	1.590	0	0.530	0.139	0.017	0	0.002
Aug05	2	4	15.908	0	0	0	0.084	0	0	0
Aug05	3	5	6.324	0	0	0	0.079	0	0	0
Aug05	3	6	10.409	0.520	0	0	0.105	0.003	0	0
Sep05	1	1	12.723	0	0	0	0.169	0	0	0
Sep05	1	2	5.695	0	0	0	0.103	0	0	0
Sep05	2	3	20.976	0	0	0	0.196	0	0	0
Sep05	2	4	7.829	0	0	0	0.076	0	0	0
Sep05	3	5	5.990	0.599	0	0	0.072	0.007	0	0
Sep05	3	6	15.574	4.193	0.599	0	0.179	0.053	0.023	0

Oct05	1	1	36.531	0	0	0	0.393	0	0	0
Oct05	1	2	13.905	12.167	0	1.158	0.163	0.146	0	0.014
Oct05	2	3	35.264	0	0	0	0.531	0	0	0
Oct05	2	4	34.174	0	0	0	0.613	0	0	0
Oct05	3	5	45.958	0	0	0	0.858	0	0	0
Oct05	3	6	51.261	1.708	0	0	0.815	0.022	0	0
Nov05	1	1	7.276	0.559	0	0	0.106	0.001	0	0
Nov05	1	2	9.898	0	0	0	0.181	0	0	0
Nov05	2	3	23.765	14.043	0	0	0.403	0.194	0	0
Nov05	2	4	22.390	17.087	0	1.178	0.448	0.242	0	0.013
Nov05	3	5	5.990	0	0	0	0.120	0	0	0
Nov05	3	6	4.055	0	0	0	0.084	0	0	0
Dec05	1	1	11.666	3.181	0	0	0.206	0.018	0	0
Dec05	1	2	12.422	0	0	0	0.266	0	0	0
Dec05	2	3	5.892	14.141	0	1.767	0.125	0.167	0	0.016
Dec05	2	4	11.391	11.391	0	0.569	0.229	0.143	0	0.006
Dec05	3	5	4.193	0	0	0	0.096	0	0	0
Dec05	3	6	8.249	0.589	0	0	0.167	0.002	0	0
Jan06	1	1	7.934	0	0.661	0	0.126	0	0.027	0
Jan06	1	2	8.209	0	0	0	0.070	0	0	0
Jan06	2	3	6.723	1.034	0	0	0.103	0.003	0	0
Jan06	2	4	18.255	6.085	0	0	0.183	0.038	0	0
Jan06	3	5	7.973	2.278	3.417	0	0.163	0.028	0.044	0
Jan06	3	6	5.568	1.856	1.856	0	0.145	0.028	0.032	0
Feb06	1	1	20.534	0	0	0	0.184	0	0	0
Feb06	1	2	8.249	2.946	0	0	0.131	0.026	0	0
Feb06	2	3	49.493	0	0	0	0.922	0	0	0
Feb06	2	4	26.171	8.298	0	0	0.312	0.104	0	0

Feb06	3	5	12.304	26.367	0	0	0.234	0.266	0	0
Feb06	3	6	25.252	15.015	1.365	0	0.526	0.171	0.011	0

Appendix VII. Results of two-way ANOVA for significant test on density and biomass of stomatopod population between strata (stratum 1, stratum 2, stratum 3) and monsoon seasons (southwest and northeast monsoons). Shaded area indicates significance at $p < 0.05$.

a.Density

	Stratum	season	{1}	{2}	{3}	{4}	{5}
1	1	SW					
2	1	NE	0.699266				
3	2	SW	0.993307	0.962508			
4	2	NE	0.615938	0.009622	0.241666		
5	3	SW	0.892380	0.999807	0.995856	0.066034	
6	3	NE	0.784823	0.026088	0.390813	0.999647	0.131286

b. Biomass

	Stratum	Season	{1}	{2}	{3}	{4}	{5}
1	1	SW					
2	1	NE	0.994018				
3	2	SW	0.999999	0.986583			
4	2	NE	0.242476	0.026625	0.295505		
5	3	SW	0.984974	0.999959	0.973089	0.057811	
6	3	NE	0.304398	0.040085	0.364316	0.999993	0.066392

Appendix VIII. Results of one-way ANOVA for significant test on density of the three stomatopod species (*Miyakea nepa*, *Oratosquillina perpensa* and *Harpiosquilla raphidea*) according to strata (stratum 1, stratum 2, stratum 3) and monsoon seasons (southwest and northeast monsoons). Shaded area indicates significance at $p < 0.05$.

a. *Miyakea nepa* by strata

	Stratum	{1}	{2}
1	1		
2	2	0.042919	
3	3	0.884267	0.012152

b. *Oratosquillina perpensa* by strata

	Stratum	{1}	{2}
1	1		
2	2	0.040764	
3	3	0.037948	0.979585

c. *Harpiosquilla raphidea* by strata

	Stratum	{1}	{2}
1	1		
2	2	0.327999	
3	3	0.000122	0.003937

d. *Miyakea nepa* by monsoon seasons

	season	{1}
1	SW	
2	NE	0.355947

e. *Oratosquillina perpensa* by monsoon seasons

	season	{1}
1	SW	
2	NE	0.003324

f. *Harpiosquilla raphidea* by monsoon seasons

	season	{1}
1	SW	
2	NE	0.001563

Appendix IX. Results of one-way ANOVA for significant test on biomass of the three stomatopod species (*Miyakea nepa*, *Oratosquillina perpensa* and *Harpiosquilla raphidea*) according to monsoon seasons (southwest and northeast monsoons). Shaded area indicates significance at $p < 0.05$.

a. *Miyakea nepa*

	Season	{1}
1	SW	
2	NE	0.391428

b. *Oratosquillina perpensa*

	Season	{1}
1	SW	
2	NE	0.009367

c. *Harpiosquilla raphidea*

	Season	{1}
1	SW	
2	NE	0.019048

Appendix X. Results of one-way ANOVA for significant test on the mean carapace length of five maturity stages for female *Miyakea nepa* and *Oratosquillina perpensa*.

a. *Miyakea nepa*

	stage	{1}	{2}	{3}	{4}
1	1				
2	2	0.000017			
3	3	0.000017	0.999503		
4	4	0.000017	0.947684	0.988800	
5	5	0.000017	0.006803	0.002718	0.000031

b. *Oratosquillina perpensa*

	stage	{1}	{2}	{3}	{4}
1	1				
2	2	0.000017			
3	3	0.000017	0.999807		
4	4	0.000017	0.999944	0.999985	
5	5	0.000017	0.619880	0.771454	0.424973

Appendix XI. Details of CCA analysis on the relationship between stomatopod larvae abundance, food items (zooplankton in three size fractions) and environmental parameters.

N	NAME	AX1	AX2	AX3	AX4	WEIGHT	N2
	EIG	0.5616	0.047	0.0089	0.0016		
1	scor	0.8431	0.0144	0.003	-0.0008	27.15	7.03
2	sp1	-0.6873	0.1571	-0.0721	-0.0168	19.74	7.43
3	sp2	-0.6597	-0.1177	0.1291	0.0355	13.07	6.05
4	nepa	-0.6065	-1.0634	0.2173	-0.3418	0.6	2.6
5	sp3	-0.3041	-1.1769	-0.4235	0.0831	1.12	2.37

N	NAME	AX1	AX2	AX3	AX4	WEIGHT	N2
	EIG	0.5616	0.047	0.0089	0.0016		
1	1NE	1.5013	0.3066	0.3375	-0.4778	2.36	1
2	1IN	1.5013	0.3066	0.3375	-0.4778	6.2	1
3	1SW	1.5013	0.3066	0.3375	-0.4778	3.37	1
4	2NE	1.2024	0.6394	-0.587	-1.5702	1.18	1.24
5	2IN	1.5013	0.3066	0.3375	-0.4778	2.9	1
6	2SW	1.5013	0.3066	0.3375	-0.4778	2.37	1
7	3NE	-0.6364	0.2472	3.1716	5.3018	1.27	2.79
8	3IN	-0.4789	1.7268	-2.7501	-3.3448	2.08	2.25
9	3SW	-1.11	1.9451	-2.827	-2.9533	1.92	1.66
10	4NE	-1.2023	0.7713	1.8315	3.8238	4.64	1.97
11	4IN	-0.1456	-2.2449	-1.7559	-0.9404	8.11	3.58
12	4SW	-1.2049	0.9274	0.0362	-3.1233	5.14	1.88
13	5NE	0.0154	0.3357	-0.6486	1.4414	11.19	2.83
14	5IN	-1.2105	1.7436	-1.9242	-1.5742	2.01	1.66
15	5SW	-1.1672	-1.595	2.6924	1.283	6.94	2.31

Tol : Species tolerance (root mean squared deviation for species)

N	NAME	AX1	AX2	AX3	AX4	RMSTOL	N2
	FR FITTED	0.7607	0.0637	0.0121	0.0022		
1	scor	0.8113	0.8477	0.6252	1.0305	84.11	7.03
2	sp1	0.5466	1.1341	1.1945	1.0171	100.58	7.43
3	sp2	0.4816	0.9893	1.2339	0.9411	95.12	6.05
4	nepa	0.4918	0.7383	1.3377	0.3535	82.18	2.6
5	sp3	0.2908	0.8235	1.1105	0.7775	80.63	2.37

Het : Sample heterogeneity (root mean squared deviation for samples)

N	NAME	AX1	AX2	AX3	AX4	RMSTOL	N2
	FR FITTED	0.7607	0.0637	0.0121	0.0022		
1	1NE	0.1972	0.9159	0.9106	0.197	66.06	1
2	1IN	0.9189	0.4093	0.0827	1.068	73.48	1
3	1SW	0.663	0.1791	0.5822	0.6126	54.45	1
4	2NE	1.4893	0.9138	0.2472	1.9713	132.29	1.24
5	2IN	0.0322	0.0454	0.0693	0.3067	15.97	1
6	2SW	0.2476	0.0497	0.3453	0.0872	21.83	1
7	3NE	0.9042	1.138	1.7528	1.8433	146.48	2.79
8	3IN	0.6932	2.6843	1.2686	0.0181	152.45	2.25
9	3SW	0.5697	1.8785	1.5418	1.2852	140.37	1.66
10	4NE	0.1492	0.6156	1.2571	0.4489	73.87	1.97
11	4IN	0.7166	1.8012	1.2566	0.3918	117.16	3.58
12	4SW	0.8231	0.2425	1.4875	1.0689	101.13	1.88
13	5NE	0.7751	0.215	0.2699	1.7041	95.18	2.83
14	5IN	0.2589	0.3246	0.2972	0.3165	30.04	1.66
15	5SW	0.1713	0.5572	1.385	0.0726	75.22	2.31

CFit: Cumulative fit per species as fraction of variance of species

N	NAME	AX1	AX2	AX3	AX4	VAR(y)	% EXPL
	FR FITTED	0.7607	0.0637	0.0121	0.0022		
1	scor	0.8726	0.8729	0.8729	0.8729	0.81	87.29
2	sp1	0.8373	0.8811	0.8903	0.8908	0.56	89.08
3	sp2	0.6718	0.6932	0.7189	0.7209	0.65	72.09
4	nepa	0.1651	0.6728	0.694	0.7464	2.23	74.64
5	sp3	0.0418	0.6676	0.7486	0.7517	2.21	75.17

SqRL: Squared residual length per sample with s axes (s=1...4)

N	NAME	AX1	AX2	AX3	AX4	SQLENG	% FIT
	FR FITTED	0.7607	0.0637	0.0121	0.0022		
1	1NE	0.1251	0.139	0.141	0.1407	1.27	88.93
2	1IN	0.044	0.0402	0.0398	0.04	1.27	96.86
3	1SW	0.0058	0.0118	0.0114	0.011	1.27	99.13
4	2NE	0.4644	0.5542	0.5572	0.5734	0.84	31.59
5	2IN	0.2735	0.2744	0.2749	0.2746	1.27	78.41

6	2SW	0.4666	0.4649	0.4639	0.4641	1.27	63.51
7	3NE	0.6358	0.6707	0.5983	0.5722	0.37	-56.61
8	3IN	0.2281	0.1384	0.09	0.0899	0.35	74.65
9	3SW	0.2633	0.0853	0.0283	0.0187	0.96	98.04
10	4NE	0.1619	0.1348	0.1888	0.1946	0.89	78.22
11	4IN	0.2663	0.0359	0.0106	0.0097	0.28	96.52
12	4SW	0.105	0.114	0.1327	0.1238	0.87	85.8
13	5NE	0.0341	0.0311	0.0287	0.0254	0.01	-102.74
14	5IN	0.2216	0.1657	0.1562	0.1548	1	84.57
15	5SW	0.2586	0.1926	0.1428	0.1428	0.95	85

Regr: Regression/canonical coefficients for standardized variables

N	NAME	AX1	AX2	AX3	AX4
	EIG	0.5616	0.047	0.0089	0.0016
1	500DEN	-0.3284	0.3552	0.8045	-0.0471
2	250DEN	-1.0926	2.0693	-0.3918	-0.962
3	125DEN	0.8555	-1.6864	-0.6688	0.5162
4	pH	2.2437	-1.4123	-3.6264	4.1627
5	Sal	-3.2162	1.4295	3.9628	-3.1263
6	Temp	-0.5297	1.5353	0.1875	0.1728
7	Do	-0.7048	0.5642	0.7379	-1.2706
8	Tur	-0.6426	0.3064	1.2769	-0.2849

tVal: t-values of regression coefficients

N	NAME	AX1	AX2	AX3	AX4
	FR EXPLAINED	0.907	0.076	0.0144	0.0026
1	500DEN	-1.0124	0.6278	0.7902	-0.0317
2	250DEN	-2.633	2.8595	-0.3008	-0.5072
3	125DEN	2.1533	-2.4342	-0.5364	0.2843
4	pH	2.129	-0.7685	-1.0964	0.8642
5	Sal	-2.8362	0.7229	1.1135	-0.6032
6	Temp	-1.8349	3.0499	0.207	0.131
7	Do	-1.9806	0.9092	0.6607	-0.7812
8	Tur	-1.6018	0.438	1.0141	-0.1554

StBi: Species coordinates for t-value biplot

N	NAME	AX1	AX2	AX3	AX4	VAR(y)	% EXPL
	EIG	0.5616	0.047	0.0089	0.0016		
1	scor	0.3115	0.0053	0	0	0.81	87.29

2	sp1	-0.2802	0.0641	0	0	0.56	89.08
3	sp2	-0.5101	-0.091	0	0	0.65	72.09
4	nepa	-0.2484	-0.4354	0	0	2.23	74.64
5	sp3	-0.1246	-0.4821	0	0	2.21	75.17

EtBi: Environmental coordinates for t-value biplot

N	NAME	AX1	AX2	AX3	AX4
	EIG	0.5616	0.047	0.0089	0.0016
1	500DEN	-0.1569	0.1697	0	0
2	250DEN	-0.4081	0.7729	0	0
3	125DEN	0.3338	-0.6579	0	0
4	pH	0.33	-0.2077	0	0
5	Sal	-0.4396	0.1954	0	0
6	Temp	-0.2844	0.8243	0	0
7	Do	-0.307	0.2457	0	0
8	Tur	-0.2483	0.1184	0	0

CorE: Inter set correlations of environmental variables with axes

N	NAME	AX1	AX2	AX3	AX4
	FR EXTRACTED	0.2409	0.0579	0.072	0.0208
1	500DEN	0.4833	0.3067	-0.004	-0.1213
2	250DEN	-0.1375	0.0496	-0.5137	-0.1866
3	125DEN	0.149	-0.0514	-0.4301	-0.1007
4	pH	-0.7852	-0.2468	-0.1139	0.161
5	Sal	-0.822	-0.2427	0.0292	0.1518
6	Temp	0.3825	0.4412	0.1912	0.2167
7	Do	-0.4024	-0.198	-0.1528	-0.1001
8	Tur	0.2289	-0.103	-0.2307	-0.0216

BipE: Biplot scores of environmental variables

N	NAME	AX1	AX2	AX3	AX4
	R(SPEC,ENV)	0.9349	0.8338	0.6428	0.4993
1	500DEN	0.517	0.3678	-0.0062	-0.243
2	250DEN	-0.1471	0.0595	-0.7992	-0.3736
3	125DEN	0.1594	-0.0616	-0.6691	-0.2017
4	pH	-0.8398	-0.2959	-0.1771	0.3224
5	Sal	-0.8792	-0.291	0.0454	0.3041
6	Temp	0.4091	0.5292	0.2974	0.4339

7	Do	-0.4304	-0.2375	-0.2377	-0.2004
8	Tur	0.2448	-0.1235	-0.3589	-0.0433

CenE: Centroids of environmental variables (mean.gt.0) in ordination diagram

N	NAME	AX1	AX2	AX3	AX4
	R(SPEC,ENV)	0.9349	0.8338	0.6428	0.4993
1	500DEN	0.4902	0.3488	-0.0059	-0.2304
2	250DEN	-0.0502	0.0203	-0.2726	-0.1274
3	125DEN	0.0759	-0.0293	-0.3186	-0.0961
4	pH	-0.032	-0.0113	-0.0068	0.0123
5	Sal	-0.1552	-0.0514	0.008	0.0537
6	Temp	0.0032	0.0041	0.0023	0.0034
7	Do	-0.0394	-0.0218	-0.0218	-0.0184
8	Tur	0.1328	-0.067	-0.1947	-0.0235

SamE: Sample scores which are linear combinations of environmental variables

N	NAME	AX1	AX2	AX3	AX4	WEIGHT	% FIT
	EIG	0.5616	0.047	0.0089	0.0016		
1	1NE	1.0404	0.9303	0.9136	-0.1977	2.36	88.93
2	1IN	1.7621	0.4238	0.0857	-1.0688	6.2	96.86
3	1SW	1.5061	-0.1647	0.5852	-0.6134	3.37	99.13
4	2NE	2.0857	-0.8826	0.2409	1.9687	1.18	31.59
5	2IN	0.8109	-0.031	-0.0663	-0.3075	2.9	78.41
6	2SW	0.5955	0.0642	0.3483	0.0864	2.37	63.51
7	3NE	0.3052	1.1431	1.7787	1.8517	1.27	-56.61
8	3IN	-0.4137	2.7637	-1.2912	-0.0098	2.08	74.65
9	3SW	-1.113	1.9665	-1.5647	-1.2898	1.92	98.04
10	4NE	-0.8238	0.6365	-1.2368	-0.442	4.64	78.22
11	4IN	-0.1242	-1.8658	-1.2639	-0.3872	8.11	96.52
12	4SW	-1.4996	-0.0985	1.4845	-1.0727	5.14	85.8
13	5NE	-0.1812	0.1169	-0.26	1.7063	11.19	-102.74
14	5IN	-0.9383	0.3827	-0.3005	-0.3182	2.01	84.57
15	5SW	-0.81	-0.5272	1.4022	-0.0134	6.94	85

Appendix XII. Details of PCA analysis on the dietary composition of the four stomatopod species according to sex and size class.

Spec: Species scores (adjusted for species variance)

N	NAME	AX1	AX2	AX3	AX4	WEIGHT	1
	EIG	0.7581	0.193	0.0207	0.0137		
1	Shrimp	-0.7953	0.5771	-0.1274	0.0633	1	1
2	Crab	-0.2153	-0.9586	-0.1093	-0.1332	1	1
3	Gastropod & bivalve	-0.944	-0.2679	0.1728	0.0496	1	1
4	Squid	0.6157	-0.6822	-0.1689	0.3434	1	1
5	Fish	0.9937	-0.0096	0.1031	-0.0029	1	1
6	Brittle star	-0.8958	-0.1037	0.3099	-0.0088	1	1
7	Sediment	-0.9333	0.1074	0.0509	-0.0742	1	1
8	Unidentified	-0.3571	0.068	0.309	0.5082	1	1

Samp: Sample scores

N	NAME	AX1	AX2	AX3	AX4	WEIGHT	1
	EIG	0.7581	0.193	0.0207	0.0137		
1	NFS	-0.8778	-0.1184	0.73	0.2968	1	1
2	NFM	-0.6154	-0.1907	1.8723	0.6394	1	1
3	NFL	-0.3151	-0.144	-0.4244	1.5347	1	1
4	NMS	-0.8509	-0.1528	0.9415	-0.4749	1	1
5	NMM	-0.6192	-0.121	1.2416	0.8661	1	1
6	NML	-0.1152	-0.1397	-1.1432	2.635	1	1
7	OFS	-0.748	-1.2341	-1.123	-1.1256	1	1
8	OFM	-0.3401	-0.9009	0.922	-1.5901	1	1
9	OFL	-0.3724	-1.0502	-0.972	-0.1943	1	1
10	OMS	-0.5938	-1.032	-0.6512	-0.5995	1	1
11	OMM	-0.4974	-0.7187	-0.4638	-0.0972	1	1
12	OML	-0.251	-0.8574	1.0462	-0.0904	1	1
13	RFS	1.2764	0.0657	-1.2268	-1.2477	1	1
14	RFM	1.5006	-0.0035	0.0935	0.9645	1	1
15	RFL	1.5012	-0.0496	-0.3127	-0.9722	1	1
16	RMS	1.4136	-0.2064	-1.2731	0.5936	1	1
17	RMM	1.6188	0.5371	1.1518	0.4656	1	1
18	RML	1.4517	1.5457	1.1585	-0.861	1	1
19	SF	-1.2669	2.4554	-1.0366	-0.379	1	1
20	SM	-1.2994	2.3154	-0.5307	-0.3638	1	1
21	ORIGIN	0.2644	0.5555	-0.8204	-6.1502	0	0

CFit: Cumulative fit per species as fraction of variance of species

N	NAME	AX1	AX2	AX3	AX4	VAR(y)	% EXPL
	FR FITTED	0.7581	0.193	0.0207	0.0137		
1	Shrimp	0.6324	0.9655	0.9817	0.9857	0.89	0
2	Crab	0.0464	0.9652	0.9772	0.9949	0.93	0
3	Gastropod & bivalve	0.8911	0.9628	0.9927	0.9952	1.85	0
4	Squid	0.379	0.8445	0.873	0.9909	0.55	0
5	Fish	0.9873	0.9874	0.9981	0.9981	3.3	0
6	Brittle star	0.8025	0.8132	0.9093	0.9094	0.27	0
7	Sediment	0.871	0.8826	0.8852	0.8907	0.14	0
8	Unidentified	0.1275	0.1322	0.2276	0.4859	0.08	0

SqRL: Squared residual length per sample with s axes (s=1...4)

N	NAME	AX1	AX2	AX3	AX4	SQLENG	% FIT
	FR FITTED	0.7581	0.193	0.0207	0.0137		
1	NFS	0.0468	0.0441	0.0331	0.0319	0.63	94.95
2	NFM	0.0858	0.0788	0.0064	0.0008	0.37	99.79
3	NFL	0.0562	0.0522	0.0485	0.0163	0.13	87.62
4	NMS	0.0535	0.049	0.0307	0.0276	0.6	95.41
5	NMM	0.0593	0.0564	0.0246	0.0143	0.35	95.91
6	NML	0.1416	0.1379	0.1109	0.0158	0.15	89.58
7	OFS	0.3492	0.0553	0.0293	0.0119	0.77	98.46
8	OFM	0.2149	0.0583	0.0407	0.0061	0.3	97.98
9	OFL	0.2556	0.0428	0.0233	0.0227	0.36	93.7
10	OMS	0.2271	0.0215	0.0128	0.0079	0.49	98.41
11	OMM	0.1106	0.0109	0.0065	0.0064	0.3	97.87
12	OML	0.1806	0.0387	0.0161	0.016	0.23	92.99
13	RFS	0.0633	0.0625	0.0314	0.0101	1.3	99.22
14	RFM	0.0528	0.0528	0.0526	0.0398	1.76	97.74
15	RFL	0.0177	0.0172	0.0152	0.0022	1.73	99.87
16	RMS	0.066	0.0578	0.0243	0.0195	1.58	98.77
17	RMM	0.0971	0.0414	0.014	0.011	2.08	99.47
18	RML	0.5187	0.0576	0.0299	0.0197	2.12	99.07
19	SF	1.1957	0.0321	0.0099	0.0079	2.41	99.67
20	SM	1.0452	0.0105	0.0047	0.0029	2.33	99.88

Appendix XIII. Results of two-way ANOVA for significant test on density of stomatopod between species (*Miyakea nepa* and *Oratosquillina perpensa*) and diel (day and night).

	Time	species	{1}	{2}	{3}	{4}	{5}
1	Day	nepa					
2	Day	oper	0.999979				
3	Day	raph	0.932727	0.969405			
4	Night	nepa	0.999998	1.000000	0.958184		
5	Night	oper	0.996902	0.999639	0.996554	0.999115	
6	Night	raph	0.855266	0.916828	0.999917	0.896539	0.980486