CHAPTER 1

INTRODUCTION

1.1. General description of zooplankton

The word zooplankton originated from the Greek words ‘zoon’ and ‘planktos’, meaning ‘animal’ and ‘drifter’ respectively. It thus describes a community of floating, often microscopic organisms inhabiting an aquatic environment. Zooplankton form a continuous size distribution from tiny flagellates, a few μm in length to giant jellyfish of 2 m in diameter. Nanozooplankton that range in size from 2 to 20 μm are heterotrophic nanoflagellates that feed on bacteria. Ciliates are one of the common examples of microzooplankton with a size range of 20 - 200 μm. This size range also covers the eggs and early stages of crustacean and non-crustacean organisms. Small hydromedusae, ctenophores, chaetognaths, appendicularians, doliolids, fish eggs and the older stages of crustacean plankton comprise the mesozooplankton (0.2 - 20 mm). Since most plankton studies use medium mesh size plankton nets (>200 μm), the mesozooplankton have been the most targeted component in zooplankton studies. The preference of using medium mesh size plankton net is primarily due to undesirable net clogging by phytoplankton if smaller mesh size nets are used (Turner, 2004). Macrozooplankton (2 - 20 cm) are the larger specimens that include hydromedusae, siphonophores, scyphomedusae, ctenophores, mysids and amphipods. Only a few planktonic organisms reach the stage of megaplankton (20 - 200 cm). This covers large jellyfish, such as siphonophores and scyphozoans, and pelagic tunicates.

Other than classification by size, zooplankton are also typified as holo- and meroplanktonic organisms. Holozooplankton are organisms that spend their whole life as plankton, which in general are largely copepods. As copepods often dominate zooplankton assemblages, they are probably the most abundant and successful metazoans in the marine environment (Longhurst, 1985; Humes, 1994; Kiørbe, 1997;

Mauchline, 1998; Ohman & Hirche, 2001). In view of their adaptations to various environmental conditions, copepods are successful inhabitants in all types of marine environment, from low to high latitude, and from estuary to deep ocean water (Paffenhöfer, 1993; Mauchline, 1998). Other important holozooplankton are chaetognaths and appendicularians. Merozooplankton are organisms which spend part of their life cycle as plankton. They include the larval stages of various benthic organisms and nekton. High survival rate of planktonic larvae is particularly important to ensure the stability of their adult population in the marine ecosystem.

However, the term 'holozooplankton' is somehow vague when it is applied to adult zooplankton. This is because many of the adult zooplankton species perform regular vertical migrations or are patchily distributed rather than drifting passively with water currents. Such cases have been reported since the early studies of zooplankton (Clarke, 1930; Johnson, 1938; Cushing, 1951; Banse, 1964; Omori & Hammer, 1982), and include many species of adult copepods, mysids and amphipods. As the adult of zooplankton species (e.g. copepods) are demersal or display patchy distribution, the existence of truly planktonic species especially in shallow coastal waters is clearly difficult to define (Reeve, 1975). Therefore, the definition of holozooplankton must be interpreted with some caution.

1.2. Overview of zooplankton distribution

The distributional patterns and community structure of zooplankton are regulated by a complex association between abiotic and biotic factors. For large-scale investigations, species richness of zooplankton in oceanic waters was reported to be higher in the tropics and subtropics as compared to high latitude regions (Hattori & Motoda, 1983; Rutherford *et* al., 1999; Boltovskoy *et* al., 1999; Woodd-Walker *et* al, 2002). Sea temperature (Rutherford *et* al., 1999) and biological factors such as primary

production (Woodd-Walker *et* al, 2002) were proposed to be the important regulators controlling the latitudinal distinctness of zooplankton community. Species richness and evenness of copepods were found to be higher and more stable in oligotrophic tropical and subtropical waters, in which the annual primary production is constant (Woodd-Walker *et* al, 2002). In poleward regions, where the primary production is highly seasonal and ephemeral, copepod community is characterized by low species richness and dominance of a few successful taxa such as *Calanus* and *Oithona* (Woodd-Walker *et* al, 2002). These taxa are evolutionarily adapted to be generalists or organisms with high lipid contents and are seasonally diapause (Atkinson, 1998). Turner (1981) and Duggan *et* al. (2008) compared the species richness of copepods in estuaries from low to high latitudes and similarly reported higher species richness in tropical and subtropical estuaries as compared to high latitude ones. Although zooplankton species richness tends to decrease towards high latitude regions, it is not advisable to directly compare their biomass or standing stock measurements in the same manner (Wickstead, 1961). Reviews on estimation of copepod biomass in different latitudinal zones revealed that the seasonal maximum of copepod biomass in high latitude waters can be higher than biomass in low latitude waters (Wickstead, 1961).

On a horizontal scale, a range of studies indicated that species richness of zooplankton generally increases from estuaries to offshore waters while the corresponding biomass or abundance is reflected in the opposite pattern (e.g. Grindley, 1984; Kimmerer, 1993; Sautour & Castel, 1993). Copepod community in estuarine systems may be dominated by only a few successful species, whereas the number of oceanic copepod species can exceed 100 species (Mauchline, 1998). For instance, in subtropical Taiwanese waters, a total of 62 copepod species was recorded in estuaries and coastal waters (Hsieh & Chiu, 1997). In oceanic waters of the same geographical zone, Hwang *et* al. (2007) recorded a total of 101 copepod species. The similar pattern

was also observed in tropical waters. Duggan *et* al. (2008) identified a total of 32 copepod species in a Australian tropical estuary, while Chew and Chong (2011) recorded a total of 48 copepod species from the surface waters of Malaysian mangrove estuaries and adjacent coastal areas. The species richness of copepods in both estuaries was about two to four orders of magnitude lower than the species richness in tropical oceanic waters of the Straits of Malacca, which recorded a total of 117 species (Rezai *et* al., 2004).

Vertical distribution of zooplankton has been studied in various marine habitats from shallow inshore systems to deep oceanic waters (e.g. Ueda, 1987; Yamaguchi *et* al., 2004). In most cases, zooplankton show distinct vertical distribution rather than being homogeneously distributed through the water column. Different copepod species or ontogenetic stages may exhibit maximum abundance at different layers of the water column. Diversity of copepods was reported to increase with depth in the top 1500 m of the water column (Binet & Dessier, 1972 cited in Mauchline, 1998). For ontogenetic vertical distribution, the young developmental stages generally inhabit the upper layers of the water column while the older stages stay close to the bottom (Mauchline, 1998). Homogeneous distribution of zooplankton often occurs when the water column is vertically well mixed by tidal- or storm-induced turbulence (e.g. Manning & Bucklin, 2005; Duggan *et* al., 2008).

1.3. Zooplankton communities in estuaries

Estuarine ecosystems are subjected to strong spatial and temporal variability in physical, chemical and biological conditions. The spatiotemporal variability is primarily mediated by seasonality of freshwater input into the estuaries as well as the degree of current mixing between estuarine and coastal waters. Undoubtedly, estuarine variability strongly affects the dynamics of biotopes especially those of planktonic organisms

(Kennish, 1990; Calbet *et* al., 2001; Hoffmeyer, 2004). Salinity and temperature are suggested to be the most important physical parameters controlling the abundance and distribution of zooplankton in most estuaries (Miller, 1983; Heip *et* al., 1995; Kibirige & Perissinotto, 2003; Froneman, 2004; Tackx *et* al., 2004) although the significance of temperature effect on tropical zooplankton is yet unknown.

In tropical estuaries, the spatiotemporal variability of zooplankton community is much related to salinity gradient. There is often a well defined species composition of zooplankton along the salinity gradient from upper estuary to coastal neritic waters (Robertson & Blaber, 1992; Duggan *et* al., 2008; Chew & Chong, 2011). The true estuarine component such as *Acartia*, *Pseudodiaptomus* and *Oithona* species are more restricted to the low salinity region of the estuary. These taxa often dominate zooplankton community in tropical estuaries especially during the wet period (Ara, 2004; Duggan *et* al., 2008). A euryhaline marine species *Parvocalanus crassirostris* (Dahl F.) is not restricted to any salinity condition and is widely distributed from the estuaries to adjacent coastal waters (Chew & Chong, 2011). The coastal neritic species are restricted to high salinity seaward regions. Freshwater species such as the copepod *Boeckella* and cladoceran *Moina* would occur when estuaries are inundated by large amount of freshwater input (McKinnon & Klumpp, 1998a).

Although zooplankton communities in estuaries are predominated by copepods, a variety of meroplanktonic larvae also occur in considerable numbers in these areas. The meroplanktonic larvae on average made up 13% of zooplankton composition in the Bay of Blanes, NW Mediterranean (Andreu & Duarte, 1996). Their contribution to zooplankton composition can be as high as 60% during the spawning season. Robertson *et* al. (1988) found that crab larvae are seasonally abundant in the tropical mangrove estuaries of Australia. Raymont (1983) also suggested that polychaete, cirripede, and decapod larvae are seasonally important in estuarine and coastal waters.

Meroplanktonic larvae, however, have received little attention in many plankton studies as compared to copepods.

Demersal zooplankton such as mysids and amphipods are probably very abundant in estuaries (Grindley, 1984). In particular, the abundance of mysids was reported to exceed 10,000 ind m^{-3} in Mngazana estuary, South Africa (Wooldridge, 1977 cited in Grindley, 1984). However, the demersal zooplankton are usually undersampled by conventional plankton tow-nets as most of these animals reside at the bottom during daytime. Because of some adaptive reasons, these animals normally migrate into the water column at night. Of course vertical migration of zooplankton is not only restricted to the so-called demersal zooplankton but also for dominant copepod species which are regularly sampled from the water column during the day (Fulton, 1984).

1.3.1 Vertical migration and its proximal cues

As mentioned earlier, zooplankton are not homogeneously distributed through the water column but show distinct vertical distribution in both shallow and deep waters. This distributional pattern is closely linked to the animals' migrating behavior that corresponds to some selective forces. Nocturnal diel vertical migration (DVM) is the most common phenomenon observed for zooplankton, with an upward migration to shallower depths during the night and a downward movement to deeper waters before sunrise (Lampert, 1989; Hays, 2003; Cohen & Forward, 2005). A reverse mode to nocturnal DVM has also been documented for a few copepod species (Ohman *et* al., 1983; Chae & Nishida, 1995). The amplitude and pattern of migration of zooplankton differ between species or between ontogenetic stages within a species (Lampert, 1989).

Light is a major environmental cue regulating the diel vertical migration of zooplankton (Forward, 1988; Ringelberg, 1995; Cohen & Forward, 2009). Several field

and laboratory studies have been conducted to examine how the intensity of light initiates zooplankton vertical migration. Tranter *et* al. (1981) investigated photobehavior of some copepod species in shallow waters and concluded that copepods were attracted to light when intensity of light declined and evaded light when light intensity increased. Stearns and Forward (1984) found that vertical migration of estuarine copepod *Acartia tonsa* Dana in the Newport River estuary was stimulated by a relative change in light irradiance. Therefore, vertical migration of zooplankton often occurs at twilight, which is the time when the relative change in light irradiance is the greatest (Cohen & Forward, 2005). Zooplankton are most sensitive to light conditions at twilight which falls in the blue-green region of the light spectrum (Mauchline, 1998).

Predator avoidance is a prime selective pressure for zooplankton to undergo vertical migration. Nocturnal upward migration of zooplankton is an adaptive mechanism to reduce the risk from being eaten by visual predators during daytime (e.g. Zaret & Suffern, 1976; Bollens *et* al., 1993; Hays, 1994). The smaller copepods such as nauplii and copepodids may adopt a reverse migrating behavior to evade non-visual predators such as chaetognaths, euphausiids and predatory copepods, which are generally nocturnal (Ohman, 1990). Diel vertical migration of zooplankton as a means of predator avoidance has been proven by the empirical studies in freshwater and marine environments (Gliwicz, 1986; Bollens & Frost, 1989). These studies showed no apparent vertical migration of copepods when zooplanktivorous fish were absent or caged.

Although diel vertical migration of zooplankton is primarily initiated by the occurrence of predators, their migration may be suspended when the ambient food concentrations are scarce (Huntley & Brooks, 1982; Daro, 1988; Fiksen & Giske, 1995). The amplitude of zooplankton vertical migration was reported to be maximal at moderate food concentrations (Fiksen & Giske, 1995). Herbivorous zooplankton do not

remain in the water column throughout the night but migrate downward after satiation (Mackas & Bohrer, 1976; Atkinson *et* al., 1992). The causal link of midnight sinking in zooplankton (Pearre, 2003), to the common pattern of vertical migration has been reported since the early study of zooplankton (Cushing, 1951).

As estuarine environments are consistently exposed to extreme tidal conditions, a specific mechanism is required for estuarine zooplankton to prevent offshore advection during ebb tide. The most common mechanism observed is through tidally induced vertical migration (TVM) (e.g. Wooldridge & Erasmus, 1980; Kimmerer & McKinnon, 1987; Kimmerer *et* al., 1998). Estuarine zooplankton tend to remain close to the bottom on ebb tide as current velocities at the bottom are much weaker than at the surface because of the bottom friction effect. Similar to DVM, adoption of tidally induced vertical migration differs among zooplankton species and among developmental stages within the species. Different stages of meroplanktonic larvae have abilities to select certain tidal phase and depth for transportation (e.g. Forward, 1987; Queiroga & Blanton, 2004).

1.4 Ecological importance of zooplankton

The pivotal role played by zooplankton as trophic links between primary producers and higher trophic levels has been well recognized in almost all marine food webs. Micro- and mesozooplankton feed primarily on phytoplankton and heterotrophic protists (review by Turner, 2004). In turn, they are consumed by a variety of planktivores including larval and juvenile fishes in the food webs. A review on 40 larval-fish diet studies from most oceans of the world indicated that 76 species of fish larvae were largely dependent on copepods as food (Turner, 1984). The spawning of estuarine fish species is often timed to synchronize with peak zooplankton abundance, indicating the importance of zooplankton energy source for larval fish survival and

growth (Harrison & Whitfield, 1990; Whitfield & Harrison, 1996). Trophic interactions between benthic animals and zooplankton in shallow waters have been the focus of recent studies, and results indicated significant consumption of zooplankton by benthic animals (Davenport *et* al., 2000).

Zooplankton are sensitive to environmental perturbations. Therefore, they are good indicators of changes in marine conditions. The occurrence of heavy metal pollutants such as copper and zinc in Elizabeth River, USA was reported to cause an abrupt reduction in survival and reproduction rates of copepods (Sunda *et* al., 1987, 1990). The growth of phytoplankton may be inhibited by heavy metal pollutants. Therefore, the reduction in zooplankton standing stock is possibly due to the limitation of phytoplankton food (Park & Marshall, 2000). Albaina *et* al. (2009) investigated zooplankton communities in two estuaries with different degrees of pollution. The authors found the elimination of sensitive taxa in the more polluted estuary, and more stable diversity of zooplankton species in the healthier estuary. *Euterpina acutifrons* (Dana) is suggested to be one of the zooplankton species sensitive to pollutants. A few tolerant species showed succession in the more polluted estuary.

The replacement of large by small copepods and the dominance of cyclopoids in a given habitat is probably an indication of eutrophication. In eutrophic waters, dominance of phytoplankton food may have been replaced by blooming of small flagellates. Flagellates are not suitable food source for large copepods because they are too small and difficult to be ingested by large animals. On the other hand, cyclopoids do not feed on phytoplankton but chiefly rely on flagellates. These may have been the reasons of elimination of large copepod species and dominance of cyclopoids in eutrophic waters (Uye, 1994). Marcus (2004) gave a collective review of the impacts of eutrophication and harmful chemical pollutants on copepods in coastal waters.

Climate change and increased sea temperature have become a global concern in recent years. The strong shifts in copepod community from its original biogeographic zone to higher latitudes, disappearance of cold-water species (Beaugrand *et* al., 2002) as well as trophic mismatch between zooplankton and phytoplankton in high latitudes (Edwards & Richardson, 2004) are important implications of climate change on marine biotopes.

Zooplankton also play an important role in nutrient recycling, which is essential for phytoplankton growth. Pagano *et* al. (2006) found that in a tropical estuary, an equivalent 10% of nitrogen and 75% of phosphorous required for phytoplankton growth are derived from metazooplankton remineralization. In oligotrophic waters, continuous phytoplankton production at steady state is chiefly maintained by grazing activity and remineralization by zooplankton (Banse, 1995). Fecal pellets with attached phytoplankton, which probably resulted from the feeding nature of larvaceans, may potentially cause sinking of phytoplankton to the ocean floor (see Kiørboe, 1997). Although the functional effect of phytoplankton sinkage still remains unclear, the sinking phytoplankton may be one of the major carbon sources for ocean benthic dwellers.

1.5 Mangrove ecosystem: hydrology, function and human impact

Mangrove forest is one of the dynamic ecosystems on earth which covers approximately 181, 000 km^2 of tropical and subtropical coastlines (Alongi, 2002). The environmental conditions in mangroves are primarily governed by a combination of climatic, hydrological, geophysical, geomorphic and biological factors (Varadachari & Kesava Das, 1984). Similar to other estuaries, the hydrological conditions of mangroves are susceptible to the variations of climatic and tidal factors. Along the mangrove channel, there are often different degrees of fresh and saline water inflow. During the

wet season, the mangrove estuary can be completely flushed by the freshwater runoff and extended to adjacent coastal waters (Robertson & Blaber, 1992). A large amount of freshwater runoff into the estuary would cause a strong stratification in water column particularly during neap tides (Madhupratap, 1987; Nelson *et* al., 1994). During the dry season, a mangrove estuary behaves like coastal environment especially when more saline water is trapped in the estuary.

The mangrove forest has high rates of leaf litter fall as in other forest systems. As most of the mangrove forests are located in the tropics, rates of bacterial decomposition are expected to be high in these areas. Oxidization of tannin and polyphenolic compounds that leached from mangrove detritus would lead to a significant drop in pH and dissolved oxygen (Boto & Bunt, 1981). There are often gradual decreases in pH and dissolved oxygen in upper reaches of mangrove estuaries, presumably caused by high production of bacteria (Boto & Bunt, 1981) and low mixing of saline water.

The significant freshwater input during the wet season is a key factor of essential nutrient enrichments in the mangrove estuaries. In particular, the freshwater runoff is a major input of phosphorous to the oceans whereas phosphorus that derived from the atmosphere is almost negligible (Tyrrell, 1999). Significant enrichment of essential nutrients during the wet seasons has been reported in a range of mangrove estuaries (Trott & Alongi, 1999; Wong, 2003, Mwashote *et* al., 2005).

Mangrove forests are considered the most productive vegetation in the marine environment (Alongi, 2002). The estimated mangrove production is on average greater than other marine vegetations such as saltmarshes, seagrasses and both macro- and microalgae (Alongi, 2002). With such high productivity, mangrove forests are significantly important in carbon fixation and sequestration thereby reducing CO_2 from

the atmosphere (Ong & Gong, 2004; Alongi et al., 2007; Suratman, 2008). The extensive aerial root systems of mangrove trees facilitate deposition of fine sediments that essentially function as a sink for nutrients and organic matters (Boto, 1982). Therefore, mangrove sediments are normally enriched with nutrients and are a source of minerals (Prasad & Ramanathan, 2008), which potentially support growth of a variety of organisms in the mangrove ecosystem. Physically, the mangrove forests can mitigate extreme current forces and protect coastal areas from erosion. It is particularly noteworthy in that during the December 2004 tsunami catastrophe, the coastal and estuarine areas with intact mangrove forest were notably less affected by the tsunami waves as compared to those areas without mangrove forest (Dahdouh-Guebas *et* al., 2005).

The estuaries with fringing mangrove forests are important interfaces in the exchange of sediments, nutrients and organic matters between land and coastal waters (Alongi *et* al., 2004). Large amounts of mangrove-based organic matters as well as essential nutrients for phytoplankton growth can be exported via interconnected mangrove waterway systems to adjacent coastal waters (Robertson *et* al., 1992; Tanaka & Choo, 2000; Dittmar & Lara, 2001). These outwelled materials are believed to be important in structuring the coastal food webs (Odum & Heald, 1975; Alongi *et* al., 1989; Alongi, 1990) although this concept is still debated upon.

Although mangrove ecosystem has low diversity of plant species, this ecosystem is recognizable as an important habitat supporting a wide range of animal species. In particular, mangrove estuaries consistently serve as nursery and feeding grounds for a variety of fish and invertebrate species (Robertson & Blaber, 1992; Nagelkerken *et* al., 2000; Chong, 2007), some of which are economically important. The dynamics of mangrove ecosystem also support high abundance of zooplankton (Robertson *et* al.,

1988; Chew & Chong, 2011), which are known to be the important food source for most estuarine fishes (Chew *et* al., 2007; Then, 2008).

Mangrove ecosystem services are not only important to those organisms utilizing the ecosystem but also to various human uses. Human activities have inevitably caused substantial losses of the current mangrove forests worldwide. Over the last quarter century, the losses of mangrove forests worldwide range between 35 and 86% (Duke *et* al., 2007). The rates of mangrove losses are estimated at 1 to 2% per year (Alongi, 2002). These rates can be even higher in those developing countries, where >90% of mangrove forests worldwide are situated (Duke *et* al., 2007). Unsustainable cutting for timber, clearing and conversion for agriculture, aquaculture and urbanization are many of the human activities that have caused substantial mangrove losses. These would ultimately lead to functional loss of mangrove ecosystem. Duke *et* al. (2007) cited several negative sequential impacts following the functional loss of mangrove ecosystem including two critical biological aspects: 1) precipitous decline in plant and animal species diversity, and perhaps extinction of less tolerant species; and 2) loss of healthy food webs and coastal fisheries. Hence, concerted efforts are needed to conserve mangrove ecosystems so as to maintain the dynamic processes and complex trophic interactions that support the variety of organisms.

1.5.1 Overview of mangrove trophodynamics

As mangrove detritus constitutes a large proportion of the organic matter in mangrove estuaries and adjacent coastal waters, there has been a general consensus that the mangrove and coastal food webs are mainly fueled by mangrove-based carbon via microorganisms that live on mangrove detritus (Odum & Heald, 1975). However, this role of mangroves has become a contentious issue as other primary producers such as phytoplankton and microphytobenthos with their higher nutritional values may be more

important sources of energy particularly in the open and nutrient-rich mangrove waterways (Robertson *et* al., 1992). Although several experimental and field observations did indicate ingestion and assimilation of vascular plant detritus by zooplankton (Roman & Rublee, 1981; Roman, 1984; DeMott, 1988; McKinnon & Klumpp, 1998b) and juvenile decapods (Rodelli *et* al., 1984; Loneragan *et* al., 1997; Fantle *et* al., 1999; Dittel *et* al., 2000; Schwamborn & Criales, 2000; Schwamborn *et* al., 2006), most of these animals given a choice, preferred live food rather than inert particles of detritus. Other studies suggested that the outwelled mangrove detritus may have little nutritional values for higher trophic levels when it is widely distributed in the adjacent coastal waters (Hatcher *et* al., 1989; Fleming *et* al., 1990).

The abundance of juvenile fish has been shown to be relatively higher in mangrove estuaries compared to other nearshore habitats (Robertson & Duke, 1987; Chong *et* al., 1990). Sasekumar *et* al. (1992) found that 90% of fish collected in mangrove estuaries were sexually immature. In terms of numbers and biomass, zooplankton-feeding fish dominated the fish community of Australian mangrove estuaries (Blaber & Blaber, 1980; Robertson & Duke, 1987). As zooplankton are generally more abundant in the mangrove estuaries than neritic coastal waters (Robertson *et* al., 1988; Chew & Chong, 2011), it is apparent that mangrove estuaries are zooplankton-rich ecosystem providing prey or food of suitable sizes for juvenile fish (Robertson & Blaber, 1992; Laegdsgaard & Johnson, 2001). This is supported by the evidence of fish stomach contents analysis. For instance, juvenile fish caught in the Australian mangrove waters fed primarily on copepods and brachyuran zoeae (Robertson & Blaber, 1992). Chew *et* al. (2007) and Then (2008) examined the stomach contents of fish collected in the Matang mangrove estuaries and found that zooplankton especially copepods and hyperbenthic shrimps constituted a large proportion of fish diets in these estuaries.

Although zooplankton are well recognized as important intermediaries between primary producers and planktivorous fish in the mangrove food web, the carbon sources being utilized by these primary consumers have not been clearly demonstrated. DeMott (1988, 1995) offered food of different sizes, nutrition and condition, such as live, dead and sterile dead algal particles, to different copepod species in laboratory experimental studies to test the hypothesis of food selectivity. The results showed different degrees of food selectivity among species but copepods were in general able to feed selectively on more nutritious than less nutritious algal particles, although it was noted that the potential food sources for copepods in natural environments are significantly more diverse than in the laboratory experiment. Based on shipboard experimental studies, Turner & Tester (1989) reported non-selective feeding in estuarine copepods. As most experimental studies on zooplankton often involved a short timescale and are different from their natural environmental conditions, the actual carbon food source utilized by zooplankton in the wild is unknown particularly in mangrove estuaries with multiple carbon food sources. Furthermore, the consumption of observed food source may not necessarily reflect its assimilation (Rodelli *et* al., 1984).

The approach of stable isotope analysis is a useful method to trace the carbon trophic pathway in marine food webs (Peterson & Fry, 1987). This method has been widely used as carbon tracer in recent mangrove trophic studies. Most of the studies focused on mangrove macrofauna (Rodelli *et* al., 1984; Newell *et* al., 1995; Lee, 2000; Chong *et* al., 2001; Bouillon *et* al., 2002; Demopoulos *et* al., 2007; Abrantes & Sheaves, 2009), and only a few concern zooplankton (Bouillon *et* al., 2000; Dehairs *et* al., 2000; Schwamborn *et* al., 2002). Stable isotope compositions of zooplankton in the above studies, however, were mostly represented by a bulk mixture of various taxonomic groups where the actual trophic position of the major taxa was not clearly defined. Stable isotope analysis of zooplankton at higher taxonomic levels could provide the

specific trophic position of a given taxon since different taxonomic groups of similar body size may not necessarily depend on similar food source. This deserves further investigation particularly in the mangrove estuaries with multiple food sources.

Malaysian mangrove estuaries and inlets receive multiple carbon sources from mangroves, phytoplankton and microphytobenthos (Rodelli *et* al., 1984; Newell *et* al., 1995; Chong *et* al., 2001). Thus, it is possible that zooplankton depend on these three carbon sources. Stable isotope analysis in these studies indicated that the macrofauna collected inside the estuaries depended heavily on mangrove carbon, but phytoplankton and microphytobenthos became more important in the offshore direction. Some macrofauna species considered in these studies fed on zooplankton, suggesting that the primary carbon source was transferred to macrofauna via zooplankton as intermediaries. However, the role of zooplankton in the Malaysian mangrove and coastal food webs is poorly understood and needs to be further investigated. Although the stable isotope analysis can measure actual and time-integrated food source assimilated by consumers, data interpretation may become complicated if the multiple primary sources have closely similar stable isotope ratios (Fry & Sherr, 1984) and there are spatial and temporal variability in isotopic composition of organisms (Boon & Bunn, 1994).

1.6 Significance and objectives of study

The Matang Mangrove Forest Reserve is one of the best sustainability managed mangrove forests in the world (Gan, 1995). The complex interactions between abiotic and biotic factors in this ecosystem provide an ideal site for numerous biological and ecological studies. Previous studies conducted in Malaysian mangrove ecosystems have shown their importance as feeding and nursery areas for juvenile marine fish, prawns and other invertebrates (Chong *et* al., 1990; Sasekumar *et* al., 1992; Chong, 2005, 2007). About 50% of the fish and almost all the prawn species in the mangrove estuaries are

economically important. Based on the Malaysian Annual Fisheries Statistics data (2008), the marine fish landing in Malaysia accounted for a total of 1,394,531 metric tonnes with a value of RM 5,627.14 million. Approximately 32% of the total landing and 15% of the total income value were contributed by the state of Perak, the highest among the states in Malaysia. The high fishery yield is credited to the presence of the large Matang Mangrove Forest Reserve along the coastline of Perak.

Studies showed that the juvenile fish and invertebrates in Malaysian mangrove estuaries depend largely on a mangrove detrital food chain, particularly those in creeks and small channels, although phytoplankton become increasingly important towards offshore (Rodelli *et* al., 1984; Newell *et* al., 1995; Hayase *et* al., 1999; Chong *et* al., 2001). Stable isotope analysis shows that the juveniles of commercially important penaeid prawns in the upstream of Matang estuaries assimilated as high as 84% of mangrove carbon (Chong *et* al, 2001). Prawns and many invertebrates have been shown to enter mangroves at the mysis or postlarval stage (Chong, 1979). Many fish species are also found to enter mangroves at the postlarval stage (Sarpedonti, 2000). These planktonic larvae form a part of the meroplankton in the estuaries, and are very much dependent on other holozooplankton taxa such as copepods as food. Although zooplankton are important as intermediaries between primary producers and predatory fish in the marine food web, the zooplankton community of Malaysian mangrove estuaries is still poorly studied, much less their exploitation by juvenile fish that use the mangroves as nursery areas.

Although the approach of stable isotope analysis has been previously used to trace energy carbon source of consumers in mangrove estuaries of Malaysia (Rodelli *et* al., 1984; Newell *et* al., 1995; Hayase *et* al., 1999; Chong *et* al., 2001), none of the studies pertains to zooplankton. While mangrove primary production was reported to be substantially high in the Matang mangrove estuaries (Ong & Gong, 2004; Alongi *et* al.,

2004), phytoplankton also yielded high standing stocks in mangrove waterways of the same estuaries (Tanaka & Choo, 2000; Alongi *et* al., 2003). Therefore, it would be interesting to know which carbon source is more important to support the zooplankton communities in turbid mangrove waters.

As zooplankton are known as an important food source for young and small mangrove fishes, it is also necessary to study their community structure and abundance in relation to the environmental conditions in order to evaluate their contribution to mangrove trophodynamics and hence to coastal fisheries (see Blaber, 2007; Chong, 2007). Furthermore, there are few studies on zooplankton ecology in the mangrove ecosystem worldwide (e.g. Grindley, 1984; Madhupratap, 1987; Robertson *et* al., 1988; Ambler *et* al., 1991; McKinnon & Klumpp, 1998a; Kouassi *et* al., 2001; Ara, 2004; Krumme & Liang, 2004; Duggan *et* al., 2008) mainly because much of mangrove forests are located in tropical developing countries, where research funding and capacity are often limited. In Malaysia, studies on marine zooplankton or copepods are few and restricted to neritic and oceanic waters (Sewell, 1933; Chong & Chua, 1975, Chua & Chong, 1975; Johan *et* al., 2002; Rezai *et* al., 2004; Rezai *et* al., 2005; Yoshida *et* al., 2006; Nakajima *et* al., 2008, 2009). There are only two studies on zooplankton in mangrove estuaries (Oka, 2000; Ooi, 2002).

The proposed study would therefore address the above problems, particularly on the relative contribution of zooplankton (and thus phytoplankton) vis-à-vis particulates of mangrove detritus as food to juvenile and small bodied fishes. The cycles of zooplankton food abundance and their predators, and how they are influenced by various environmental factors, also provide good reasons for an interesting research.

The aims of the present study were: 1) to determine the dynamics of zooplankton in terms of abundance and community structure in the mangrove estuaries

and adjacent coastal waters, 2) to relate zooplankton community structure to environmental factors, and 3) to determine the contribution of zooplankton as intermediate components linking the primary producers to small-sized fishes in the mangrove and coastal food webs.

Two hypotheses were tested in the present study: 1) the abundance and community structure of zooplankton are regulated by sequential effects of abiotic (salinity, light and nutrients) and biotic (phytoplankton and predators) factors (Chapter 3 & 4), and 2) zooplankton support juvenile and small-sized fish nutrition by utilizing phytoplankton as an energy source in turbid mangrove waters (Chapter 5).

The following investigations were carried out to fulfill the above objectives:

1. Spatial and temporal variability of zooplankton abundance and community structure in the mangrove estuaries and adjacent coastal waters (Chapter 3)
2. Short-term variability of zooplankton abundance and community structure in the mangrove estuaries (Chapter 4) and
3. Role of zooplankton as food for juvenile and small-sized fishes in the mangrove waters (Chapter 5).

CHAPTER 2

MATERIALS AND METHODS

2.1 General description of the study site

The general study site was located at the Matang Mangrove Forest Reserve (MMFR) on the west coast of Peninsular Malaysia (4^{o} 50'N, 100^{o} 35'E) (Fig. 2.1). The MMFR covers a total of 41,711 ha and has been regarded as the best sustainably managed mangrove forest in the world (Gan, 1995). The MMFR covers seven deltaic islands (Pulau Gula, P. Kelumpang, P. Selinsing, P. Sangga Kecil, P. Sangga Besar, P. Terong and P. Pasir Hitam) and is dominated by silvicultured *Rhizophora apiculata* Blume. About 95% of the mangrove forest floor is exposed to tidal inundation (Gan, 1995). The mangrove waterways that separate the deltaic islands as well as the mudflats adjoining the mangrove fringes have been known to be the pivotal areas for numerous organisms in sustaining the coastal fisheries (Chong, 2007). Cockle cultivation and floating fish cage-culture are among the most important aquaculture activities in the estuaries, both of which are more centralized in the Kuala Sepetang area (Madin, 2010).

The water depths are relatively shallow, with the maximum depth not exceeding 10 m across the sampling stations. The tidal regime is semidiurnal and tidal levels at MHWS, MHWN, MLWN and MLWS have been reported as 2.1, 1.5, 0.9 and 0.3 m above chart datum (National Hydrographic Centre, Malaysia).

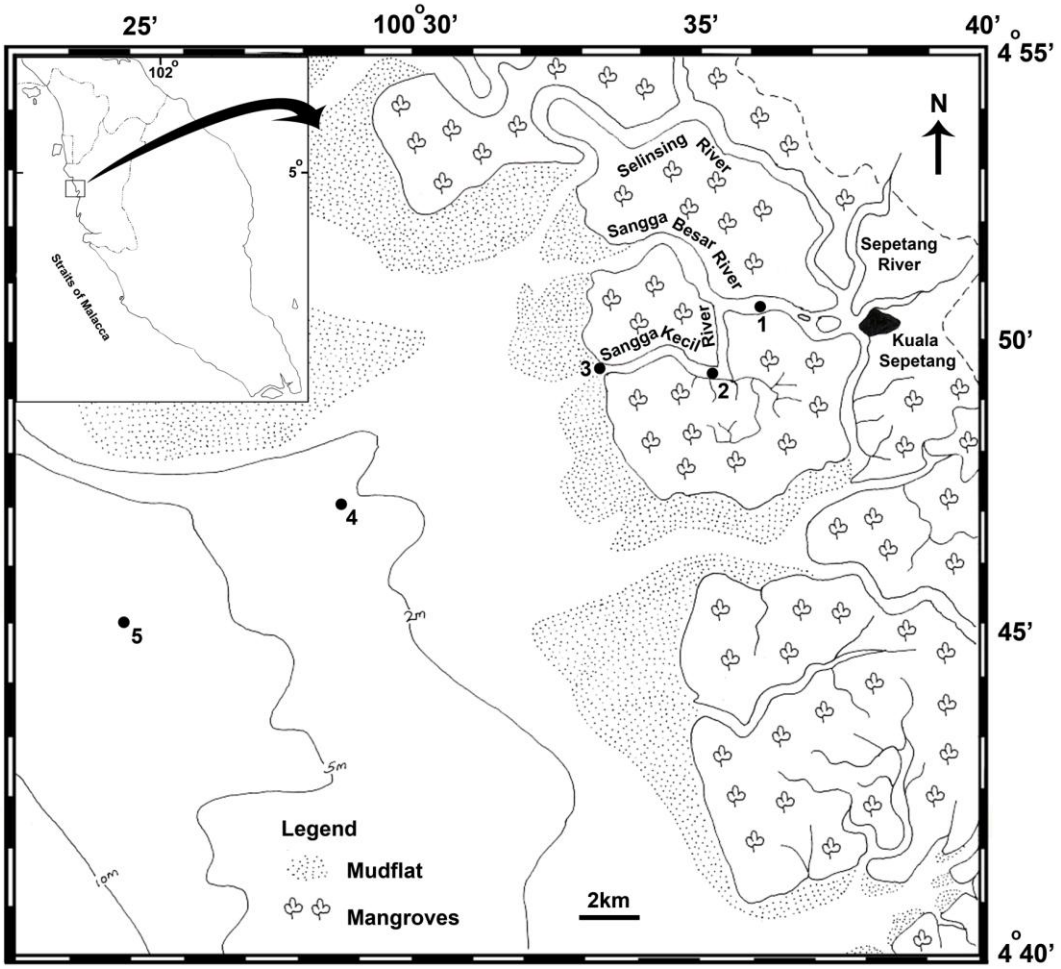


Fig. 2.1. Location map of sampling stations in the Matang mangrove estuaries and adjacent coastal waters during the routine monthly sampling. Stations: 1 = upper estuary; 2 = mid-estuary; 3 = lower estuary; 4 = nearshore waters; 5 = offshore waters.

In the present study, three empirical investigations were carried out in the Matang mangrove estuaries and adjacent coastal waters to elucidate the dynamics and ecological importance of zooplankton in this mangrove system. The materials and methods of each study are described in separate section as follow:

2.2 Spatial and temporal variability of zooplankton abundance and community structure

2.2.1 Field collection

The upper (thereafter UE), middle (ME) and lower (LE) regions of the complex interconnected estuaries of the Sangga rivers that were sampled for zooplankton were located 7, 3.5 and 0 km from the river mouth of Sangga Kecil (Table 2.1; Fig. 2.1). The adjacent coastal waters were sampled at their nearshore (NS) and offshore (OS) sites located 8 km and 16 km from the mouth of Sangga Kecil, respectively.

Table 2.1. Station location and mean water depth of zooplankton routine monthly sampling in the Matang mangrove estuaries and adjacent coastal waters.

Station	Location		Distance from river mouth (km)	Mean water depth (m)
Upper estuary	4°50'N	100°36'E	-7	3.46
Mid-estuary	4°49'N	100°35'E	-3.5	7.25
Lower estuary	4°49'N	100°33'E	0	5.75
Nearshore waters	4°47'N	100°29'E	8	3.3
Offshore waters	4°45'N	100°25'E	16	7.04

Routine monthly sampling of zooplankton was carried out from May 2002 to October 2003 from the upper estuary to offshore waters. Samplings were conducted during neap tides when the water parameters were less fluctuating (Chong *et* al., 1999). Duplicate zooplankton samples were taken by 45 cm-diameter bongo nets (363 µm, 180 µm) fitted with calibrated flow-meters. Two horizontal tows (0.5 – 1 m depth) were made at each station during the day, one on the seabound journey and the other on the return. Tow durations ranged between 3 - 10 min depending on net clogging. The volume of water filtered for each tow ranged from 48 to 203 m^3 (appendix I).

Zooplankton samples were preserved in 10% buffered formaldehyde in seawater and kept in 500 ml plastic bottles before subsequent analysis.

At each collection of zooplankton, physical parameters (salinity, temperature, pH, dissolved oxygen and turbidity) were measured by a metered multi-parameter sonde (Model YSI 3800 and Hydrolab 4a). All water parameters were taken at 0.5 m depth. Rainfall data from 1995 to 2006 were obtained from the Malaysian Meteorological Department based on measurements recorded at Taiping, a town located 10 km to the east of MMFR.

Wind Rose data that summarized the monthly average wind speed and direction were obtained for three meteorological stations located at Kota Bharu, Langkawi Island and Lubok Merbau (Fig. 2.2). Kota Bharu (northwest) and Langkawi Island (northeast) are the most exposed meteorological stations to monsoonal winds in Peninsular Malaysia, while Lubok Merbau is the nearest wind station to MMFR. Wind Rose data were also provided by the Malaysian Meteorological Department.

For the estimation of chlorophyll *a* and dissolved inorganic nutrient concentrations, triplicates of water samples from 0.5 m depth were taken at each of the zooplankton collection by using the Van Dorn Water sampler. Water samples were poured into a pail and mixed well before they were transferred into 1-l acid rinsed bottles. The sample bottles were screw-capped, labeled and kept on ice. At base camp, 100 ml of seawater was poured out from the sample bottle and immediately filtered through GF/C Whatman glass microfibre filter paper before two drops of 1% of $MgCO_3$ were added for acidification. The filter paper was then folded twice into a quadrant, kept in a plastic screw-capped container and stored in a -20 ^{o}C freezer until subsequent chlorophyll content analysis.

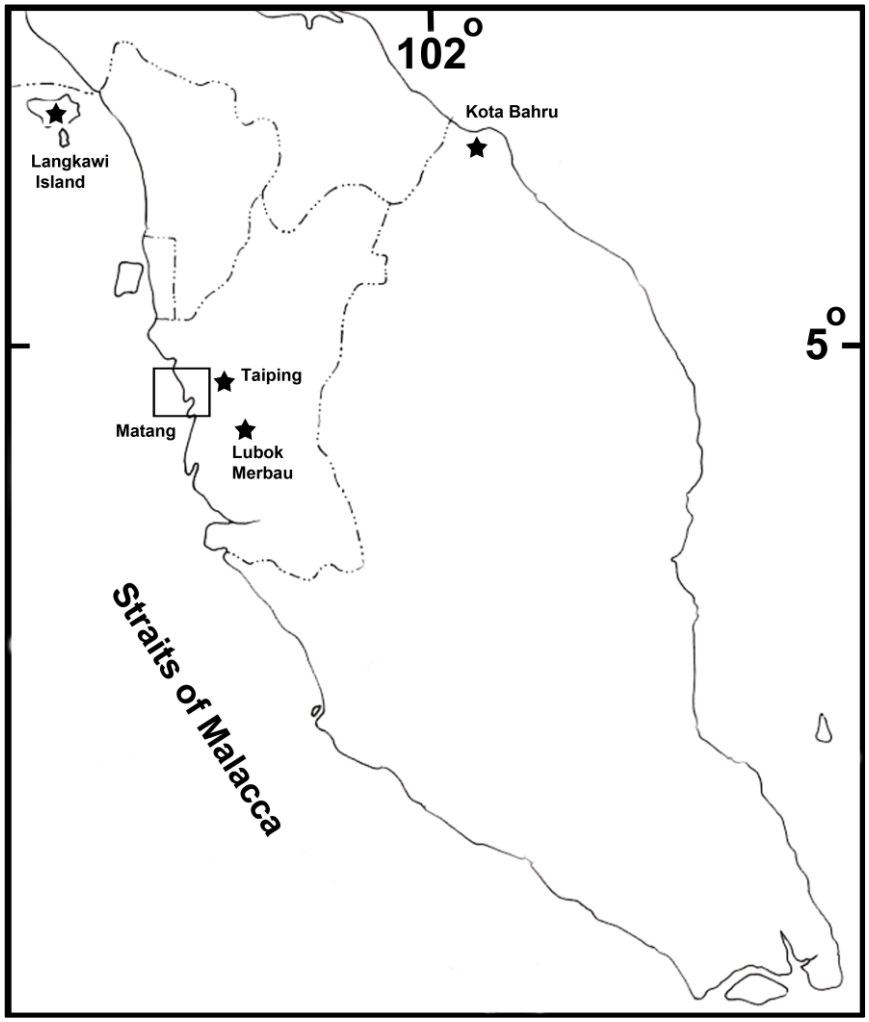


Fig. 2.2. Location map of meteorological stations (★) for rainfall and Wind Rose data.

The water filtration was repeated two times for the same bottle of water sample to collect the filtered seawater which was kept in a new acid rinsed bottle. The bottle was screw-capped, labeled and frozen before subsequent dissolved inorganic nutrient analysis.

2.2.2 Laboratory procedures

2.2.2.1 Zooplankton

a) Wet biomass

Only the 180 μm-net samples were analyzed and the results reported. Individual samples were gently and quickly wet sieved through stacked 1000 μm, 500 μm, 250 μm and 125 μm Endecott sieves using running tap water. The sieved zooplankton size fractions were transferred onto pre-weighed steel gauze and excess moisture was absorbed by a blotting paper. The plankton wet weight in gram (g) was measured to 2 decimal points. The raw zooplankton wet weight (b) was converted to wet biomass (B) in mg per m^3 (mg m^{-3}) from the following equation:

$$\mathbf{B = \frac{1000b}{DA}}$$

where D is the distance of the tow path in metres, and A is the area of the mouth of the bongo-net. D was calculated from the calibrated flowmeter as:

D = FR

where F is the calibration factor in metres per revolution and R is the number of flowmeter revolutions during the tow (appendix I).

b) Abundance

The various zooplankton fractions were immediately resuspended in 80% alcohol in separate 100-ml vials after weighing. For enumeration, the samples were split between 1 - 8 times using a Folsom plankton splitter. Adult copepods were

identified to species or the lowest possible taxon. Copepodids were identified to genus level. Juveniles that could not be identified were classified as unidentified copepodids or nauplii. Other zooplankton (except for fish larvae) were also identified to the lowest possible taxon. All large zooplankton (>1 mm) were counted in a Petri dish. Small zooplankton (<1 mm) were subsampled using a 1 ml Stempel pipette before transferring them into a 1 ml Sedgewick-Rafter cell for total counts. Zooplankton abundance (A) was estimated as number of individuals per m^3 (ind m^{-3}) using the following equation:

$$\mathbf{A = \frac{fv\,(N)}{DA}}$$

where f is the multiplication factor; v is the diluted sample volume; N is the number of individuals counted from the Sedgewick-Rafter cell; and D and A are as described above.

The wet biomass (or abundance) of the 1000 µm fraction and 500 µm fraction was combined and reported as 500 µm fraction. Since the mesh size was 180 µm, there was a potential loss of zooplankton smaller than this size. Nevertheless, the fractionation procedure showed the capture of zooplankton smaller than 180 µm due to blockage by larger zooplankton. Therefore, the 125 (-250) µm fraction contained 180 - 250 µm size zooplankton plus an underestimated portion of <180 µm size zooplankton.

2.2.2.2 Chlorophyll a

Chlorophyll *a* (chl. *a*) concentrations were measured monthly using the fluorometric method (Parsons *et* al., 1984) from July 2002 to October 2003. The folded filtered paper with seston was torn into small pieces and put into a polypropylene test tube. Five milliliters of acetone was added by using a pipette. The sample in acetone was repeatedly crushed with a rod. Another 5 ml of acetone and two drops of $MgCO_3$ were added. The tube was screw-capped and stored in the refrigerator at 4 ^oC for 24 hours of chlorophyll extraction. Tubes were centrifuged at 3000 rpm for 10 min and the

supernatant was measured for chl. *a* concentration by a Turner Quantech fluorometer based on a pre-set standard curve.

To develop a standard curve of chl. *a* for fluorometer, a pure *Chlorella* culture obtained from the Algae Research Laboratory, University of Malaya was extracted using the same procedure described above. The pure extracted chl. *a* was measured using a Shimadzu UV-VIS Spectrophotometer based on the three absorbance wavelengths of 665, 645 and 630 nm. The chl. *a* concentration was estimated using a Strickland & Parsons (1968) equation:

$$\mathbf{C = 11.6 \times OD_{665} - 1.31 \times OD_{645} - 0.14 \times OD_{630}}$$

where OD = the absorbance at different wavelengths

C = concentration of chl. *a* in [(mg) (ml^{-1})] per 10^3 = µg ml^{-1}

The concentration of chl. *a* in µg l^{-1} was estimated using the following equation:

$$\textbf{Chlorophyll } a \textbf{ (µg } l^{-1}\textbf{)} = \frac{\textbf{C x 10 ml of extracted sample}}{\textbf{100 ml of filtered water sample x 1000}}$$

The pure chl. *a* extraction was half-diluted to obtain a series of five different chl. *a* concentrations. The standard curve was set using a five-point calibration as instructed in the Quantech Turner Fluorometer operation manual.

2.2.2.3 Dissolved inorganic nutrients

The concentrations of dissolved inorganic nutrients NH_4^+, NO_2^-, NO_3^+ and PO_4^{3-} were measured by using the HACH DR/2010 spectrophotometer. Frozen filtered seawater samples were thawed to room temperature. Dissolved inorganic nutrient concentrations were determined based on the HACH Water Analysis Handbook (1997). Each sample bottle was measured repeatedly two to three times depending on the consistency of the nutrient reading. Nutrient concentrations in mg l^{-1} unit were

converted to μmol l^{-1}, where NH_4^+, NO_2^- and NO_3^+ were divided by the molecular weight of nitrogen (N = 14) and PO_4^{3-} was divided by the molecular weight of phosphate (PO_4^{3-} = 95). Concentrations of NO_2^- and NO_3^+ were combined and reported as $NO_2^- + NO_3^+$.

2.2.3 Data and statistical analyses

2.2.3.1 Rainfall data

The standard precipitation index (SPI) developed by Mckee *et* al. (1993) was used to define the precipitation pattern in the study area. Monthly SPI over a 12-year timescale period was calculated based on the following equation:

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

where X_i is the total rainfall of the *i*th month**;** $\bar{X}$ is the mean monthly total rainfall over a 12-year timescale; and SD is the standard deviation of the monthly total rainfall over 12 years timescale.

The SPI values and precipitation categories are given as follow:

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

2.2.3.2 Univariate analyses

a) Copepod species diversity

Copepod diversity was determined for all adults and *Hemicyclops* copepodids using four diversity indexes viz. Shannon-Wiener diversity index (H') (Shannon, 1948), Pielou's evenness (J') (Pielou, 1969), average individual taxonomic distinctness (Δ*)

and average specific taxonomic distinctness (Δ^+) (Warwick & Clarke, 1995; Pienkowski *et* al., 1998). H' and J' are the measures using the abundance data at specific taxonomic level (species level in the present study). These measures illustrate the distribution of abundance among species. Higher values of these measures reflect many species of the community are about equally abundant and thus less dominance of the community, whereas lower values of these measures reflect low number of species or only a few species are abundant and thus high dominance of the community (Brower *et* al., 1998). Δ^* is a measure of average taxonomic distances between every pair of individuals in the sample. Δ^* estimation precludes the species dominant effects, and thus reflecting a pure taxonomic relatedness of individuals in the sample (Warwick & Clarke, 1995). Δ^+ is a measure based on the presence/absence data. This measure reflects the average taxonomic distances between every pair of species in the sample (Pienkowski *et* al., 1998).

The algebraic equations of the four diversity indexes are given as follow:

Shannon-Wiener diversity index, H' = -Σ *pi* ln *pi*

where *pi* is the proportion of total number of individuals that belong to *i*th species.

Pielou's evenness, J' = H'/H' max

where H' max = ln (total number of species).

$$\textbf{AITD, } \Delta^* = \frac{\Sigma\Sigma_{i<j}\,\omega_{ij}X_iX_j}{\Sigma\Sigma_{i<j}\,X_iX_j}$$

where X_i (i = 1,…,s) is the abundance of the *i*th species; ω_{ij} is the 'weighted' taxonomic distances link between species *i* to *j* in the hierarchical taxonomy where individuals in the same species were weighted as 25, genus as 50, family as 75, and order as 100; and double summations denote over all pairs of species *i* and *j*.

$$\textbf{ASTD, } \Delta^{+} = 2\,\frac{\Sigma\Sigma_{i<j}\,\omega_{ij}}{S(S-1)}$$

where S is the species richness; ω_{ij} is the 'weighted' taxonomic distances link between species i and j in the hierarchical taxonomy with weightings are given above; and double summations denote ranges over all pairs i and j of these species ($i<j$).

The four diversity indexes were computed by using the Plymouth Routines in Multivariate Ecological Research (PRIMER 6) software.

b) Statistical analysis

Two-way factorial ANOVA with unequal and proportional replication was used to examine effects due to seasonal monsoon (NE monsoon, SW monsoon and IN monsoon period) and station (UE, ME, LE, NS and OS) on the zooplankton biomass (total and size-fractionated components), zooplankton abundance (total, size-fractionated components, total copepods, *Parvocalanus crassirostris*, *Acartia spinicauda* Mori, *Acartia* copepodid, *Oithona simplex* Farran, *Bestiolina similis* (Sewell), *Euterpina acutifrons*, cirripede larvae, total decapods, polychaete larvae and unidentified eggs), copepod diversity indexes (H', J', Δ^* and Δ^+) and the various environmental variables (salinity, temperature, pH, dissolved oxygen, turbidity and chlorophyll *a* and dissolved inorganic nutrient concentrations). If the ANOVA test was significant, Tukey HSD test was further conducted for multiple comparisons of the means. Data were first tested for normality and homogeneity of variance. Skewed data were either fourth rooted, $\log_{10}$ (x) (environmental variable) or $\log_{10}$ (x + 1) (zooplankton abundance) transformed. Kruskal-Wallis test was conducted if the variable (e.g. abundance of *Parvocalanus elegans* Andronov, *Metacalanus aurivilli* Cleve, Harpacticoida sp. 1, Luciferidae, Sergestidae, Brachyura, Diogenidae, Protozoa, Chaetognatha, Gastropoda, Bivalve, Larvacea, Bryozoa larvae and Ophiopluteus larvae)

did not fulfill parametric assumptions even after data transformation. If the Kruskal-Wallis test was significant, Mann-Whitney U test was further applied for multiple comparisons of the means. Significance level at $\alpha = 0.05$ was applied to determine significant difference.

Pearson's *r* correlation was used to examine the relationship between zooplankton wet biomass and respective numerical abundance. Significance level was set at $\alpha = 0.05$. The correlation is supposed to be weak if zooplankton sample is severely contaminated with plant material or with the presence of large bodied animals.

All statistical analyses were conducted using the Statistica Version 8 software on a PC.

2.2.3.3 K-dominance curves

K-dominance curves are distributional plots of cumulative ranked abundance against species rank or log species rank (Lambshead *et* al., 1983). The smooth curves are plotted based on the information extracted from the relative species abundance patterns without losing information to a single summary statistic such as a biological diversity index (Clarke & Warwick, 2001). The most elevated curve represented the lowest diversity or the highest dominance of the community. This technique was used to provide additional information to species diversity indexes in comparing the dominance of copepods at different sampling stations. To generate the curves, copepod species abundance data were averaged for each sampling station and $\log_{10}(x + 1)$ transformed before the transformed data was computed by the PRIMER 6 software.

2.2.3.4 Multivariate analyses

a) Similarity between zooplankton communities

The hierarchical cluster analysis and non-metric multidimensional scaling (MDS) were used to reduce the complexity of zooplankton community data based on the similarity approach. To apply these analyses, the monthly mean abundance data comprising of all zooplankton taxa (n = 94) were $\log_{10}$ (x + 1) transformed to reduce the weight of the dominant taxa. The Bray-Curtis (BC) similarity matrix with all pairwise comparisons of samples was then generated from the transformed zooplankton abundance data based on the following similarity coefficient:

$$\mathbf{S_{jk} = 100\ \{1-(\Sigma_{i=1}^{p}\ |y_{ij} - y_{ik}|/\Sigma_{i=1}^{p}(y_{ij} + y_{ik})\}}$$ (Clarke & Warwick, 2001).

where S_{jk} is a similarity between *j*th and *k*th samples; and y_{ij} and y_{ik} are the abundance for *i*th species in *j*th and *k*th sample respectively.

From the BC similarity matrix, a dendrogram was constructed for cluster analysis using an average group linking method. The dendrogram is interpreted in such a way that samples within a group or cluster are supposed to be more similar to each other compared to samples in other groups (Quinn & Keough, 2002; Clarke & Warwick, 2001). MDS is generally displayed by a 2-dimensional configuration which is generated from a rank similarity matrix. The closer proximity of two samples on the plots indicates the more similar the zooplankton communities are among these samples (Clarke & Warwick, 2001). A stress coefficient is a measure of whether the distances among sample plots accurately reflect their similarities. A stress value of less than 0.1 corresponds to a good ordination, while a stress value of more than 0.3 corresponds to sample points that are close to being arbitrarily placed on the 2-dimentional ordination.

The significant spatial and monsoonal variations in zooplankton community structure were tested using a non-parametric 2-way crossed Analysis of Similarities (ANOSIM) with replicates (Clarke & Warwick, 2001), which is analogous to the parametric two-way ANOVA. This analysis uses an R statistic calculated from a rank

similarity matrix (BC for this study), which is scaled from -1 to +1. R value of 0 indicates no separation of the community structure between groups for the comparing factor (stations or monsoonal seasons), while R value of 1 indicates perfect separation of the community structure. The significance level of ANOSIM was determined by referring the observed R value to its permutation distribution which was generated from a repeating process of arbitrarily reshuffling the sample labels and recalculating the R value.

All similarity analyses were computed by using the PRIMER 6 software.

b) Redundancy analysis

The relationships between zooplankton abundance and environmental variables were analyzed by redundancy analysis (RDA) using the CANOCO 4.5 program. RDA is a constrained linear ordination method that assumes the species-environment relations are linear based on direct ordination (Ter Braak, 1994). RDA which is a short-gradient analysis was used because the zooplankton community variation in the study area was not wide, <2 SD (Ter Braak & Prentice, 1988). Eighty-eight samples containing 47 selected zooplankton taxa (those that accounted for at least 0.2% of the total abundance for each sample) were related to 9 environmental parameters (salinity, pH, temperature, dissolved oxygen, turbidity, and chl. *a* and dissolved inorganic nutrient concentrations). Zooplankton abundance was $\log_{10}$ (x + 1) transformed while turbidity, chlorophyll *a* and dissolved inorganic nutrient concentrations were $\log_{10}$ (x) transformed because of skewed data.

2.2.3.5 Relationships between potential food and consumers

It has been suggested that the timing of larval spawning or recruitment is closely linked to the availability of larval food production (Cushing, 1976). The production

cycle of organisms are often cued by the seasonal cycle of environmental stimuli (such as temperature and irradiance in temperate waters or salinity in tropical waters) as to ensure that the newly-recruited larvae are ready to exploit the seasonal abundant food. To show such relationships, overall mean monthly data (all stations combined) of six major groups including phytoplankton, protozoans, copepods, non-copepod zooplankton (except for carnivorous zooplankton), carnivorous zooplankton (chaetognaths, cnidarians and ctenophores combined) and fish larvae were log (x + 1) transformed and standardized to number of standard deviations. Since salinity is mediated by rainfall, the standardized biological data were thus compared to respective standardized precipitation index as reported in section 3.1.2.

2.3 Short-term variability of zooplankton abundance and community structure

2.3.1 Field collection

A 30 cm-mouth diameter Clarke-Bumpus sampler with 160-μm mesh size net and opening-closing mechanism was used to collect zooplankton at two depth strata of the water column. Towing depths were near surface (0.5 m from the surface) and bottom (0.5 m from the sediment bottom) water at a fixed station located at the lower estuary of Sangga Kecil River (station LE, see Fig. 2.1). 24-h samplings at 2-hour intervals (2 high tides and 2 low tides) were carried out on 7 - 8 July (neap, 1st quarter), 14 - 15 July (spring, full moon), 21 - 22 July (neap, 3rd quarter) and 28 - 29 July (spring, new moon) in year 2003 in the dry period. Another series for wet period was carried out in the same year on 2 - 3 November (neap, 1st quarter), 9 - 10 November (spring, full moon), 17 - 18 November (neap, 3rd quarter) and 24 - 25 November (spring, new moon). Duplicate samples of zooplankton were collected at each depth stratum. Each zooplankton sample collection was conducted at 5 min duration. Total volume filtration

for each tow ranged from 23 to 111 m^3 (appendix II). Samples were collected into the bottle and preserved with 10% buffered formaldehyde for laboratory analysis.

Physical water parameters were measured for surface and bottom layers of the water column at each sampling interval by using the multi-parameter sonde Hydrolab 4a, while water samples for chl. *a* and nutrient analyses were collected only at the surface layer. The water samples were collected and treated in the same manner as described for routine monthly sampling in section 2.2.1.

2.3.2 Laboratory procedures

Samples of zooplankton, seston and filtered seawater were processed and analyzed based on the same procedure applied to the samples of routine monthly sampling (2.2.2).

The wet biomass of mangrove detritus contamination in the spring tide samples was estimated under a compound microscope by using an eye-estimation method (Pillay, 1953; McHugh, 1940). The percentage volume of mangrove contaminants in zooplankton aliquot laid on a Sedgewick-Rafter cell was estimated using an eyepiece grid (10 x 10 squares). The estimated percentage volume of mangrove contaminants was then converted to wet biomass. The ultimate zooplankton wet biomass was equal to raw zooplankton wet biomass minus the wet biomass of mangrove contaminants.

2.3.3 Data and statistical analyses

2.3.3.1 Univariate analyses

a) Copepod species diversity

Four biodiversity indexes H', J', Δ^* and Δ^+ were computed for all adult copepod species and *Hemicyclops* copepodids (n = 47) by the PRIMER 6 routine. Details of the four indexes were elaborated in section 2.2.3.2 (a).

b) Statistical analysis

One-way ANOVA was used to compare the variation in zooplankton biomass (total and size-fractionated components), zooplankton abundance (total, size-fractionated components, total copepods, *Acartia* copepodids, *A. spinicauda, B. similis, P. crassirostris, O. simplex*, mysids, decapods, cnidarians, polychaete larvae, gastropods, bivalves, bryozoan larvae, protozoans and unidentified eggs) and all environmental parameters between dry and wet period. All zooplankton biomass and abundance data subjected to ANOVA were fourth-rooted or $\log_{10}$ (x + 1) transformed as to fulfill the requirements of normality and homogeneity of variance for parametric test (Zar, 1998). Environmental variable was $\log_{10}$ (x)-transformed if data were not normally distributed. Non-parametric Mann-Whitney U test was performed on various zooplankton taxa (*Acartia* sp. 1, *P. elegans, Oithona dissimilis* Lindberg, *Oithona aruensis* Früchtl, *E. acutifrons*, cirripede larvae, chaetognaths and larvaceans) which did not attain the parametric assumptions even though after data transformation.

For each series of sampling period, a 4-way factorial ANOVA was applied to transformed zooplankton biomass (total and size-fractionated components) and abundance (total, size-fractionated components, total copepods, *Acartia* copepodids, *A. spinicauda, B. similis, P. crassirostris, O. simplex*, cirripede larvae, decapods, chaetognaths, cnidarians, polychaete larvae, gastropods, larvaceans, protozoans and unidentified eggs) data to examine if the influencing factors of moon phase (1^{st} quarter, full moon, 3^{rd} quarter and new moon), diel cycle (day and night), tide (ebb and flood) and depth (surface and bottom) had significant effects on zooplankton abundance. In order to achieve the parametric assumptions, zero values of *B. similis* in the dry period were not included in the 4-way ANOVA.

A 3-way ANOVA was conducted on physical parameters to compare the variation of moon phase, tidal and depth effects, while a 2-way ANOVA was conducted

to examine the effects of moon phase and tide on dissolved inorganic nutrient concentrations (except for ammonium in the wet period). The effect of moon phase, diel and tidal effects on chl. *a* concentration was tested by a 3-way ANOVA. If the multiple-factorial ANOVA test was significant, Tukey HSD test was further applied for multiple comparisons of the means.

A non-parametric Kruskal-Wallis test was used to examine the effect of moon phase on mysid abundance. Mann-Whitney U test was further conducted for pairwise comparisons among moon phases if Kruskal-Wallis test was significant. For each moon phase, Mann-Whitney U test was conducted to test whether diel, tide and depth effects had significant influence on mysids.

Pearson's *r* correlation was used to examine the association between zooplankton wet biomass and respective abundance for each moon phase. Significance level for statistical tests was set at $\alpha = 0.05$. All statistical tests were computed by using the Statistica Version 8 software package.

2.3.3.2 Multivariate analyses

a) Similarity between zooplankton communities

To avoid an enormous dataset, zooplankton abundance of all taxa (n = 106) were averaged in accordance with the diel-tidal cycle for each moon phase and depth stratum. Average of all zooplankton abundance was logarithmic transformed [$\log_{10}$ (x + 1)] to reduce the distributional skewness caused by the extreme values. A Bray-Curtis (BC) similarity matrix was generated from the transformed abundance data using the PRIMER 6 software package. The dendrogram of hierarchical clustering and 2-dimensional MDS plots were constructed based on the BC similarity generated from the transformed abundance dataset.

Two-way crossed ANOSIM routine with replicates was used to test the significant difference in zooplankton community structure between moon phase and diel cycle. Other tests of 2-way crossed ANOSIM routine were also conducted to examine the variation of zooplankton community structure with moon phase and tide and moon phase and depth as influencing factors.

2.4 Trophic structure in the Matang mangrove estuaries and adjacent coastal waters

2.4.1 Field collection

a) Fish

Fish samplings for stomach content analysis were carried out monthly from June 2003 to June 2004. All sampling occasions corresponded to neap tide except for November 2003 and June 2004, which corresponded to spring tide. Juvenile and small fishes were sampled along the banks of Sangga Kecil, Sangga Besar, Sepetang, Selinsing and Jaha Rivers (Fig. 2.3) using a small otter trawl net of 2 cm stretched cod end mesh size and head rope length of 11.3 m. Trawling durations ranged from 5 - 10 min each. Eight to 10 trawls were made per sampling occasion. Trawl catches were normally sub-sampled but if the catch was small, the entire catch was taken. Samples were kept in ice on board the boat and frozen at -20 ^{o}C in laboratory until subsequent analysis.

Fish samples for stable isotope analysis were collected in April 2005. Fish collections were conducted at various stations located on Selinsing (SL1, SL2 and SL3) and Sangga Kecil (SK2 and SK3) Rivers and shallow water (ca. 2 m deep) near mudflat areas (NS2 and NS3) (Fig. 2.3). Sampling locations recorded by a geographic position system (GPS) were shown in Table 2.2. Duplicate trawls were conducted at each sampling station.

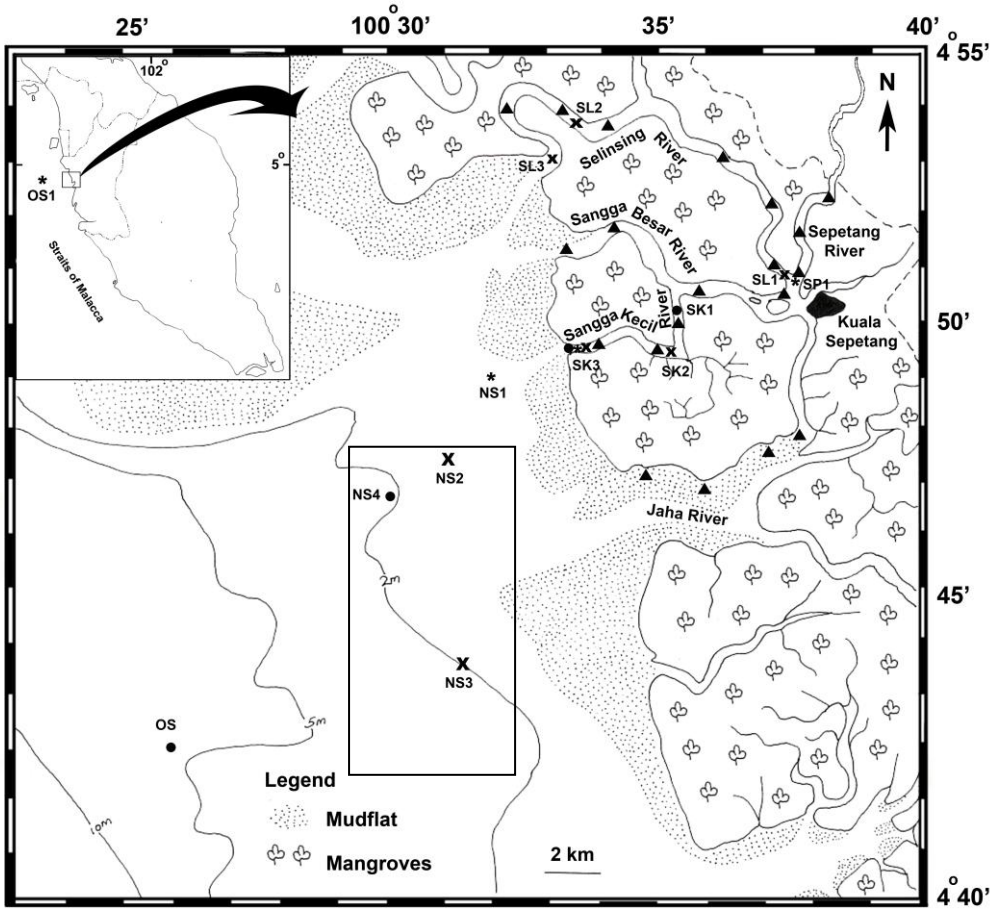


Fig. 2.3. Location map of sampling stations for fish stomach contents and stable isotope analyses in the Matang mangrove estuaries, nearshore and offshore waters. Sample collection sites for stable isotope analysis: '*' seston, '●' zooplankton, 'x' fish; sampling locations within the square box were considered as nearshore waters. '▲' fish collection sites for stomach contents analysis.

Table 2.2. Sampling location of primary producers and consumers for stable isotope analysis in the Matang mangrove estuaries, nearshore and offshore waters.

Station	Location		Type of sample collection
SP1	4°51'N	100°37'E	Seston
SK1	4°50'N	100°35'E	Senescent mangrove leaves, zooplankton
SK2	4°49'N	100°35'E	Senescent mangrove leaves, fish
SK3	4°49'N	100°33'E	Senescent mangrove leaves, seston, zooplankton, fish
SL1	4°51'N	100°37'E	Fish
SL2	4°54'N	100°34'E	Fish
SL3	4°53'N	100°33'E	Fish
NS1-4	4°43'-4°49'N	100°30'-100°32'	Seston, zooplankton, fish
OS	4°42'N	100°25'E	Zooplankton
OS1	4°48'N	100°03'E	Seston

b) Zooplankton

Zooplankton for stable isotope analysis were sampled by using the 45 cm-diameter bongo nets (363 µm, 180 µm). Duplicate zooplankton samples were collected across the water column by an oblique tow for 5 to 8 min duration. Sample collections were carried out at the upper (SK1) and lower (SK3) reaches of Sangga Kecil River to nearshore (NS4) and offshore (OS) waters (Fig. 2.3; Table 2.2). Samplings were conducted from midnight to early morning before sunrise on 19 February 2005. The samples were taken during neap tide and nighttime so as to facilitate the capture of demersal and adult zooplankters and to reduce contamination by mangrove detritus. The sample of zooplankton was screened through 1000 µm, 500 µm and 250 µm Endecott sieves onboard with filtered seawater. The fractionated zooplankton samples were transferred into individual sample bottles, screw-capped and frozen at -20 ^{o}C before laboratory sorting.

c) Mangrove leaves and seston

Seston samples were collected by using the Van Dorn sampler at four stations on two sampling occasions. The first sampling (8 June 2004) was conducted at station located 55 km off Matang (OS1) during the first Scientific Expedition to the Seas of Malaysia (SESMA I) (Fig. 2.3, Table 2.2).The second sampling (21 December 2005) was carried out at three sampling stations located at lower reaches of Sepetang (SP1) and Sangga Kecil (SK3) Rivers and nearshore waters (NS1), respectively (Fig. 2.3; Table 2.2). Duplicate samples were collected at each sampling station. To obtain seston samples, about 50 litres of seawater from the OS1 station and 4 litres from estuarine and coastal stations were pre-filtered through a 63-µm mesh size plankton net in the field before filtration through a pre-combusted GF/C Whatman glass microfibre filter paper was made. Seston retained on the filter paper was thoroughly rinsed with distilled water,

transferred into a screw-capped container and stored in a freezer at -20 ^{o}C until seston samples were oven dried.

Drifting senescent mangrove leaves were collected at the upper, mid- and lower reaches of the Sangga Kecil River using a scoop net. Senescent leaves were kept in different plastic zip-log bags according to sampling stations and stored in ice for further treatment.

2.4.2 Laboratory procedures

2.4.2.1 Fish stomach contents analysis

Juvenile fish belonging to 26 species were studied for their stomach contents. The fish species were selected based on size (<14 cm) and fish family commonly found in the Matang mangrove estuaries as reported in Chong (2005).These species altogether made up approximated 87.6% of the total fish density in Matang mangrove estuaries (Then, 2008). Frozen fish samples were thawed under running tap water before examination. Each fish specimen was identified, before its standard length (SL in cm) was measured. The fish abdomen was dissected and stomach was removed. All stomachs were thoroughly rinsed with 70% alcohol to remove the external residual before preservation. Stomach fullness was classified as empty, ¼ full, ½ full, ¾ full, full and gorged. The stomach was then slit open and its entire contents were washed with 70% alcohol onto a watch glass.

Large prey items were examined under a stereomicroscope and their volumes estimated with the aid of a gridded Sedgewick-Rafter cell. Small items were examined under a compound microscope and their volumes estimated with the aid of a 10 x 10 squares eyepiece grid. Subsampling of the stomach content was carried out using a Stempel pipette if large numbers of small prey items, such as copepods and ostracods,

were present. Food or prey items were identified and enumerated to the lowest taxonomic level. Food present as an amorphous mass and difficult to identify was classified as unidentified material. Frequency of occurrence (%) was calculated from the number of stomachs containing a particular food item, excluding empty stomachs.

2.4.2.2 Stable isotope analysis

Six important zooplanktivorous fish species from the Matang mangrove estuaries and nearshore waters (*Arius maculatus* (Thunberg), *Leiognathus brevirostris* (Valenciennes), *Johnius weberi* Hardenberg, *Stolephorus baganensis* Hardenberg, *Thryssa kammalensis* (Bleeker) and *Upeneus sulphureus* Cuvier), which were not previously studied for their stable isotope composition in the mangrove system of Matang, were selected for the analysis. Fish muscle tissues were dissected and rinsed thoroughly with distilled water. Tissues of small juveniles or small-sized fish, the same species and trawl, were pooled together as one sample for stable isotope analysis. Frozen zooplankton samples were thawed and sorted according to each taxon. Each sorted sample which weighed at least 2 mg dry weight was placed on a precombusted glass microfibre filter paper (Whatman GF/C) and rinsed thoroughly with distilled water before it was oven dried. Senescent mangrove leaves were also rinsed thoroughly with distilled water before they were dried in oven. All samples for stable isotope analysis were oven dried at 70 ^{o}C for 3 days. Dried samples were cooled, sealed in different plastic bags and kept in a dessicator until they were sent to Marine Biological Laboratory (MBL), Wood Hole, USA (August 05) or The University of Waikato, New Zealand (September 05) for stable isotopic carbon and nitrogen analyses.

At stable isotope laboratory, dried samples were ground to a fine powder before they were combusted to N_2 and CO_2 gasses by Europa ANCA-SL (Automated Nitrogen Carbon Analysis for Solids and Liquids) elemental analyzer. Only samples from

ostracods were acid treated before the combustion. The stable isotope carbon and nitrogen ratios were determined by Europa 20-20 mass spectrometer after the purified N_2 and CO_2 gasses were introduced into the spectrometer. Results were expressed in the standard δ notation, and values were determined based on the following equation:

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

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

The standard reference materials for carbon and nitrogen in stable isotope analysis were Peedee Belemnite (PDB) and N_2 in air, respectively. The precision of the spectrophotometer was ± 0.1 ‰ for both measurements of $\delta\,^{15}N$ and $\delta\,^{13}C$.

Although a high lipid content potentially decreases the $\delta^{13}C$ value of animals (DeNiro & Epstein 1977; McConnaughey & McRoy 1979), all animal samples were not defatted in the present study. This was because stable isotope values of defatted tissue (Hayase *et* al., 1999; Tanaka *et* al., 2011) and non-defatted tissue of the same species (Chong *et* al., 2001; Then, 2008) gave no significant differences ($p > 0.05$).

2.4.3 Data and statistical analyses

2.4.3.1 Fish stomach contents analysis

Fish vacuity index (VI) is a percentage of empty stomachs over total stomachs examined for each species (Hajisamae *et* al., 2003). The Levin's dietary niche breath (B) is a measure of animal's food specialization in a given habitat (Levins, 1968). Species with lower niche breadth or known as specialist depends on very few food resources. Species with larger niche breadth utilize more food resources and are known as generalists. The measure of Levin's niche breadth was calculated based on the following equation:

$$B = \frac{1}{\sum_{j=1}^{n} Pj^2}$$

where P*j* is the proportion of individuals of same species consuming food item *j* (ΣP*j* = 1).

This measure often is standardized on scale from 0 to 1 by the following equation:

$$Bs = \frac{B-1}{n-1}$$

where Bs is the Levin's standardized niche breadth and n is the total number of food resources (27 in this study after pooling).

Principle component analysis (PCA) was used to explore the diet preference of the 26 common fish species found in the Matang mangrove estuaries using the CANOCO 4.5 software. PCA is a linear ordination method to reduce dimensionality of possibly correlated variables by transformation of the original data set to another set of uncorrelated variables called principal components (PCs) (Jolliffe, 2002). These components are ordered so that most of the variations occur in the original variables are retained in the first few components (e.g. PC1 and PC2). To apply this procedure, the percentage volumetric of food item was averaged in accordance with fish species. Averaged data were arsine-transformed before they were analyzed for PCA. Results of PCA were generally depicted by a 2-dimension ordination biplot diagram.

To examine the ontogenetic shift in diets of combined ariids and sciaenids as well as *Pomadasys kaakan* (Cuvier), the percentage volumetric of their food item were averaged into size classes accordingly. Averaged data were arsine-transformed for PCA.

2.4.3.2 Stable isotope analysis

To determine the isotopic trophic position of zooplankton and fish in the Matang mangrove food web, animals' $\delta^{15}N$ values across stations were averaged for each taxon.

The isotopic trophic position was then estimated based on the method described in Vander Zanden and Rasmussen (1999):

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

where $\delta^{15}N_{consumer}$ is the $\delta^{15}N$ value for a given consumer; $\delta^{15}N_{base}$ is the value of a representative baseline at trophic position 2 (herbivorous copepod *Pseudodiaptomus* in the present study); and $\Delta\delta^{15}N$ is the trophic fractionation value of $\delta^{15}N$ (3 ‰ in this study). As trophic fractionation of $\delta^{15}N$ value between *Pseudodiaptomus* and secondary consumer across sampling stations was more consistent (ca. 3 ‰ in the present study) than the trophic fractionation value between seston and zooplankton primary consumer, the copepod *Pseudodiaptomus* was assigned as the representative baseline at trophic position 2 in the Matang mangrove food web.

The significant difference in $\delta^{13}C$ value between senescent mangrove leaves and seston collected at each sampling location was statistically compared using a non-parametric Mann-Whitney U test. The significant spatial variation in $\delta^{13}C$ and $\delta^{15}N$ values of seston was also statistically tested by using the non-parametric Kruskal-Wallis test. Mann-Whitney U test was further applied for comparisons between two samples if the Kruskal-Wallis test was significant. To test if sampling location had a significant influence on zooplankton $\delta^{13}C$ and $\delta^{15}N$ values, data were pooled in accordance with their trophic position before the non-parametric Kruskal-Wallis test was applied. Comparisons between two samples were further made by using the Mann-Whitney U test if there was a significant difference among sampling locations. Significance level for statistical tests was set at $\alpha = 0.05$.

CHAPTER 3

SPATIAL AND TEMPORAL VARIABILITY OF ZOOPLANKTON ABUNDANCE AND COMMUNITY STRUCTURE IN THE MATANG MANGROVE ESTUARIES AND ADJACENT COASTAL WATERS

Part of the content of this chapter was published in ISI indexed journal as follow:

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 (Appendix III).

3.1 Results

3.1.1 Wind direction

Monthly average wind directions from Wind Rose data (33 years) for Kota Bharu and Langkawi Island shows a significant seasonality of wind cycles, namely, the northeast (NE) monsoon and southwest (SW) monsoon (Figs. 3.1 and 3.2). The NE monsoon generally occurs from November to March, whilst SW monsoon occurs from May to September. At both places, and in particular Langkawi on the same coast as Matang on the west coast of Peninsular Malaysia, northeast to easterly winds are dominant with the arrival of the NE monsoon in December or January but retreat gradually with the advent of the SW monsoon in May. South to westerly winds dominate both places during the SW monsoon. The transition or inter monsoon (IN) period generally occurs in April and October. However, at Lubok Merbau, which is the nearest wind data station to the study site, did not exhibit a distinct seasonality of wind cycles. Its annual wind distribution is consistent with prevailing winds blowing in north-northeast and south-west directions, during the NE and SW monsoon, respectively (Fig. 3.3).

3.1.2 Rainfall

Monthly standardized precipitation index (SPI) over a 12-year timescale (1995 - 2006) for Taiping is given in Fig. 3.4. Precipitation below-average (SPI <0) generally

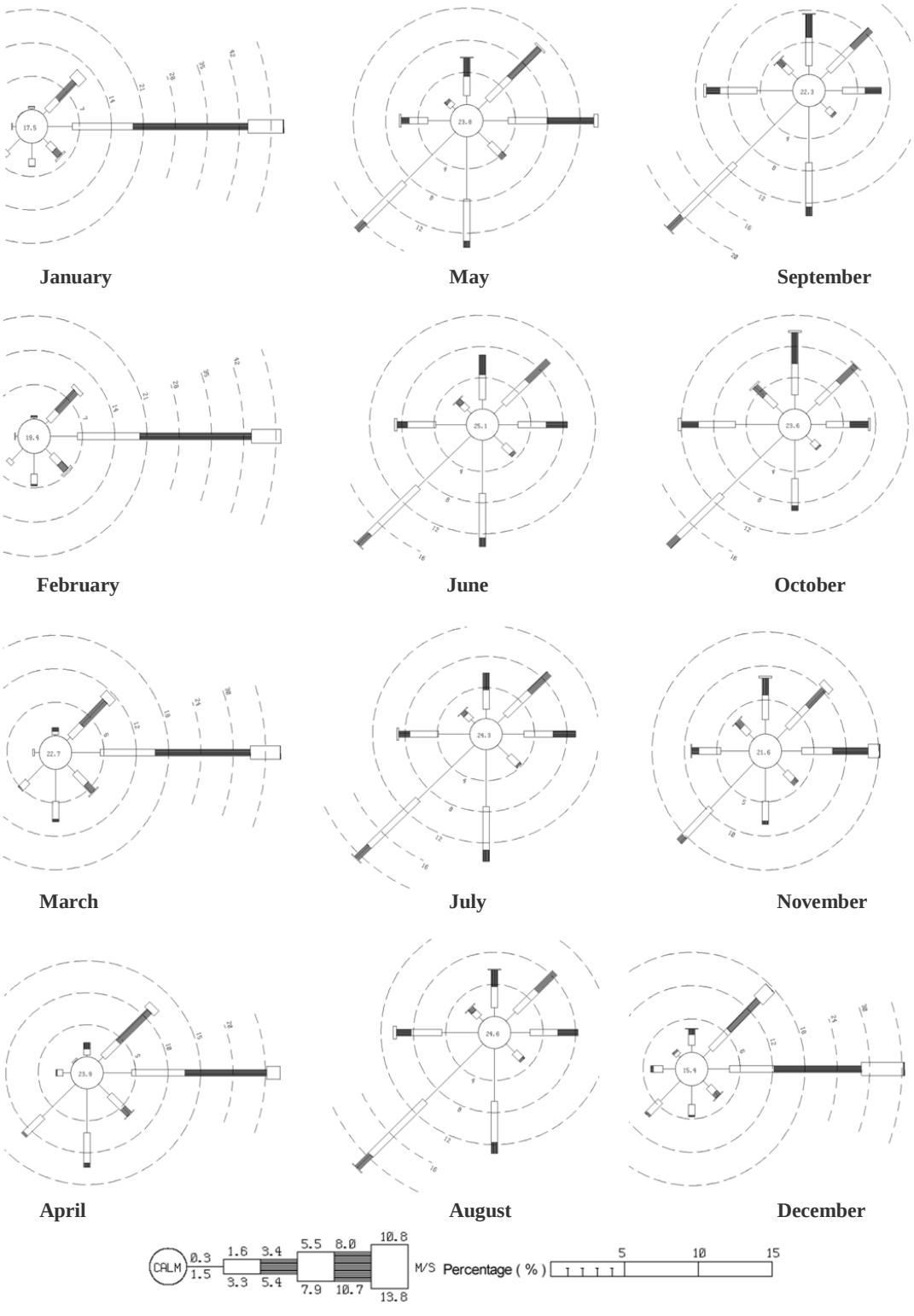


Fig. 3.1. Monthly mean of wind direction and speed from year 1975 to 2007 for Kota Bharu (data provided by Malaysian Meteorological Department).

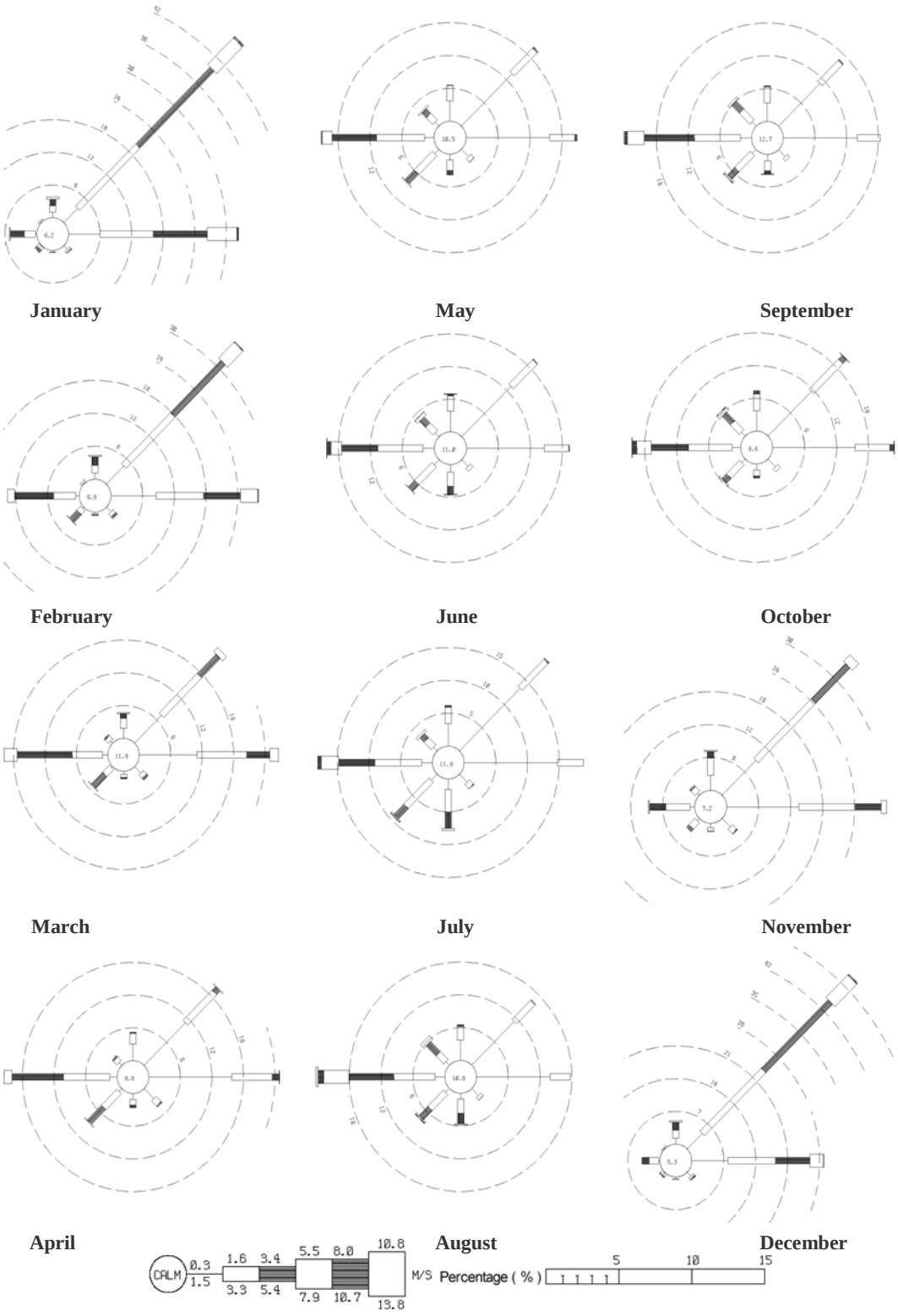


Fig. 3.2. Monthly mean of wind direction and speed from year 1988 to 2007 for Langkawi Island (data provided by Malaysian Meteorological Department).

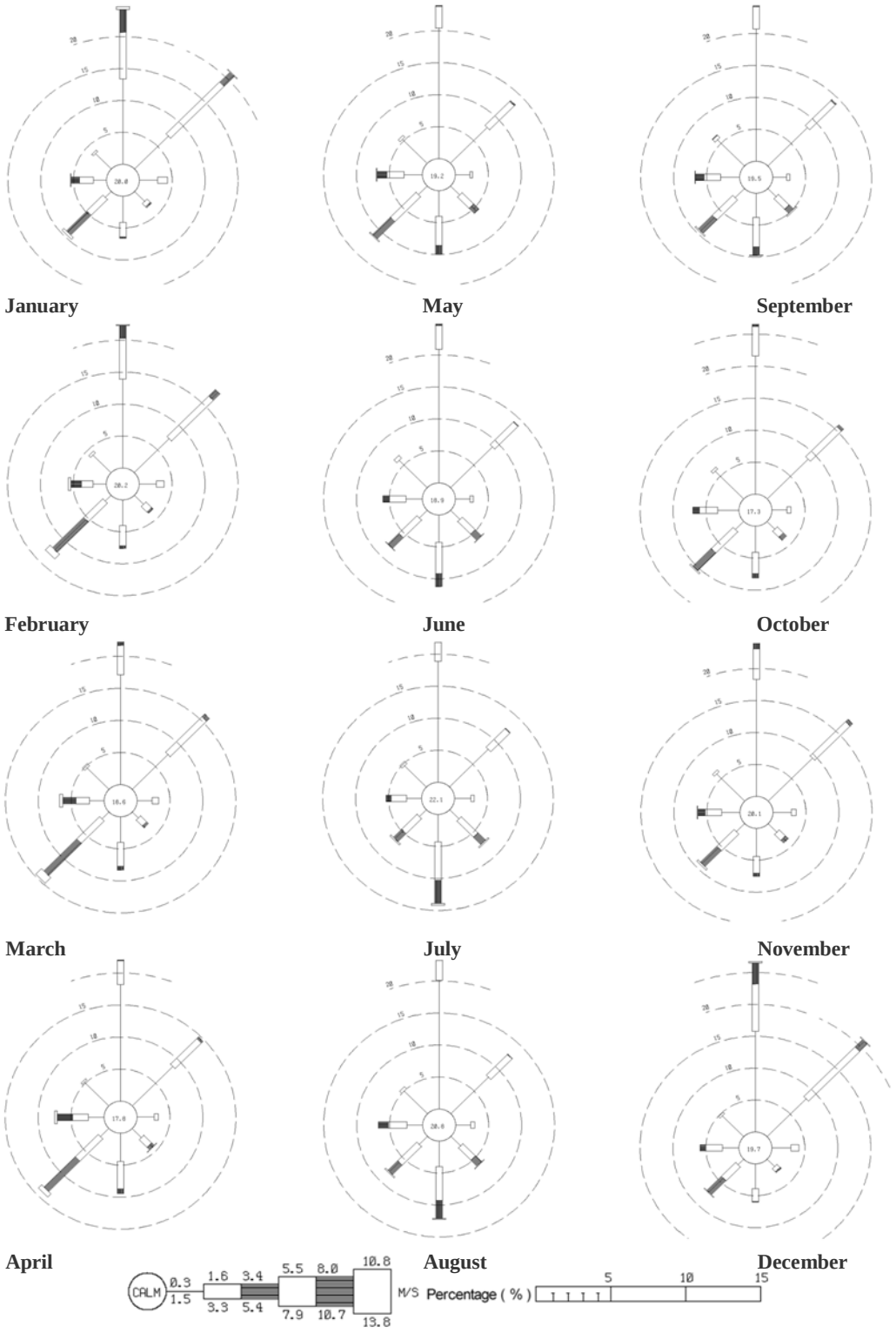


Fig. 3.3. Monthly mean of wind direction and speed from year 1993 to 2007 for Lubok Merbau (data provided by Malaysian Meteorological department).

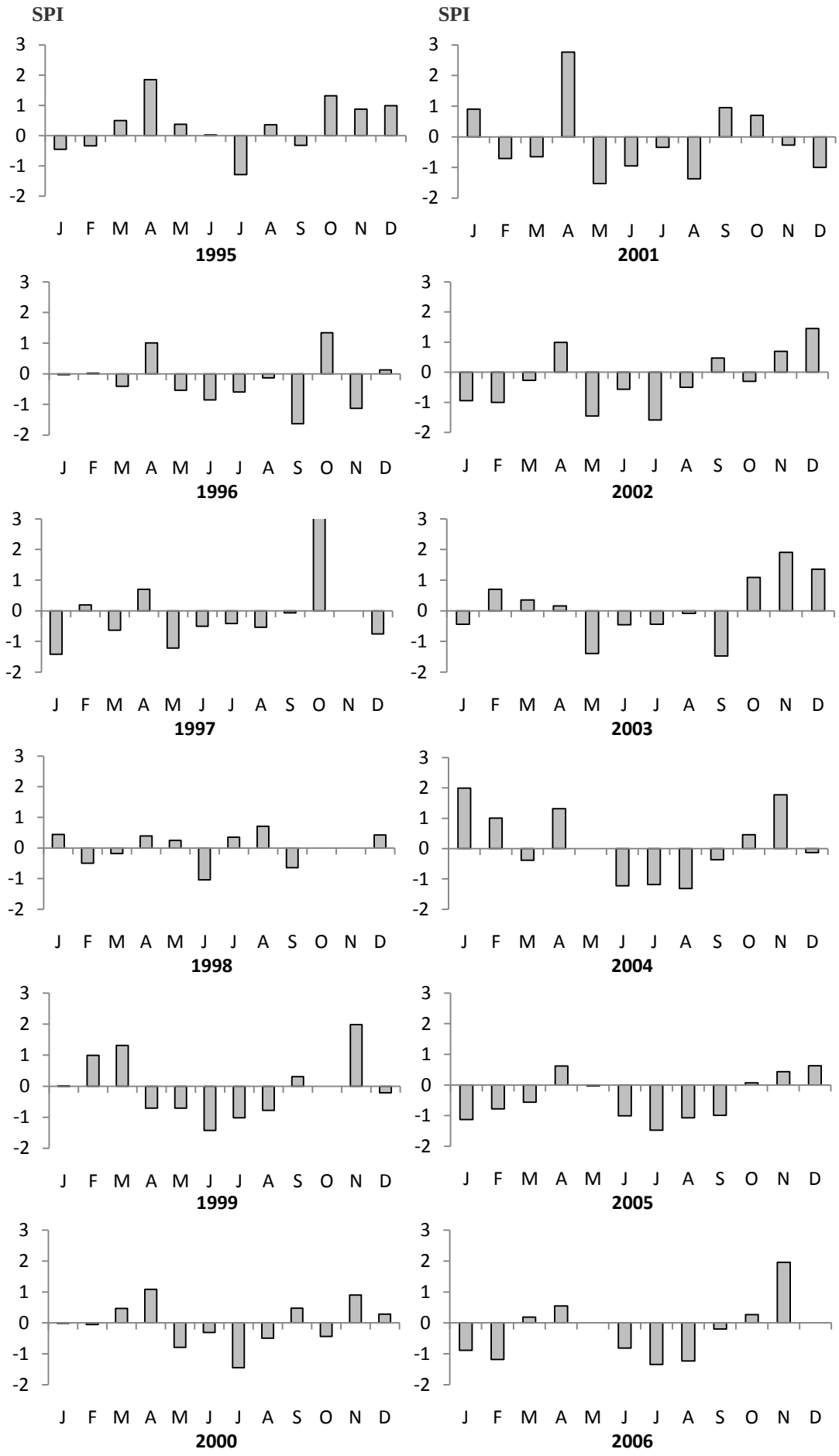


Fig. 3.4. Standardized precipitation index (SPI) from 1995 to 2006 at Taiping (data provided by Malaysian Meteorological Department).

occurred from May - September, coinciding with the SW monsoon. All severely-dry events (SPI <-1.5 to -2) occurred during the SW monsoon in July 1995, September 1996, July 2000, May 2001, May and July 2002, September 2003 and July 2005. No extreme-dry event (SPI <-2) was observed over the 12-year timescale. On the other hand, all severe- and extreme-wet events (SPI >1.5) coincided with the NE monsoon and IN monsoon periods (from October to April). Severely-wet events were observed in November 1999, December 2002, November - December 2003 and November 2004 while extreme-wet events were observed in April 1995, October 1997, April 2001 and January 2004 (Fig. 3.4).

Monthly rainfall recorded at Taiping over the sampling period (May 2002 - November 2003) ranged from 67 mm to 650 mm, with the lowest rainfall recorded in July 2002 and the highest rainfall in November 2003 (Fig. 3.5). Monthly number of rainy days ranged from 9 to 29 days. Mean monthly rainfall was 316 mm (SD: ± 167 mm) and mean monthly number of rainy day was 20 days (SD: ± 6 day). One-way ANOVA revealed significant higher rainfall ($p < 0.05$) during NE monsoon as compared to that of the SW monsoon and IN period. Mean rainfall of NE monsoon, IN period and SW monsoon was 462 mm (SD: ± 137 mm), 384 mm (SD: ± 118 mm) and 208 mm (SD: ± 116 mm) respectively (Table 3.1).

Since monthly rainfall of Taiping was highly influenced by the seasonal monsoons, samples collected over the 18-month sampling period were pooled as NE (November - March), IN (April and October) and SW (May - September) samples for the subsequent analysis. Study of short-term variations of zooplankton in July 2003 coincided with the dry period while November 2003 coincided with the wet period (Chapter 4).

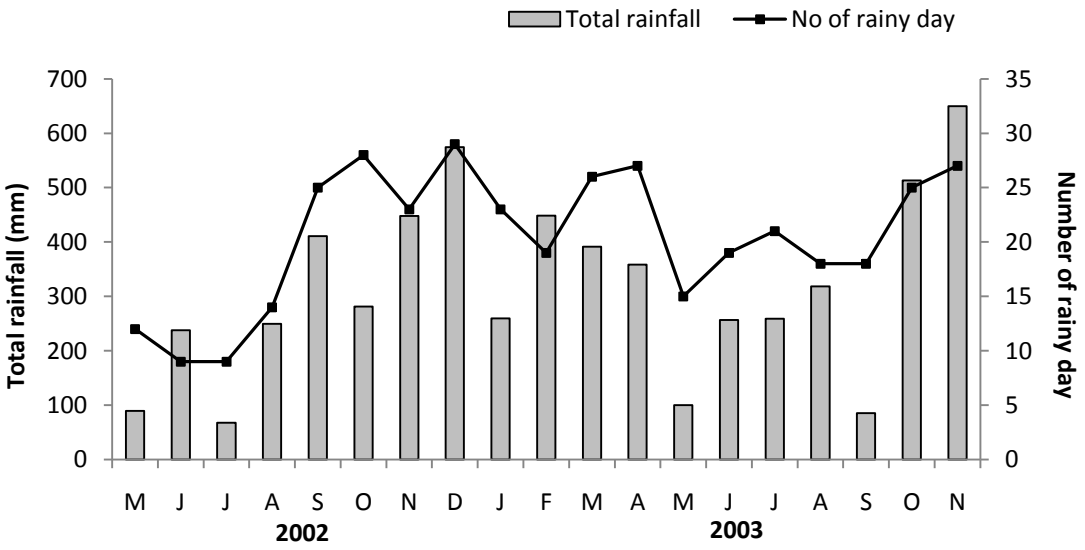


Fig. 3.5. Monthly total rainfall and number of rainy days recorded from May 2002 to November 2003 at Taiping, located 10 km east of the study site (data provided by Malaysian Meteorological Department).

Table 3.1. Summary results of one-way ANOVA and post-hoc Tukey HSD tests on monthly total rainfall between monsoon seasons. $\bar{x}$ = mean; n = sample size; homogenous groups indicated by superscripts a and b; ** significance at $p < 0.01$.

	Season	$\bar{x}$	± SD	n	p-level
Monthly total rainfall	SW[a]	208	116	10	0.003**
	IN[a,b]	384	118	3	
	NE[b]	462	137	6	

3.1.3 Hydrographic conditions

3.1.3.1 Salinity

The monthly surface salinity recorded over the sampling period for the upper estuary to offshore waters ranged from 12.2 to 33.6 ppt. Mean salinity increased gradually from the upper estuary (20.4 ± 3.75 ppt) to offshore (30.5 ± 1.18 ppt) stations (Table 3.2). The lowest monthly mean salinity was measured at the upper estuary station in February 2003 while the highest salinity was recorded at the offshore station in May 2002, coinciding with the month of highest and lowest rainfall respectively (Fig. 3.6a; see Fig. 3.5). In general, a longitudinal salinity gradient developed from the upper estuary to offshore waters. This estuary-to-offshore gradient, however, disappeared in

August 2002, which corresponded to strong wind event (Fig. 3.6a). Homogeneity of salinity that was confined within the mangrove estuaries was also observed in January, March and July 2003 (Fig. 3.6a). The fluctuations in salinity were greater in the mangrove stations as compared to the nearshore and offshore stations. Seasonality of salinity was pronounced with significantly higher ($p < 0.01$) value during the SW monsoon (26.8 ± 3.9 ppt; all stations combined) as compared to the NE monsoon (23.9 ± 5 ppt) and IN period (24.3 ± 4.8 ppt). There was no significant interaction effect between monsoon season and station (Table 3.2).

3.1.3.2 Temperature

Mean water temperatures at the five stations were generally similar ranging from 30 ^{o}C to 31 ^{o}C, while mean monthly temperature at station was rather consistent with <1.5 ^{o}C fluctuation during the sampling period (Fig. 3.6b). Water temperatures of both mangrove and adjacent coastal waters were not significantly different between monsoon seasons (Table 3.2).

3.1.3.3 pH

The surface pH values at all stations ranged from 6.6 to 8.2. Mean pH value of 7.2 recorded at the upper estuary increased to 8.0 in offshore waters. pH values were significantly lower (ANOVA, $p < 0.01$) and more variable in the mangrove stations as compared to the nearshore and offshore stations. Although the mean pH values between seasons were almost similar, ANOVA results showed that the SW monsoon (7.7) had significantly higher ($p < 0.01$) pH value than that of the NE monsoon (7.6). No interaction effect was detected between monsoon season and station (Table 3.2).

3.1.3.4 Dissolved oxygen (DO) concentrations

Surface dissolved oxygen (DO) concentrations fluctuated between 2.5 mg l^{-1} and 7.9 mg l^{-1} (Table 3.2). Mean DO concentrations increased in the offshore direction with significantly highest mean at the offshore station (6.0 ± 0.61 mg l^{-1}). The lowest mean DO concentration was recorded during the NE monsoon (4.8 ± 1.5 mg l^{-1}) (Table 3.2). Nevertheless, depletion of DO concentration to minimal level was not detected with the onset of the NE monsoon but in the later part of the NE monsoon (Fig. 3.6d).

3.1.3.5 Turbidity

Mean turbidity showed the highest at the lower estuary with mean of 35.6 NTU, and generally decreased in both upstream and offshore directions. The clearest water was observed in offshore waters (15.2 NTU). Peak turbidity was observed in the mangrove stations in January 2003 (Fig. 3.6). Turbidity was significantly different between monsoon seasons (ANOVA, $p < 0.01$). Nevertheless, the values tended to fluctuate greatly over the sampling period (Table 3.2). The waters measured during the NE monsoon were more turbid than that of the SW monsoon due to high turbidity values recorded in the mangrove stations in January 2003 (Fig. 3.6e).

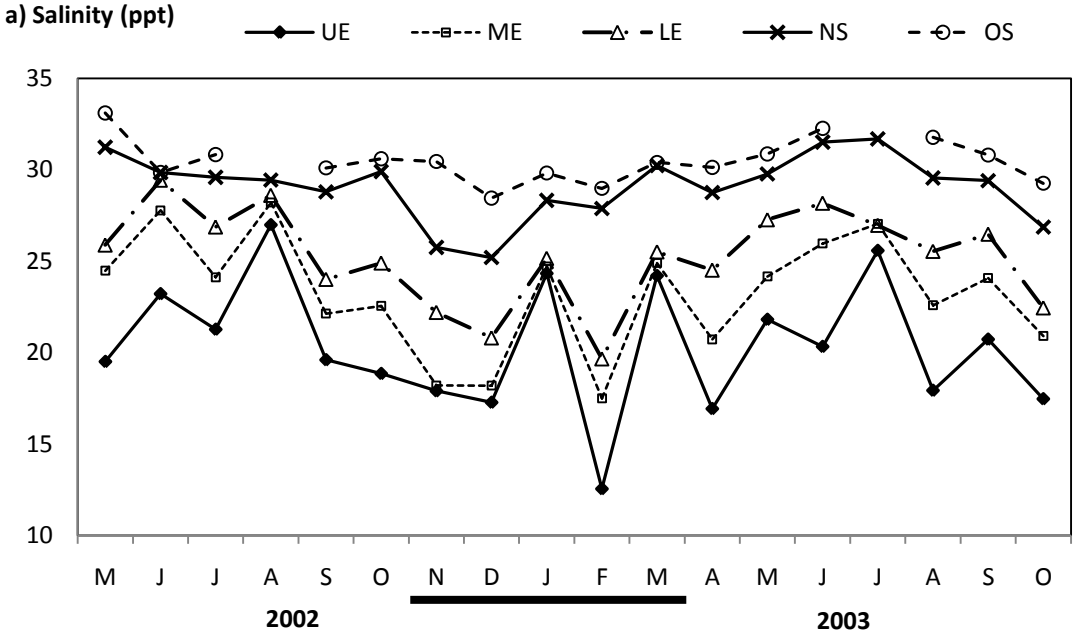
Table 3.2. Summary results of two-way ANOVA and post-hoc Tukey HSD tests on various environmental variables with respect to station, season and their interaction. $\bar{x}$ = mean; n = sample size; Min = minimum, Max = maximum; stations: UE = upper estuary, ME = mid-estuary, LE = lower estuary, NS = nearshore waters, OS = offshore waters; season: SW = Southwest monsoon, IN = inter-monsoon period, NE = Northeast monsoon; homogenous groups indicated by superscripts a, b, c and d; * significance at $p < 0.05$, ** significance at $p < 0.01$.

Variable		Source of Variation										
		Station						Season				Station x Season
		UE	ME	LE	NS	OS	p-level	SW	IN	NE	p-level	p-level
Salinity (o/oo)	$\bar{x}$	20.4[a]	23.2[b]	25.2[c]	29.1[d]	30.5[d]	<0.001**	26.8[a]	24.3[b]	23.9[b]	<0.001**	0.194
	± SD	3.75	3.26	2.7	1.82	1.18		3.9	4.8	5		
	n	36	36	36	36	32		96	30	50		
	Min	12.2	17.1	19.7	25	28.4		16.4	14.4	12.2		
	Max	27.9	29	31.5	31.7	33.6		33.6	30.7	30.7		
Temperature (^{o}C)	$\bar{x}$	30.8[a]	30.9[a]	30.8[a]	30.3[a]	30.5[a]	0.037*	30.5	30.7	30.9	0.069	0.810
	± SD	0.98	0.85	1.08	0.8	0.82		0.9	1.2	0.8		
	n	36	36	36	36	32		96	30	50		
	Min	29	29	28.7	29.1	29.1		28.7	29	29.3		
	Max	33.6	32.9	32.4	31.7	31.9		32.9	33.6	32.4		
pH	$\bar{x}$	7.2[a]	7.5[b]	7.6[c]	7.9[d]	8.0[d]	<0.001**	7.7[a]	7.7[a,b]	7.6[b]	0.002**	0.198
	± SD	0.3	0.22	0.18	0.08	0.08		0.3	0.4	0.4		
	n	36	36	36	36	32		96	30	50		
	Min	6.6	7.2	7.3	7.8	7.9		6.9	6.9	6.6		
	Max	8	8	8.2	8.2	8.2		8.2	8.1	8.2		
DO (mg l^{-1})	$\bar{x}$	4.8[a]	5.2[a,b]	5.6[b,c]	6.0[c]	6.0[c]	<0.001**	5.8[a]	6.0[a]	4.8[b]	<0.001**	0.115
	± SD	1.47	1.19	1.12	0.75	0.61		0.9	0.8	1.5		
	n	35	36	36	36	32		95	30	50		
	Min	2.3	1.9	2	4.4	4.8		3.3	4.3	1.9		
	Max	9.6	7.8	8	8	7.3		9.6	7.9	8		

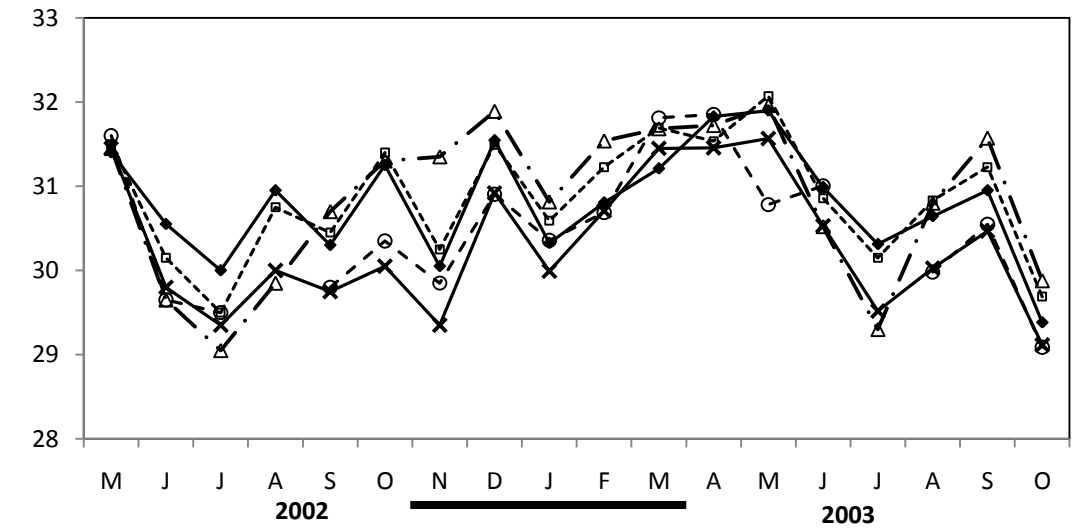
Table 3.2, continued

Variable		Source of Variation										
		Station						Season				Station x Season
		UE	ME	LE	NS	OS	p-level	SW	IN	NE	p-level	p-level
Turbidity (NTU)	$\bar{x}$	29.9 [a]	30.9 [a]	35.6 [a]	28.5 [a]	15.2 [b]	0.005**	20.1 [a]	27.1 [a]	45.4 [b]	0.001**	0.770
	± SD	38.5	43.9	71.2	22.5	14.3		15.5	32.3	72.8		
	n	36	36	36	36	31		96	30	49		
	Min	5.4	6.4	1.6	4	1.9		1.6	2.2	5.4		
	Max	205.6	229.8	436.4	81.6	63.2		81	154.3	436.4		
chl. *a* ($\mu g\ l^{-1}$)	$\bar{x}$	21.0 [a]	20.2 [a]	22.8 [a]	12.3 [b]	9.2 [b]	<0.001**	14.3 [a]	11.5 [a]	25.4 [b]	<0.001**	0.196
	± SD	15.5	19.6	21.8	7.2	4.6		8.5	5.5	24.5		
	n	32	32	32	32	28		76	30	50		
	Min	5.3	7.5	6.8	5	4.9		4.9	5	5.3		
	Max	73.4	93.9	94.2	31.8	28.9		50.8	25.7	94.2		
$NO_2^-+NO_3^-$ (μM)	$\bar{x}$	7.08 [a]	5.67 [a,b]	4.66 [a,b]	4.22 [b]	4.14 [b]	0.005**	3.89 [a]	5.89 [b]	6.64 [b]	<0.001**	0.600
	± SD	5.38	4.75	3.19	2.22	2.27		2.21	5	4.58		
	n	31	32	32	32	28		75	30	50		
	Min	2.5	1.5	0.75	1	0.27		0.27	1	1.79		
	Max	26.43	20.57	14	9.94	10.83		12.86	26.43	20.57		
NH_4^+ (μM)	$\bar{x}$	3.10 [a]	2.45 [a,b]	1.26 [b]	1.84 [a,b]	1.31 [a,b]	0.038*	2.42 [a,b]	2.2 [b]	1.45 [a]	0.022*	0.991
	± SD	3.39	2.56	1.38	2.01	1.4		3.1	1.51	1.5		
	n	29	28	27	27	22		61	26	46		
	Min	0.16	0.16	0.08	0.27	0.14		0.14	0.71	0.08		
	Max	13.57	10	5	9.29	5.71		13.57	7.14	5.71		
PO_4^{3-} (μM)	$\bar{x}$	1.59	1.02	1.42	1.47	1.2	0.875	1.07	1.58	1.59	0.078	0.895
	± SD	1.99	0.79	1.29	1.35	1.19		1.04	1.49	1.63		
	n	29	32	31	29	28		72	27	50		
	Min	0.11	0.11	0.11	0.11	0.08		0.08	0.21	0.11		
	Max	7.58	3.16	4.88	5.58	4.32		5.58	7.37	7.58		

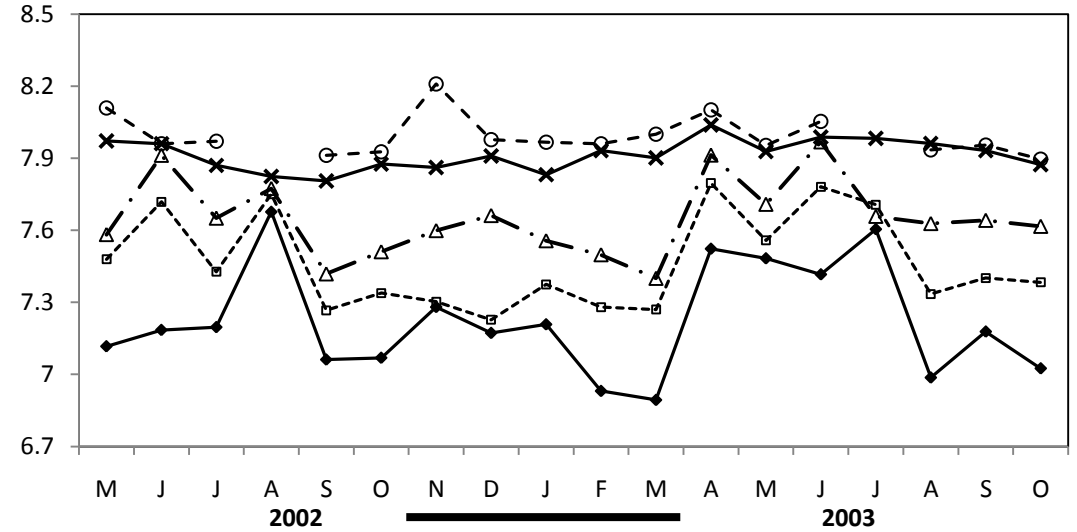
a) Salinity (ppt)



b) Temperature (°C)



c) pH



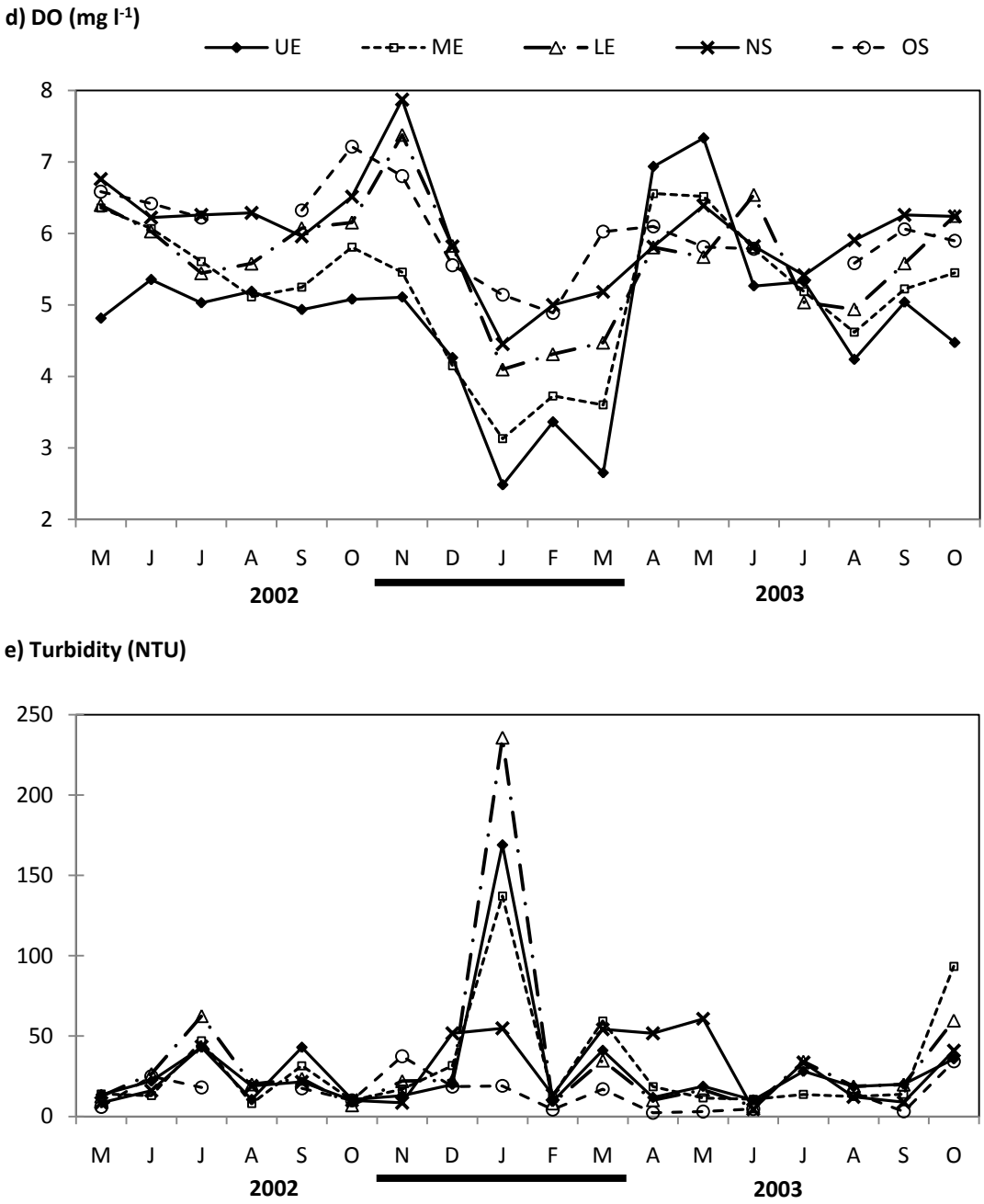


Fig. 3.6. Monthly mean of hydrographic conditions (SD not shown) at five sampling stations from May 2002 to October 2003. Horizontal bar indicates Northeast monsoon. Stations: UE = upper estuary; ME = mid-estuary; LE = lower estuary; NS = nearshore waters; OS = offshore waters.

3.1.4 Dissolved inorganic nutrients

Monthly mean concentrations of dissolved inorganic nutrients are shown in Fig. 3.7. At all stations, concentrations of nitrite + nitrate (NO_2^- + NO_3^-), ammonium (NH_4^+) and phosphate (PO_4^{3-}) ranged from 0.27 - 26.43 µM, 0.08 - 13.57 µM and 0.08 - 7.58 µM respectively (Table 3.2). NO_2^- + NO_3^- concentration was significantly higher (ANOVA, $p < 0.01$) in the upper estuary and its concentration declined in the offshore direction. Mean NH_4^+ showed the lowest at the lower estuary while the highest concentration was measured at the upper estuary. PO_4^{3-} did not differ significantly between stations (ANOVA, $p > 0.05$). Concentrations of dissolved inorganic nitrogen (NO_2^- + NO_3^- and NH_4^+) were significantly affected by seasonal monsoons (ANOVA, $p < 0.05$). Tukey HSD test showed that the wetter IN period and NE monsoon had significantly higher NO_2^- + NO_3^- concentration as compared to that of SW monsoon (ANOVA, $p < 0.001$). However, the lowest NH_4^+ was recorded during the NE monsoon. Seasonality differences in PO_4^{3-} were not significant (ANOVA, $p > 0.05$) (Table 3.2). Notwithstanding, maximum PO_4^{3-} was recorded in the upper estuary station in December 2002, coinciding with the month of severely-wet precipitation (Fig. 3.7 and see Fig. 3.5).

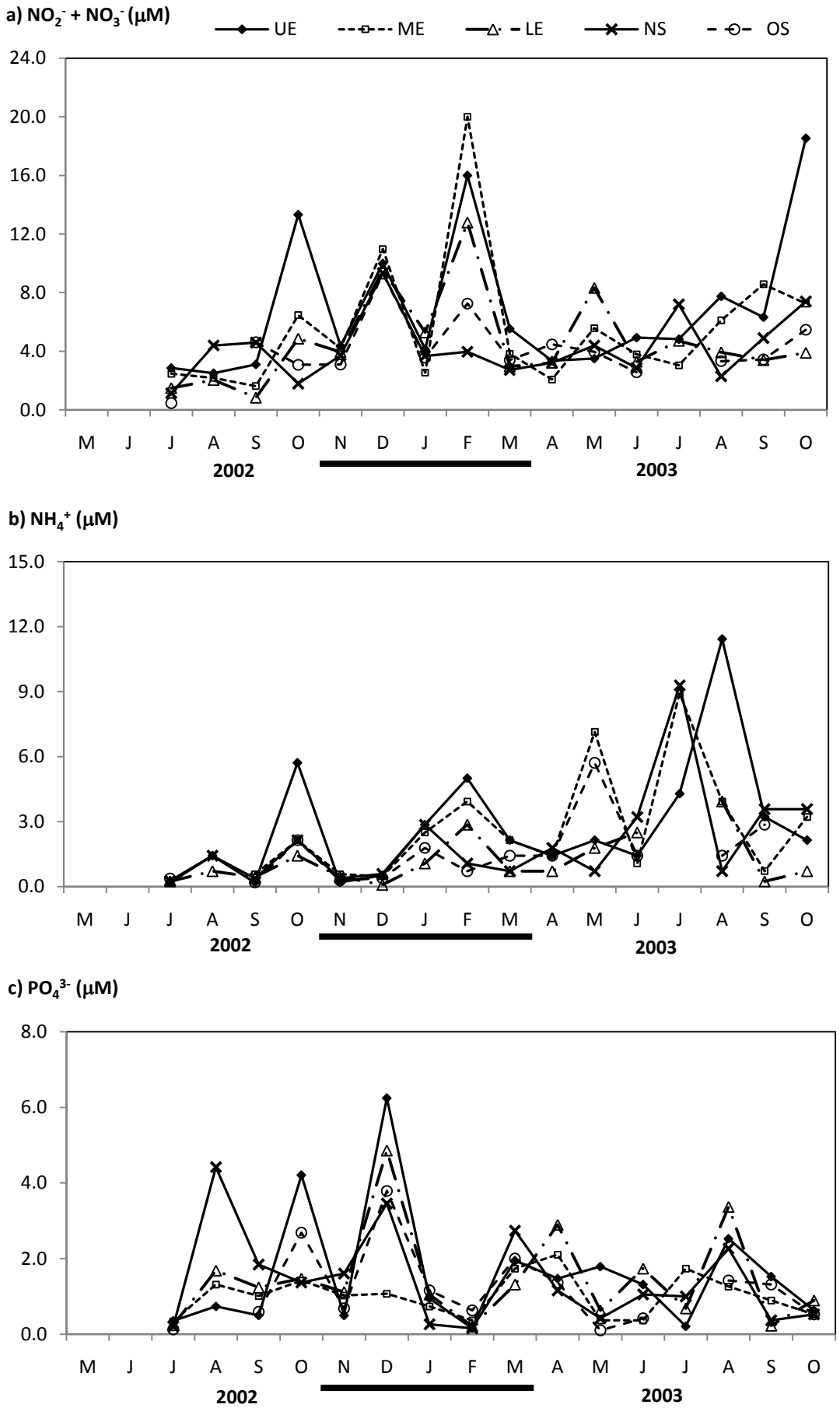


Fig. 3.7. Monthly mean of dissolved inorganic nutrients at five sampling stations from July 2002 to October 2003. Horizontal bar indicates Northeast monsoon.

3.1.5 Chlorophyll *a* concentrations

Mean chlorophyll *a* concentration (chl. *a*) was higher in the mangrove stations (21.0, 20.2, 22.8 µg l^{-1}) than in the nearshore (12.3 µg l^{-1}) or offshore station (9.2 µg l^{-1}) (Table 3.2). After pooling the above data, the mean chl. *a* was found to be significantly higher (ANOVA, $p < 0.01$) inside the mangrove estuary (40.1 ± 21.9 µg l^{-1}) than the adjacent coastal waters (26.8 ± 7.7 µg l^{-1}), and in the NE monsoon (25.4 ± 24.49 µg l^{-1}) than in the SW monsoon (14.3 ± 8.51 µg l^{-1}) and IN period (11.5 ± 5.45 µg l^{-1}). Phytoplankton blooms apparently occurred in the mangrove estuary with a major peak in January 2003 (Fig. 3.8).

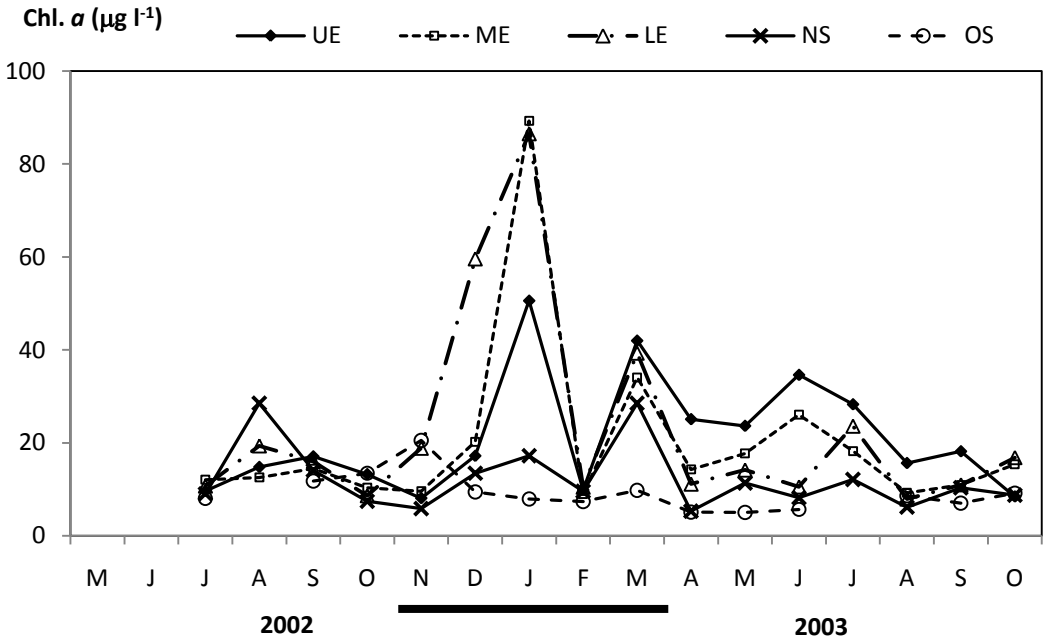


Fig. 3.8. Monthly mean of chlorophyll a concentration at five sampling stations from July 2002 to October 2003. Horizontal bar indicates Northeast monsoon.

3.1.6 Zooplankton wet biomass and abundance by size fractions

Total zooplankton biomass and density of all samples ranged from 46.1 mg m^{-3} to 2718.9 mg m^{-3} and 3,425 ind m^{-3} to 469,666 ind m^{-3}, respectively (Tables 3.3 and 3.4). The spatial patterns in total biomass and numerical abundance were significantly different among stations (ANOVA, $p < 0.001$). Mean values of total biomass and

density increased progressively from the upper estuary through mid- and lower estuary to nearshore and decreased further offshore (Tables 3.3 and 3.4).

Zooplankton biomass in mangrove stations largely composed of large-sized zooplankton (500 µm fraction) whereas medium-sized zooplankton (250 µm fraction) dominated the nearshore and offshore waters. Small-sized zooplankton (125 µm fraction) contributed a small proportion (<22%) to the wet biomass across all sampling stations (Table 3.3). In terms of numerical abundance, medium-sized zooplankton was by far the most abundant component at all sampling stations followed by small-sized zooplankton except for the nearshore station where large-sized zooplankton were on average more numerous than small-sized zooplankton (Table 3.4).

ANOVA results revealed a significant seasonal difference in total biomass and abundance, respectively ($p < 0.05$). Mean values of total biomass and abundance were highest during the IN period as compared to SW and NE monsoons. This was due to the exceptional peak biomass and abundance of medium- and large-sized zooplankton in October 2002 and 2003 particularly in nearshore waters (Figs. 3.9 and 3.10). Although significantly higher abundance of zooplankton occurred during the IN period, greater zooplankton abundance was also observed during the SW and NE monsoons at mid-estuary and lower estuary, and during the NE monsoon at upper estuary (Fig. 3.10).

Results of Pearson's correlation (r) between zooplankton wet biomass and abundance for each station are shown in Table 3.5. Total and all size fractions wet biomasses were very highly positively correlated with their respective abundance across all stations ($p < 0.01$) except for the small-sized zooplankton in nearshore and offshore waters. Although the correlation of small-sized zooplankton in nearshore waters was significant ($p < 0.05$), the r value (0.4) obtained at this station was much lower than

Table 3.3. Net zooplankton biomass: summary results of two-way ANOVA and post-hoc Tukey HSD tests on total and size fraction biomasses of zooplankton, with respect to station, season and their interaction. $\bar{x}$ = mean; n = sample size; stations: UE = upper estuary, ME = mid-estuary, LE = lower estuary, NS = nearshore waters, OS = offshore waters; season: SW = Southwest monsoon, IN = inter-monsoon period, NE = Northeast monsoon; Min = minimum, Max = maximum; homogenous groups indicated by superscripts a, b, c and d; * significance at $p < 0.05$, ** significance at $p < 0.01$, ns no significance.

Size fraction		Source of Variation										
		Station (1)						Season (2)				Interaction
		UE	ME	LE	NS	OS	p-level	SW	IN	NE	p-level	(1) x (2)
	n	36	36	36	36	32		96	30	50		p-level
500 µm	$\bar{x}$	246.5 [a]	350.5 [a,b]	344.6 [b]	312.8 [b]	220.8 [a,b]	*	276.7	485.1	222.2	ns	ns
	± SD	393.4	364.0	322.2	213.3	152.1		231.3	524.2	203.6		
	Min	6.8	6.5	69.3	55.1	24.4		7.3	10.1	6.5		
	Max	2204.8	1281.6	1167.9	1040.3	624.4		1281.6	2204.8	1123.8		
250 µm	$\bar{x}$	142.8 [a]	188.0 [a,b]	233.0 [b,c]	398.8 [d]	396.8 [c,d]	**	234.0 [a]	399.7 [b]	257.9 [a,b]	**	ns
	± SD	152.9	189.5	185.7	241.1	329.7		237.5	349.6	151.9		
	Min	11.8	9.4	41.7	18.5	65.6		11.8	46.8	9.4		
	Max	741.0	986.6	881.6	1031.4	1432.6		1432.6	1072.2	608.1		
125 µm	$\bar{x}$	85.3 [a]	114.9 [a,b]	150.5 [b,c]	193.0 [c]	157.7 [b,c]	**	101.7 [a]	213.2 [b]	169.1 [b]	**	ns
	± SD	70.8	94.6	109.6	203.0	81.5		73.5	234.0	85.3		
	Min	9.5	20.1	17.7	9.5	55.0		9.5	28.3	30.2		
	Max	289.0	482.5	488.5	1017.9	356.8		324.9	1017.9	488.5		
Total	$\bar{x}$	474.6 [a]	653.4 [a,b]	728.0 [b,c]	904.5 [c]	775.3 [b,c]	**	612.3 [a]	1098.0 [b]	649.3 [a,b]	*	ns
	± SD	505.8	568.8	548.9	427.7	394.9		382.6	831.0	353.9		
	Min	83.1	46.1	176.6	207.8	240.6		96.2	86.5	46.1		
	Max	2535.6	2718.9	2328.6	2157.7	1874.3		1903.9	2718.9	2039.0		

Table 3.4. Net zooplankton density: summary results of two-way ANOVA and post-hoc Tukey HSD tests on total and size fraction abundances of zooplankton, with respect to station, season and their interaction. $\bar{x}$ = mean; n = sample size; stations: UE = upper estuary, ME = mid-estuary, LE = lower estuary, NS = nearshore waters, OS = offshore waters; season: SW = Southwest monsoon, IN = inter-monsoon period, NE = Northeast monsoon; Min = minimum, Max = maximum; homogenous groups indicated by superscripts a, b, c and d; * significance at $p < 0.05$, ** significance at $p < 0.01$, ns no significance.

Size fraction		Source of Variation										
		Station (1)						Season (2)				Interaction
		UE	ME	LE	NS	OS	p-level	SW	IN	NE	p-level	(1) x (2)
	n	36	36	36	36	32		96	30	50		p-level
500 µm	$\bar{x}$	3114^{a}	5436^{b}	5130^{b}	12366^{b}	$2707^{a,b}$	**	4769	14730	2492	ns	ns
	± SD	7337	7060	4892	46588	3265		6690	50902	3101		
	Min	8	53	201	203	171		8	84	8		
	Max	43048	29311	17904	280471	15199		45061	280471	15199		
250 µm	$\bar{x}$	10378^{a}	$11474^{a,b}$	$18614^{b,c}$	22530^{c}	$11013^{a,b,c}$	**	12279^{a}	21998^{a}	15630^{a}	*	ns
	± SD	15554	10372	17496	29501	8824		12894	32816	14871		
	Min	778	414	1670	389	1581		389	2520	414		
	Max	88675	45461	90086	179182	42191		90086	179182	88675		
125 µm	$\bar{x}$	$5376^{a,c}$	$9113^{a,b}$	11211^{b}	$8065^{a,b}$	3708^{c}	**	5955^{a}	8809^{b}	9966^{b}	**	ns
	± SD	4597	8904	11386	6734	3680		7596	5580	9382		
	Min	752	937	897	1356	211		211	2047	418		
	Max	19140	43660	51522	37249	14873		44901	22033	51522		
Total	$\bar{x}$	18868^{a}	$26024^{a,b}$	34955^{b}	42961^{b}	17428^{a}	**	23003^{a}	45536^{b}	$28088^{a,b}$	**	ns
	± SD	20776	20705	25040	75330	13086		20441	82747	21484		
	Min	3569	4309	5673	6080	3425		3425	6116	4465		
	Max	108565	92072	94067	469666	61123		94067	469666	108565		

those of the larger sized and total zooplankton (r > 0.7). There was no significant correlation (p > 0.05) observed for the small-sized zooplankton in offshore waters.

Table 3.5. Pearson's correlation coefficients (r) between zooplankton wet biomass and density. ** Significance at p < 0.01, * significance at p < 0.05. n = number of pairwise.

Station		500 µm	250 µm	125 µm	Total
Upper estuary	r	0.79**	0.83**	0.63**	0.72**
	n	36	36	36	36
Mid-estuary	r	0.52**	0.94**	0.77**	0.83**
	n	36	36	36	36
Lower estuary	r	0.77**	0.87**	0.76**	0.82**
	n	36	36	36	36
Nearshore waters	r	0.71**	0.83**	0.40*	0.72**
	n	36	36	36	36
Offshore waters	r	0.75**	0.52**	0.25	0.57**
	n	32	32	32	32

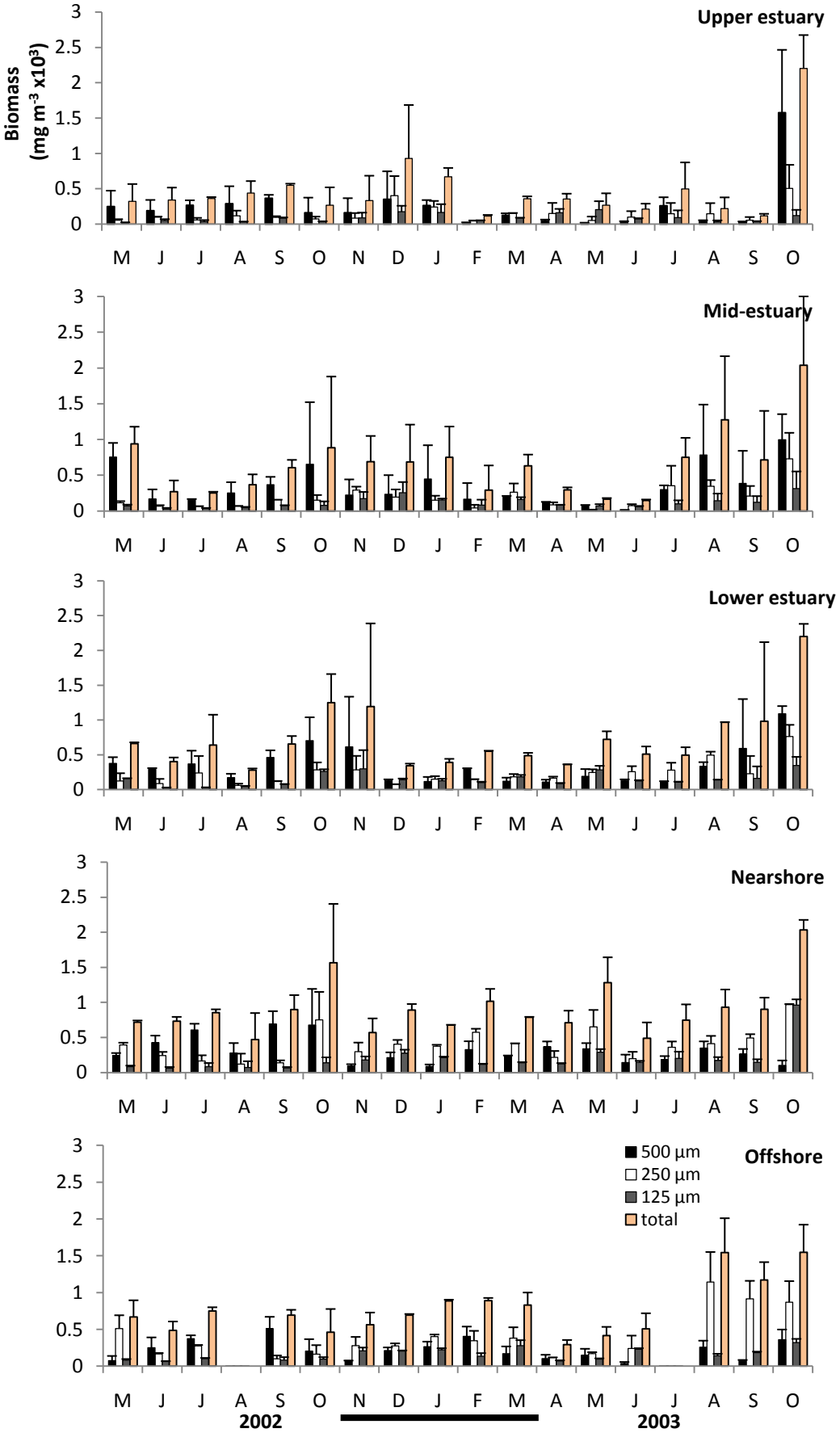


Fig. 3.9. Mean monthly zooplankton biomass recorded in Matang mangrove estuaries and adjacent coastal waters from May 2002 to October 2003. Error bars indicate SD; horizontal bar indicates Northeast monsoon.

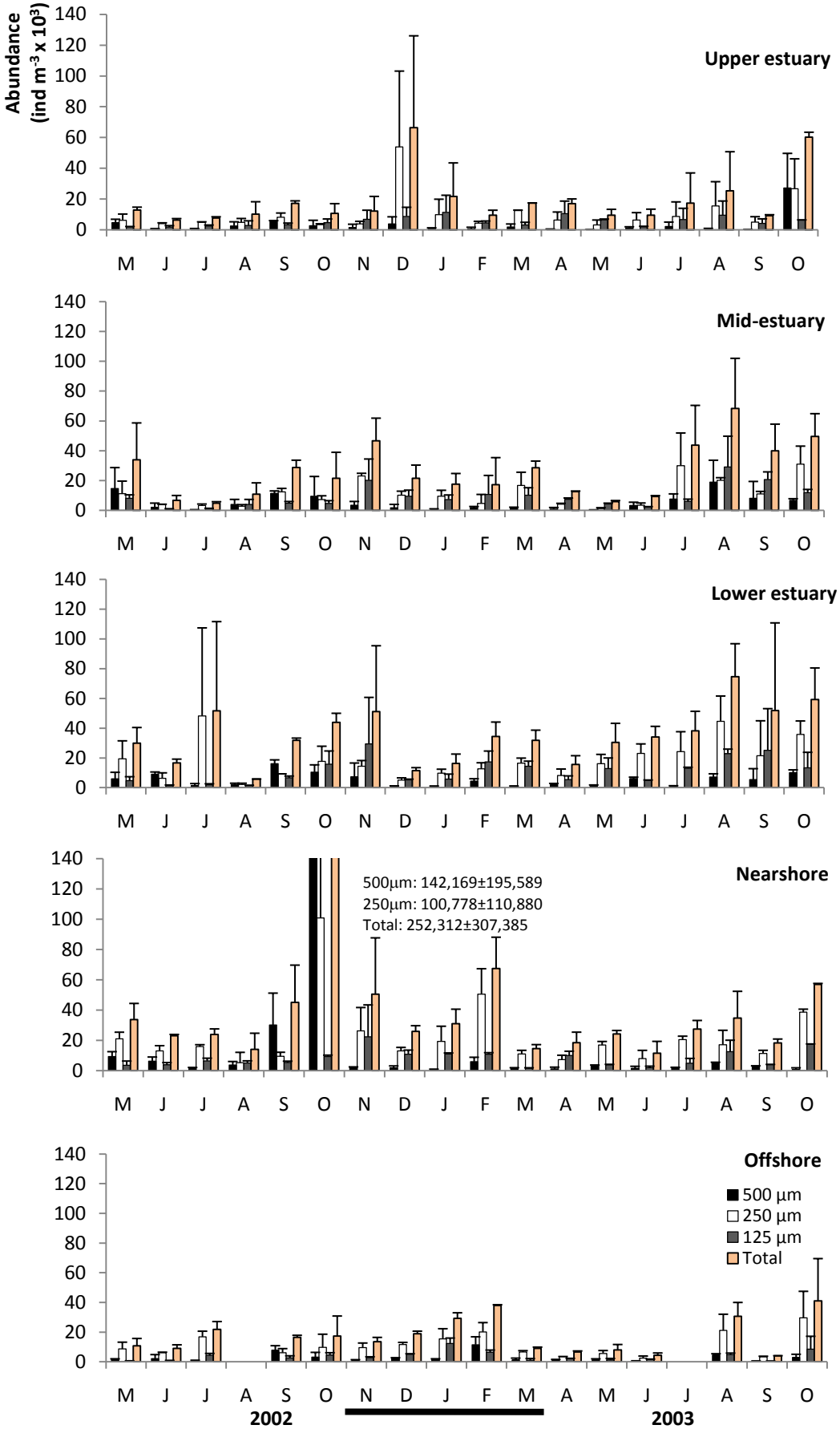


Fig. 3.10. Mean monthly zooplankton abundance recorded in Matang mangrove estuaries and adjacent coastal waters from May 2002 to October 2003. Error bars indicate SD; horizontal bar indicates Northeast monsoon.

3.1.7 Zooplankton abundance and composition by taxonomic groups

3.1.7.1 General abundance and composition

Overall mean abundance and percentage composition of the main zooplankton groups are given in Figs. 3.11and 3.12. Copepods were numerically dominant (17,467 ± 15,575 ind m^{-3}, n = 176), comprising 62% of the overall zooplankton abundance followed by cirripede larvae (18%) and both polychaete larvae and unidentified eggs (4%). Zooplankton groups that accounted for 1 - 3% of the overall abundance were protozoans, decapods, gastropods, chaetognaths, larvaceans and bryozoan larvae. Zooplankton grouped as 'others' comprised of cnidarians, ctenophores, bivalves, ophiopluteus larvae, mysids, ostracods, isopods, cumaceans, *Phoronis* larvae, nematods, amphipods, cephalopods and *Lingula* sp.. These taxa altogether represented 1% of the overall zooplankton abundance.

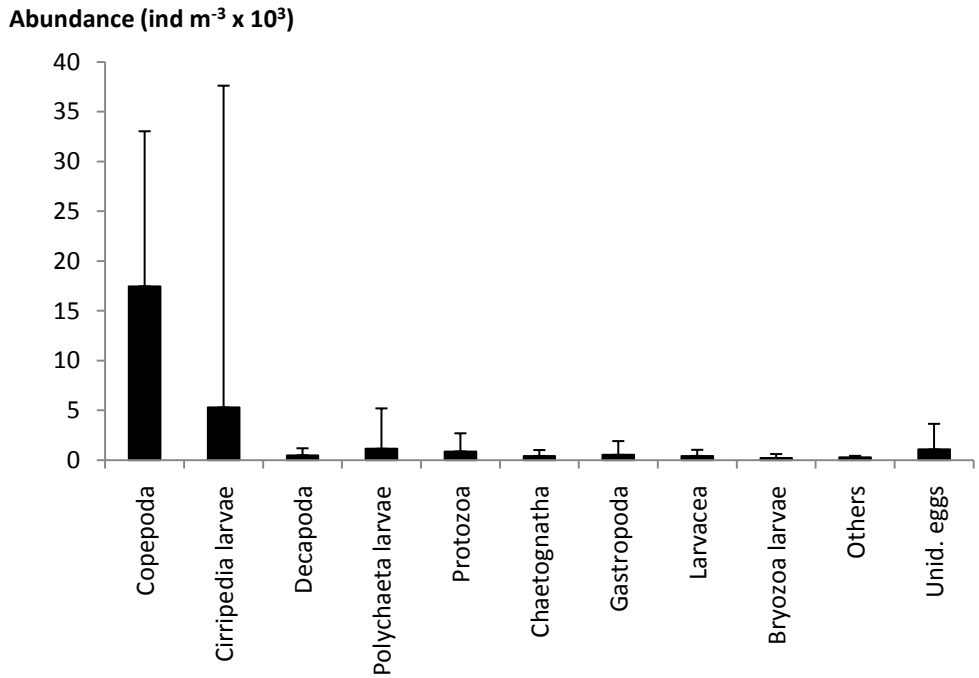


Fig. 3.11. Mean abundance of major zooplankton groups for all stations combined. Error bars indicate SD.

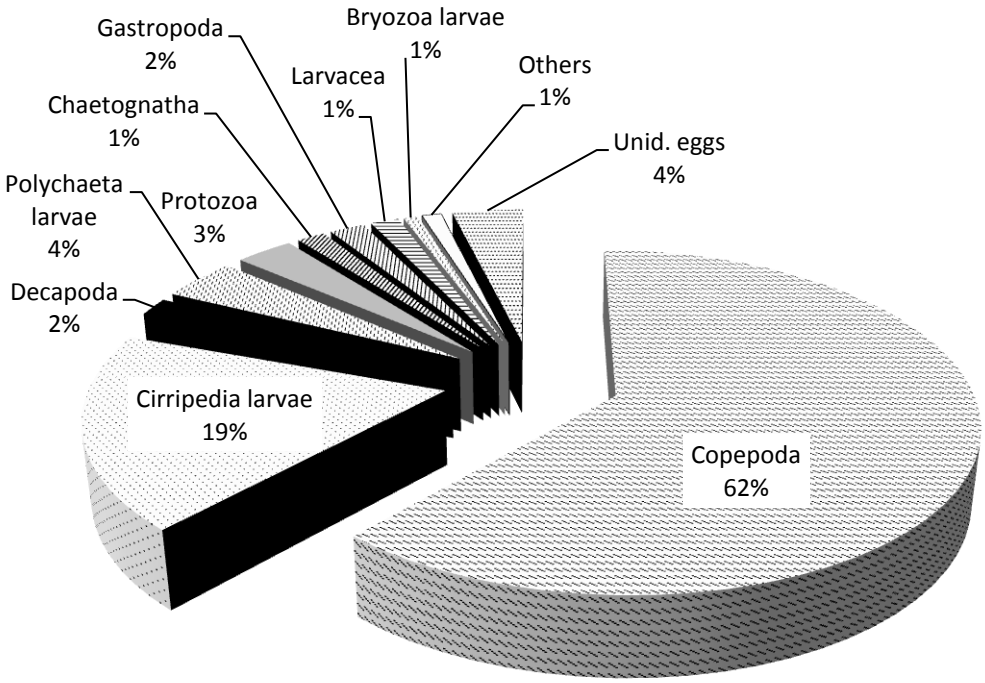


Fig. 3.12. Overall percentage composition of major zooplankton groups.

3.1.7.2 Spatial variations

a. Copepods

The spatial pattern in abundance of copepods were similar to that of total zooplankton, with mean value that increased from the upper estuary (15,572 ± 20,171 ind m^{-3}) to nearshore waters (20,311 ± 12,892 ind m^{-3}), and decreased towards offshore waters (12,330 ± 11,046 ind m^{-3}). ANOVA results indicated a significant difference in copepod abundance among sampling stations ($p < 0.05$; Table 3.6). Copepods dominated the zooplankton at all stations, accounting for 47 to 83% of the total abundance (Table 3.7). Copepods of mainly adults, collected in nearshore and offshore waters, represented 73% and 66% of the total copepod abundance respectively. Juvenile copepods (copepodid and naupliar stages) of mainly *Acartia* copepodids constituted 43% to 51% of the total copepod abundance in mangrove waters (Table 3.8).

Table 3.6. Mean abundance (ind m^{-3}), relative abundance (% Rel) and occurrence (% Occ) of main zooplankton groups sampled from the upper estuary to offshore. Stations: UE = upper estuary, ME = mid-estuary, LE = lower estuary, NS = nearshore waters, OS = offshore waters; '+' indicates present but constituted <0.1% of relative abundance; number of zooplankton groups in parentheses.

	Station														
	UE			ME			LE			NS			OS		
Taxon	$\bar{x}$	% Rel	% Occ	$\bar{x}$	% Rel	% Occ	$\bar{x}$	% Rel	% Occ	$\bar{x}$	% Rel	% Occ	$\bar{x}$	% Rel	% Occ
Copepoda	15572	83	100	18796	72	100	19759	57	100	20311	47	100	12330	71	100
Cirripedia larvae	884	5	100	2503	10	100	6239	18	100	15274	36	100	1127	6	88
Decapoda	132	1	100	147	1	100	273	1	100	1098	3	100	869	5	100
Polychaeta larvae	36	0.2	67	872	3	89	3617	10	94	854	2	100	289	2	100
Protozoa	1037	5	83	396	2	100	1243	4	100	1128	3	89	553	3	69
Chaetognatha	244	1	100	423	2	100	589	2	100	440	1	100	447	3	100
Gastropoda	72	0.4	89	86	0.3	78	662	2	100	1462	3	100	374	2	100
Bivalvia	12	0.1	67	39	0.2	61	76	0.2	78	248	1	94	137	1	100
Larvacea	81	0.4	61	184	1	94	540	2	94	699	2	100	683	4	100
Bryozoa larvae	20	0.1	61	84	0.3	94	302	1	94	509	1	89	204	1	69
Ophiopluteus larvae	33	0.2	44	30	0.1	39	32	0.1	44	288	1	89	255	1	81
Cnidaria	10	0.1	83	24	0.1	100	48	0.1	100	84	0.2	89	17	0.1	75
Ctenophora	+	+	78	+	+	89	+	+	89	+	+	44	+	+	44
Others	+ (5)	+	6-33	+ (4)	+	11-39	+ (7)	+	6-39	106 (8)	0.2	6-72	19 (5)	0.1	13-38
Egg	724	4	100	2432	9	100	1558	4	100	459	1	100	125	1	100
Total	18868	100		26024	100		34955	100		42961	100		17428	100	

Table 3.7. Summary results of parametric (two-way ANOVA and post-hoc Tukey HSD tests) and non-parametric (Kruskal-Wallis ANOVA and Man-Whitney U tests) analyses on abundance of various zooplankton taxa, with respect to station, season and their interaction (only for two-way ANOVA). $\bar{x}$ = mean; n = sample size; stations: UE = upper estuary, ME = mid-estuary, LE = lower estuary, NS = nearshore waters, OS = offshore waters; season: SW = Southwest monsoon, IN = inter-monsoon period, NE = Northeast monsoon; '^' indicates non-parametric tests; '+' present but constituted <1 ind m^{-3}; homogenous groups indicated by superscripts a, b, c and d; * significance at $p < 0.05$, ** significance at $p < 0.01$, ns no significance.

		Source of variation										
		Station (1)						Season (2)				Interaction (1) x (2)
		UE	ME	LE	NS	OS	p-level	SW	IN	NE	p-level	
Variable	n	36	36	36	36	32		96	30	50		
Total Copepods	$\bar{x}$	15572[a]	18796[a,b]	19759[a,b]	20311[b]	12330[a]	*	13819[a]	23780[b]	20686[b]	**	ns
	± SD	20171	15040	16195	12892	11046		11653	19269	17953		
Parvocalanus crassirostris	$\bar{x}$	5051	4211	4516	4043	3174	ns	3056[a]	5127[a]	5918[b]	**	ns
	± SD	9467	4196	4590	3791	3835		3233	6162	7980		
Acartia spinicauda	$\bar{x}$	1104[a]	1374[a]	1157[a]	300[a,b]	112[b]	**	532[a]	2163[b]	585[a,b]	**	ns
	± SD	3340	2872	1972	363	137		1492	4182	1285		
Acartia copepodids	$\bar{x}$	4524[a]	6129[a]	4251[a]	605[b]	313[b]	**	2626[a]	4729[b]	3487[a,b]	**	ns
	± SD	6381	5866	4329	833	485		4230	6783	4734		
Oithona simplex	$\bar{x}$	855[a]	1251[a,d]	2462[b]	5720[c]	1701[b,d]	**	1672[a]	1964[a]	4107[b]	**	ns
	± SD	1972	2268	3431	6993	2707		2551	2855	6633		
Bestiolina similis	$\bar{x}$	249[a]	275[a,b]	437[b,c]	1102[c]	607[c]	**	510	937	332	ns	ns
	± SD	471	377	484	1536	665		625	1601	576		
Euterpina acutifrons	$\bar{x}$	12[a]	63[b]	221[b]	1865[c]	1037[c]	**	365	1412	671	ns	0.0489
	± SD	37	140	333	3362	1255		639	3546	1513		
Cirripedia larvae	$\bar{x}$	884[a]	2503[b]	6239[b]	15274[b]	1127[a]	**	3582	16353	1960	ns	ns
	± SD	1521	3537	13470	69841	1665		9011	76604	2966		
Decapoda	$\bar{x}$	132[a]	147[a,b]	273[b,c]	1098[d]	869[d]	**	445[a]	407[a,b]	646[b]	**	ns
	± SD	233	189	263	1056	670		774	430	686		
^Luciferidae	$\bar{x}$	1[a]	4[b]	7[b]	113[c]	220[c]	**	40	17	144	ns	
	± SD	2	8	14	231	426		97	34	389		
^Sergestidae	$\bar{x}$	41[a]	53[a]	165[b]	527[c]	428[c]	**	238	205	260	ns	
	± SD	85	103	206	826	472		551	303	411		
^Brachyura	$\bar{x}$	74[a,b]	70[a,b,c]	35[b]	118[c]	68[a,c]	**	39[a]	92[a]	127[b]	**	
	± SD	175	132	62	162	128		82	192	168		
^Diogenidae	$\bar{x}$	+[a]	+[a]	22[a]	312[b]	124[c]	**	113	68	63	ns	
	± SD	2	1	96	373	249		276	170	176		

Table 3.7, continued

		Source of variation										
		Station (1)						Season (2)				Interaction (1) x (2)
Variable	n	UE 36	ME 36	LE 36	NS 36	OS 32	p-level	SW 96	IN 30	NE 50	p-level	
Polychaeta larvae	x̄	36 [a]	872 [b]	3617 [c]	854 [c]	289 [b,c]	**	1942 [a]	311 [b]	142 [b]	**	**
	± SD	113	2729	8064	1056	403		5358	668	198		
^Protozoa	x̄	1037 [a]	396 [a]	1243 [b]	1128 [a, b]	553 [a]	**	513 [a]	1245 [a]	1361 [b]	**	
	± SD	2840	490	1608	2022	1113		1017	2954	2032		
^Chaetognatha	x̄	244 [a]	423 [b]	589 [b]	440 [b]	447 [b]	**	348	352	628	ns	
	± SD	500	551	649	459	757		387	542	855		
^Gastropoda	x̄	72 [a]	86 [a]	662 [b]	1462 [c]	374 [b]	**	334	1387	409	ns	
	± SD	103	123	1451	2434	456		627	2947	642		
^Bivalvia	x̄	12 [a]	39 [a,b]	76 [b]	248 [c]	137 [c]	**	112	84	92	ns	
	± SD	24	72	126	335	198		229	136	183		
^Larvacea	x̄	81 [a]	184 [b]	540 [c]	699 [c]	683 [c]	**	504 [a]	550 [a]	222 [b]	**	
	± SD	157	375	605	728	736		710	528	367		
^Bryozoa larvae	x̄	20 [a]	84 [a,b]	302 [b]	509 [c]	204 [c]	**	311 [a]	87 [b]	140 [a,b]	*	
	± SD	28	126	404	629	249		484	165	234		
^Ophiopluteus larvae	x̄	33 [a]	30 [a,b]	32 [b]	288 [c]	255 [c]	**	71 [a]	37 [b]	281 [a]	**	
	± SD	152	91	84	552	440		151	126	574		
Unidentified eggs	x̄	724 [a]	2432 [a]	1558 [a]	459 [a]	125 [b]	**	940	914	1452	ns	ns
	± SD	1143	4537	2744	422	105		2588	1500	3020		

Table 3.8. Mean abundance (ind m^{-3}), relative abundance (% Rel) and occurrence (% Occ) of copepods recorded from upper estuary to offshore. Stations: UE = upper estuary, ME = mid-estuary, LE = lower estuary, NS = nearshore waters, OS = offshore waters; '+' indicates present but constituted <0.2% of relative abundance; number of taxa of grouped copepods in parentheses.

Taxon	Station														
	UE			ME			LE			NS			OS		
	x̄	% Rel	% Occ	x̄	% Rel	% Occ	x̄	% Rel	% Occ	x̄	% Rel	% Occ	x̄	% Rel	% Occ
Adult															
Parvocalanus crassirostris (Dahl F.)	4871	31.8	100	4211	22.4	100	4516	22.9	100	4043	19.9	100	3174	25.7	100
Acartia spinicauda Mori	1103	7.2	100	1374	7.3	94	1157	5.9	97	300	1.5	100	112	0.9	88
Oithona simplex Farran	843	5.5	92	1251	6.7	92	2462	12.5	100	5720	28.2	100	1701	13.8	100
Parvocalanus elegans Andronov	618	4	33	229	1.2	14	151	0.8	31	73	0.4	36	106	0.9	13
Oithona dissimilis Lindberg	569	3.7	100	568	3	100	484	2.4	86	60	0.3	19	+	+	3
Oithona aruensis Früchtl	287	1.9	97	391	2.1	94	664	3.4	100	214	1.1	69	93	0.8	22
Bestiolina similis (Sewell)	248	1.6	72	275	1.5	75	437	2.2	92	1102	5.4	92	607	4.9	100
Acartia sp. 1	175	1.1	89	774	4.1	97	394	2	97	+	+	8	+	+	6
Euterpina acutifrons (Dana)	+	+	31	63	0.3	69	221	1.1	69	1865	9.2	100	1037	8.4	97
Oithona attenuata Farran	+	+	11	+	+	14	56	0.3	25	300	1.5	78	392	3.2	91
Centropages dorsispinatus Thompson & Scott	+	+	11	+	+	25	+	+	25	326	1.6	69	123	1	69
Paracalanus aculeatus Giesbrecht							+	+	6	55	0.3	42	246	2	53
Oithona brevicornis Giesbrecht	+	+	6				+	+	6	+	+	11	228	1.9	47
Microsetella norvegica Dana	+	+	3	+	+	17	+	+	25	132	0.7	53	20	0.2	41
Corycaeus andrewsi Farran							+	+	19	118	0.6	56	121	1	75
Pseudomacrochiron sp. 1	+	+	6	+	+	17	45	0.2	36	52	0.3	33	+	+	13
Tortanus barbatus (Brady)	+	+	31	+	+	56	+	+	61	84	0.4	86	30	0.2	66
Metacalanus aurivilli Cleve	+	+	3	+	+	6	+	+	6	59	0.3	17	+	+	9
Tortanus forcipatus (Giesbrecht)	+	+	6	+	+	25	+	+	39	57	0.3	69	22	0.2	59
Harpacticoida sp. 1	+	+	14	+	+	22	84	0.4	33	+	+	22	+	+	6
Hemicyclops sp. 1	+	+	6	+	+	8	+	+	11	35	0.2	36	21	0.2	19
Acartia erythraea Giesbrecht							+	+	11	39	0.2	36	49	0.4	69
Acrocalanus gibber Giesbrecht							+	+	6	31	0.2	28	+	+	41
Other adults	+ (6)	+	3-25	+ (11)	+	3-28	+ (11)	+	3-39	54 (19)	0.3	3-56	70 (16)	0.6	3-66
% of copepod (adult)		57.2			49			54.6			72.7			66.4	

Table 3.8, continued

Taxon	Station														
	UE			ME			LE			NS			OS		
	x̄	% Rel	% Occ	x̄	% Rel	% Occ	x̄	% Rel	% Occ	x̄	% Rel	% Occ	x̄	% Rel	% Occ
Nauplius and copepodid															
Acartia spp.	4501	29.4	100	6129	32.6	100	4251	21.5	100	605	3	97	313	2.5	97
Parvocalanus spp.	881	5.8	97	1828	9.7	100	2272	11.5	100	1629	8	100	1129	9.2	100
Unidentified nauplii	710	4.6	100	566	3	100	720	3.6	100	612	3	100	448	3.6	100
Bestiolina sp.	172	1.1	69	497	2.6	83	778	3.9	92	922	4.5	92	573	4.6	91
Pseudodiaptomus spp.	172	1.1	86	278	1.5	97	279	1.4	86	110	0.5	69	86	0.7	72
Oithona spp.	95	0.6	69	163	0.9	72	323	1.6	69	131	0.6	81	75	0.6	72
Tortanus spp.	26	0.2	42	92	0.5	72	225	1.1	89	1056	5.2	97	543	4.4	94
Pontellidae spp.	+	+	19	29	0.2	47	59	0.3	53	256	1.3	89	495	4	100
Other juveniles	+ (2)	+	3-6	+ (3)	+	3-6	55 (6)	0.3	6-19	227 (7)	1.1	3-36	478 (10)	3.9	3-72
% of copepod (juvenile)		42.8			51			45.4			27.3			33.6	

Dominant species that comprised at least 5% of the total abundance or present in at least one station were *Parvocalanus crassirostris, Acartia spinicauda, Oithona simplex, Bestiolina similis* and *Euterpina acutifrons*. The small calanoid copepod *P. crassirostris* comprised 20% to 32% of the copepod population and was present in all samples collected throughout the study period (100% occurrence) (Table 3.8). *P. crassirostris* was also the most abundant species at all sampling stations except at mid-estuary and nearshore waters which were dominated by *Acartia* copepodids and *O. simplex* respectively (Fig. 3.13). Copepodids of *Parvocalanus* constituted 6% to 12% of the total abundance and were absent in only a few samples from the upper estuary. *P. crassirostris* abundance showed no significant difference among sampling stations suggesting that the euryhaline species could tolerate a wider range of salinities (Fig. 3.13). *Acartia* copepodid abundance was always higher than their adults at all stations (Table 3.8). Juvenile stages of *Acartia* were as dominant as *P. crassirostris*, but they were more confined to mangrove estuaries (ANOVA, $p < 0.01$; Table 3.6). Mean total abundance of *Acartia* copepodids (6,129 ± 5,866 ind m^{-3}) exceeded *P. crassirostris* (4,211 ± 4,196 ind m^{-3}) at mid-estuary (Tables 3.6 and 3.8). A similar distribution pattern was observed for *A. spinicauda* with higher abundance in mangrove than coastal waters (Fig. 3.13). In contrast, *O. simplex* showed preference for higher salinity water although it was sampled at all stations. The abundance of *O. simplex* was significantly higher at the river mouth to coastal stations (ANOVA, $p < 0.01$) than at the upper and mid estuaries (Table 3.6). It was more abundant than even *P. crassirostris* in nearshore waters (Fig. 3.13, Tables 3.6 and 3.8). A similar trend of distribution as *O. simplex* was also observed for *B. similis* and its juveniles (Fig. 3.13). *E. acutifrons* preferred nearshore (9%) and offshore (8%) waters more than mangrove waters (<1%) (Fig. 3.13, Table 3.8).

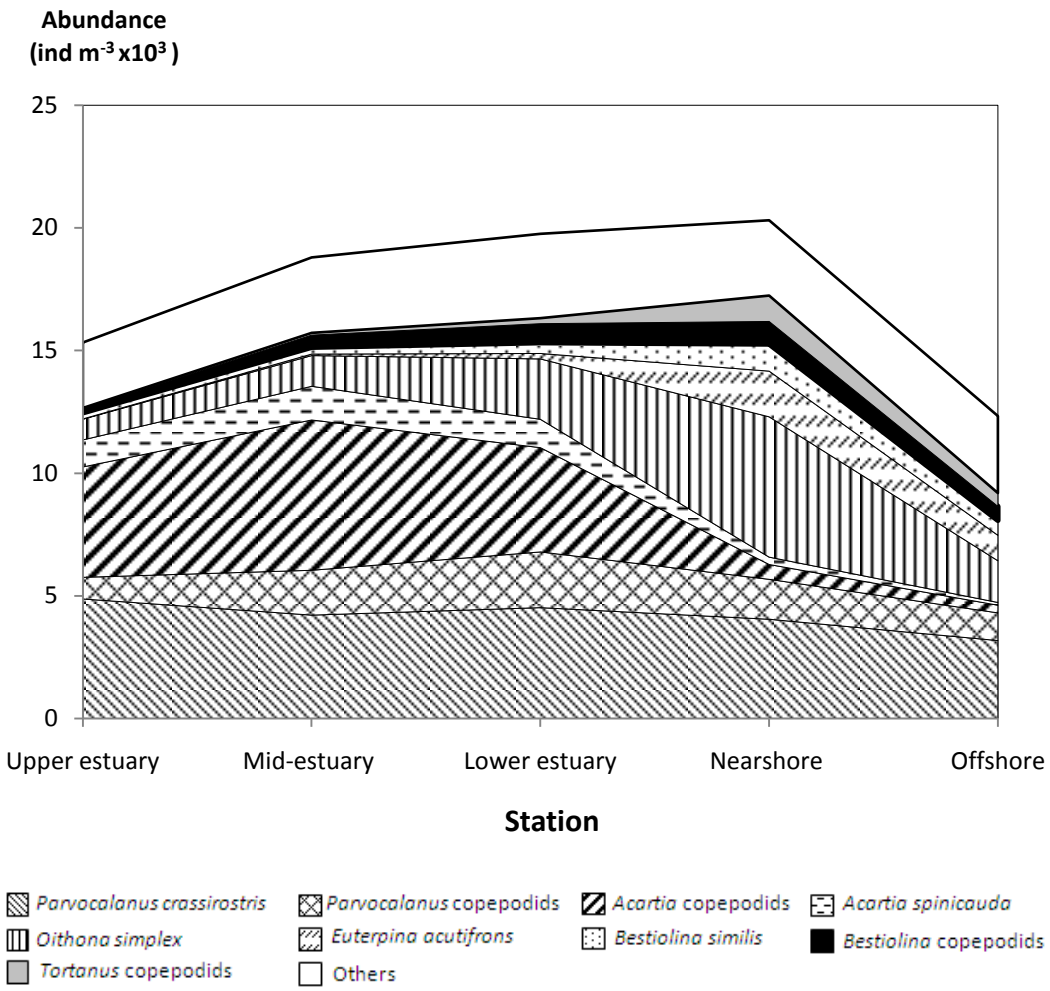


Fig. 3.13. Mean abundance of copepod species (those comprising >5% of total abundance) by sampling stations.

Tortanus barbatus (Brady) and *Tortanus forcipatus* (Giesbrecht) each constituted less than 1% of the overall copepod abundance, but copepodids of *Tortanus* comprised 5% of the total copepod abundance in nearshore waters (Fig. 3.13). *Tortanus* copepodids were frequently sampled in nearshore and offshore with >90% of occurrence (Table 3.8). Other copepods such as *Oithona dissimilis*, *Oithona aruensis*, *Acartia* sp. 1, copepodids of *Pseudodiaptomus*, *Oithona attenuata* Farran and copepodids of Pontellidae were also frequently collected. The former first four taxa were more abundant in estuarine waters whereas the Pontellidae mainly occurred in offshore waters (Table 3.8).

b. Cirripedia larvae

Cirripede larvae were the next most abundant group after copepods, representing <6% of the total zooplankton abundance in upper estuary and offshore to as high as 36% in nearshore waters (Table 3.7). Almost all cirripede larvae were captured as naupliar stages (ca. 99%) whereas cyprids were consistently sparse in all samples. The spatial abundance pattern of cirripede larvae was similar as those observed for total zooplankton and copepods, with mean value that increased from the upper estuary to nearshore waters and decreased in offshore waters. ANOVA results showed that the cirripede larvae were significantly lowest in the upper estuary ($p < 0.001$; Table 3.6).

c. Decapods

The decapods that mostly occurred as larval forms comprised ca. 1% of the total zooplankton abundance in mangrove waters and were 2 to 4% higher in nearshore and offshore waters. In terms of numerical abundance, decapods in nearshore and offshore waters were 3 to 8 times greater than in mangrove waters (ANOVA, $p < 0.001$; Tables 3.6). This was largely due to the important taxa of Sergestidae, Brachyura, Diogenidae and Luciferidae which were more abundant in adjacent coastal waters.

Sergestidae represented 48% of the total decapod abundance while Luciferidae, Brachyura and Diogenidae constituted 13 - 18% respectively. The Sergestidae and Luciferidae mostly occurred as protozoeal stages, and both were significantly more abundant in nearshore and offshore waters as compared to mangrove waters (Kruskal-Wallis ANOVA, $p < 0.001$). The adults of Sergestidae represented by the genus *Acetes* were rare in the surface waters. Conversely, the adults of Luciferidae represented by *Lucifer hanseni* Nobili were commonly captured at the surface water at all stations (66% - 100% occurrence). Interestingly, *Lucifer* was present only as adults at the upper estuary. Diogenid zoeae were also significantly more abundant in nearshore and

offshore waters as compared to that in mangrove waters (Kruskal-Wallis ANOVA, $p < 0.001$). Diogenid zoeae were present in all nearshore samples (100% occurrence) and only absent in few samples from offshore waters (88% occurrence). However, these larvae rarely occurred in the mangrove waters (<33% occurrence). Brachyuran zoeae were most abundant at nearshore station (118 ± 162 ind m^{-3}). However, these larvae were commonly captured at all sampling stations (>88% occurrence; Tables 3.6 and 3.9). Other taxa that were not regularly captured throughout the sampling period included the larvae of penaeids and carideans. The abundance and occurrence of penaeid larvae were relatively higher in the lower estuary and towards offshore compared with the upper and mid estuaries. Penaeid larvae were captured mainly as naupliar stages (Table 3.9). As opposed to penaeid prawns, the carideans mainly of Alpheidae were more abundant in mangrove waters than in nearshore and offshore. Porcellanid zoeae were commonly encountered over the sampling period but occurred in very few numbers. The larvae of Thalassinidae and Polychelidae were present only in one sample throughout the monthly sampling period.

d. Non-crustacean zooplankton

The polychaetes composed largely of larval stages were most abundant at the lower estuary with mean values that decreased in both the upstream and seaward directions (ANOVA, $p < 0.001$; Table 3.6). At lower estuary, polychaetes ranked third in abundance after copepods and cirripede larvae, comprising 10% of the total zooplankton abundance. However, very few larvae were found in the upper estuary (Table 3.7). The larvae of the families Sabellariidae and Spionidae were most abundant, comprising 96% of the overall polychaete abundance. The holoplanktonic polychaete *Tomopteris* was rarely captured over the sampling period and occurred only in nearshore and offshore samples (see Table 3.10).

Table 3.9. Mean abundance (ind m^{-3}), relative abundance (% Rel) and occurrence (% Occ) of decapods recorded from upper estuary to offshore. Stations: UE = upper estuary, ME = mid-estuary, LE = lower estuary, NS = nearshore waters, OS = offshore waters; '+' indicates present but constituted <0.1% of relative abundance; number of taxa of grouped decapods in parentheses.

Taxon	Life stage	Station														
		UE			ME			LE			NS			OS		
			% Rel	% Occ		% Rel	% Occ		% Rel	% Occ		% Rel	% Occ		% Rel	% Occ
Acetes	protozoea	36	27.8	52.8	46	31.5	55.6	163	59.8	80.6	525	47.9	100.0	423	49.1	96.9
	juvenile	3	2.6	22.2	6	4.0	38.9	2	0.6	25.0	2	0.2	19.4	6	0.7	31.3
								+			+					
	Adult	1 (3)	1.1	8-20	1 (3)	0.4	5-8	(2)	+	3.0	(1)	+	3.0			
Lucifer	protozoea				1	0.8	11.1	1	0.5	5.6	64	5.9	50.0	162	18.9	68.8
	juvenile				+	+	11.1	1	0.3	25.0	33	3	75.0	32	3.8	75.0
	adult	1	0.7	50.0	3	2.3	86.1	4	1.6	80.6	16	1.5	88.9	25	3.0	87.5
Diogenidae	zoea	0.36	0.3	5.6	0.141	0.1	2.8	22	7.9	16.7	312	28.5	94.4	124	14.4	78.1
	Juvenile				+	+	8.3	+	+	5.6	+	+	8.3	+	+	25.0
Brachyuran	zoea	74	57.3	69.4	70	47.9	80.6	34	12.4	75.0	118	10.7	88.9	68	7.9	84.4
	megalopa	+	+	2.8				1	0.2	5.6	+	+	5.6	+	+	12.5
	juvenile	+	+	2.8	+	+	8.3	+	+	5.6	+	+	11.1	+	+	6.3
Caridean																
Alpheidae	zoea	10	7.6	77.8	12	8.5	88.9	13	4.6	83.3	4	0.3	69.4	4	0.5	75.0
Palaemonidae	zoea	1	1.1	41.7	2	1.3	41.7	5	2	38.9	2	0.1	33.3	+	+	18.8
Penaeidae	Nauplius	2	1.4	5.6	4	2.8	8.3	24	8.9	16.7	15	1.4	8.3	9	1.1	12.5
	Protozoea	+	+	2.8				2	0.6	5.6	2	0.2	8.3	1	0.1	21.9
	mysis										1	0.1	13.9	3	0.4	15.6
	post-larva				+	+	2.8							+	+	6.3
Porcellanidae	zoea	0.3	0.2	38.9	1	0.4	63.9	1	0.4	41.7	1	0.1	22.2	2	0.2	25
Thalassinidae	zoea													+	+	3.1
Polychelidae larvae														+	+	3.1

The remaining groups were protozoans, chaetognaths, gastropods, bivalves, larvaceans, bryozoan larvae, ophiopluteus larvae, cnidarians and ctenophores altogether making up 5 - 15% of the total zooplankton abundance (Table 3.7). Chaetognaths were present in all samples with occurrence of 100% (Table 3.7). The chaetognaths were relatively equal in abundance across sampling stations except for the lowest mean abundance at upper estuary station (Kruskal-Wallis ANOVA, $p < 0.01$; Table 3.6). For protozoans, there was no clear spatial pattern in abundance along the gradient from the upper estuary to offshore waters. The only significant lower mean value was observed at mid-estuary (Kruskal-Wallis ANOVA, $p < 0.01$; Table 3.6). The protozoans were mainly represented by *Favella*, *Tintinnopsis* and *Noctiluca* while foraminiferans were rare over the sampling period (see Table 3.10; pg. 89). Gastropods, bivalves, larvaceans, larvae of bryozoans and ophiopluteus were mainly sampled in lower estuary and towards offshore compared with the upper and mid estuaries (Kruskal-Wallis ANOVA, $p < 0.01$; Table 3.6). Although the cnidarians and ctenophores were consistently found in few numbers (<0.2%), these taxa occurred regularly in the mangrove waters throughout the study period (occurrence >78%; Table 3.7).

e. Unidentified eggs

Unidentified eggs constituted 4 to 9% of the total zooplankton abundance in mangrove waters but made up just 1% in nearshore and offshore waters (Table 3.7). The unidentified eggs were least abundant at offshore station (ANOVA, $p < 0.001$; Table 3.6).

3.1.7.3 Seasonal variations

a. Copepods

Monthly mean density of copepods at the 5 stations ranged from 3,030 ind m^{-3} to 62,650 ind m^{-3}, with the lowest density recorded at mid-estuary in May 2003 and the highest at upper estuary in December 2002 (Fig. 3.14). The abundance of copepods was significantly higher (ANOVA, $p < 0.001$) during IN period and NE monsoon, which experienced a higher rainfall (Table 3.6, see also Fig. 3.5). Seasonal variation in copepod abundance was distinctly observed at upper estuary with two large peaks in December 2002 and October 2003 (Fig. 3.14) that coincided with the period of heaviest rainfall. Upper estuary copepods sampled monthly rarely exceeded 20,000 ind m^{-3} but densities in these months were much higher at ca 60,000 ind m^{-3} (Fig. 3.14). Multiple peaks in abundances were also observed at mid-estuary and offshore during the IN period and NE monsoon particularly in November 2002, February 2003 and October and copepodids varied seasonally and were significantly more abundant (ANOVA, $p < 0.001$) during the wetter periods of IN and NE monsoon (Fig. 3.14, Table 3.6). The coastal species, *O. simplex*, was also significantly more abundant (ANOVA, $p < 0.01$) during the NE monsoon particularly in November 2002 and February 2003 (Fig. 3.14, Table 3.6). The abundance of *E. acutifrons* and *B. similis* was not significantly affected by seasonal monsoon (ANOVA, $p > 0.05$). No significant interaction effects (ANOVA, $p > 0.05$) between station and monsoon period were detected for dominant copepod abundances except *E. acutifrons* with marginally significant interaction effect (ANOVA, $p = 0.0486$; Table 3.6).

b. Cirripede larvae

Monthly mean abundance of cirripede larvae ranged from 0 to 214,269 ind m^{-3}, with no specimen sampled in April and May 2003 offshore. Cirripede larval abundance peaked in October 2002 in nearshore waters. Mean abundance of cirripede larvae

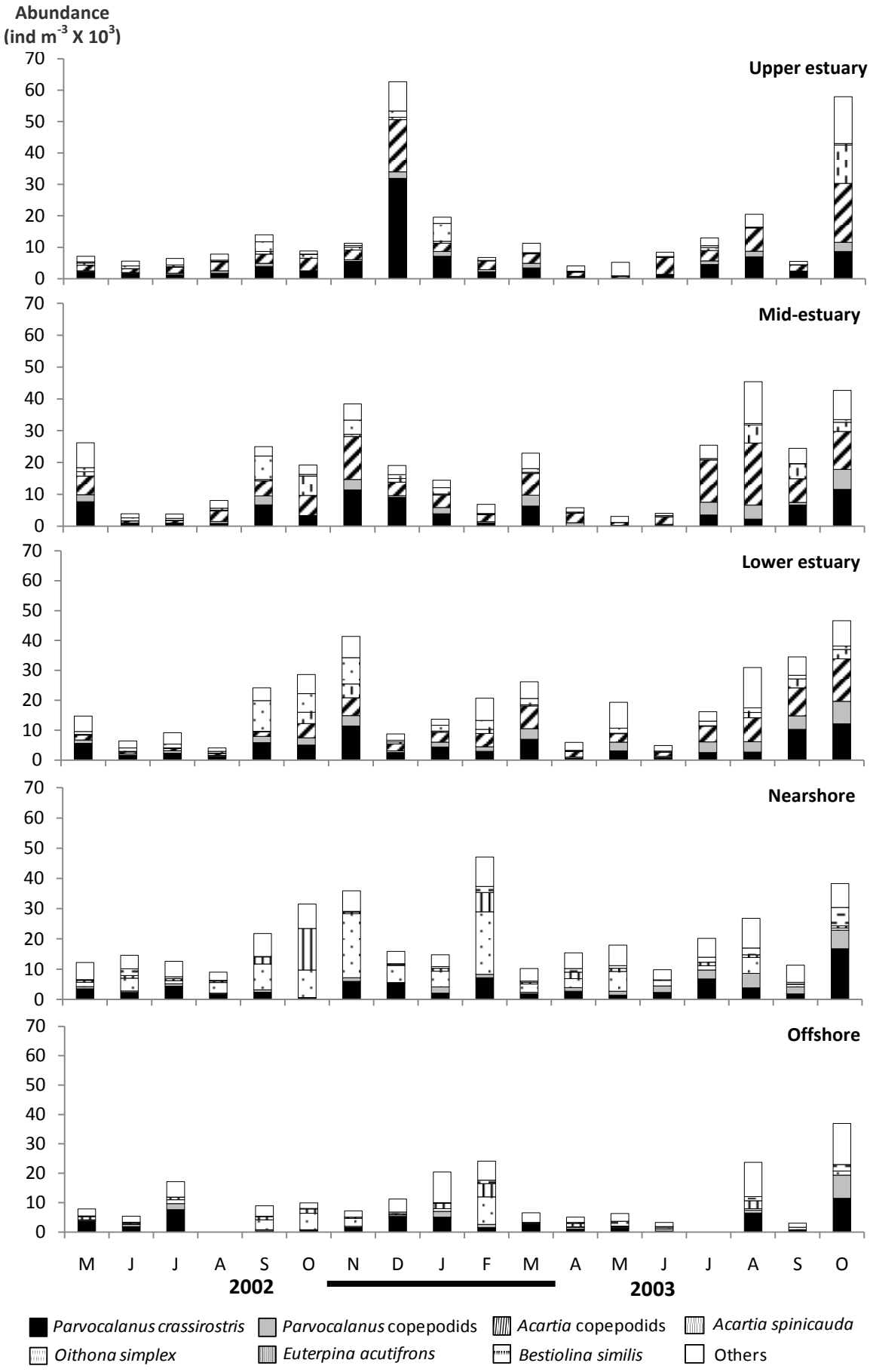


Fig. 3.14. Monthly composition of major copepod taxa by station, from May 2002 to October, 2003. Only the five most abundant taxa of each station are shown. 'Others' grouped the remainder species. Horizontal bar indicates Northeast monsoon; error bar not shown.

during the IN period was 4 and 8 times greater than the SW and NE monsoon respectively (Table 3.6). However, ANOVA results did not show significant seasonality on the pooled abundance data of cirripede larvae (ANOVA, $p > 0.05$). Other than the above-mentioned strong peak abundance, large numbers of cirripede larvae also occurred randomly over the sampling period. It was noted that the cirripede larvae appeared to be more numerous than the copepods in July 2002 at lower estuary, and in May and October 2002 at nearshore waters, and made up 75%, 44% and 88% of zooplankton abundance respectively (Figs. 3.15 and 3.16).

c. Decapods

The abundance of decapods was significantly higher during the NE monsoon as compared to IN period and SW monsoon (ANOVA, $p < 0.01$; Table 3.6). However, the maximum abundance of decapods was attained in September 2002 at nearshore waters due to the presence of large quantities of sergestid protozoeae (Fig. 3.17). In general, the lowest number of decapods always coincided with the SW monsoon in all sampling stations (Fig. 3.17).

Kruskal-Wallis ANOVA test performed on the abundance data of the four most abundant decapod taxa revealed that significant seasonality was only observed for the brachyuran larvae (Table 3.6). With few exceptions, higher number of brachyuran larvae generally coincided with the NE monsoon whereas the lowest number was observed during the SW monsoon (Fig. 3.17). Despite there was no significant seasonality in abundance of *Lucifer*, the highest abundance was recorded in February 2003 in coastal waters (Fig. 3.17). In nearshore waters, diogenids occurred in greater numbers between May and September 2002 and 2003 as compared to the rest of the sampling months. In contrast, higher numbers of diogenids in offshore waters were

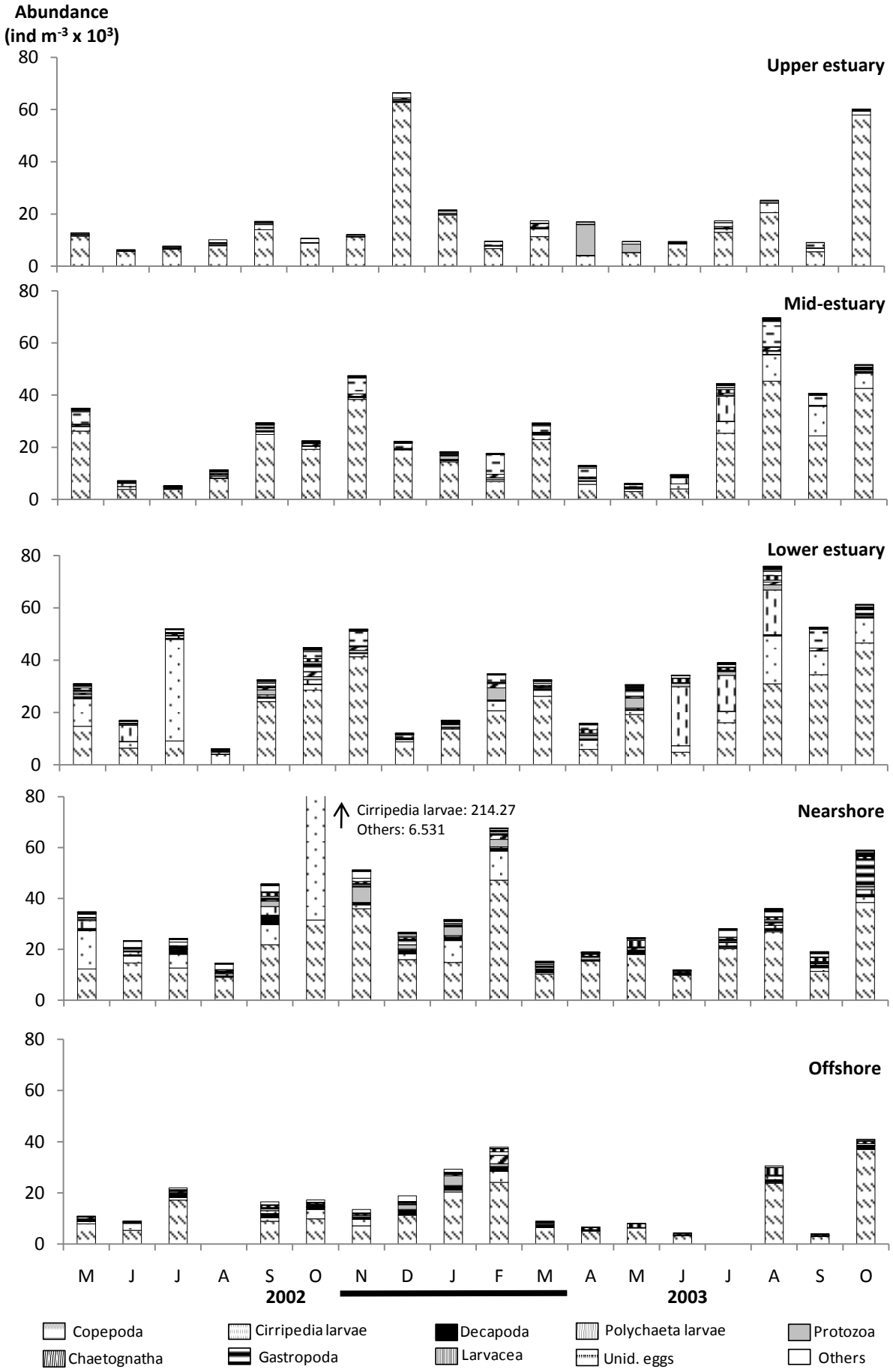


Fig. 3.15. Monthly abundance of major zooplankton taxa. 'Others' grouped the remainder taxa. Horizontal bar indicates Northeast moonsoon; error bar not shown.

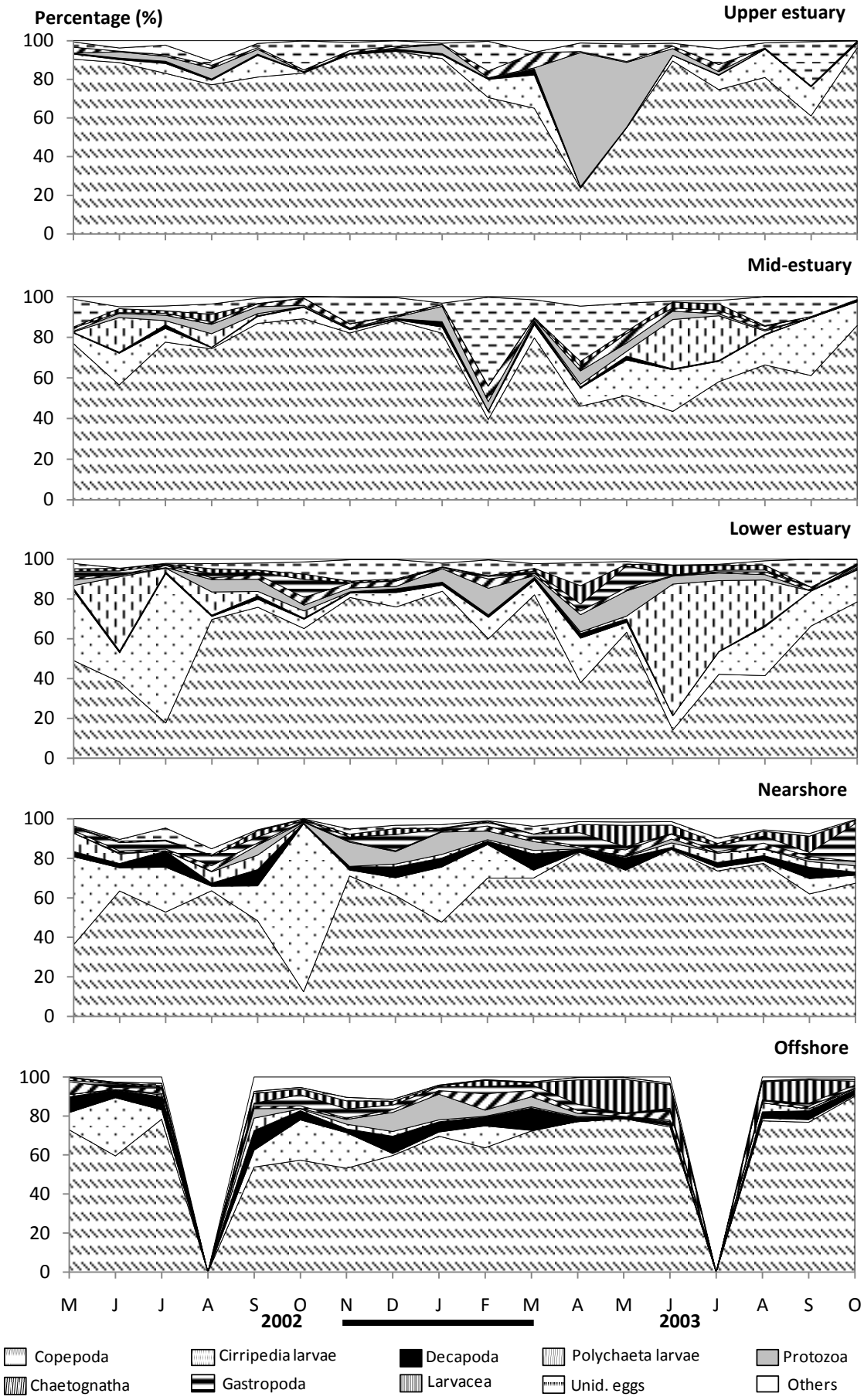


Fig. 3.16. Monthly percentage composition of major zooplankton taxa. 'Others' grouped the remainder taxa. Horizontal bar indicates Northeast monsoon.

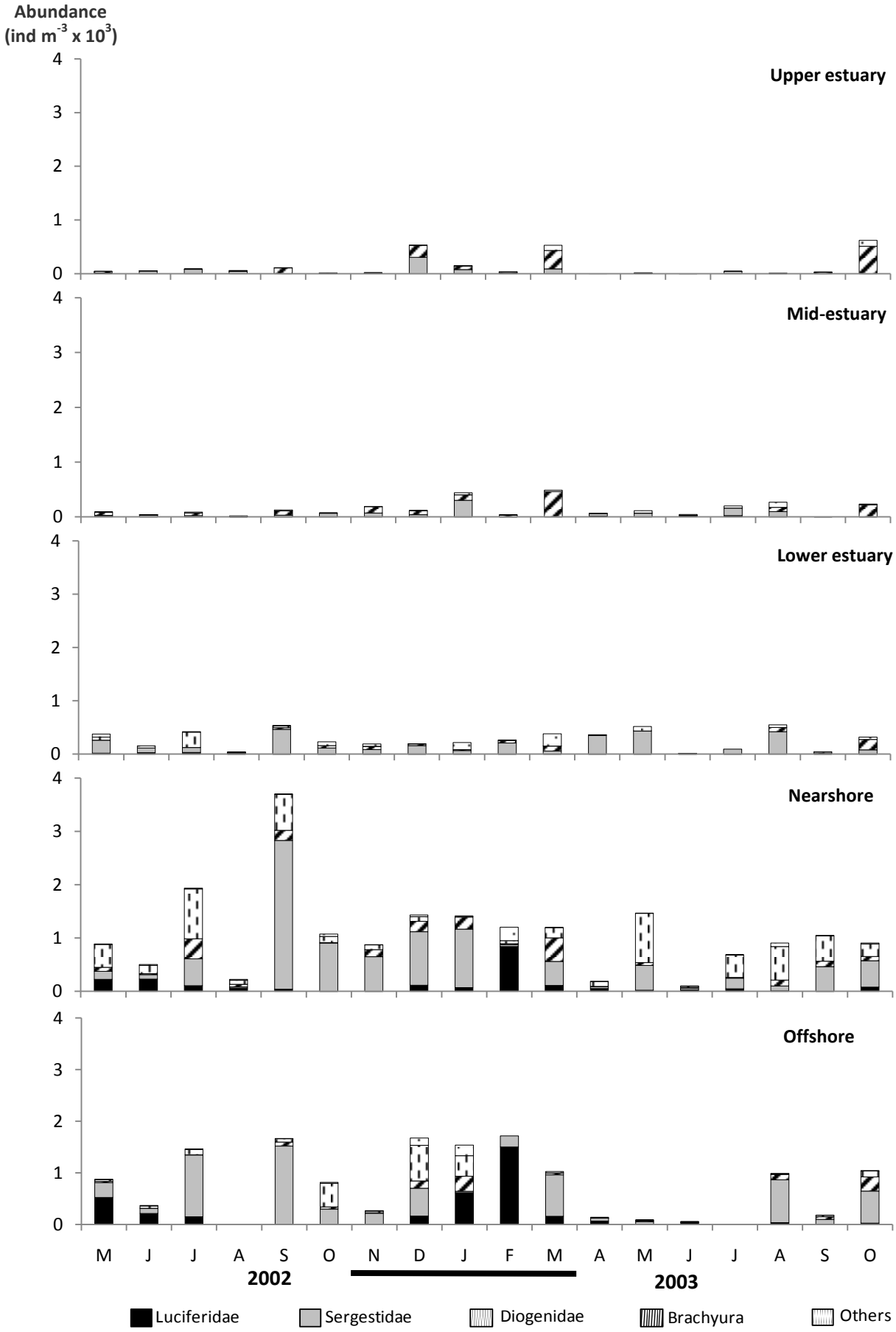


Fig. 3.17. Monthly abundance of major components of decapods. 'Others' grouped the remainder taxa. Horizontal bar indicates Northeast moonsoon; error bar not shown.

observed between October 2002 and January 2003 and coincided with wetter period (Fig. 3.17). Sergestids were uniformly distributed throughout the sampling period in nearshore and offshore waters (Fig. 3.17).

d. Non-crustacean zooplankton

As opposed to copepods and decapods, the abundance of polychaetes were significantly highest during the SW monsoon (ANOVA, $p < 0.001$; Table 3.6). The significant interaction effect in abundance between station and monsoon season indicated that the seasonality of polychaetes was obvious mainly at mid and lower estuaries ($p < 0.01$, Fig. 3.15). At both stations, polychaetes peaked in June 2002 and between June and August 2003 with abundance of over 6,000 ind m^{-3} (Fig. 3.15). In particular, polychaetes appeared to be more numerous than copepods in June 2003 at the lower estuary, comprising 66% of the total zooplankton abundance while copepods constituted only 14% (Fig. 3.16). It was noteworthy in that the initial increase of polychaetes was observed after the lowest precipitation events in May 2002 and 2003 (Fig. 3.15; see also Fig. 3.5).

Kruskal-Wallis ANOVA test on common non-crustacean zooplankton revealed a significant seasonality for five taxa, namely protozoans, larvaceans, bryozoan larvae and ophiopluteus larvae (Table 3.6). Larvaceans and bryozoans larvae that were more abundant in coastal waters were found in higher number during the SW monsoon than the IN period and NE monsoon (Table 3.6). Although the distribution of ophiopluteus larvae was more restricted to coastal waters, these larvae were found in higher number during the NE monsoon as compared to both IN period and SW monsoon (Table 3.6). Protozoans appeared to be more abundant particularly in adjacent coastal waters during the NE monsoon as compared to IN period and SW monsoon (Fig. 3.15). There was no significant seasonality for chaetognaths, gastropods and bivalves (Table 3.6).

e. Unidentified eggs

There was no clear seasonal pattern in abundance of unidentified eggs (ANOVA, $p > 0.05$). Eggs were observed all year-round and peak abundances were observed at mid-estuary in May and November 2002, February and August 2003 and at lower estuary in November 2002 and September 2003 (Fig. 3.15).

3.1.7.4 Zooplankton community structure

3.1.7.4 .1 Species richness

A total of 99 taxa of zooplankton were recorded throughout the monthly sampling period. Copepods comprised the most diverse group, representing 48 taxa. Forty-six taxa of the zooplankton were present in all sampling stations, while 26 taxa occurred only at the lower estuary and stations further offshore. Out of the 26 taxa, 16 species comprised of copepods. Three taxa (*P. crassirostris, O. simplex* and Chaetognatha) were present in all samples (100% occurrence; see Table 3.7). Nearshore recorded the highest number of zooplankton taxa (82) followed by offshore (78), lower estuary (72), mid-estuary (66) and upper estuary (61). Similarly, nearshore station also recorded the highest number of copepod species (42) followed by offshore (39), lower estuary (34), mid-estuary (29) and upper estuary (25). Table 3.10 gives a complete list of zooplankton found in the Matang mangrove estuaries and adjacent coastal waters.

3.1.7.4 .2 Copepod species diversity

Mean of the four diversity indexes of copepods and summary results of 2-way ANOVA are given in Table 3.11. Each of the four biodiversity indexes was significantly different among stations (ANOVA, $p < 0.001$). Pielou's evenness (J') and Shannon-Wiener diversity index (H') were highest at lower estuary and lowest at upper estuary. K-dominance curve also reflected a decrease in copepod diversity from the

Table 3.10. List of zooplankton found in Matang mangrove estuaries and adjacent coastal waters during monthly and 24-hour samplings. UE= upper estuary, ME= mid-estuary, LE= lower estuary, NS= nearshore waters, OS= offshore waters; D= dominant with over 5% of the total zooplankton abundance and occurrence of ≥ 50%, C= common with occurrence of ≥ 50%, '+'= present but with occurrence between 13 to 49%, R= rare with occurrence of <13%, '-'= absent; Abbr.= abbreviations used in RDA; $^{\Psi}$= only family level was considered for species richness during monthly routine sampling.

Taxon	Abbr.	Monthly routine sampling					24-hour sampling			
		Station					Dry period		Wet period	
		UE	ME	LE	NS	OS	Neap	Spring	Neap	Spring
Copepoda										
Acartiidae										
Acartia erythraea Giesbrecht	Aery	-	-	R	C	C	-	R	-	-
Acartia sp1	Asp1	C	C	C	R	R	C	C	C	C
Acartia spinicauda Giesbrecht	Aspi	D	D	C	C	C	C	C	D	D
Arietellidae										
Metacalanus aurivilli Cleve	Arie	R	R	R	R	R	R	R	-	-
Calanidae										
Canthocalanus pauper (Giesbrecht)	Capau	-	-	-	-	R	-	R	-	-
Centropagidae										
Centropages dorsispinatus Thompson I.C. & Scott A.	Cdor	R	+	+	C	C	+	+	R	R
Centropages furcatus (Dana)	Cfur	-	-	-	+	C	-	R	R	-
Eucalanidae										
Eucalanus subcrassus Giesbrecht	Eusub	-	R	R	C	C	R	R	R	R
Paracalanidae										
Acrocalanus gibber Giesbrecht	Acgib	-	-	R	+	+	-	R	-	-
Acrocalanus gracilis Giesbrecht	Acgra	-	-	-	-	R				
Bestiolina similis (Sewell)	Bsim	C	C	C	C	C	C	C	C	C
Paracalanus aculeatus Giesbrecht	Pacu	-	-	R	C	C	R	R	R	-
Parvocalanus crassirostris (Dahl F.)	Pcras	D	D	D	D	D	D	D	D	D
Parvocalanus elegans Andronov	Pele	C	R	C	C	R	+	+	+	C
Pontellidae										
Calanopia thompsoni Scott A.	Cthom	-	R	R	R	-	+	+	+	R
Labidocera euchaeta Giesbrecht	Leuch	-	-	-	-	-	-	R	-	-
Labidocera jaafari Othman	Ljaa	R	+	R	+	R	+	+	+	+
Labidocera pectinata Thompson I.C. & Scott A.	Lpec	R	+	C	R	R	C	+	+	+
Labidocera sp1	Lsp1	-	R	R	R	R	+	+	R	R
Pontella danae Giesbrecht	Pdan	-	-	R	R	R				
Pseudodiaptomidae										
Pseudodiaptomus annandalei Sewell	Pana	R	-	-	-	-	-	+	+	+
Pseudodiaptomus bowmani Walter	Pbow	-	R	R	C	C	+	+	R	R
Pseudodiaptomus thailandensis Walter	Pthai	-	R	R	-	-	+	+	+	R
Pseudodiaptomus trihamatus Wright S.	Ptri	+	R	+	R	-	+	+	+	C
Temoridae										
Temora discaudata Giesbrecht	Tedis	-	-	-	R	-				
Temora turbinata (Dana)	Tetur	-	-	-	-	R	R	-	-	-
Tortanidae										
Tortanus barbatus (Brady)	Tbar	+	C	C	C	C	C	C	C	+
Tortanus forcipatus (Giesbrecht)	Tfor	R	+	C	C	C	+	C	R	R

Table 3.10, continued

Taxon	Abbr.	Monthly routine sampling					24-hour sampling			
		Station					Dry period		Wet period	
		UE	ME	LE	NS	OS	Neap	Spring	Neap	Spring
Oithonidae										
Oithona aruensis Früchtl	Oaru	C	C	C	C	R	C	C	C	+
Oithona attenuata Farran	Oatte	R	R	+	C	C	R	+	R	-
Oithona brevicornis Giesbrecht	Obre	R	-	R	R	C	-	R	-	-
Oithona dissimilis Lindberg	Odiss	C	C	C	+	R	C	C	C	C
Oithona simplex Farran	Osim	C	C	D	D	D	C	C	C	D
Oithona rigida Giesbrecht	Orig	-	-	-	R	R	R	R	-	-
Clausidiidae										
Hemicyclops sp1	Hem	R	R	R	C	R	R	R	+	+
Corycaeidae										
Corycaeus andrewsi Farran	Cand	-	-	R	C	C	R	R	-	R
Corycaeus dahli Tanaka	Cdah	-	-	-	R	-	-	R	-	-
Corycaeus erythraeus Cleve	Cery	-	-	-	R	R	-	R	-	-
Kelleriidae										
Kelleria sp1	Kell	-	-	-	R	R	+	+	+	R
Macrochironidae										
Paramacrochiron amboinense Mulyadi	Pamb	-	-	-	-	-	-	R	-	-
Pseudomacrochiron sp1	Pseu	R	R	C	C	R	+	R	+	+
Oncaeidae										
Oncaea clevei Früchtl	Ocle	-	-	R	R	R	-	R	R	-
Caligidae										
Caligus sp.	Cali	R	R	-	R	-	R	R	-	-
Adenopleurellidae sp.	Aden	-	-	-	-	-	-	R	-	-
Clytemnestridae										
Clytemnestra scutellata Dana	Clyt	-	R	-	R	-	R	R	R	R
Ectinosomatidae										
Microsetella norvegica (Boeck)	Mnor	R	+	+	C	+	+	+	R	+
Ectinosomatidae sp.	Ect	R	-	R	R	R	R	R	R	+
Euterpinidae										
Euterpina acutifrons (Dana)	Eacu	C	C	C	C	D	C	C	C	C
Miraciidae										
Macrosetella gracilis (Dana)	Mgra	-	-	-	R	R				
Longipediidae										
Longepedia sp.	Lon	-	R	-	-	-	-	R	R	-
Harpacticoida sp1	H	R	+	+	+	R	R	R	R	R
		25	**29**	**34**	**42**	**39**	**34**	**46**	**33**	**29**
Total number of copepod species				**48**			**47**		**34**	
								47		
						51				

Table 3.10, continued

Taxon	Abbr.	Monthly routine sampling					24-hour sampling			
		Station					Dry period		Wet period	
		UE	ME	LE	NS	OS	Neap	Spring	Neap	Spring
Cirripedia larvae	Cirri	C	D	D	D	D	D	D	D	D
Mysidae										
Acanthomysis sp.	Acan	R	-	R	-	-	+	+	+	C
Erythrops sp.	Ery	-	-	-	-	-	R	R	-	-
Mesopodopsis sp.	Meso	R	-	-	-	-	R	+	+	+
Notacanthomysis sp.	Noto	R	R	+	R	-	+	C	+	+
Rhopalophthalmus sp.	Rhopa	R	R	-	-	-	+	+	+	+
Decapoda										
Luciferidae	Luci	C	C	C	C	C	C	C	C	C
Ψsergestidae (larval and juvenile stages)	Ser	C	C	C	C	C	C	C	C	C
Acetes japonicus Kishinouye	Ajap	R	R	R	R	-	+	+	+	+
Acetes indicus H. Milne Edwards	Aind	R	R	R	-	-	R	+	R	+
Acetes sibogae Hansen	Asib	R	R	-	-	-	+	R	R	R
Alpheidae larvae	Alp	C	C	C	C	C	C	+	C	C
Brachyura larvae	Bra	C	C	C	C	C	C	C	C	C
Diogenidae larvae	Dio	R	R	+	C	C	+	+	C	+
Palaemonidae larvae	Palae	C	C	C	C	R	+	+	C	R
Pasiphaeidae larvae	Pasi	-	-	-	-	-	-	R	-	-
Penaeidae larvae	Pena	R	R	R	C	C	C	C	+	+
Polychelidae larvae	Poly	-	-	-	-	R	-	-	R	-
Porcellanidae larvae	Por	C	C	C	+	+	C	+	C	+
Thalassinidae larvae	Thall	-	-	-	-	R	R	R	-	+
Amphipoda										
Caprella sp.	Capre	-	-	-	-	-	R	R	-	-
Corophium sp.	Corr	-	-	-	-	-	-	R	-	R
Grandidierella sp.	Gran	R	-	-	R	R	+	+	R	R
Synchelidium sp.	Syn	-	-	-	R	R	R	+	+	R
Hyperiidae sp.	Hyp	-	-	-	-	R	R	R	R	R
Cumaceae	Cum	+	R	R	R	-	R	+	+	+
Isopoda	Iso	R	+	R	C	+	+	C	+	+
Ostracoda	Ost	R	R	R	R	R	+	+	R	+
Stomatopoda	Sto	C	C	C	C	C	C	+	C	+
Protozoa										
Foramineferan	Foram	-	R	R	R	-	R	R	R	R
Favella sp.	Fav	C	C	C	C	C	C	C	C	C
Tintinnopsis sp.	Tint	C	C	C	C	+	+	+	R	R
Noctiluca sp.	Noc	R	R	R	R	R	D	+	+	R
Chaetognatha	Chae	C	C	C	C	C	C	C	C	C
Cnidaria										
Hydrozoa	Hydro	C	C	C	C	C	C	C	C	C
Scyphozoa	Scy	R	R	-	-	-	-	R	-	R
Ctenophora										
Pleurobrachia sp.	Pleu	C	C	C	R	+	C	C	C	+
Beroe sp.	Bero	R	-	R	R	R	R	+	+	-

Table 3.10, continued

Taxon	Abbr.	Monthly routine sampling					24-hour sampling			
		Station					Dry period		Wet period	
		UE	ME	LE	NS	OS	Neap	Spring	Neap	Spring
Polychaeta										
Capitellidae	Cap	-	-	-	-	-	R	-	-	-
Chrysopetalidae larvae	Chry	-	R	R	R	R	R	R	R	-
Flabelligeridae	Flab	-	-	-	-	-	R	R	-	-
Glyceridae	Gly	-	-	-	-	-	R	R	-	R
Magelonidae larvae	Mage	-	-	-	R	R	R	R	R	R
Nereididae larvae	Nere	-	R	R	+	R	R	R	+	+
Opheliidae	Ophe	-	-	-	-	-	-	R	-	-
Oweniidae larvae	Owen	R	R	R	-	-	R	R	R	-
Phyllodocidae	Phyll	-	-	-	-	-	-	-	-	R
Polynoidae larvae	Poly	-	-	R	R	R	-	-	R	R
Sabellariidae larvae	Sabe	C	C	D	C	C	C	C	C	+
Spionidae larvae	Spio	+	C	C	C	C	C	+	+	+
Syllidae	Scyll	-	-	-	-	-	R	R	-	-
Terebellidae larvae	Tere	R	R	R	C	C	+	+	R	R
Tomopteridae	Tomo	-	-	-	R	R	-	-	+	-
Bivalvia	Bv	C	C	C	C	C	C	C	C	C
Cephalopoda	Cep	R	-	-	-	-	R	R	R	R
Gastropoda	Ga	C	C	C	C	C	C	C	C	C
Ophiopluteus larvae	Ophio	+	+	+	C	C	+	+	R	R
Bryozoa larvae	Bry	C	C	C	C	C	C	C	C	+
Larvacea	Lar	C	C	C	C	C	C	C	C	C
Phoronis larvae	Pho	-	-	R	+	R	+	+	R	-
Lingula larvae	Lin	-	-	R	R	-	R	R	-	-
Nematoda	Nema	-	-	R	R	R	R	R	-	R
		61	**66**	**72**	**82**	**78**	**88**	**103**	**81**	**77**
							104		**88**	
Total number of zooplankton taxa				**99**				**108**		
						112				

Table 3.11. Summary table of ANOVA results for biodiversity indexes of copepods with respect to station, season and their interaction. Boldface indicates overall value of combined stations. $\bar{x}$ = mean; n = sample size; stations: UE = upper estuary, ME = mid-estuary, LE = lower estuary, NS = nearshore waters, OS = offshore waters; season: SW = Southwest monsoon, IN = inter-monsoon period, NE = Northeast monsoon; diversity indexes: S = species richness, J' = Pielou's evenness, H' = Shannon-Wiener diversity indexes, Δ* = average individual taxonomic distinctness and Δ^+ = average specific taxonomic distinctness; Min = minimum, Max = maximum; homogenous groups indicated by superscripts a, b and c; ** significance at $p < 0.01$, ns no significance. H' computed on log-base e.

		Source of variation											**Mangrove**	**Adjacent coastal waters**
		Station (1)						Season (2)				Interaction (1) x (2)		
	n	UE 36	ME 36	LE 36	NS 36	OS 32	p-level	SW 96	IN 30	NE 50	p-level			
S		25	29	34	42	39		44	31	40			**38**	**45**
J'	$\bar{x}$	0.54 [a]	0.60 [a,b]	0.63 [b]	0.57 [a,b]	0.56 [a]	<0.001**	0.60 [a]	0.59 [a]	0.53 [b]	<0.01**	ns	**0.48**	**0.50**
	± SD	0.15	0.12	0.10	0.11	0.10		0.11	0.15	0.12				
	Min	0.21	0.32	0.44	0.23	0.33		0.23	0.22	0.21				
	Max	0.80	0.85	0.83	0.76	0.74		0.83	0.85	0.83				
H'	$\bar{x}$	1.17 [a]	1.39 [b]	1.55 [b]	1.53 [b]	1.49 [b]	<0.001**	1.50 [a]	1.41 [a,b]	1.29 [b]	<0.001**	ns	**1.73**	**1.91**
	± SD	0.35	0.34	0.28	0.36	0.29		0.30	0.41	0.36				
	Min	0.35	0.62	1.10	0.56	0.93		0.48	0.35	0.38				
	Max	1.82	2.02	2.03	2.10	2.06		2.10	2.02	1.98				
Δ*	$\bar{x}$	84.04 [a,c]	82.77 [a]	85.05 [a,c]	90.35 [b]	87.99 [b,c]	<0.001**	85.38 [a]	81.53 [b]	89.85 [c]	<0.001**	ns	**82.29**	**90.28**
	± SD	8.90	8.89	5.20	6.70	8.19		6.67	12.17	5.69				
	Min	49.82	58.84	69.80	68.78	64.22		58.84	49.82	74.80				
	Max	98.54	94.91	95.65	99.53	98.72		97.51	98.92	99.53				
Δ^+	$\bar{x}$	81.56 [a]	84.82 [b]	85.72 [b,d]	87.67 [c]	87.04 [c,d]	<0.001**	85.65	84.57	85.16	ns	ns	**88.37**	**89.09**
	± SD	3.59	3.49	2.56	2.29	2.02		3.09	3.81	4.23				
	Min	76.67	76.67	80.36	83.89	81.36		76.67	77.68	76.67				
	Max	88.26	90.97	90.38	91.82	90.91		91.82	90.91	90.97				

coastal waters towards the upper part of the estuaries (Fig. 3.18). The two taxonomic indexes of copepods, average individual taxonomic distinctness (Δ*) and average specific taxonomic distinctness (Δ^+), were higher in nearshore and offshore as compared to mangrove waters. The lowest mean values of Δ* and Δ^+ were obtained at mid-estuary and upper estuary respectively (Table 3.11).

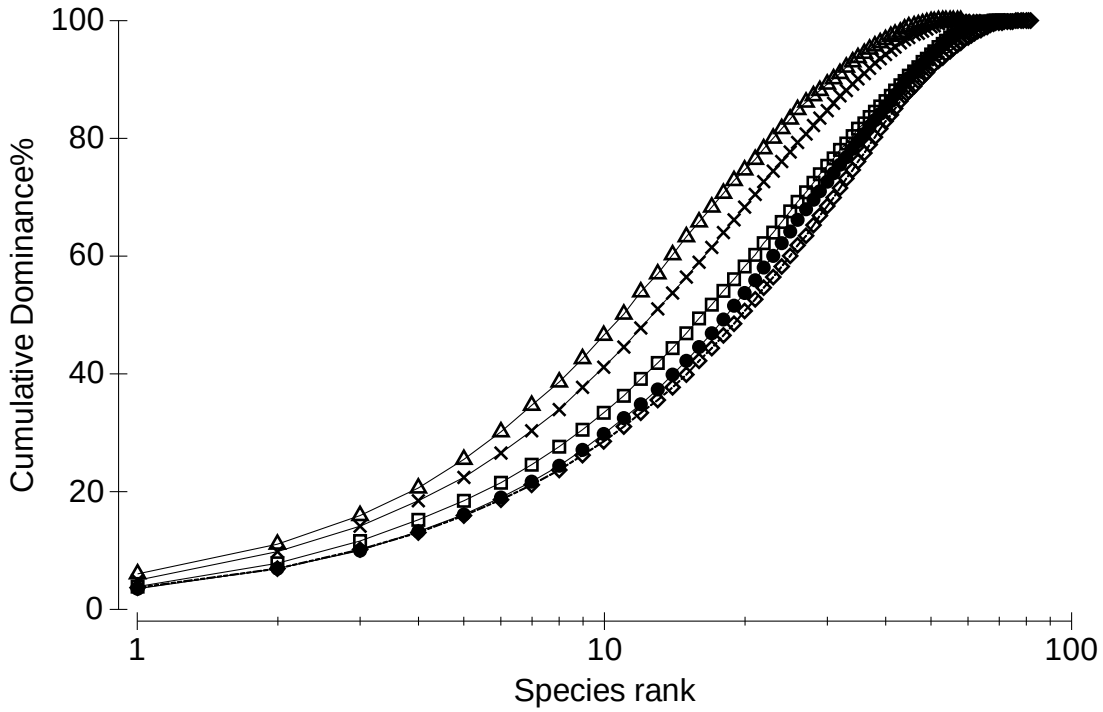


Fig. 3.18. K-dominance curve of copepods by stations. Δ = upper estuary, x = mid-estuary, □ = lower estuary, ◊ = nearshore waters, ● = offshore waters.

Results of ANOVA showed a significant seasonality on the pooled data of copepod diversity indexes except for Δ^+ (Table 3.11). J' and H' were lowest during the NE monsoon and highest during the SW monsoon. However, the lower values of J' and H' were initially observed in October prior to the period of NE monsoon. These values continued to remain at low levels during the early NE monsoon (November to December) but increased thereafter in the latter part of NE monsoon (January to March) (Fig. 3.19). J' and H' were generally at higher levels during the SW monsoon (Fig. 3.19). In contrast, Δ* was highest during the NE monsoon and lowest during the IN period as resulted by the lowest value in October 2003 (Table 3.11 and Fig. 3.20).

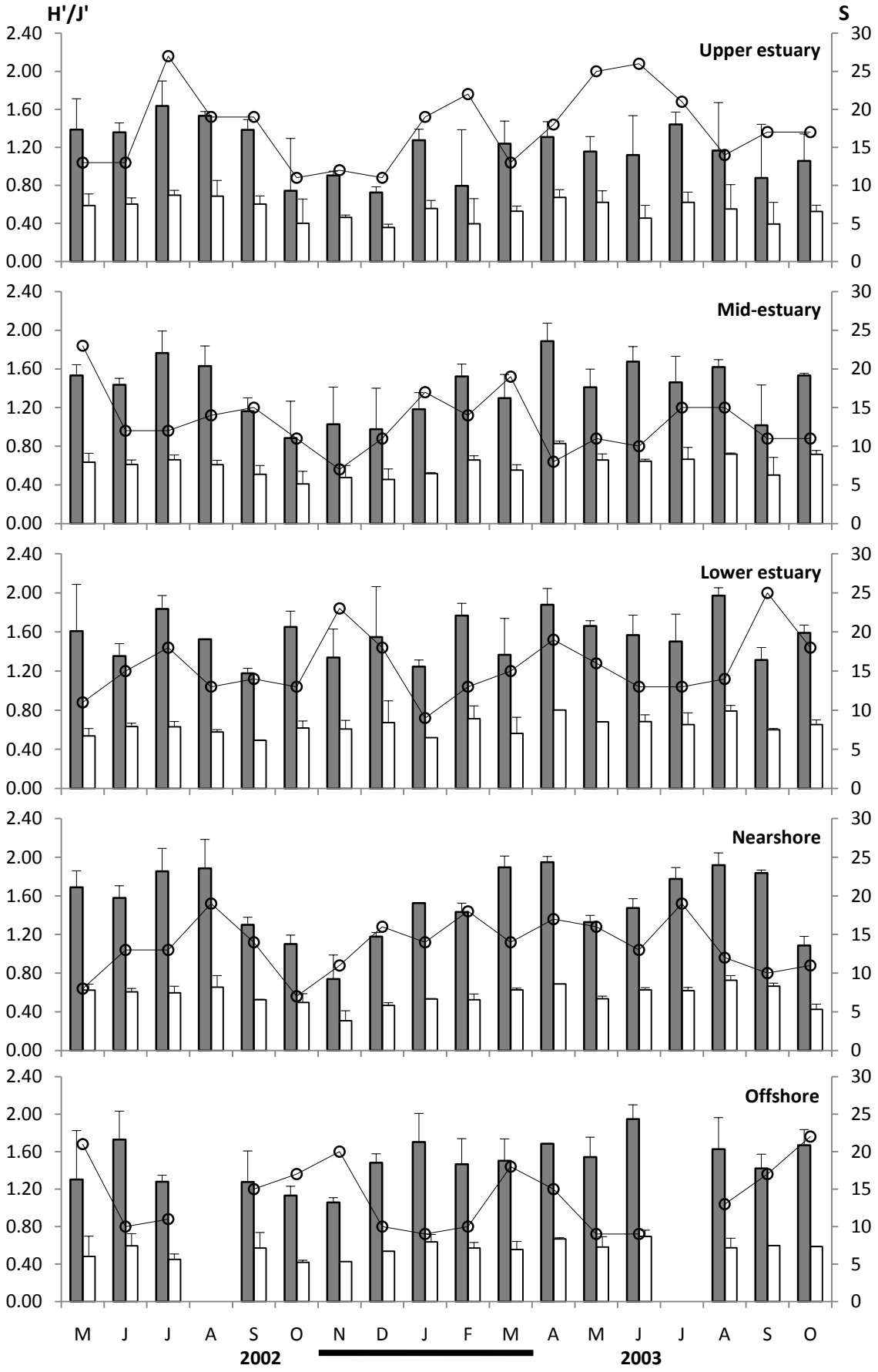


Fig. 3.19. Monthly Shannon-Wiener index (■) , Pielou's evenness (□) and species richness (○) of copepods by station, from May 2002 to October 2003. Error bars indicate SD; horizontal bar indicates Northeast monsoon.

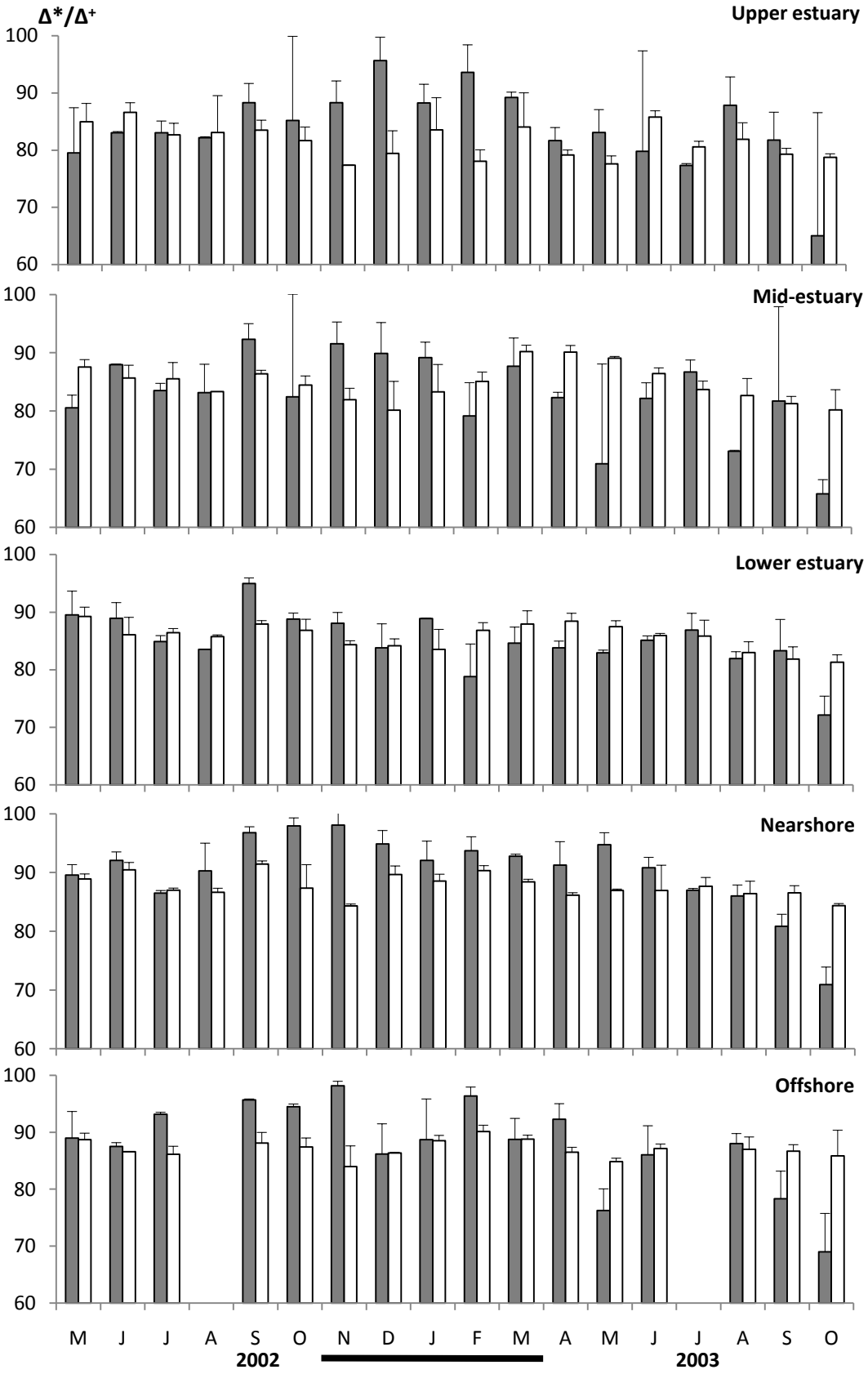


Fig. 3.20. Monthly taxonomic indexes of copepods by station, from May 2002 to October 2003. Error bars indicate SD; horizontal bar indicates Northeast monsoon; Δ* = individual average taxonomic distinctness (■), Δ^+ = species average taxonomic distinctness (□).

The values of J', H', Δ* and Δ^+ for overall copepods in mangrove waters (mangrove stations combined) were 0.48, 1.73, 82.29 and 88.37 respectively while the adjacent coastal waters (nearshore and offshore stations combined) were 0.5, 1.91, 90.28 and 89.09 respectively (Table 3.11).

3.1.7.4.3 Similarity between zooplankton communities

The dendrogram of group-average link cluster analysis and MDS ordination plot of zooplankton samples generated from the Bray-Curtis similarity matrix are given in Figs. 3.21 and 3.22. Zooplankton communities in the mangrove stations were clustered together, apart from that in adjacent coastal waters at 53% similarity, except for two lower estuary samples collected during the SW monsoon (Fig. 3.21). These two samples were clustered together with the nearshore and offshore samples. The MDS plot with stress value of 0.15 shows gradual changes in zooplankton community from the upper estuary through lower estuary to offshore waters (Fig. 3.22). Results of ANOSIM revealed a significant separation of zooplankton community across stations (Global R = 0.529; $p < 0.001$). Pairwise tests of any two stations showed that the degree of separation in community structure increased with increasing distance between two sampling stations. The community structure at the upper estuary was most distinct from that of offshore waters with R value of 0.94. Conversely, community structure at mid-estuary was not significantly separable from that of upper and lower estuary ($R < 0.1$, $p > 0.05$; Table 3.12). Global R value of ANOSIM indicated a significant seasonal difference ($p < 0.001$) in zooplankton community although the value (0.186) was barely small in group separation (Table 3.12).

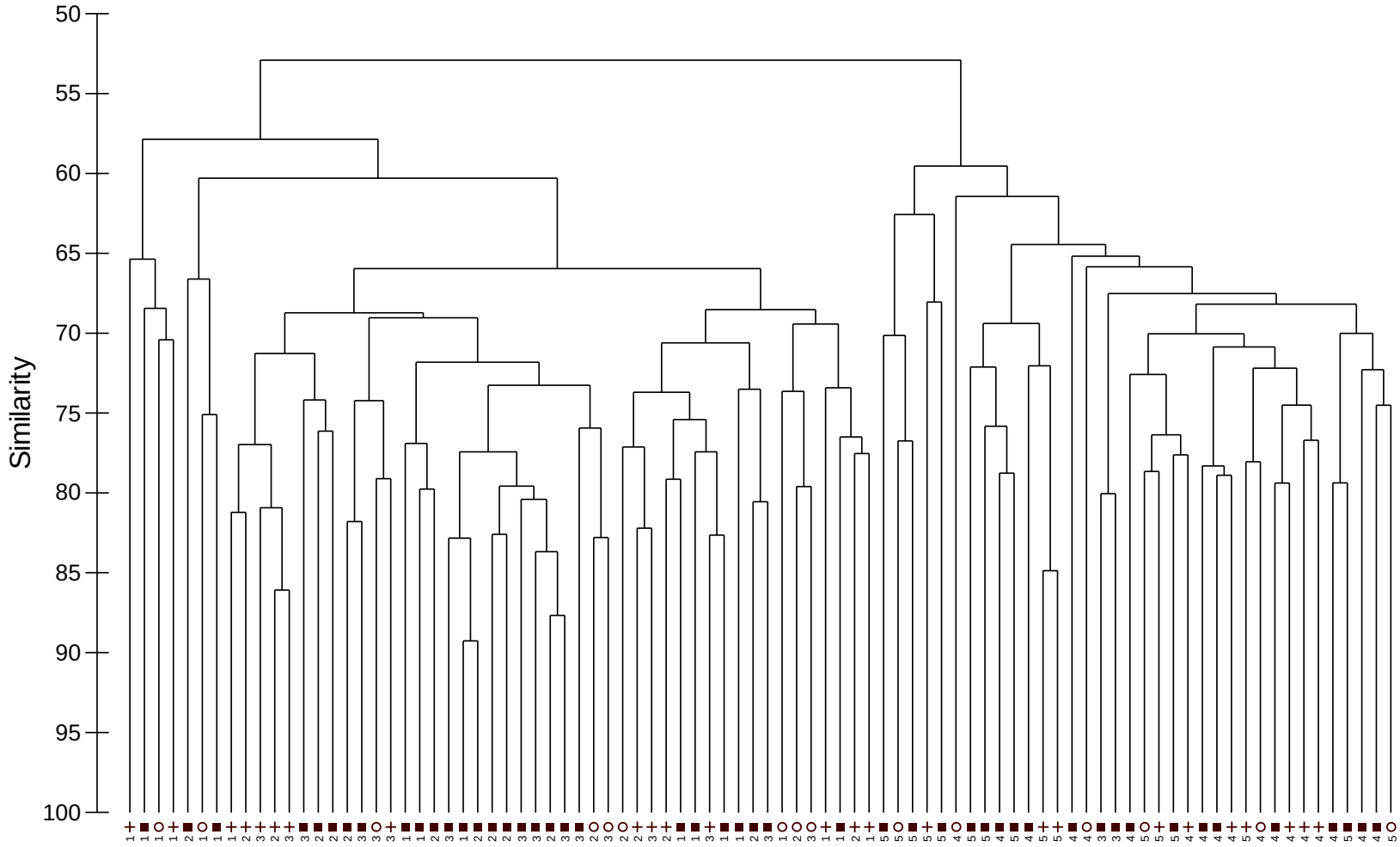


Fig. 3.21. Dendrogram of group average clustering from Bray-Curtis similarities on log-transformed zooplankton abundance data. Numbers on horizontal axis indicate sampling stations: 1 = upper estuary, 2 = mid-estuary, 3 = lower estuary, 4 = nearshore waters, 5 = offshore waters; symbols indicate monsoonal season: ■ = Southwest monsoon, ○ = inter-monsoon period, '+' = Northeast monsoon.

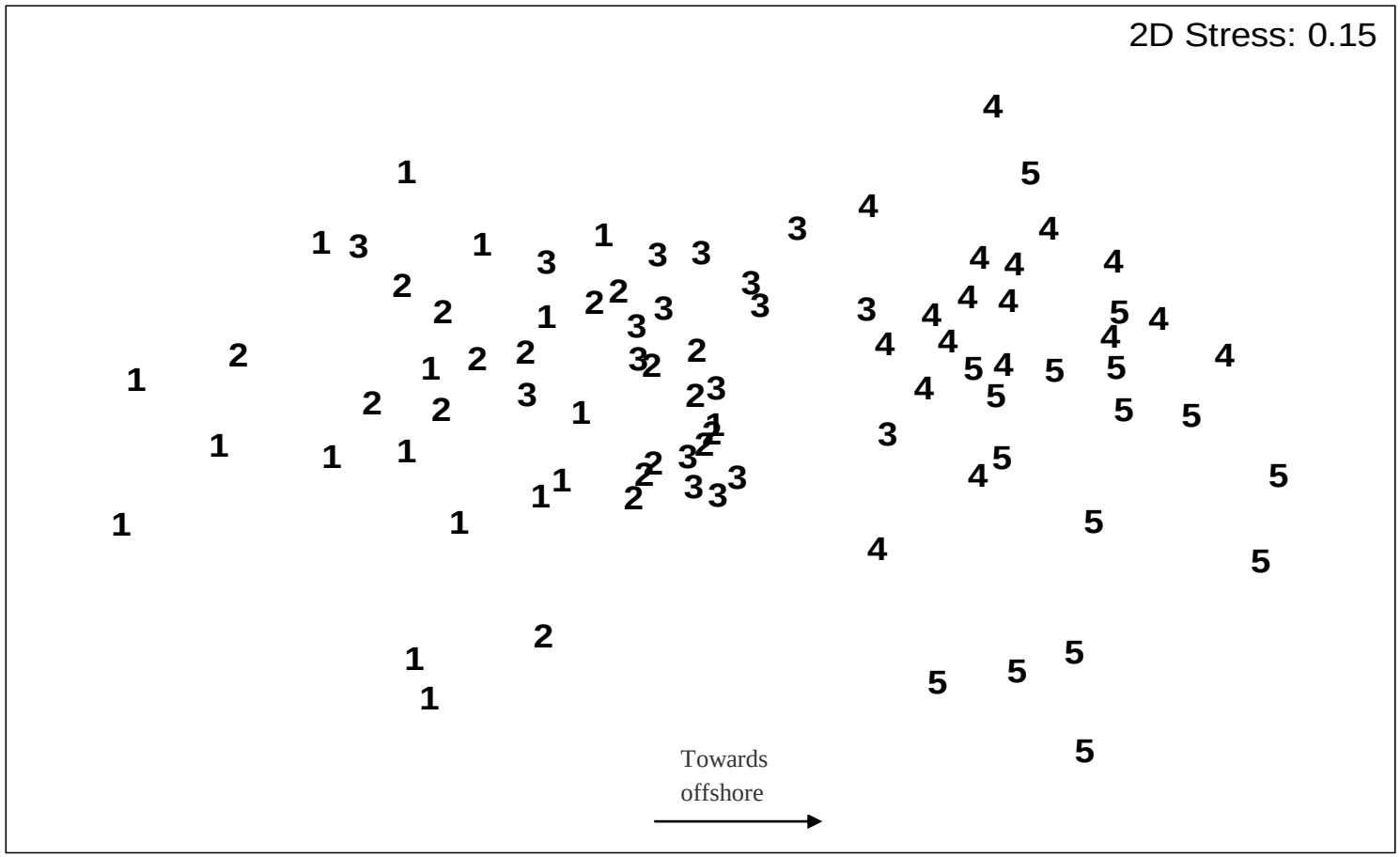


Fig. 3.22. MDS plots of zooplankton assemblages sampled from upper estuary to offshore. Sampling stations: 1 = upper estuary, 2 = mid-estuary, 3 = lower estuary, 4 = nearshore waters and 5 = offshore waters. Higher proximity of points indicates higher similarity of the community structure.

Table 3.12. Summary results of two-way crossed ANOSIM and pairwise tests comparing zooplankton assemblages between stations and seasons. Boldface indicates significant separation at $p < 0.05$. Stations: UE = upper estuary, ME = mid-estuary, LE = lower estuary, NS = nearshore waters, OS = offshore waters; season: SW = Southwest monsoon, IN = inter-monsoon period, NE = Northeast monsoon.

Groups	R Statistic	Significance p-level
Station	**0.529**	**0.001**
Pairwise tests		
UE, ME	0.085	0.066
UE, LE	**0.342**	**0.001**
UE, NS	**0.918**	**0.001**
UE, OS	**0.943**	**0.001**
ME, LE	0.027	0.283
ME, NS	**0.812**	**0.001**
ME, OS	**0.874**	**0.001**
LE, NS	**0.586**	**0.001**
LE, OS	**0.765**	**0.001**
NS, OS	**0.254**	**0.005**
Season	**0.186**	**0.001**
Pairwise tests		
SW, I	**0.196**	**0.015**
SW, NE	**0.189**	**0.005**
I, NE	**0.268**	**0.005**

3.1.7.5 Environment-species relationship

The Monte Carlo permutation test on the first canonical axis as well as the sum of all other canonical axes showed a significance of the environment-species correlation at $p = 0.002$. The first two axes explained 26.8% of the variance in the zooplankton abundance data and 77.3% of the variance in the correlation of zooplankton taxa and environmental parameters (Table 3.13). The canonical coefficients or eigen vectors of the first four axes and inter-set correlations of the environmental parameters with these axes are given in appendix IV. The interpretation of the results derived from RDA is best illustrated by the ordination biplots (Fig. 3.23).

Table 3.13. Summary results of Redundancy analysis (RDA) for zooplankton assemblages from upper estuary to offshore in relation to environmental parameters.

Axes	1	2	3	4	Total variance
Eigenvalues :	0.237	0.032	0.025	0.018	1
Species-environment correlations :	0.881	0.716	0.725	0.556	
Cumulative percentage variance					
of species data :	23.7	26.8	29.3	31.1	
of species-environment relation:	68.2	77.3	84.4	89.5	
Sum of all eigenvalues					1
Sum of all canonical eigenvalues					0.347

All four eigenvalues reported above are canonical and correspond to axes that are constrained by the environmental variables.

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

Test of significance of first canonical axis: eigenvalue = 0.237
F-ratio = 24.208
P-value = 0.0020

Test of significance of all canonical axes : Trace = 0.347
F-ratio = 4.607
P-value = 0.0020

(499 permutations under reduced model)

The first canonical axis (axis 1) was primarily a descriptor of salinity and pH in the negative direction and NO_2^- + NO_3^- and chlorophyll *a* concentrations in the positive direction. Turbidity was positively associated with the second canonical axis (axis 2) on the positive side as opposed to dissolved oxygen on the negative side. The biplots of the environmental parameters and sample points in Fig. 3.23a shows that stations in mangrove waters (1, 2, 3) were generally positively correlated to higher turbidity values, dissolved inorganic nitrogen and chlorophyll *a* concentrations (positive direction on axis 1), but negatively correlated to salinity and pH values (negative direction on axis). Coastal stations (4, 5) however showed the exact opposite.

The 47 selected zooplankton taxa displayed in the RDA plot can be generally classified into stenohaline, estuarine and euryhaline groups based on their relative abundance along the salinity gradient over spatial and temporal scales. As can be seen from the plots, most of the zooplankton taxa were more associated with higher salinity

(stenohaline). Seventeen out of 27 copepod species were closely associated with higher salinity and pH or classified as stenohaline species (Fig. 3.23b). The seven major stenohaline copepods that were only present at the lower estuary and further offshore stations were *Paracalanus aculeatus* Giesbrecht, *Acartia erythraea* Giesbrecht, *Centropages furcatus* (Dana), *Corycaeus andrewsi* Farran, *Corycaeus erythraea* Cleve, *Acrocalanus gibber* Giesbrecht and *Canthocalanus pauper* (Giesbrecht) (see Table 3.10). Other stenohaline copepod species that were sporadically found inside the estuary included the calanoids, *Centropages dorsispinatus* Thompson & Scott, *T. barbatus*, *T. forcipatus*, *Pseudodiaptomus bowmani* Walter, the cyclopoids, *Oithona attenuata*, *Oithona brevicornis* Giesbrecht, *Hemicyclops* sp. 1, *Pseudomacrochiron* sp. 1 and the harpacticoids, *E. acutifrons* and *Microsetella norvegica* Dana.

The four decapod taxa that were closely associated with high salinity and pH were Sergestidae, Luciferidae, Diogenidae and Penaeidae (Fig. 3.23c). The non-crustacean zooplankton that inhabit mostly in higher salinity waters included the larvaceans, polychaete larvae of Sabellaridae, Spionidae and Terebellidae, ophiopluteus larvae, gastropods, bivalves and *Phoronis* larvae (Fig. 3.23d).

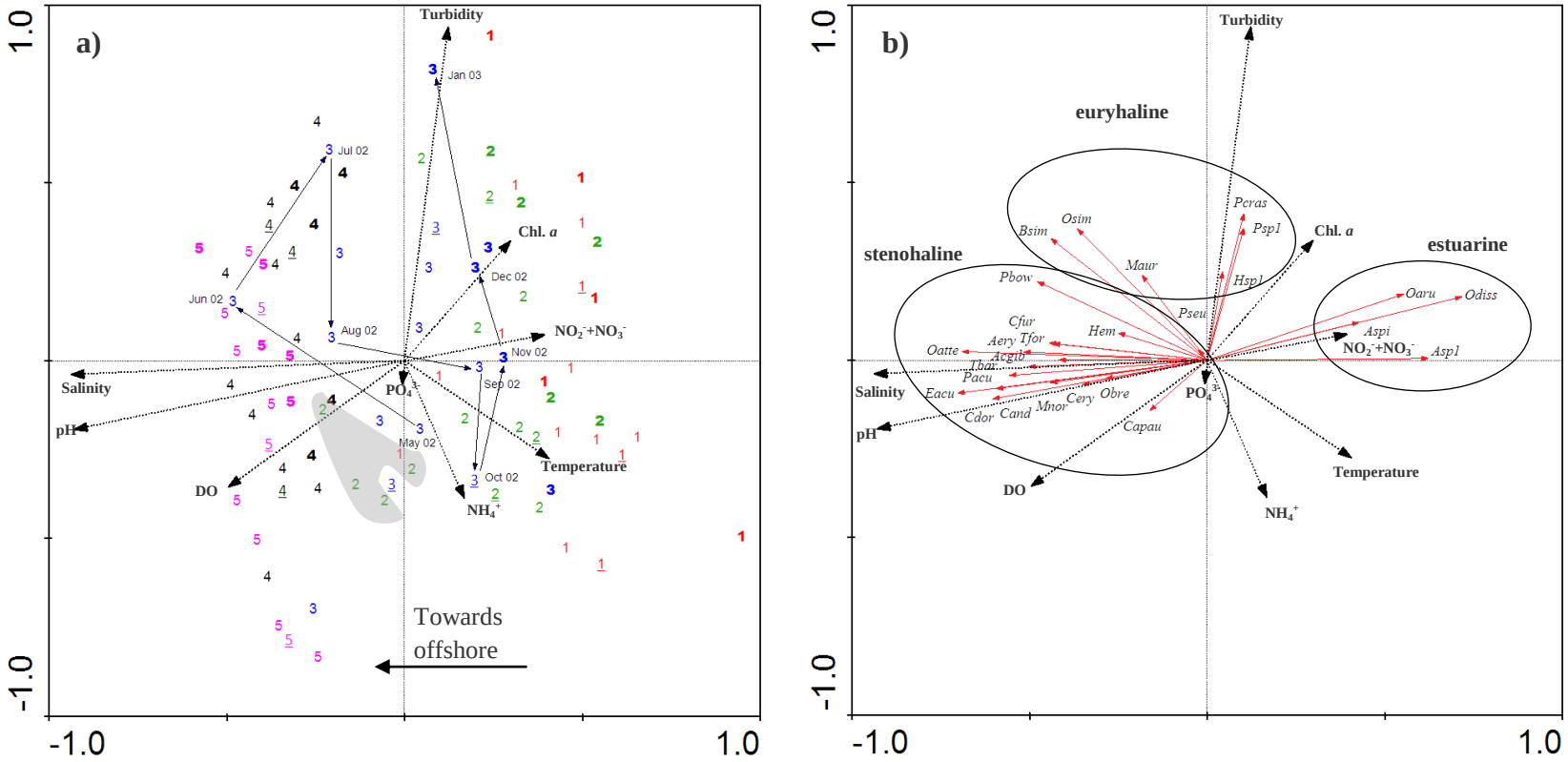
Very few zooplankton taxa inhabit mangrove waters in abundance except for the three copepod species *A. spinicauda*, *Acartia* sp. 1, *O. dissimilis* and *O. aruensis*. Their abundances were highly negatively correlated with salinity and pH (Fig. 3.23a).

The euryhaline copepods were oriented closer to axis 2 in the positive direction. Within the group, the copepod species that correlated with higher salinity were *O. simplex*, *B. similis* and *M. aurivilli*. The arrow orientations of *P. crassirostris*, *P. elegans* and Harpacticoida sp. 1 were almost perpendicular to the salinity gradient, implying that salinity did not have significant effect on their distribution. In fact, these species were more closely associated with turbidity and chl. *a*. The distribution of

cirripede and brachyuran larvae were not much affected by the salinity gradient despite being most abundant in nearshore waters. These taxa were also regularly found in the mangrove waters (see Table 3.7).

The euryhaline non-crustacean zooplankton composed of the protozoans *Favella*, *Tintinnopsis* and *Noctiluca*, the chaetognaths and the medusa of hydrozoans. These taxa showed weak correlation with salinity except for *Favella*, which appeared to be more related to the lower salinity. Noteworthy, *Favella* was oriented similar to that of chl. *a*, indicating a strong positive correlation between both components. *Favella, Tintinnopsis* and hydrozoans were positively associated with axis 2 as opposed to chaetognaths and *Noctiluca* on the negative side. Interestingly, the small size copepods *P. crassirostris* and *P. elegans* were exactly in the opposite side of chaetognaths, suggesting a strong negative correlation between these animals (Fig. 3.23).

Zooplankton community of the mangrove waters (Stn. 1, 2 and 3), with few exceptions, appeared to be quite distinct from that of nearshore and offshore stations (Stn. 4 and 5) (Fig. 3.23a). A seasonal shift in zooplankton community structure was evident particularly at lower estuary. For instance, stenohaline and euryhaline zooplankton dominated in the lower estuary during the dry period from June - September (thin line arrows joining station 3), but the community soon changed to one dominated by estuarine zooplankton with the onset of the wet period from October – January (thin line arrows joining station 3 in boldface). Neritic zooplankton invaded the lower estuary and reached the upper estuary in the driest months of June - August (indicated by shaded area enclosing stations 1 and 2) when high salinity water penetrated upstream.


a)
Turbidity
Jan 03
Jul 02
Chl. a
Dec 02
Jun 02
Aug 02
$NO_2^-+NO_3^-$
Nov 02
Salinity
PO_4^{3-}
Sep 02
pH
May 02
Temperature
DO
Oct 02
NH_4^+
Towards
offshore
1.0
-1.0
-1.0
1.0
b)
Turbidity
euryhaline
stenohaline
estuarine
Pcras
Psp1
Chl. a
Osim
Bsim
Maur
Hsp1
Pbow
Pseu
Oaru
Odiss
Cfur
Aery
Tfor
Hem
Aspi
$NO_2^-+NO_3^-$
Asp1
Oatte
Acgib
Tbai
Pacu
Salinity
Eacu
Cery
Obre
PO_4^{3-}
pH
Cdor
Cand
Mnor
Capau
Temperature
DO
NH_4^+
1.0
-1.0
-1.0
1.0

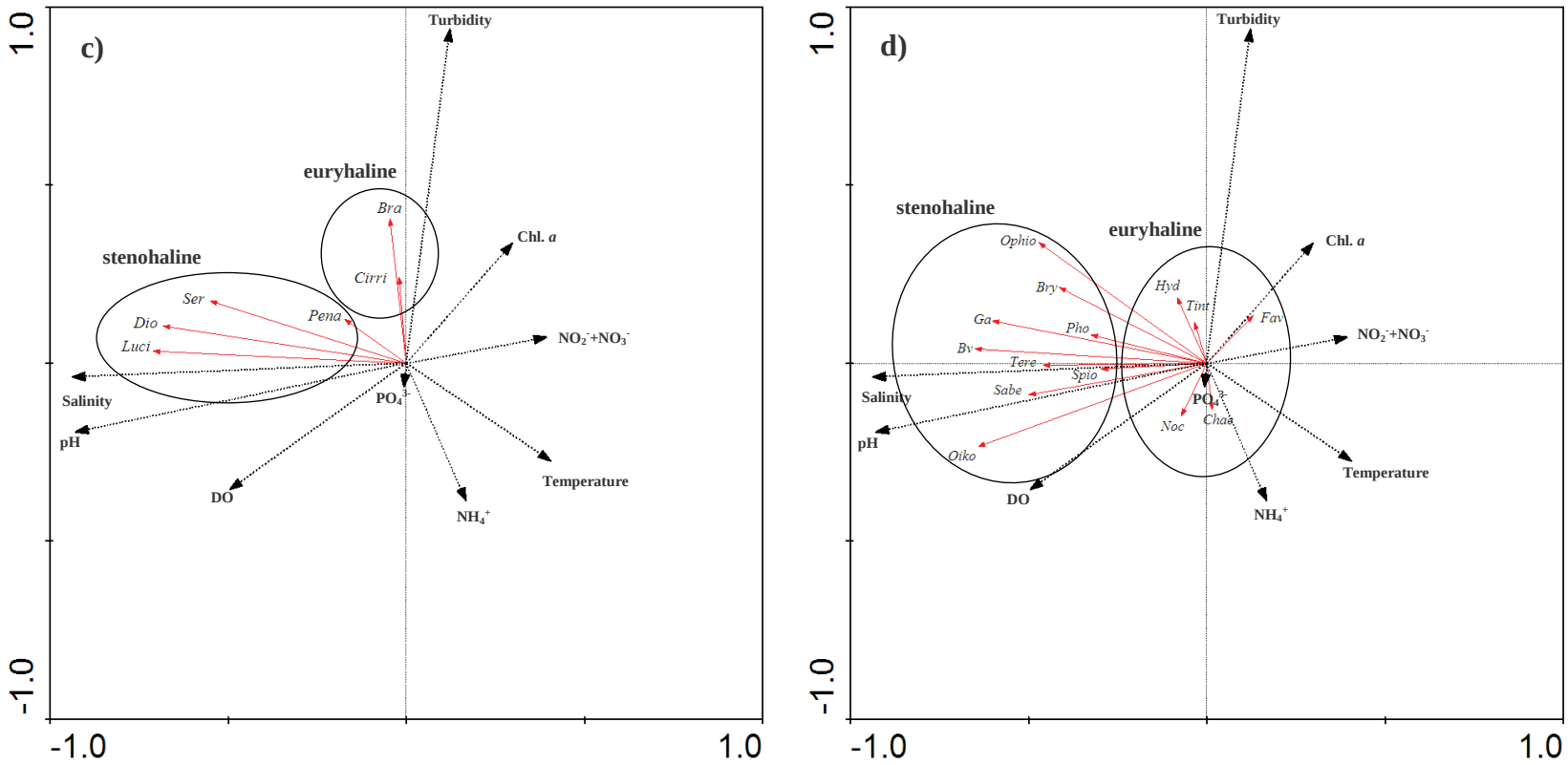


Fig. 3.23. RDA ordination diagrams showing (a) biplots of environmental parameters (dotted line arrows) and station samples (1-5), and (b: copepods, c: other crustacean zooplankton and d: non-crustacean zooplankton) biplots of environmental parameters (dotted line arrows) and zooplankton taxa (small arrow heads). Thin line arrows in (a) show seasonal shift of environmental parameters and zooplankton community structure from June - August 2002 (dry period) and from October to January 2003 (wet period) in the lower estuary. Numbers indicate sampled stations at: 1, upper estuary; 2, mid-estuary; 3, lower estuary; 4, nearshore waters; and 5, offshore waters. Boldface numbers indicate sampling during NE monsoon, regular numbers indicate sampling during SW monsoon and underlined numbers indicate IN period. Species abbreviations are given in Table 3.10.

3.1.8 Relationships between potential food and consumers

As discussed in section 3.2.1, phytoplankton blooms in Matang mangrove estuaries were not observed during the onset of heavy rainfall but after a lag period of freshwater flushing (e.g. January 2003 and March 2003). Interestingly, secondary peaks of chl. *a* in August 2002 and July 2003, which were not mentioned earlier (Fig. 3.24) coincided with strong SW and westerly winds (see section 3.2.1, pg. 62). This could be due to resuspension of benthic diatoms or nutrient replenishment for phytoplankton production as a result of wind mixing currents. Protozoans showed a good correspondence with phytoplankton peaks except in July 2003. The mismatch between protozoans and phytoplankton during this period could be due to high abundance of copepods (above annual mean), which may have fed on protozoans. However, the abundance of protozoans might be underestimated by the plankton net (180 µm) used in the present study.

Monthly copepod abundance above annual mean was closely linked to phytoplankton and protozoan peaks except in October 2003. Monthly abundance of other zooplankton was relatively close to annual mean over the sampling period. This was due to a combination of various taxonomic groups (e.g. cirripede and polychaete larvae) which have different timing of mass spawning. The carnivorous zooplankton, which have been known to feed voraciously on copepods showed good matches with their potential prey items except in May 2002 and October 2003. The mismatches could not be ascertained as there were no data available beyond the sampling period.

Fish larvae peaks were closely linked to phytoplankton or zooplankton food from August 2002 to March 2003. It was noted that two extreme low fish larvae abundance in February and May 2003 corresponded to peak carnivorous zooplankton or low abundance of zooplankton food source, suggesting an intense predation pressure and food limitation for fish larvae. On the other hand, high larval fish abundance might

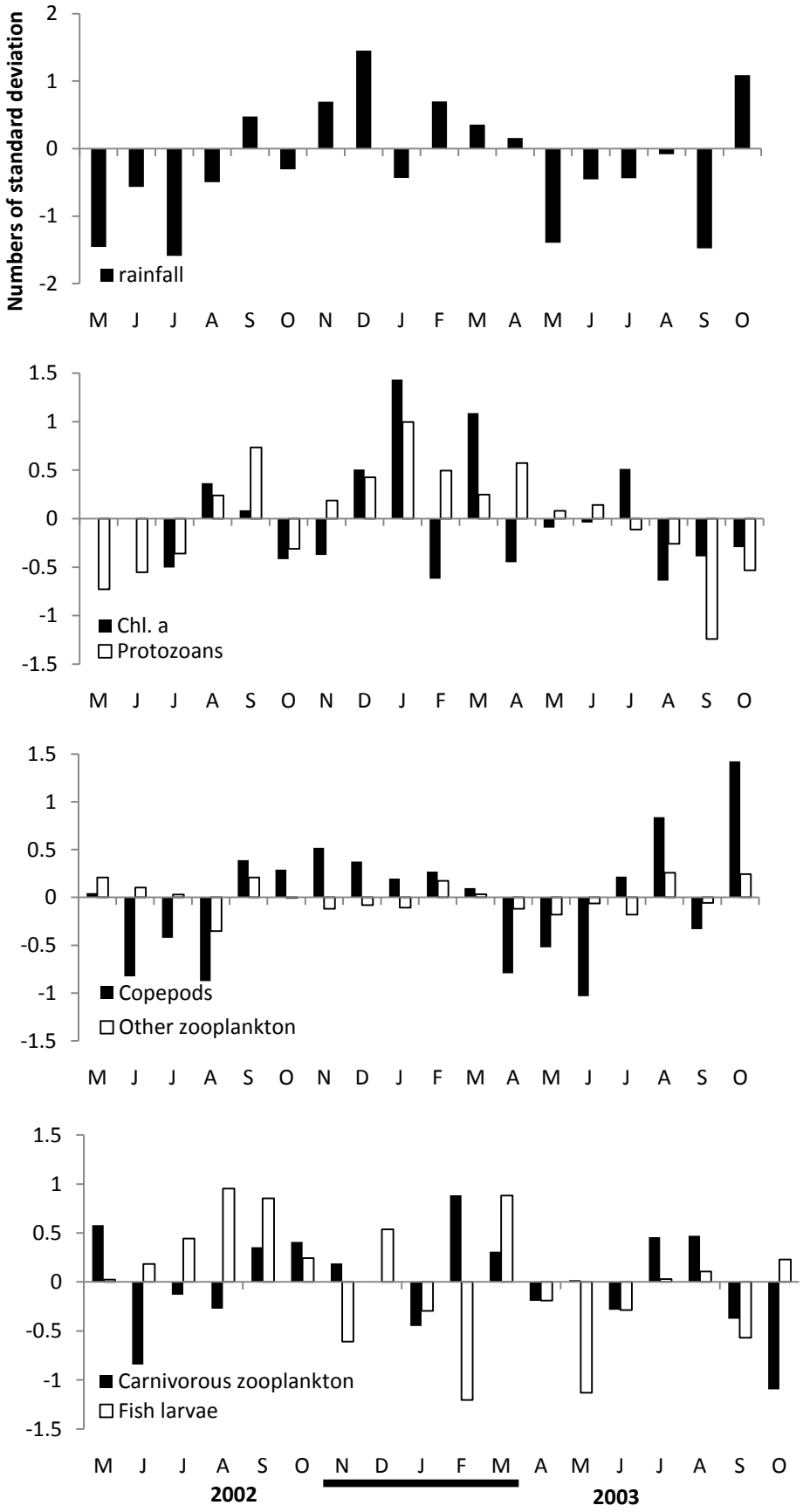


Fig. 3.24. Monthly variations of rainfall, chl. a, zooplankton and fish larvae (Ooi & Chong, 2011) in Matang mangrove estuaries. The zero baseline indicates mean of these variables over the 18 months of sampling. Positive values indicate plankton yields above the average, whereas negative values indicate below the average. Horizontal bar indicates Northeast monsoon.

reduce the copepod abundance through predation in August 2002.

3.2 Discussion

3.2.1 Climate, hydrography and phytoplankton of the study area

The precipitation pattern in Malaysia is closely linked to the seasonal monsoon with relatively drier months during the SW monsoon and wetter months during the IN period and NE monsoon although wind and rain patterns in Peninsular Malaysia can be very localized (Malaysian Meteorological Department). Cheang (1988a, b) reported that heavy rainfall normally occurs during the early part of the NE monsoon followed by dry spells during the later part, but the SW monsoon brings diminished rainfall. Peak rainfall was reported generally during the intermonsoon periods (Leyu & Ling, 1988). The SPI of Taiping over a 12-year period is analogous to the general Malaysian climate.

The hydrographic conditions of Matang mangrove estuaries and adjacent coastal waters show strong spatiotemporal variations except for temperature. As compared to previous studies by Sasekumar *et* al. (1994) and Chong *et* al. (1999) in the same estuaries, mean water temperature of Matang mangrove estuary over a decade remained constant at approximately 30 to 31 ^{o}C. The maximum range of mean monthly surface water temperatures from the upper estuary to offshore waters was merely 1.5 ^{o}C for the present study. Chong *et* al. (1999) reported that water temperature did not vary seasonally in the Matang mangrove estuary.

A longitudinal gradient of salinity, pH and DO always develops from the upper estuary of Matang to offshore waters. The gradient particularly salinity however, tends to diminish when the strong SW and westerly winds generate a horizontal mixing between mangrove and adjacent coastal waters. Salinity was spatially homogeneous from the upper estuary of Matang to nearshore waters in August 2002, a month after the severely-dry event and coincident with the strong wind event. Homogeneity of salinity

that was confined inside the mangrove estuaries was also observed during the months of lower rainfall in January, March and July 2003 (see Figs. 3.5 and 3.6). Heavy rainfall during the onset of NE monsoon has depressive effect on salinity and pH in Matang and adjacent coastal waters as also reported by the previous study in the same study area (Chong *et* al., 1999). Unlike pH and salinity, DO values in Matang mangrove estuaries tended to increase in the early part of NE monsoon due to a large quantity of well oxygenated freshwater input (Singh, 2003). DO values were relatively lower in the later part of NE monsoon, coincident with peak chl. *a* concentration (see Figs. 3.6 and 3.8). This paradoxical situation is likely the consequence of high bacterial activity. Lee and Bong (2008) reported that the nearshore waters of Peninsular Malaysia were net-heterotrophic and peak bacterial abundance could occur with high chl. *a* concentration. In the Matang waters, Alongi *et* al. (2003) similarly reported moderate to high rates of bacteria respiration (2003). Thus, low DO values were attributable to increased heterotrophic bacteria respiration in the mangrove estuary.

The Matang mangrove and nearshore waters are characterized by high turbidity as compared to offshore waters. This implies that the mangrove estuary and nearshore waters are loaded with suspended particles from sediment load and particulate organic matter. Peak turbidity was observed to be coincident with phytoplankton bloom (see Figs. 3.6 and 3.8).

The phytoplankton productivity is mainly governed by the nutrient availability in the water column. The present study showed that essential nutrients for the primary production are more available in the Matang mangrove estuaries than in the offshore waters. As a result, phytoplankton is more abundant in the mangrove than offshore waters. The wet season is a key factor for nutrient enrichment prior to phytoplankton blooms. In the temperate estuary of Arcachon Bay, rates of phytoplankton production were low during a very dry spring period due to low dissolved inorganic nitrogen and

silicate, whereas high rates of phytoplankton production were observed in the wet spring period when river plume was intense (Glé *et* al, 2008). Tropical mangrove estuaries also experience the correspondence of phytoplankton bloom to wet season replete with nutrients (Trott & Alongi, 1999; Mwashote *et* at, 2005). In Matang mangrove estuary, the effect of high rainfall on nutrient elevation was significant and the phytoplankton blooms were observed after a time lag.

3.2.2 Zooplankton composition and community structure

As in other estuarine systems (Grindley, 1984; McKinnon & Klumpp, 1998a; Plourde *et* al., 2002; Osore *et* al., 2004; Li *et* al., 2006; Marques *et* al., 2006; Duggan *et* al., 2008; Marques *et* al., 2008; Primo *et* al., 2009), zooplankton community structure in the Matang mangrove estuaries is always susceptible to spatial and temporal variations of the environmental conditions. It is generally accepted that species diversity of zooplankton including fish larvae increases with increasing salinity in both tropical and temperate estuaries (Grindley, 1984; Madhupratap, 1987; McKinnon & Klumpp, 1998a; Li *et* al., 2006; Marques *et* al., 2006; Ramos *et* al., 2006). It was also suggested that zooplankton were most diverse at the river mouth (Grindley, 1984; Osore, 1992; Osore *et* al., 2004; Primo *et* al., 2009) due to a combination of both estuarine and marine species (Grindley, 1984; Primo *et* al., 2009). Low diversity of zooplankton in the estuaries was mainly attributed to high abundance of the dominant estuarine species (Lee & Chen, 2003; Primo *et* al., 2009). Zooplankton community in the Matang mangrove estuaries was similar to those of previous studies. The simultaneous fish larvae study also exhibited a similar pattern (Ooi & Chong, 2011).

Zooplankton diversity appeared to be closely related to salinity in subtropical Pearl River estuary, China (Li *et* al., 2006). Zooplankton community was found to be more diverse in the water salinity of >25 ppt whereas less diverse community was

observed in the water salinity of <5 ppt (Li *et* al., 2006). Miyashita *et* al. (2009) suggested that copepod diversity tends to increase towards oceanic waters. In this study, mean salinity of >25 ppt were recorded at the lower estuary and towards offshore waters (see Table 3.2). Therefore, zooplankton particularly copepods were more diverse at these areas compared with inner part of the estuaries.

The preliminary survey on pelagic zooplankton in 55 km offshore from the Matang mangrove estuaries displayed an unexpected low species richness of zooplankton (47 taxa) as well as copepods (28 taxa) (see Table 3.14). This might be related to the zooplankton sampling depth at the top 30 m while the estimated depth at this station was about 50 m. Since most of the adult copepods are nocturnal migrators, the preliminary survey might have undersampled the adult copepods that reside near sea bottom during the day. As species richness is highly sensitive to sample size and sampling effort (Clarke & Warwick, 2001), the reason for low species richness is more likely the result of undersampling since only one sample was collected at the far offshore station. In such a situation, the rarefaction index ES (*n*), which generates an expected number of species found in a sample of *n* individuals (Hurlbert, 1971) but not applied in the present study, may be more appropriate to compare the species richness between samples of uneven sizes.

Grindley (1984) categorized mangrove zooplankton into four components based on their salinity preference: 1) freshwater, 2) estuarine, 3) stenohaline and 4) euryhaline. All four components were found in the North Queensland mangrove estuaries but the freshwater component appeared to be transient (McKinnon and Klumpp, 1988a). In Alligator creek, zooplankton were composed of mainly the representatives of euryhaline and stenohaline species, but no freshwater and estuarine species were observed due to a consistent salinity of >30 ppt (Robertson *et* al., 1988). All components except for freshwater species were observed in the present study. There was also no freshwater fish

larvae sampled in the Lima estuary, Portugal (Ramos *et* al., 2006). The authors suggested that the absence of the freshwater species might be related to salinity intolerance which exceeded 15 ppt. The minimum salinity in this study was 12 ppt at the upper estuary (see Table 3.2), possibly inhibiting the intrusion of freshwater zooplankton into the study area.

Copepods, cirripede larvae and polychaete larvae constituted the most dominant mesozooplankton in the Matang mangrove estuaries and adjacent coastal waters while protozoans formed the important part of microzooplankton. Nevertheless, the numerical abundance of microzooplankton was highly underestimated in the present study due to the potential loss of individuals smaller than 180 µm and the use of formaldehyde as fixative. The latter was reported to cause a significant loss of aloricate ciliates (Leakey *et* al., 1994). Chaetognaths, cnidarians, ctenophores, larvaceans, decapods, bryozoans, gastropods, bivalves, and echinoderms constituted the common taxa in this study. Because of time and technical constraints, identification at species level was made only for copepods and sergestid shrimps. Other holoplankton and meroplankton were identified at the best possible taxonomic level.

A total of 48 copepod species were identified for the near surface waters of Matang mangrove estuaries and adjacent coastal waters. The unidentified *Acartia* sp. 1 appeared be a new species, while *Pseudodiaptomus thailandensis* Walter is a first record for Malaysian waters. Compared with the 24-hour samplings conducted at the lower estuary (see Chapter 4), the species composition of copepods between both surveys was relatively similar except for the four rare species which might have been sampled by chance (see Table 3.10). In marine pelagic realms, copepods generally constitute 55 - 95% of the metazooplankton abundance (Longhurst, 1985). In the present study, copepods constituted 47 - 83% of the mangrove and coastal zooplankton

Table 3.14. Preliminary results of zooplankton abundance, relative composition (% Rel) and species richness in 55 km offshore from Matang mangrove estuaries. '+' indicates present but constitutes <0.1% of total zooplankton abundance; number in parenthesis indicates relative abundance of copepods.

Taxon	Abundance	% Rel	Taxon	Abundance	% Rel
CRUSTACEA					
COPEPODA					
Copepod nauplius	1319	9	CYCLOPOIDA		
CALANOIDA			Corycaeidae		
Acartiidae			*Corycaeus andrewsi*	11	0.1
Acartia erythraea	34	0.2	*Onychocorycaeus catus* (Dahl F.)	44	0.3
A. spinicauda	+	+	*Corycaeus erythraeus*	+	+
Acartia sp.	+	+	*Corycaeus speciosus* Dana	+	+
Acartia copepodid	660	4	*Corycaeus* copepodid	271	2
Candaciidae			Oncaeidae		
Candacia discaudata Scott A.	144	1	*Oncaea clevei*	+	+
Candacia copepodid	87	1	*Oncaea* spp.	908	6
Centropagidae			Oithonidae		
Centropages furcatus	84	1	*Oithona attenuata*	17	0.1
			Oithona brevicornis	1039	7
Eucalanidae			*Oithona plumifera* Baird	198	1
Eucalanus subcrassus	18	0.1	*Oithona simplex*	17	0.1
Eucalanus copepodid	218	1	*Oithona* copepodid	704	5
Paracalanidae			Sapphirinidae		
Acrocalanus gracilis	16	0.1	*Copilia mirabilis platyonyx* Paiva	+	+
Paracalanus denudatus Sewell	44	0.3	*Copilia longistylis* Mori	+	+
Parvocalanus crassirostris	122	1			
Paracalanus parvus (Claus)	262	2	HARPACTICOIDA		
Paracalanidae copepodid	908	6	Euterpinidae		
			Euterpina acutifrons	476	3
Pontellidae					
Labidocera acuta (Dana)	+	+	Ectinosomatidae		
Pontellopsis krameri (Giesbrecht)	+	+	*Microsetella norvegica*	66	0.4
Pontellopsis tenuicauda (Giesbrecht)	+	+			
Pontellidae copepodid	16	0.1	Miraciidae		
			Macrosetella gracilis	175	1
Temoridae					
Temora discaudata	+	+			
Temora copepodid	87	1			
Total copepod	**7977**	**52**			
Number of adult copepod species	**28**				
Adult copepod	2797	18 (35)			
Copepod nauplius and copepodid	5180	34 (65)			

Table 3.14, continued

Taxon	Abundance	% Rel	Taxon	Abundance	% Rel
DECAPODA			POLYCHAETA		
Sergestidae			Terebellidae larvae	+	+
Unidentified Sergestidae protozoea	11	0.1	Unidentified polychaete larvae	888	6
Luciferidae			CHAETOGNATHA		
Lucifer protozoea	480	3	Chaetognaths	207	1
Lucifer juvenile	107	1			
Lucifer penicillifer Hansen	+	+	MOLLUSCA		
			GASTROPODA		
Penaeidae	+	+	Gastropods	96	1
Caridea			BIVALVIA		
Unidentified caridean zoea	18	0.1	Bivalves	302	2
Brachyura			ECHINODERMATA		
Brachyuran zoea	+	+	Ophiuluteus larvae	1330	9
Thallasinidae			CHORDATA		
Thallasinidae zoea	+	+	UROCHORDATA		
			Oikopleura spp.	3388	22
STOMATOPODA			*Fritillaria* spp.	+	+
Stomatopod larvae (Alima type)	+	+			
Stomatopod larvae (Erichthus type)	+	+	Unidentified eggs	87	1
Cladoceran	175	1			
CNIDARIA					
Siphonophora	129	1			
Medusa of hydrozoa	+	+			
Total zooplankton	**15215**	**100**			
Number of zooplankton taxa	**47**				

abundance. Ara (2004) reported a higher percent in Cananéia mangrove system, Brazil, with up to 98% of the zooplankton being copepods.

In general, estuarine copepods are mainly dominated by only one or few species whereas about 10 to 15 species are subdominant and the rest are rare (Mauchline, 1998). It was suggested that *Acartia* is the most important calanoid copepod in shallow waters, and it always co-occurs with the smaller copepods *Oithona* and *P. crassirostris* in tropical estuaries (Mauchline, 1998). Acartiidae, Paracalanidae and Oithonidae were the predominant copepod taxa in the Matang mangrove estuaries and adjacent coastal waters, comprising 70% - 98% of total copepod population. This feature is also common in the mangrove systems elsewhere (McKinnon & Klumpp, 1998a; Ara, 2004; Duggan *et* al., 2008).

Three species of *Acartia* were found in the Matang and adjacent coastal waters with two being estuarine and one stenohaline. The estuarine species, *A. spinicauda* and *Acartia* sp. 1, were mostly sampled at their copepodid stages. Low abundance of adults as compared to copepodids implied the recruitment of a new generation and mortality during their development. The adults of this genus could have been undersampled near surface water as they undergo diel vertical migration even though in the shallow waters of Matang mangrove estuaries (see Chapter 4). McKinnon & Klumpp (1998a) found that the larger species such as *Acartia* were rare in mangrove estuary of Queensland, Australia due to their sampling method that mainly targeted the small size species.

The distribution of *Acartia* species is affected by salinity and temperature (Ueda, 1987; Cervetto *et* al., 1999; Gaudy *et* al., 2000). *Acartia californiensis* Trinast and *Acartia clausi* Giesbrecht found in the San Francisco Bay exhibited different responses to these parameters (Ambler *et* al., 1985). The former occurs mainly during the dry-warm period when salinity (>25 ppt) and temperature (>15 ^{o}C) are higher while the

latter prefers lower temperature (<20 ^{o}C) but has wider salinity tolerance (5-30 ppt) (Ambler *et* al., 1985). In tropical waters, Yoshida *et* al. (2006) suggested that *Acartia pacifica* Steuer prefers water of higher salinity and lower temperature as opposed to *A. spinicauda*. In the present study, temperature appeared to be constant throughout the sampling period. Therefore, salinity was the main factor that affected the distribution of *Acartia*. *A. erythraea* was found in more saline water but was not present inside the Matang mangrove estuary over the sampling period. On the other hand, *Acartia* sp. 1 was more confined to mangrove waters, while *A. spinicauda* was more dispersed including the adjacent coastal waters. *A. spinicauda*, which is known to have a broad salinity tolerance, was the most abundant Acartiidae sampled from the Matang mangrove estuaries and adjacent waters.

Parvocalanus crassirostris is widely distributed from the upper mangrove estuary to offshore waters. This species has been identified as a common species of Australian mangroves estuaries (McKinnon & Klumpp, 1998a; Duggan *et* al., 2008) and constituted an important small calanoid in subtropical Pearl River estuary (Chen *et* al., 2003). The species is considered eurythermal and euryhaline species since they are found to inhabit waters of 3.4 to 55 ppt and 1 to 30 ^{o}C (Lawson & Grice, 1973). Because of its ability to adapt to a wide range of salinities and temperatures, *P. crassirostris* has successfully dominated the copepod community of Matang and adjacent waters. The closely similar *P. elegans* is also, but sporadically present, while *B. similis* prefers more saline coastal waters but also frequently encountered in the Matang mangrove estuaries. The three Paracalanidae species have been reported to be among the dominant species of copepod found in the Straits of Malacca (Rezai *et* al., 2005). The stenohaline species *P. aculeatus* only occurred at the lower estuary of Matang and offshore waters and reported to be abundant in salinities that ranged from 30 to 32 ppt (Chen *et* al., 2003).

The cyclopoids, *Oithona simplex*, *O. attenuata*, *O. plumifera* Baird, *O. rigida* Giesbrecht and *O. nana* Giesbrecht are commonly encountered in Malaysian waters (Chua & Chong, 1975; Rezai *et* al., 2004). However, only the former two were commonly collected in Matang mangrove estuaries and its adjacent waters in the present study. As also reported by Oka (2000), the estuarine oithonids, *O. dissimilis* and *O. aruensis* are also common in Matang waterways but were not reported in the Straits of Malacca by Rezai *et* al. (2004) and Chua & Chong (1975). In the present study, *O. brevicornis* and *O. rigida* were both restricted to more saline waters. However, *O. rigida* was rare although it was found to be abundant in the Straits of Malacca (Chua & Chong, 1975; Rezai *et* al., 2004).

Our samples generally comprised of planktonic copepods. The so-called '*Saphirella*-like' copepodids of *Hemicyclops* were occasionally collected in both mangrove and adjacent coastal waters but were more abundant in the latter. The genus *Hemicyclops* with its first-stage copepodid occurring as plankton is closely associated with various benthic borrowers that are normally found in the estuary, coastal inlet and mudflat (Boxshall & Halsey, 2004; Itoh, 2006; Itoh & Nishida, 2007). Thus, as in our study, *Hemicyclops* copepodids were more abundant in nearshore waters close to coastal mudflats. Nevertheless, the ecology of this genus in the mudflat region of MMFR has not been documented before. Similarly, *Pseudomacrochiron* sp. 1 which is commonly associated with scyphozoans and hydrozoans (Boxshall & Halsey, 2004) was occasionally present in our samples.

Although cirripede larvae were the second most abundant mesozooplankton in temperate and tropical estuaries (Ooi, 2002; Muxagata *et* al., 2004; Highfield *et* al., 2010), the distribution and composition of these larvae have received few investigations of study as compared to copepods (Muxagata *et* al., 2004; Highfield *et* al., 2010). Cirripede larvae contributed an average of 13% to zooplankton abundance in the

Southampton estuary and their contribution sometimes can be up to 60% (Muxagata *et* al., 2004). Percentage composition of cirripede larvae in the Matang mangrove estuaries and adjacent coastal waters was comparable to the observation by Muxagata *et* al. (2004). These larvae, however, occurred in low numbers in more saline coastal waters (>28 ppt) of the Straits of Malacca (Yoshida *et* al., 2006) and entirely absent in open waters located in 55 km off Matang (see Table 3.14). The lack of hard surfaces for larval settlement in open waters probably accounts for the low abundance of these larvae compared with mangrove estuaries and rocky shores where cirripede adults occur in abundance.

Muxagata *et* al. (2004) identified a total of eight species of cirripede larvae in the Southampton estuary while Lang and Ackenhusen-Johns (1981) recorded six species in Rhode Island waters. There is no data on species composition of cirripede larvae in the Matang mangrove estuaries. The only adult species reported in this area was *Balanus amphitrite* Darwin, which occurs as biofouler on fish net-cages (Madin *et* al., 2009). This species together with *Balanus thailandicus* Puspasari, Yamaguchi & Angsupanich, *Euraphia withersi* (Pilsbry) and *Fistulobalanus patelliformis* (Bruguière) were major infesters on mangrove plants in other coastlines of Peninsular Malaysia (Tan, personal communication). Therefore, the cirripede larvae are likely to be released by more than one species in the Matang mangrove estuaries. Further research is required to identify both larvae and adults of cirripedes in Matang at higher taxonomic resolution. The coupling between larval release and settlement also deserves further investigation.

Decapods constitute another important component of mesozooplankton in Matang mangrove estuaries and its coastal waters despite their abundances being much lower than the copepods and cirripede larvae. Larvae of the four taxonomic groups (Brachyura, Sergestidae, Luciferidae and Diogenidae) dominated the decapod assemblages in Matang mangrove estuaries and adjacent coastal waters. Out of the four

groups, only Luciferidae remains planktonic through its life cycle while the other three groups were benthic at adult stage. Luciferidae was represented by *L. hanseni,* which was frequently observed at all sampling stations. This species was reported to have a wide range of salinity tolerance (4 - 34.5 ppt) in Cochin backwaters, India (Madhupratap, 1987). However, it was not found in more oceanic waters of the Straits of Malacca but replaced by other species namely *Lucifer penicillifer* Hansen (see Table 3.14; Chew *et* al., 2008).

Species composition of benthic polychaetes in the Matang mangrove estuaries was previously documented by Muhammad Ali (2004) and Natin (2001) in their M. Sc. dissertations. However, the planktonic polychaete larvae were only reported at general taxonomic level by Ooi (2002) and Madin *et* al (2009) in the same estuaries. Because of difficulties in determining the larval stages taxonomically, the planktonic polychaete larvae have drawn little interest of many zooplankton studies. The present study is the first to report the planktonic polychaete larvae at family level in the Matang mangrove estuaries. The larvae were composed mainly of Sabellariidae and Spionidae. Compared with their benthic counterparts, Sabellariidae was not reported in the Matang mangrove estuaries by Muhammad Ali (2004). Nevertheless, there is a similar trend in overall abundance between both benthic and planktonic polychaetes, with greater numbers collected at the lower part of the estuaries as compared to the upper part (present study; Muhammad Ali, 2004; Chong, 2007). This may suggest that most of the polychaete larvae are retained in the vicinities of their parental habitats rather than widely dispersed by current forces.

Other general groups of zooplankton found in the Matang mangrove estuaries and adjacent coastal waters were similarly reported for the other studies in the Straits of Malacca (Yoshida *et* al., 2006; Chew *et* al., 2008) with few exceptions. For example, siphonophores, salps and cladocerans were commonly sampled in more marine waters

of the Straits of Malacca (see Table 3.14; Yoshida *et* al., 2006; Chew *et* al., 2008) but almost no specimens of these taxa were collected in the Matang mangrove estuaries and its adjacent coastal waters even during the dry periods when high salinities prevailed.

3.2.3 Zooplankton abundance and biomass

The strong positive correlation between size-fractionated biomass and abundance in this study suggested no severe contamination of plant materials or significant influence of large bodied zooplankton such as *Acetes*, cnidarians and ctenophores on biomass in the samples, except the weak correlation for smaller sized fractions (<250 μm) in adjacent coastal waters with some extent of large size centric diatom mixture in the samples. However, this should not be a major problem when interpreting the abundance-biomass data since the spatial and seasonal pattern of total zooplankton abundance is reflective of total biomass.

In the present study, zooplankton showed strong spatiotemporal variations in abundance and biomass arising from heterogeneous environments along the sampling transect. On average, zooplankton yielded greater numbers at the lower estuary and nearshore waters and the numbers decreased in both upstream and seaward directions. Chong *et* al. (2004) reported a similar spatial pattern in the same estuaries. Kibirige *et* al. (2006) similarly exhibited the highest zooplankton abundance at the mouth of temporally open estuaries. The concurrent fish larvae abundance (Ooi & Chong, 2011), however, did not match the spatial abundance pattern of zooplankton in the Matang mangrove estuaries.

Although zooplankton abundance data may not be comparable among studies due to different mesh sizes of plankton nets used for sampling, zooplankton abundances reported for most of the studies conducted in mangrove estuaries and coastal waters are generally in the range of 10^4 to 10^5 ind m^{-3} (Robertson and Blaber, 1992). Mean

zooplankton abundances by sampling stations for the present study (ca. 10^4 ind m^{-3}; see Table 3.4) were comparable with the previous studies reviewed by Robertson and Blaber (1992). Compared with studies done in offshore waters of the Straits of Malacca (Yoshida *et* al., 2006; Chew *et* al., 2008), zooplankton abundance in the vicinities of Matang mangrove estuaries was higher than those areas with less influence of riverine discharge. This was similarly reported in the previous studies that specifically focused on copepods (Chong & Chua, 1975; Chua & Chong, 1975; Rezai *et* al., 2004). Zooplankton abundance at 55 km offshore waters in the Straits of Malacca was slightly lower than the present study but on the other hand higher in wet biomass (see Table 3.14; Chew *et* al., 2008). The 55 km offshore sample was composed mainly of gelatinous zooplankton such as larvaceans and siphonophores. Therefore, higher wet biomass might be attributed to high water content of these animals.

Seasonality of zooplankton has been documented in tropical and temperate estuaries and coastal waters (Grindley, 1984; Ambler *et* al., 1985; Madhupratap, 1987; Osore, 1992; Wong *et* al., 1993; Mackinnon & Klumpp, 1998a; Plourde *et* al., 2002; Lee & Chen, 2003; Krumme & Liang, 2004; Li *et* al., 2006; Duggan *et* al., 2008), and most of the studies showed higher zooplankton abundance during the wet season than the dry season or a time lag of freshwater runoff. Seasonal abundance patterns of zooplankton in Matang mangrove estuaries and adjacent coastal waters varied among taxa. Copepods dominated by *A. spinicauda* and its copepodids, *P. crassirostris* and *O. simplex* were more abundant during the NE monsoon. The former two species contributed to abrupt increases of copepods by up to 60,000 ind m^{-3} in the estuaries (see Fig. 3.14). The previous studies conducted at fish net-cages in the same estuaries similarly reported higher copepod abundance during the NE monsoon (Ooi, 2002; Madin, 2010). Tranter & Abraham (1971) in contrast recorded ca. 55,000 ind m^{-3} of copepods in Cochin backwaters, India during the drier post and premonsoon period.

Subbaraju & Krishnamurthy (1972) showed an even higher abundance of 286,000 ind m^{-3} in the Vellar estuary, India. In comparison, the offshore waters of the Straits of Malacca yielded a mean total copepod abundance of only 3,000 ind m^{-3} and no significant monsoonal differences being observed along the north-south transect of the Straits (Rezai *et* al., 2004). Comparison of abundance data among studies, however, must be cautiously interpreted as different mesh sizes of nets were used.

Large amount of freshwater input is likely to favour proliferation of *Acartia* in some tropical and subtropical estuaries. For example, in Mida creek, Kenya, *Acartia* abundance peaked during the rainy season whereas most of the other zooplankton found in the same area were more abundant during the dry season (Osore *et* al., 2004). Similarly, increases in *Acartia* abundance during the rainy summer were observed in the inner region of Tapong Bay, Taiwan (Hsu *et* al., 2008) and Pearl River estuary, China (Lee & Chen, 2003). Unlike temperate estuaries (e.g. Sullivan & McManus, 1986; Katajitso *et* al., 1998), the mechanisms that are responsible for the timing of *Acartia* reproduction and seasonal succession in tropical mangrove estuaries are still poorly understood. Further research is needed to understand how freshwater runoff regulates the timing and magnitude of reproduction of *Acartia* in tropical mangrove estuaries.

The spawning of meroplanktonic larvae in temperate waters always corresponded to phytoplankton bloom during the warm summer, in which the environmental conditions are favourable for larval release (Goncalves *et* al., 2003; Highfield *et* al., 2010). However, the timing of larval release in Matang mangrove estuaries was inconsistent among the taxa. Increases of planktonic larvae during the NE monsoon were observed for brachyurans, Luciferidae and echinoderms. The former was also found to be more abundant during the wet season in Alligator creek (Robertson *et* al., 1988).

There were no significant seasonal variations of cirripede larvae in the Matang mangrove estuaries. This observation was consistent to a study conducted in Rhode Island waters (Lang & Ackenhusen-Johns, 1981), and in contrast to those studies in temperate waters with distinct seasonal pattern (Muxagata *et* al., 2004; Highfield *et* al., 2010). Lee *et* al. (2006) reported non-seasonal larval settlement for cirripede *Chthamalus malayensis* Pilsbry on the coast of Peninsular Malaysia. The highest settlement rate observed in their study occurred in October and November, which was comparable to peak abundance of cirripede larvae in the Matang mangrove estuaries. Madin *et* al. (2009), however, reported low cirripede larval settlement rate on fish net-cages during the wet season in the Matang mangrove estuaries. This discrepancy may be related to their sampling location at the upper part of the estuaries which experienced the lowest salinity of 5 ppt during the wet season. This low saline water location was far below the threshold level for cirripede larvae (Chan *et* al., 2001) and is thus unfavourable for the colonization of the larvae.

The success of meroplanktonic larvae is closely associated with their adult population and vice versa through benthic-pelagic coupling. The seasonal variations of planktonic gastropods, bivalves and polychaetes were consistent to their benthic forms as reported in the previous study (Muhammad Ali, 2004). Both gastropods and bivalves did not show a clear monsoonal variability, whereas the polychaetes preferred drier SW monsoon. Because of the limited long-term data, whether these patterns are inter-annually consistent remains unclear.

Chaetognaths, cnidarians and ctenophores were frequently encountered in the Matang mangrove estuaries but occurred in low numbers. These animals prey mainly on copepods and thus their abundances are undoubtedly linked to the abundance of copepods (Froneman *et* al., 1998; Sullivan *et* al., 2001; Osore *et* al., 2004; Purcell & Decker, 2005; Tönnesson & Tiselius, 2005), although in the estuaries they are subject to

large salinity changes. The abundance of this component was closely linked to copepod abundance in the present study (see sections 3.1.7.5 & 6).

3.2.4 Factors influencing zooplankton dynamics

Estuarine zooplankton abundance and distribution are subject to unstable physical-chemical conditions, biological interactions and combinations of these factors (Grindley, 1984; Ambler *et* al., 1985; Kibirige & Perissinotto, 2003; Froneman, 2004; Marques *et* al., 2008; Duggan *et* al., 2008). As mentioned earlier, temperature in the Matang mangrove estuaries has been inter-annually constant over the past decade, and therefore its influence on zooplankton community is considered to be minor as compared to other environmental parameters. Gouda and Panigrahy (1995) found that copepod abundance was not significantly affected by temperature in a tropical Indian estuary. Other environmental parameters in the Matang mangrove estuaries and adjacent coastal waters are significantly altered by annual rainfall patterns that are dictated by the seasonal monsoons. Of the physical-chemical parameters, salinity is a key factor controlling zooplankton distribution of Matang mangrove estuaries both in space and time albeit other factors are also important. Using a regression logistic model, Marques *et* al. (2008) defined that salinity is the most reliable parameter to predict zooplankton distribution in temperate estuaries. In this study, lower estuary and nearshore waters recorded on average higher zooplankton abundance and species diversity than other sampling stations, suggesting an optimal salinity range for most of the zooplankton taxa sampled during the study period.

In terms of biological alterations, species-specific physiology, food availability and quality and predation pressure are known to have significant impact on zooplankton in estuaries and coastal waters. The dominance of *P. crassirostris, Oithona* and *Acartia* can be attributed to their physiological adaptation with high reproduction and growth

rates and low metabolic and mortality rates (Paffenhöfer, 1993; Mauchline, 1998; Turner, 2004). These taxa occur year-round in the Matang mangrove estuaries but their spawning and larval production are timed to peak during the early NE monsoon just prior to phytoplankton bloom. Larvae and *Oithona* spp. (Nishibe *et* al., 2010) could alternatively feed on associated blooms of motile food such as naked ciliates, flagellates and dinoflagellates. Salinity depressed by freshwater runoff may act as a cue for massive reproduction of these taxa.

Although zooplankton may have fed on a wide range of food items, diatoms appear to be an important diet for secondary zooplankton consumers such as copepods in the marine food webs (Kleppel, 1993; Irigoien *et* al., 2004). Vargas *et* al. (2010) suggested that large size diatoms contain relatively high lipid concentrations such as HUFA and PUFA that are essential for copepod egg production and growth in productive coastal waters. Schwamborn *et* al. (2006) demonstrated high selectivity of brachyuran zoeae on diatoms over animal food. Although phytoplankton composition has not been documented in the Matang mangrove estuaries and adjacent coastal waters, the large size centric diatoms that incidentally caught by the zooplankton net are notably more abundant in nearshore waters as compared to inner part of the estuaries (personal observation). Chai *et* al. (2011) examined the composition of microphytobenthos in the mudflat areas adjacent to Matang mangrove estuaries and found a considerable proportion of planktonic centric diatom species, *Coscinodiscus subtilis* Ehrenberg in their sediment samples. In addition to optimal salinity range, the prevalence of large centric diatoms may explain why nearshore waters accommodate such high diversity and abundance of zooplankton including most of the meroplanktonic larvae sampled. The stable isotope results of zooplankton collected from nearshore waters did indicate utilization of nutritious diatom food source (see Chapter 5). Qasim *et* al. (1969) reported

that seasonality of zooplankton in mangrove estuaries is largely dependent on the type of local phytoplankton.

Zooplankton population dynamics are often linked to their food availability and predation pressure in marine ecosystem (Kiørboe, 1997). The synchronicity between peak zooplankton abundance and phytoplankton is particularly important to ensure sufficient food source for the survival of newly-spawned juveniles, and in a similar way supports higher trophic levels in the food webs. The timing of larval fish spawning and zooplankton peaks in relation to temperature has been well documented in temperate waters (Lara-Lopez & Neira, 2008 and references therein). In tropical coastal waters of Peninsular Malaysia, the larval recruitments of penaeids (Chong, 1993) and engraulids (Sarpedonti, 2000) were closely linked to peak phytoplankton, zooplankton and annual rainfall. The authors suggested that the variability in food concentrations was related to rainfall pattern that is monsoonal-dictated.

The present study is generally in agreement that spawning of zooplankton was closely related with their potential food abundance in the Matang mangrove system, and therefore there is evidence that the match-mismatch hypothesis may be applicable to tropical waters (see Cushing *et* al., 1990). Ooi & Chong (2011) also reported strong correlation between fish larvae and zooplankton abundance in these estuaries. Although zooplankton loss by predation was not quantitatively measured in the present study, high dependency of juvenile and small-sized fish on zooplankton (see Chapter 5) indicates significant impact of predation on zooplankton community. Nevertheless, the relationships between the temporal variation of food and consumers, as discussed here, may be difficult to prove conclusively based on the simple comparisons of the temporal patterns of abundance. The exact trophic interactive processes are much complicated by various factors, including the different time scales and time lags of the different components of the food chain.

3.2.5 Limitations of the present study

Hopcroft *et* al. (1998) reported that the small copepods and their early developmental stages such as nauplii and copepodids were not adequately sampled by the standard 200-µm plankton net. In fact, this component was found to dominate the copepod community in tropical waters of Kingston Harbour, Jamaica (Hopcroft *et* al., 1998) and Darwin Harbour, Australia (Duggan *et* al., 2008). While it captured mainly medium and large sized zooplankton (>250 µm), the use of coarser mesh net (180 µm) in the present study may have undersampled a large proportion of microzooplankton including the protozoans and early developmental stages of various zooplankton taxa. Therefore, the relative importance of zooplankton functional groups in trophodynamics must be considered with caution.

Since sampling was undertaken near surface waters and during diurnal neap tide, the effects of short-term variations such as moon phase, diel and tidal cycles on zooplankton community as well as their depth profile pattern were not detected. For example, adults of *Pseudodiaptomus* spp. were rarely encountered in daytime samples although fish diet analysis showed that large numbers of *Pseudodiaptomus annandalei* Sewell were eaten by small or juvenile demersal fish during the day (see Chapter 5; Chew *et* al., 2007). This suggests that some species particularly the nocturnal migrants were unrepresented in this sampling design. Therefore, further research is required to determine how the short-term variations affect zooplankton community in mangrove estuaries (see Chapter 4).

3.3 Conclusion

The abundance and community structure of zooplankton in the Matang estuary and adjacent coastal waters showed strong spatiotemporal variations in relation to the physical and chemical parameters that varied with the prevailing rainfall pattern.

Zooplankton abundance and chlorophyll *a* concentrations were higher in mangrove and nearshore waters than in offshore waters. Copepods dominated by *Acartia*, *Parvocalanus* and *Oithona* spp. were timed to peak in abundance prior to phytoplankton bloom during the NE monsoon when rainfall was highest. Conversely, mass spawning of polychaete larvae occurred during the drier SW monsoon. There was no significant seasonal pattern observed for cirripede larvae. Salinity and biological interactions such as phytoplankton availability and predation pressure appear to be the major controlling factors of zooplankton community in the estuary.

CHAPTER 4

SHORT-TERM VARIABILITY OF ZOOPLANKTON ABUNDANCE AND COMMUNITY STRUCTURE

4.1 Results

4.1.1 Hydrographic conditions

4.1.1.1 Salinity

Salinity ranged from 13.6 to 30.1 ppt and was significantly different between dry (27.9 ± 1.2 ppt) and wet (21.7 ± 3.4 ppt) periods (ANOVA, $p < 0.01$; Table 4.1). Differences in salinity among moon phases were smaller during the dry period (<4 ppt) as compared to during the wet period (ca. 10 ppt). Average bottom salinity was significantly higher than that of surface in both the dry and wet periods (ANOVA, $p < 0.01$; Tables 4.1 & 4.2). However, the marginally significant interaction effect between moon phase and depth ($p = 0.045$) in the dry period indicated a significant stratification in salinity during the 3rd quarter (Fig. 4.1, appendix Va). In the wet period, significant stratification in salinity was observed particularly during neap tide (Fig. 4.1, appendix Vb). Water column became vertically well mixed during spring tide (Fig. 4.1). Salinity tended to decrease from high water to low water and increased vice versa. This was more pronounced in the wet period during spring tide (Fig. 4.1).

4.1.1.2 Temperature

Surface and bottom temperatures recorded over 24-hour sampling varied between 28 ^{o}C and 33 ^{o}C (Table 4.1). Mean temperatures were approximately 30 to 31 ^{o}C. Although the differences in temperatures between dry and wet period and among moon phases were fairly small, the differences were statistically significant (ANOVA, $p < 0.01$; Tables 4.1, 4.2 & 4.3). In general, water temperature tended to peak in the

Table 4.1. Summary results of one-way ANOVA on various environmental parameters between dry and wet period. $\bar{x}$ = mean; n = sample size; Min = minimum, Max = maximum; ** significance at $p < 0.01$, ns no significance.

Variable		Period		
		Dry	Wet	p-level
Salinity	$\bar{x}$	27.9	21.7	**
(ppt)	n	96	96	
	± SD	1.2	3.4	
	Min	24.8	13.6	
	Max	30.1	27.5	
Temperature	$\bar{x}$	30.0	30.5	**
(^{o}C)	n	96	96	
	± SD	0.6	0.8	
	Min	28.5	28.6	
	Max	31.4	32.9	
pH	$\bar{x}$	7.7	7.5	**
	n	96	96	
	± SD	0.1	0.3	
	Min	7.5	6.8	
	Max	8.1	8.4	
DO	$\bar{x}$	4.2	4.8	**
(mg l^{-1})	n	96	96	
	± SD	0.9	1.8	
	Min	2.5	1.0	
	Max	6.3	12.3	
Turbidity	$\bar{x}$	89.8	99.7	ns
(NTU)	n	96	96	
	± SD	120.8	164.1	
	Min	9.4	9.8	
	Max	798.3	846.4	
NO_2^-+NO_3^-	$\bar{x}$	4.01	2.76	**
(µM)	n	47	35	
	± SD	1.71	1.17	
	Min	1.07	1.14	
	Max	7.71	5.07	
NH_4^+	$\bar{x}$	7.59	7.78	ns
(µM)	n	42	19	
	± SD	6.71	5.60	
	Min	0.71	0.71	
	Max	30.71	20.00	
PO_4^{3-}	$\bar{x}$	0.89	0.62	ns
(µM)	n	46	35	
	± SD	2.14	0.46	
	Min	0.11	0.11	
	Max	13.05	2.00	
chl. *a*	$\bar{x}$	19.0	17.6	ns
(µg l^{-1})	n	48	48	
	± SD	16.4	17.0	
	Min	5.6	6.7	
	Max	102.3	72.0	

Table 4.2. Summary results of three-way ANOVA and post-hoc Tukey HSD tests on physical parameters with respect to moon phase, tide, depth and their interaction in the dry period. $\bar{x}$ = mean; n = sample size; Min = minimum, Max = maximum; homogenous groups indicated by superscripts a, b, c and d; * significance at $p < 0.05$, ** significance at $p < 0.01$, ns no significance.

Variable		Source of Variation											
		Moon phase (1)					Tide (2)			Depth (3)			Significant interaction
		1st quarter	Full moon	3rd quarter	New moon	p-level	Ebb	Flood	p-level	Surface	Bottom	p-level	effect ($p < 0.05$)
	n	24	24	24	24		48	48		48	48		
Salinity (ppt)	$\bar{x}$	26.9[a]	27.5[b]	28.0[b]	29.2[c]	**	28.1	27.6	**	27.6	28.2	**	1 x 3 ($p = 0.045$)
	± SD	0.7	1.2	0.7	0.6		1.1	1.3		1.2	1.1		
	Min	25.0	24.8	26.5	27.9		26.3	24.8		24.8	24.9		
	Max	28.0	28.8	29.0	30.1		30.1	29.5		29.8	30.1		
Temperature (^oC)	$\bar{x}$	29.7[a]	29.7[a]	30.5[b]	29.9[a]	**	29.9	30.0	ns	30.0	29.9	ns	-
	± SD	0.7	0.1	0.7	0.3		0.5	0.7		0.7	0.6		
	Min	28.5	29.5	29.0	29.4		28.8	28.5		28.5	29.1		
	Max	31.3	29.8	31.4	30.4		31.2	31.4		31.4	31.2		
pH	$\bar{x}$	7.7[a]	7.7[a]	7.8[a]	7.6[b]	**	7.7	7.7	*	7.7	7.7	ns	-
	± SD	0.1	0.2	0.1	0.1		0.1	0.1		0.1	0.1		
	Min	7.5	7.5	7.5	7.5		7.5	7.5		7.5	7.5		
	Max	7.8	8.1	7.9	7.7		8.1	7.9		8.1	8.0		
DO ($mg\ l^{-1}$)	$\bar{x}$	4.7[a]	3.3[b]	5.2[c]	3.7[d]	**	4.3	4.1	ns	4.4	4.0	**	1 x 3
	± SD	0.5	0.3	0.6	0.6		0.9	1.0		1.0	0.7		
	Min	3.7	2.5	4.1	2.8		3.1	2.5		2.5	2.5		
	Max	5.7	3.6	6.3	4.9		6.0	6.3		6.3	5.2		
Turbidity (NTU)	$\bar{x}$	102.1[a]	110.6[b]	24.8[a]	121.5[a]	**	77.0	102.6	**	42.4	137.2	**	-
	± SD	121.1	109.4	17.0	165.2		137.2	101.7		42.7	151.9		
	Min	11.4	17.5	9.4	15.8		9.4	10.1		9.4	19.1		
	Max	540.1	471.0	73.5	798.3		798.3	471.0		240.0	798.3		

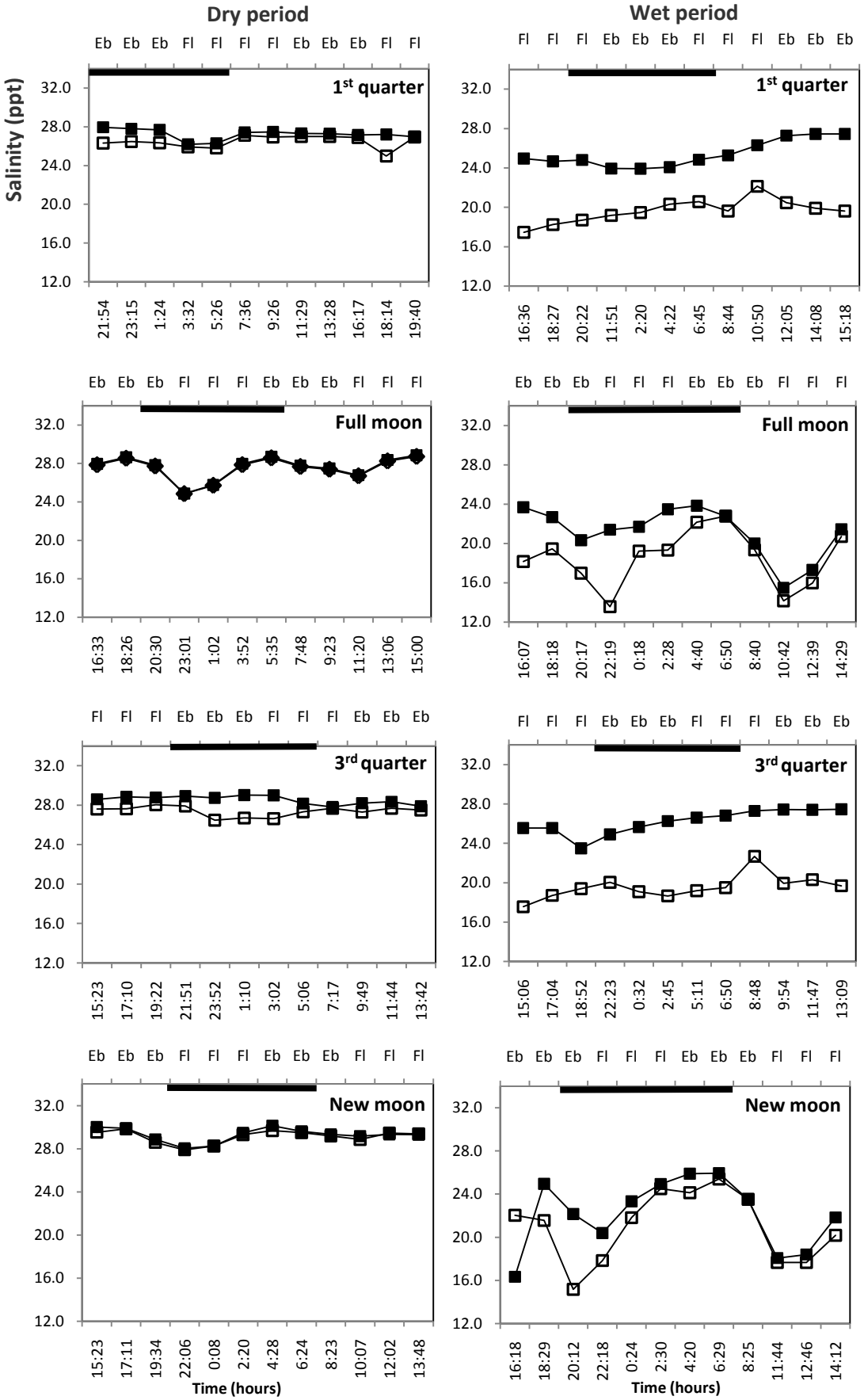


Fig. 4.1. Mean salinity of surface (□) and bottom (■) waters recorded over 24 hours and four consecutive moon phases in the dry and wet periods. Eb denotes ebb tide, Fl flood tide; horizontal bar indicates nighttime. SD not plotted in order to show clearer trend.

Table 4.3. Summary results of three-way ANOVA and post-hoc Tukey HSD tests on physical parameters with respect to moon phase, tide, depth and their interaction in the wet period. $\bar{x}$ = mean; n = sample size; Min = minimum, Max = maximum; homogenous groups indicated by superscripts a, b, c and d; * significance at $p < 0.05$, ** significance at $p < 0.01$, ns no significance.

Variable		Source of Variation											
		Moon phase (1)					Tide (2)			Depth (3)			Significant interaction
		1st quarter	Full moon	3rd quarter	New moon	p-level	Ebb	Flood	p-level	Surface	Bottom	p-level	effect ($p < 0.05$)
	n	24	24	24	24		48	48		48	48		
Salinity (ppt)	$\bar{x}$	22.5 [a]	19.8 [b]	22.9 [a]	21.6 [a]	**	22.3	21.0	**	19.7	23.7	**	1 x 3
	± SD	3.2	3.0	3.6	3.2		3.2	3.5		2.4	3.1		
	Min	17.5	13.6	17.6	15.2		15.2	13.6		13.6	15.5		
	Max	27.5	23.8	27.5	25.9		27.5	27.3		25.4	27.5		
Temperature (^{o}C)	$\bar{x}$	30.7 [a]	30.3 [a,b]	31.1 [c]	29.9 [b]	**	30.6	30.4	ns	30.7	30.3	**	1 x 3
	± SD	0.5	0.8	0.7	0.6		0.6	0.9		1.0	0.5		
	Min	30.0	29.2	30.6	28.6		29.5	28.6		28.7	28.6		
	Max	32.0	32.9	32.9	30.7		32.9	32.9		32.9	31.2		
pH	$\bar{x}$	7.6 [a]	7.6 [a]	7.6 [a]	7.3 [b]	**	7.6	7.4	**	7.5	7.5	ns	-
	± SD	0.1	0.4	0.1	0.4		0.2	0.4		0.3	0.3		
	Min	7.3	6.8	7.3	6.8		6.9	6.8		6.8	6.8		
	Max	7.8	8.4	8.0	7.8		8.4	8.0		8.4	8.0		
DO (mg l^{-1})	$\bar{x}$	5.5 [a]	5.7 [a]	4.5 [b]	3.6 [b]	**	5.3	4.4	**	5.4	4.2	**	1 x 3
	± SD	1.0	1.9	1.6	1.7		1.6	1.8		1.9	1.4		
	Min	4.1	2.6	2.6	1.0		2.3	1.0		1.1	1.0		
	Max	7.8	12.3	8.0	6.2		12.3	8.0		12.3	6.7		
Turbidity (NTU)	$\bar{x}$	32.5 [a]	137.7 [b]	31.5 [a]	197.2 [b]	**	87.0	112.4	*	68.0	131.5	**	-
	± SD	20.9	197.6	21.2	224.3		161.6	167.3		116.9	196.7		
	Min	9.8	18.4	11.7	25.0		9.8	11.7		9.8	17.9		
	Max	82.8	766.9	85.8	846.4		766.9	846.4		558.5	846.4		

afternoon and decreased during nighttime. Lower temperatures were generally recorded in the morning (0700- to 1200-hour) (Fig. 4.2). ANOVA results showed significant cooler water at the bottom than at surface water during neap tide in the wet period as indicated by significant interaction effect between moon phase and depth (ANOVA, $p < 0.01$; Table 4.3). Differences between surface and bottom temperature were not significant in the dry period. Temperature was not significantly affected by tide (ANOVA, $p > 0.05$; Tables 4.2 & 4.3).

4.1.1.3 pH

The surface and bottom pH values in the dry and wet periods varied between 7.5 and 8.1 and 6.8 and 8.4 respectively. Dry period had significantly higher pH values as compared to that of wet period (ANOVA, $p < 0.01$; Table 4.1). The variations in pH values between moon phases were small but the differences were significantly different (ANOVA, $p < 0.01$) for both dry and wet periods. There was no significant difference (ANOVA, $p > 0.05$) in pH values with respect to depth (Tables 4.2 & 4.3). pH tended to decrease from high tide to low tide and increased vice versa during spring tide (Fig. 4.3).

4.1.1.4 Dissolved oxygen (DO) concentrations

In the dry period, DO concentrations of both surface and bottom waters ranged from 2.5 to 6.3 mg l^{-1}, while in the wet period they ranged from 1.0 to 12.3 mg l^{-1}. Mean DO values of the wet period (4.8 ± 1.8 mg l^{-1}) was significantly higher (ANOVA, $p < 0.01$) than that of the dry period (4.2 ± 0.9 mg l^{-1}) (Table 4.1). Low oxygen was observed during spring tide except an exceptional high DO value at 1607-hour during full moon in the wet period (Fig. 4.4). Tide did not have any effect on DO concentration in the dry period but significantly higher (ANOVA, $p < 0.01$) DO concentration was observed during ebb tide than flood tide in the wet period. Mean DO value at surface

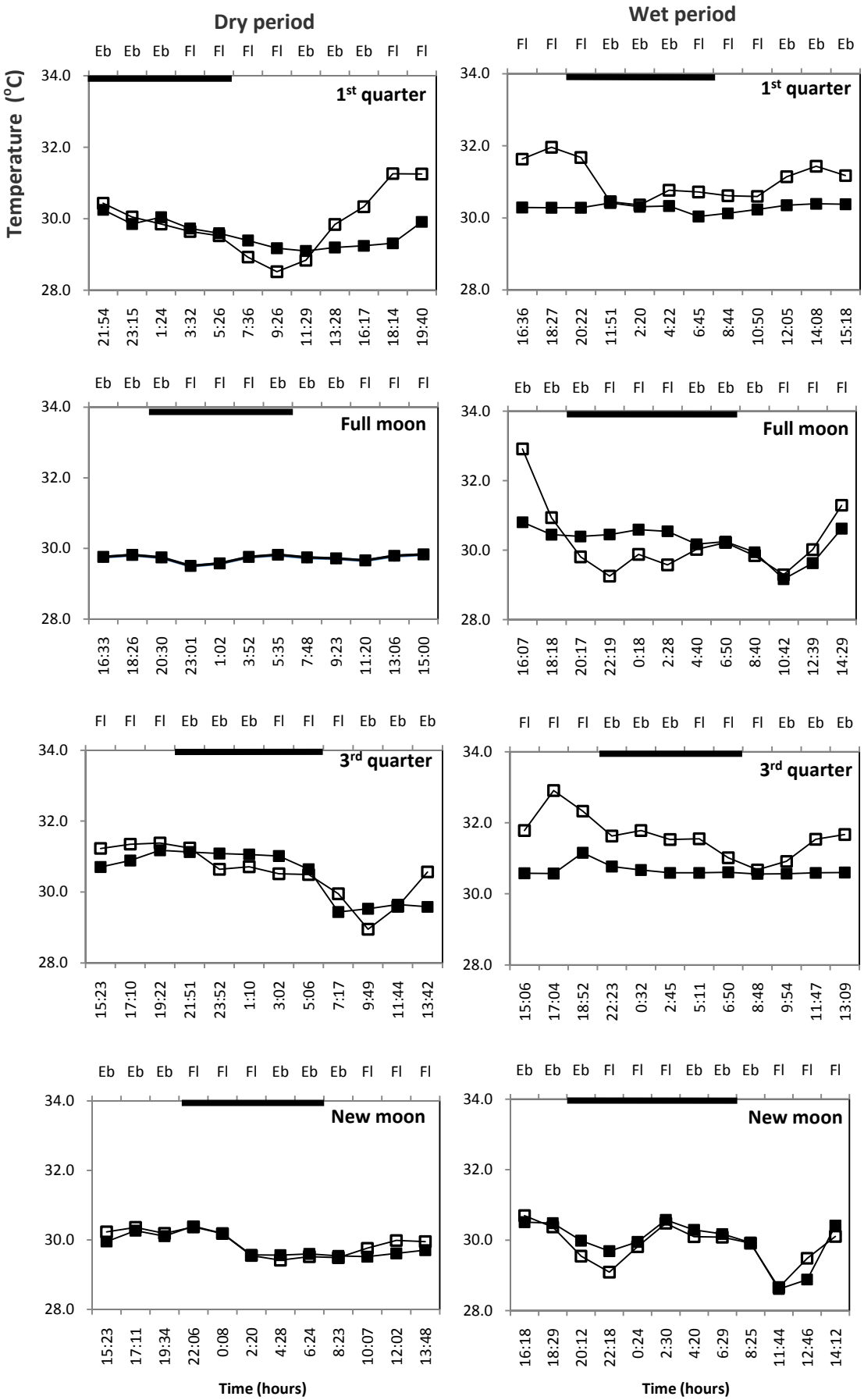


Fig. 4.2. Mean temperature of surface (□) and bottom (■) waters recorded over 24 hours and four consecutive moon phases in the dry and wet periods. Eb denotes ebb tide, Fl flood tide; horizontal bar indicates nighttime. SD not plotted in order to show clearer trend.

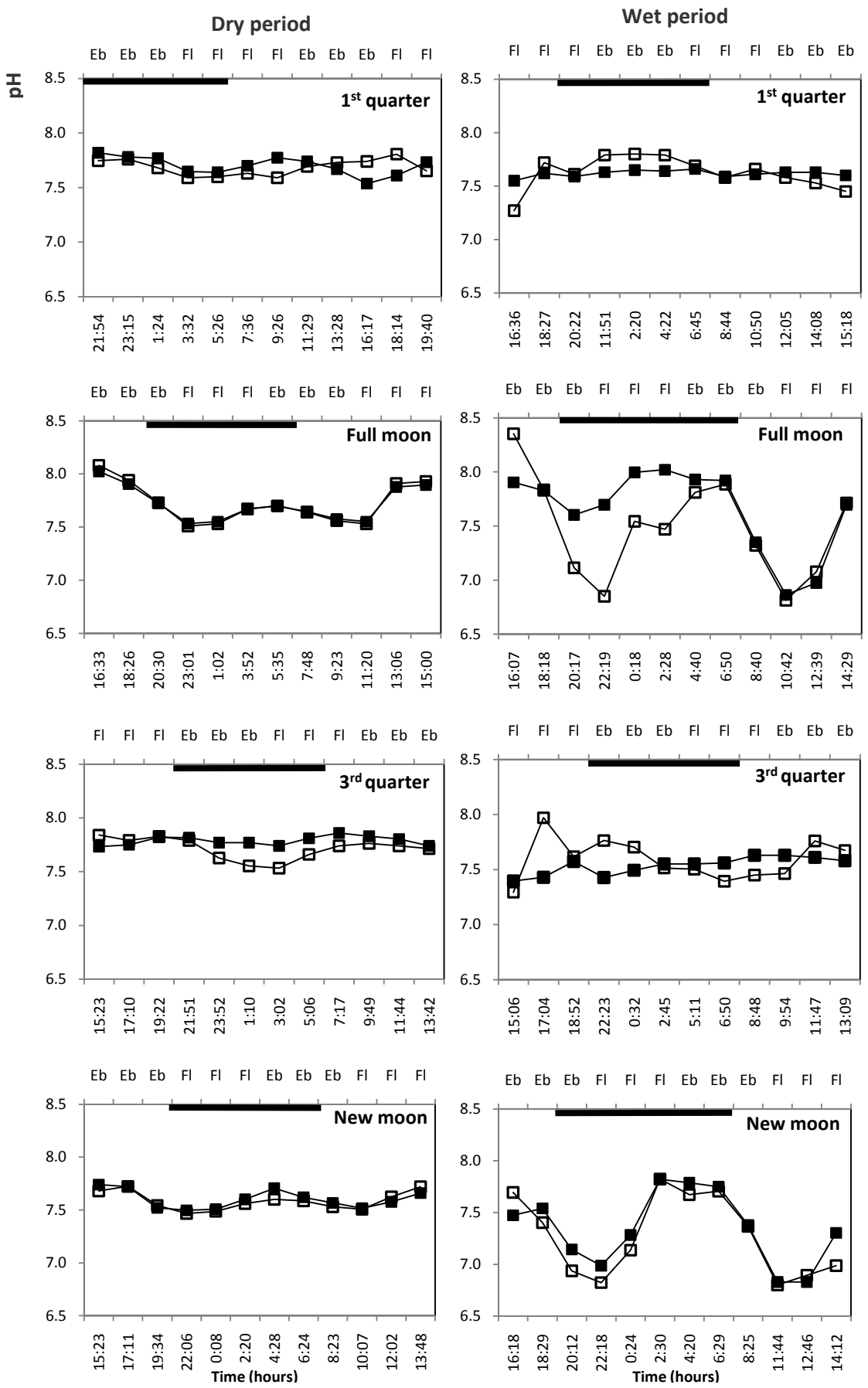


Fig. 4.3. Mean pH of surface (□) and bottom (■) waters recorded over 24 hours and four consecutive moon phases in the dry and wet periods. Eb denotes ebb tide, Fl flood tide; horizontal bar indicates nighttime. SD not plotted in order to show clearer trend.

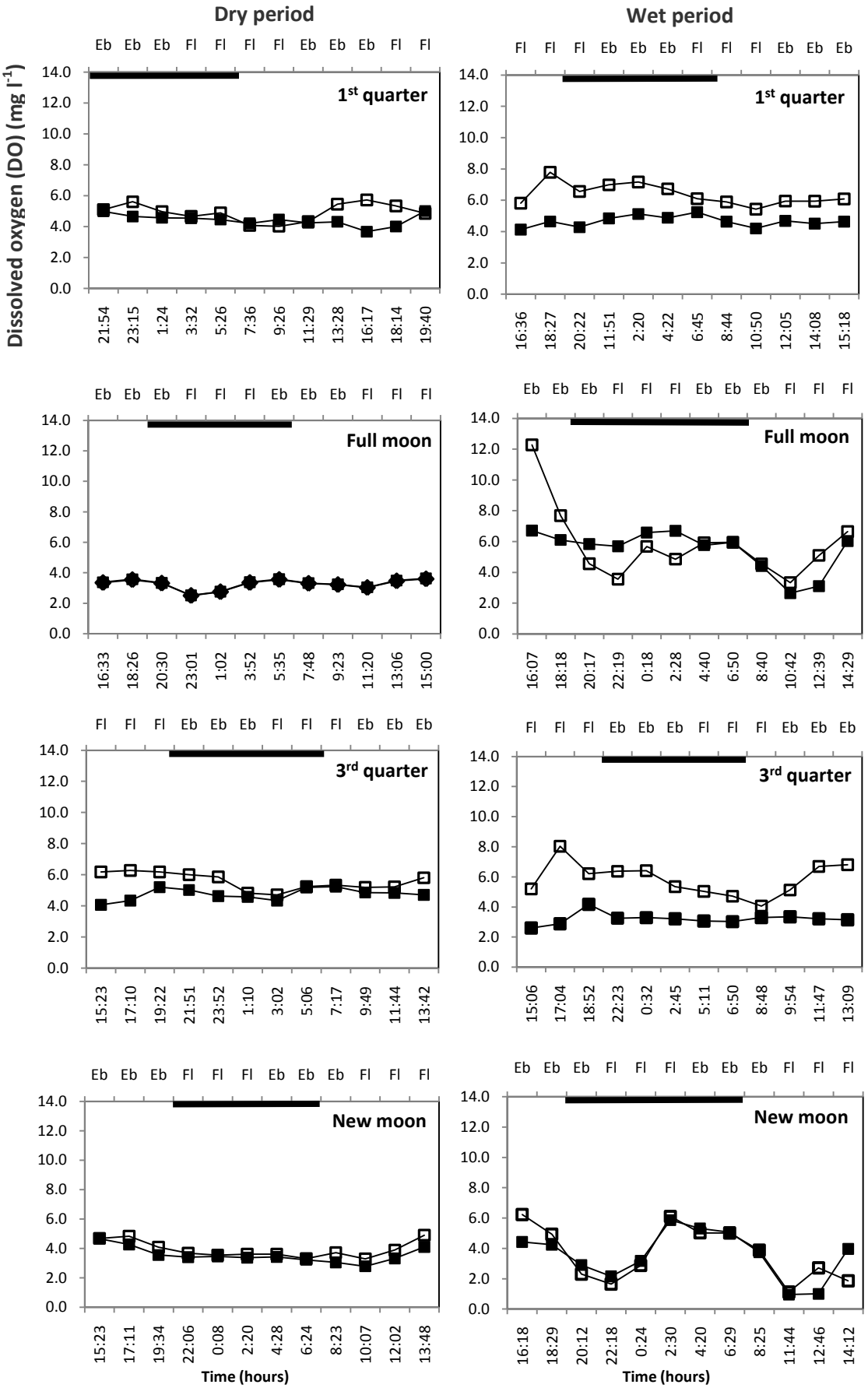


Fig. 4.4. Mean DO of surface (□) and bottom (■) waters recorded over 24 hours and four consecutive moon phases in the dry and wet periods. Eb denotes ebb tide, Fl flood tide; horizontal bar indicates nighttime. SD not plotted in order to show clearer trend.

water was significantly higher ($p < 0.01$) than bottom water. Similar to salinity, significant difference in DO value between water depth was observed during the 3rd quarter in the dry period (Fig. 4.4, appendix Vc). In the wet period, the depth difference in DO concentration was significant during neap tide (Fig. 4.4, appendix Vd).

4.1.1.5 Turbidity

There was a large variation in turbidity values that ranged from 9 to 846 NTU. Turbidity values were not significantly different between dry and wet periods (ANOVA, $p > 0.05$; Table 4.1). In general, turbidity was significantly higher during flood tide than ebb tide, and at the river bottom than at the surface water (ANOVA, $p < 0.01$) (Tables 4.2 & 4.3; Fig. 4.5).

4.1.2 Dissolved inorganic nutrients

The concentrations of $NO_2^- + NO_3^-$, NH_4^+ and PO_4^{3-} ranged from 1.07 to 7.71 µM, 0.71 to 30.71 µM and 0.11 to 13.05 µM, respectively. $NO_2^- + NO_3^-$ concentrations were significantly higher in the dry period than the wet period (ANOVA, $p < 0.01$), but differences were not significant for PO_4^{3-} (Table 4.1). The difference in NH_4^+ concentration between the dry and wet period was not statistically tested due to almost half (46%) of the water samples collected in the wet period had concentration that exceeded the detection range of the spectrophotometer (>35 µM). These over range data were collected mainly during the 3rd quarter and new moon phases (Fig. 4.7). Significantly higher dissolved inorganic nitrogen concentrations (4.94 ± 1.58 µM for $NO_2^- + NO_3^-$ and 12.56 ± 5.37 µM for NH_4^+) were observed during the new moon in the dry period (ANOVA, $p < 0.05$; Table 4.4). However, $NO_2^- + NO_3^-$ concentrations were not significantly different among moon phases in the wet period (ANOVA, $p > 0.05$) (Table 4.5; Fig. 4.7). PO_4^{3-} was not significantly different among moon phases, but the

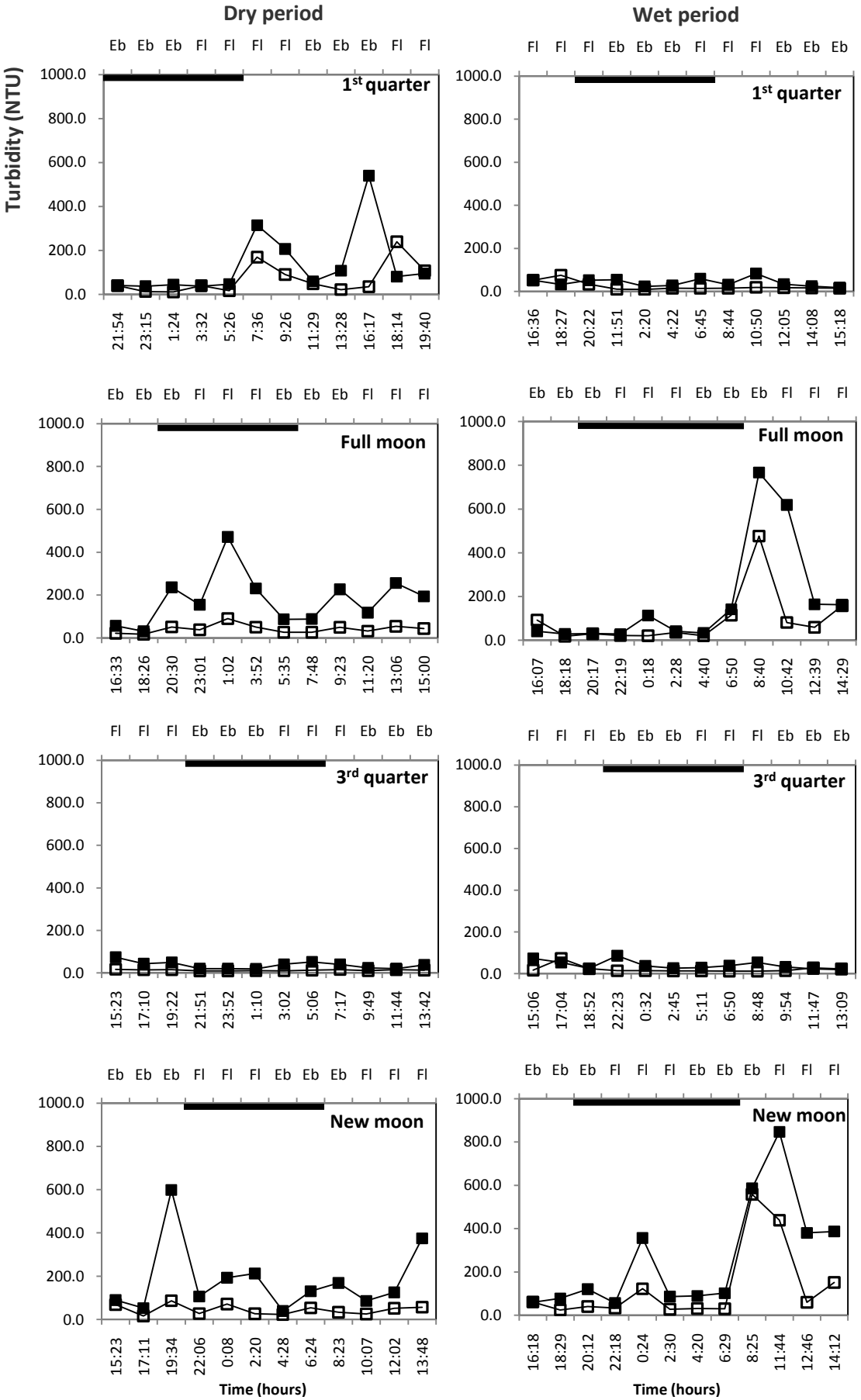


Fig. 4.5. Mean turbidity of surface (□) and bottom (■) waters recorded over 24 hours and four consecutive moon phases in the dry and wet periods. Eb denotes ebb tide, Fl flood tide; horizontal bar indicates nighttime. SD not plotted in order to show clearer trend.

highest concentration (13.05 µM) was observed at 0923-hour during full moon in the dry period (Fig. 4.8). Two-way ANOVA was not performed on the NH_4^+ concentrations in the wet periods as too limited data was available for the analysis. Dissolved inorganic nutrients were not significantly affected by tide (ANOVA, $p > 0.05$) (Tables 4.4 & 4.5).

Table 4.4. Summary results of two-way ANOVA and post-hoc Tukey HSD tests on dissolved inorganic nutrients with respect to moon phase, tide and their interaction in the dry period. $\bar{x}$ = mean; n = sample size; Min = minimum, Max = maximum; homogenous groups indicated by superscripts a, b and c; * significance at $p < 0.05$, ** significance at $p < 0.01$, ns no significance.

Variable		Source of Variation								
		Moon phase (1)					Tide (2)			(1) x (2)
		1st-quarter	Full moon	3rd quarter	New moon	p-level	Ebb	Flood	p-level	p-level
$NO_2^-+NO_3^-$ (µM)	$\bar{x}$	2.88 [a]	3.84 [a,b]	4.42 [a,b]	4.94 [b]	*	3.7	4.4	ns	ns
	n	12	12	11	12		24	23		
	± SD	0.98	0.64	2.53	1.58		1.8	1.5		
	Min	1.50	2.93	1.07	2.79		1.1	1.8		
	Max	4.71	5.36	7.71	7.71		7.7	7.6		
NH_4^+ (µM)	$\bar{x}$	3.04 [a]	3.44 [a,b]	9.61 [b,c]	12.56 [c]	**	7.5	7.7	ns	ns
	n	8	11	11	12		23	19		
	± SD	2.85	2.30	8.51	5.37		8.2	4.6		
	Min	0.71	0.71	0.71	6.43		0.7	1.4		
	Max	8.57	7.86	30.71	22.14		30.7	19.3		
PO_4^{3-} (µM)	$\bar{x}$	0.63	1.83	0.94	0.18	ns	1.3	0.5	ns	ns
	n	12	12	10	12		23	23		
	± SD	1.06	3.72	1.65	0.08		2.9	0.8		
	Min	0.11	0.11	0.11	0.11		0.1	0.1		
	Max	3.79	13.05	5.47	0.32		13.1	3.8		

Table 4.5. Summary results of two-way ANOVA and post-hoc Tukey HSD tests on dissolved inorganic nutrients with respect to moon phase, tide and their interaction in the wet period. $\bar{x}$ = mean; n = sample size; Min = minimum, Max = maximum; ns no significance, TFA too few data for ANOVA.

Variable		Source of Variation								
		Moon phase (1)					Tide (2)			(1) x (2)
		1st quarter	Full moon	3rd quarter	New moon	p-level	Ebb	Flood	p-level	p-level
$NO_2^-+NO_3^-$ (µM)	$\bar{x}$	2.92	2.45	2.13	3.34	ns	2.4	3.1	ns	ns
	n	6	12	6	11		17	18		
	± SD	1.15	1.07	0.72	1.30		0.8	1.4		
	Min	1.21	1.14	1.21	1.79		1.1	1.2		
	Max	4.79	4.64	3.00	5.07		4.3	5.1		
NH_4^+ (µM)	$\bar{x}$	9.76	5.78	10.00	15.71	TFA	5.4	10.5	TFA	TFA
	n	6	11	1	1		10	9		
	± SD	5.40	5.33	0.00	0.00		4.5	5.7		
	Min	4.29	0.71	10.00	15.71		0.7	0.7		
	Max	20.00	16.43	10.00	15.71		15.7	20.0		
PO_4^{3-} (µM)	$\bar{x}$	0.51	0.64	0.40	0.77	ns	0.6	0.6	ns	ns
	n	6	12	6	11		17	18		
	± SD	0.40	0.58	0.37	0.36		0.5	0.4		
	Min	0.11	0.11	0.11	0.21		0.1	0.1		
	Max	1.05	2.00	0.95	1.37		2.0	1.3		

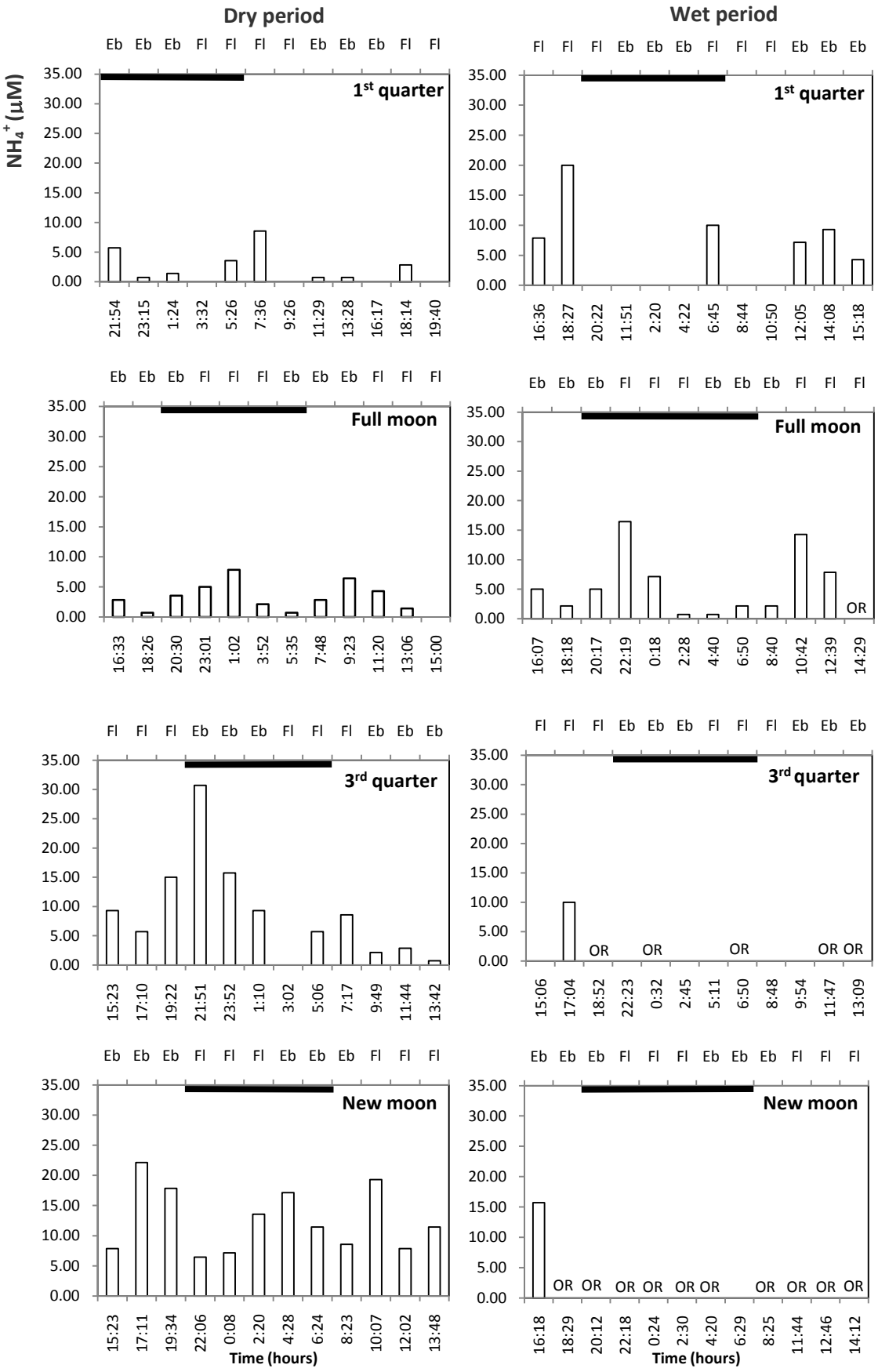


Fig. 4.6. Mean NH_4^+ of surface waters recorded over 24 hours and four consecutive moon phases in the dry and wet periods. Blank indicates data not available; OR over range data; Eb ebb tide, Fl flood tide; horizontal bar indicates nighttime. SD not plotted in order to show clearer trend.

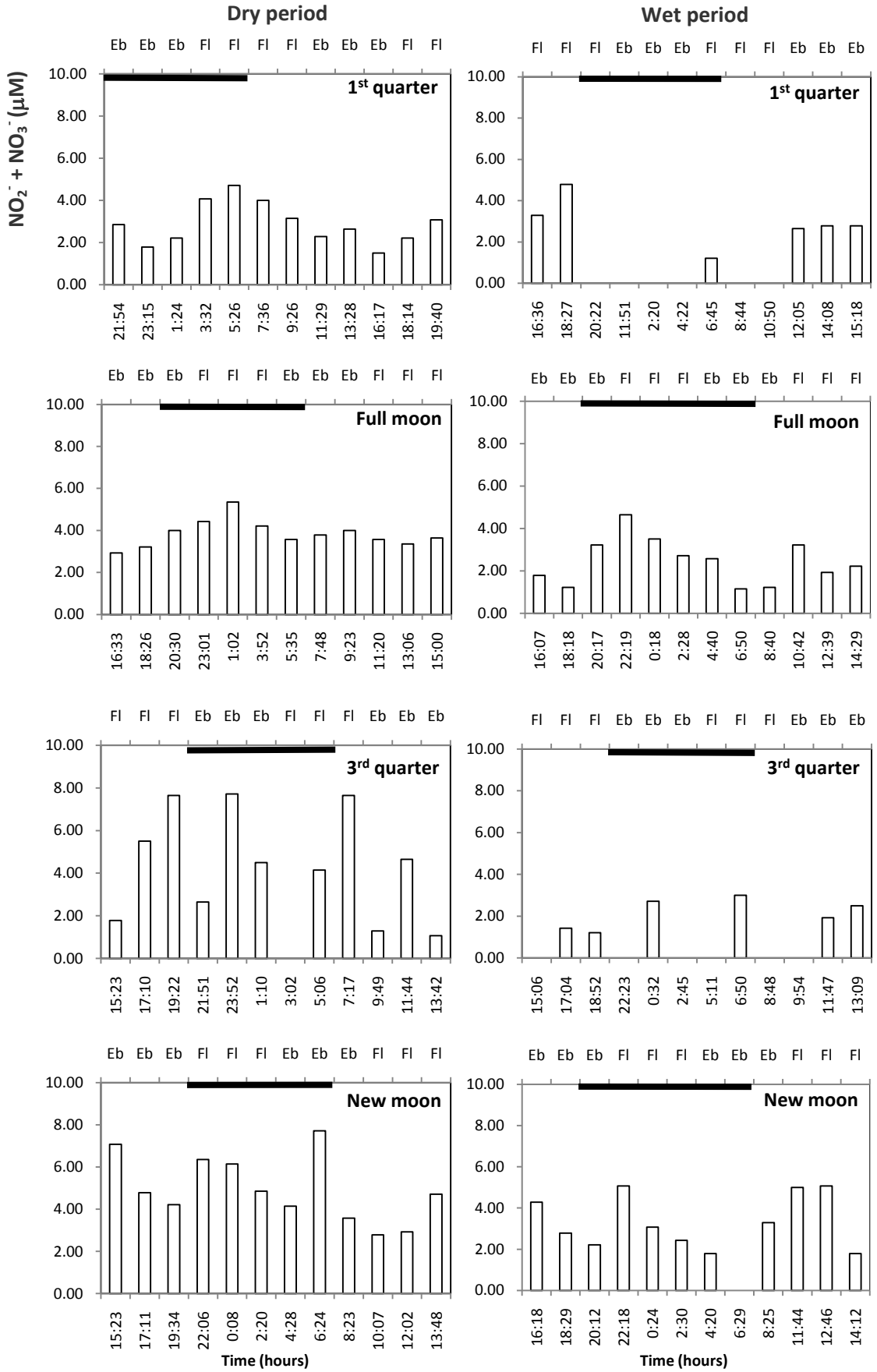


Fig. 4.7. Mean NO_2^- + NO_3^- of surface waters recorded over 24 hours and four consecutive moon phases in the dry and wet periods. Blank indicates data not available; Eb ebb tide, Fl flood tide; horizontal bar indicates nighttime. SD not plotted in order to show clearer trend.

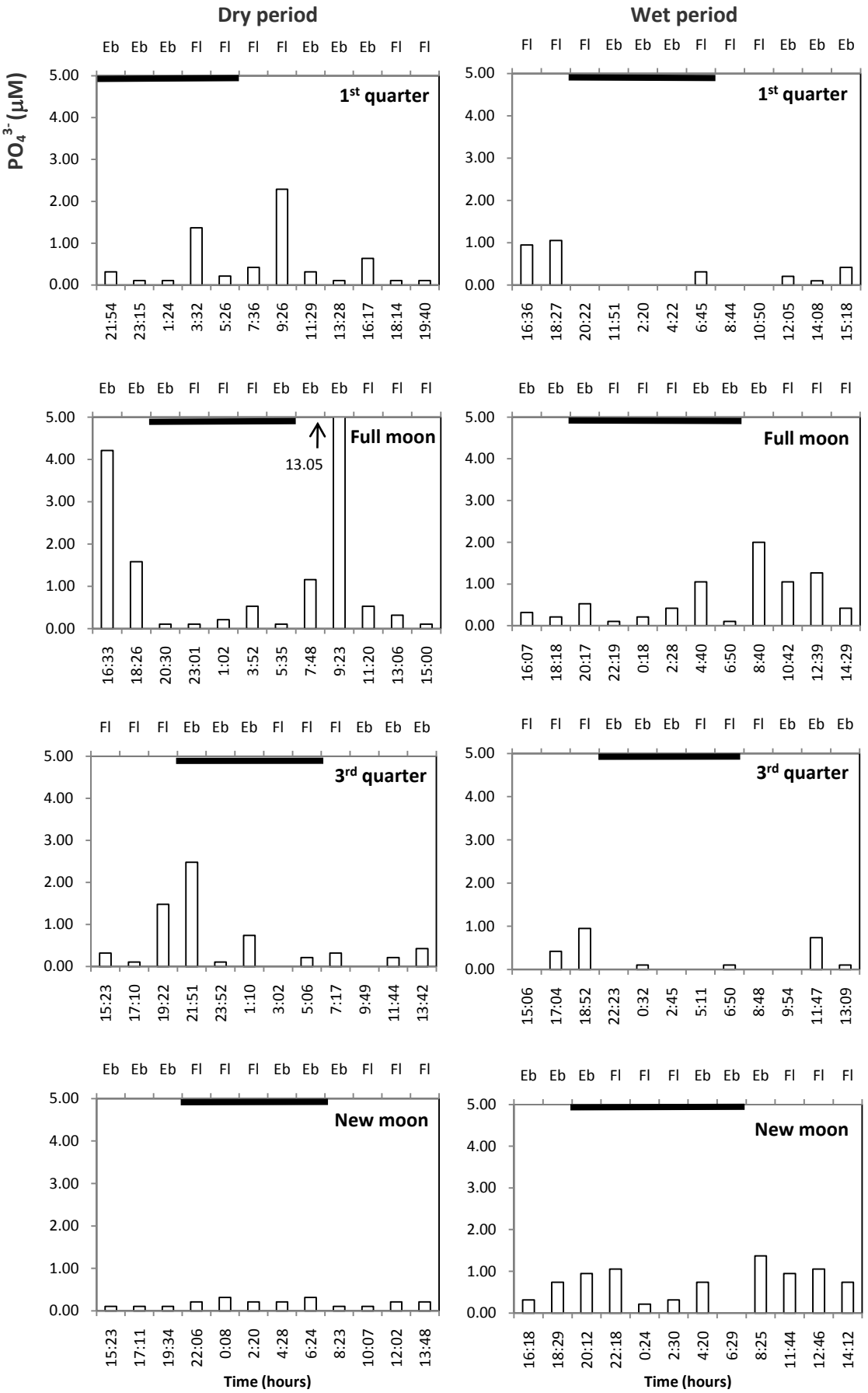


Fig. 4.8. Mean PO_4^{3-} of surface waters recorded over 24 hours and four consecutive moon phases in the dry and wet periods. Blank indicates data not available; Eb ebb tide, Fl flood tide; horizontal bar indicates nighttime. SD not plotted in order to show clearer trend.

4.1.3 Chlorophyll *a* concentrations

The chl. *a* concentrations were measured to determine how the phytoplankton responded to diel-tidal rhythms in the mangrove estuaries. The surface chl. *a* values fluctuated greatly between 5.6 µg l^{-1} and 102.3 µg l^{-1} (Table 4.1). Maximum chl. *a* for the dry period was recorded at 1814-hour during the 1st quarter (102.3 µg l^{-1}), while for the wet period it was recorded at 1147-hour during the 3rd quarter (72 µg l^{-1}) (Fig. 4.9). The mean chl. *a* of the dry period (19.0 ± 16.4 µg l^{-1}) was not significantly different (ANOVA, $p > 0.05$) from the wet period (17.6 ± 17.0 µg l^{-1}) (Table 4.1).

In the dry period, mean chl. *a* appeared to be higher during neap tide as compared to spring tide (ANOVA, $p < 0.01$), but it was the other way around in the wet period (ANOVA, $p < 0.01$; Table 4.6). Significantly higher (ANOVA, $p < 0.01$) chl. *a* was observed during daytime as compared to during nighttime for both periods (Fig. 4.9). The significant interaction effect between moon phase and diel in the wet period indicated that chl. *a* measured during the 1st quarter daytime was relatively similar to that measured during the night (Tukey HSD test, $p > 0.05$; Fig. 4.9; appendix Ve). The effect of tide on chl. *a* was neither significant in the dry nor wet period (ANOVA, $p > 0.05$) (Table 4.6).

Table 4.6. Summary results of three-way ANOVA and post-hoc Tukey HSD tests on chlorophyll *a* concentration (µg l^{-1}) with respect to moon phase, diel, tide and their interaction for dry and wet periods. $\bar{x}$ = mean; n = Sample size; Min = minimum, Max = maximum; homogenous groups indicated by superscripts a and b; * indicates significance at $p < 0.05$, ** significance at $p < 0.01$, ns no significance.

		Source of Variation											
		Moon phase (1)					Diel (2)			Tide (3)			Significant interaction
		1st quarter	Full moon	3rd quarter	New moon	p-level	Day	Night	p-level	Ebb	Flood	p-level	effect ($p < 0.05$)
Dry period	$\bar{x}$	22.1 [a,b]	15.9 [a,b]	24.5 [a]	13.4 [b]	**	25.2	10.3	**	17.3	20.7	ns	-
	n	12	12	12	12		28	20		24	24		
	± SD	26.5	6.4	14.6	10.3		19.0	3.9		11.3	20.4		
	Min	6.8	7.3	11.3	5.6		6.2	5.6		6.3	5.6		
	Max	102.3	30.2	55.9	41.8		102.3	19.0		55.9	102.3		
Wet period	$\bar{x}$	8.3 [a]	23.8 [b]	17.6 [a,b]	20.7 [b]	**	25.9	7.8	**	18.0	17.2	ns	1 x 2
	n	12	12	12	12		26	22		24	24		
	± SD	2.8	20.9	19.2	16.7		19.7	1.2		18.1	16.3		
	Min	6.8	6.8	7.0	6.7		7.3	6.7		6.9	6.7		
	Max	16.8	61.2	72.0	54.4		72.0	11.0		72.0	61.2		

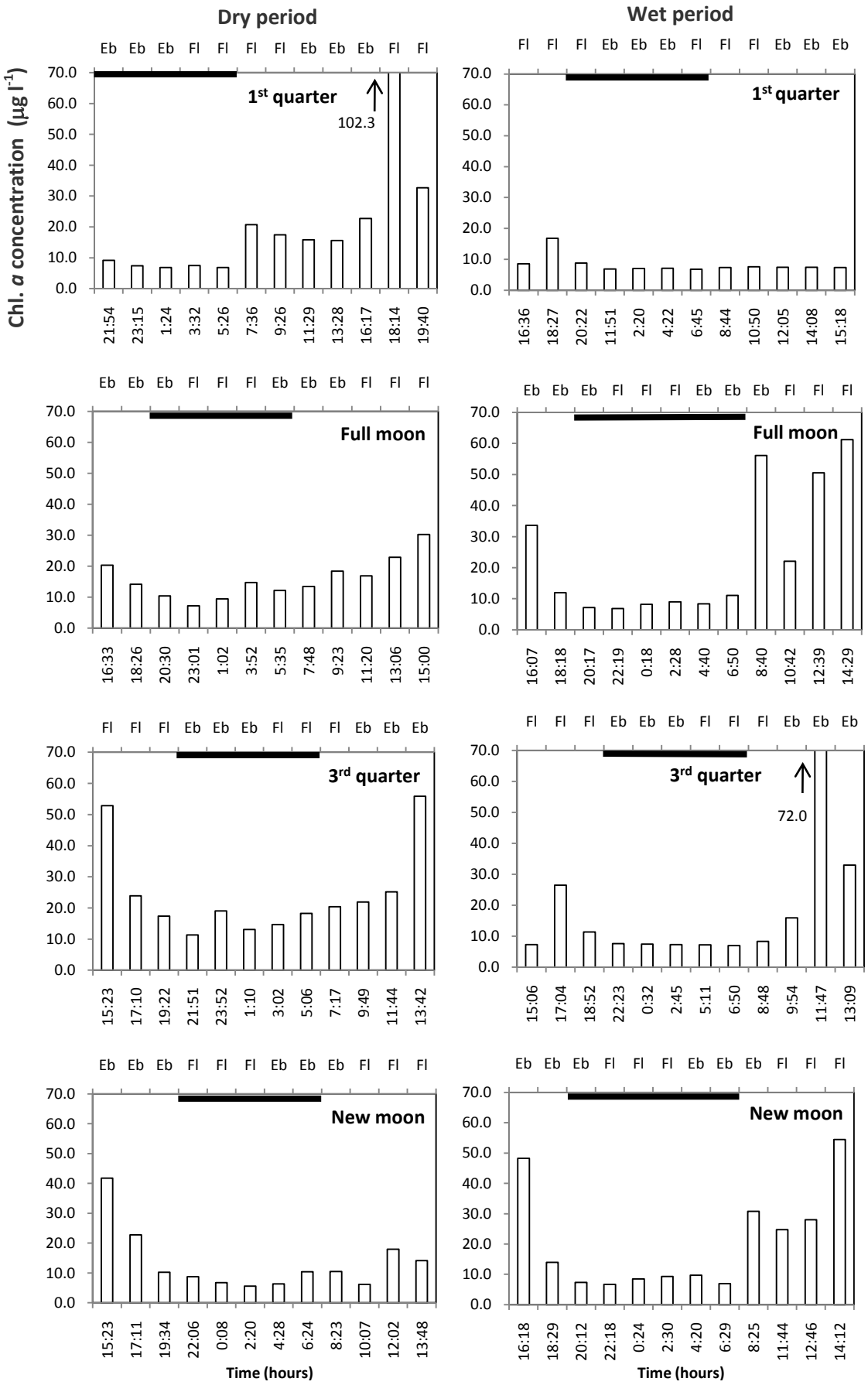


Fig. 4.9. Mean chlorophyll *a* concentration of surface waters recorded over 24 hours four and four consecutive moon phases in the dry and wet periods. Eb denotes ebb tide, Fl flood tide; horizontal bar indicates nighttime. SD not plotted in order to show clearer trend.

4.1.4 Zooplankton wet biomass and abundance by size fractions

4.1.4.1 Comparisons between dry and wet period

Total wet biomass of all zooplankton sampled in both the dry and wet periods ranged from 27.6 mg m^{-3} to 1095.7 mg m^{-3} and 63.5 mg m^{-3} to 6122.4 mg m^{-3}, respectively. Mean total zooplankton biomass in the wet period (651.8 ± 618 mg m^{-3}) was significantly higher than that in the dry period (322.7 ± 219.5 mg m^{-3}; ANOVA, $p < 0.001$) mainly due to significantly higher mean value of large-sized zooplankton in the wet period (481.3 ± 575.8 mg m^{-3}) as compared to dry period (134 ± 154.5 mg m^{-3}; ANOVA, $p < 0.001$). Mean biomass of medium-sized zooplankton was not significantly different between the dry and the wet period (ANOVA, $p > 0.05$). Small-sized zooplankton had higher mean value in the dry period (82.5 ± 85.8 mg m^{-3}) than in the wet period (52 ± 61.6 mg m^{-3}; ANOVA, $p < 0.001$) (Table 4.7).

Table 4.7. Summary results of one-way ANOVA on wet biomass and density of zooplankton between dry and wet periods. $\bar{x}$ = mean; n = sample size; Min = minimum, Max = maximum; ** significance at $p < 0.01$.

Size fraction		Biomass			Density		
		Dry	Wet	p-level	Dry	Wet	p-level
	n	192	192		192	192	
500 µm	$\bar{x}$	134.0	481.3	<0.001**	398	1189	<0.001**
	± SD	154.6	575.8		400	1196	
	Min	0.9	36.4		5	7	
	Max	888.3	6034.8		2668	9133	
250 µm	$\bar{x}$	106.2	118.6	0.9290	4989	3998	<0.001**
	± SD	74.2	182.0		3839	6210	
	Min	15.7	11.8		674	223	
	Max	380.2	2395.4		26749	68260	
125 µm	$\bar{x}$	82.5	52.0	<0.001**	2581	1570	<0.001**
	± SD	85.8	61.6		1510	1322	
	Min	4.0	5.4		84	41	
	Max	473.1	608.7		7717	9092	
Total	$\bar{x}$	322.7	651.8	<0.001**	7968	6757	<0.001**
	± SD	219.5	618.0		4774	7335	
	Min	27.6	63.5		1180	510	
	Max	1095.7	6122.4		31258	77741	

Zooplankton abundance in the dry and wet periods ranged from 1,180 ind m^{-3} to 31,258 ind m^{-3} and 510 ind m^{-3} to 77,741 ind m^{-3}, respectively. As opposed to biomass, mean total abundance in the dry period (7,957 ± 4,784 ind m^{-3}) was significantly higher

than in the wet period (6,757 ± 7,335 ind m^{-3}; ANOVA, $p < 0.001$). This was mainly due to the significantly greater numbers of medium- and small-sized zooplankton during the dry period as compared to the wet period (ANOVA, $p < 0.001$). In contrast, large-sized zooplankton had significant higher abundance in the wet period as compared to the dry period (ANOVA, $p < 0.001$) (Table 4.7).

4.1.4.2 Dry period survey

a. Wet biomass

Bihourly mean zooplankton biomass recorded over the 24-hour sampling in the dry period is given in Fig. 4.10. Mean total biomass was significantly higher during neap tides (1st and 3rd quarter) as compared to spring tides (full and new moon) (ANOVA, $p < 0.001$; Table 4.8). Large-sized zooplankton (>500 µm) constituted the largest proportion of the biomass during the 3rd quarter, with mean value of at least 2 times greater than the biomass of medium- and small-sized zooplankton (<500 µm) (Table 4.8, Fig. 4.10).

ANOVA results showed significant differences in total biomass for the main effects of diel and sampling depth ($p < 0.001$; Table 4.8). Mean total biomass obtained during the night and at the bottom was significantly higher than during the day and at surface water, respectively. There was no significant difference in total biomass between ebb and flood tide (ANOVA, $p > 0.05$; Table 4.8). Among size fractions, only the large-sized zooplankton were significantly different in biomass between diel cycle (ANOVA, $p < 0.001$), with greater mean value during the night (209.4 ± 202.2 mg m^{-3}) than during the day (80.1 ± 70.7 mg m^{-3}) (Table 4.8). Biomass of zooplankton in smaller size fractions was not significantly different between day and night (ANOVA, $p > 0.05$; Table 4.8). Mean bottom biomass was significantly higher than mean surface biomass for all size fractions zooplankton (ANOVA, $p < 0.01$). The only significant

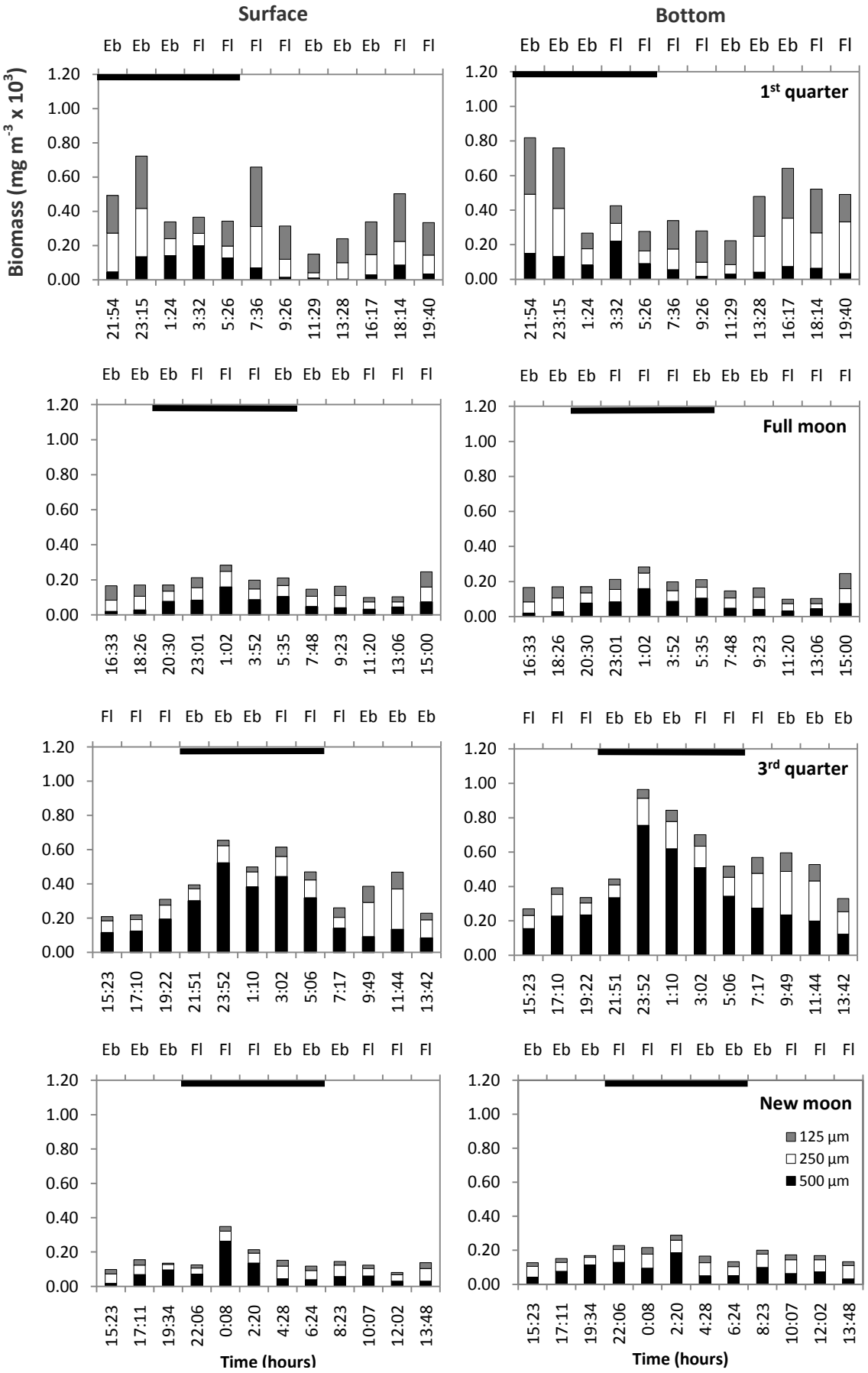


Fig. 4.10. Mean surface and bottom zooplankton biomass recorded over 24 hours and four consecutive moon phases in the dry period. Horizontal bar denotes nighttime; Eb = ebb tide, Fl = flood tide. SD not plotted in order to show clearer trend.

Table 4.8. Zooplankton wet biomass: summary results of four-way ANOVA and post-hoc Tukey HSD tests by size fractions in the dry period with respect to moon phase, tide, diel, depth and their interaction. $\bar{x}$ = mean; n = sample size; Min = minimum, Max = maximum; superscripts a, b and c indicate homogeneous groups; * significance at $p < 0.05$, ** significance at $p < 0.01$.

Size fraction		Source of variation														
		Moon phase (1)					Diel (2)			Tide (3)			Depth (4)			Significant interaction effect ($p < 0.05$)
		1st quarter	Full moon	3rd quarter	New moon	p-level	Day	Night	p-level	Ebb	Flood	p-level	Surface	Bottom	p-level	
	n	48	48	48	48		112	80		96	96		96	96		
500 µm	$\bar{x}$	78.3[a]	92.6[a]	285.4[b]	79.6[a]	<0.001**	80.1	209.4	<0.001**	132.4	135.6	0.059	112.8	155.1	<0.001**	1 x 2, 2 x 4,
	± SD	72.3	126.6	201.9	61.1		70.7	202.2		169.2	139.3		130.0	173.9		3 x 4,
	Min	0.9	14.1	47.2	3.7		0.9	17.9		0.9	5.3		0.9	5.5		1 x 2 x 3
	Max	297.0	856.8	888.3	312.9		405.7	888.3		888.3	856.8		888.3	856.8		
250 µm	$\bar{x}$	155.4[a]	81.0[b]	126.5[a]	62.0[c]	<0.001**	107.0	105.1	0.858	116.9	95.5	0.028*	90.5	122.0	<0.001**	1 x 2 x 3
	± SD	101.1	30.1	71.5	24.3		75.4	72.9		85.3	59.7		66.9	78.0		
	Min	18.1	25.4	53.4	15.7		15.7	21.6		18.1	15.7		15.7	33.9		
	Max	380.2	147.6	326.7	134.0		376.4	380.2		380.2	376.4		364.8	380.2		
125 µm	$\bar{x}$	196.4[a]	54.2[b]	55.1[b]	24.5[c]	<0.001**	86.6	76.8	0.263	88.1	77.0	0.085	78.2	86.8	0.004**	1 x 2,
	± SD	100.7	24.3	28.4	11.2		83.4	89.3		92.5	78.7		86.9	85.0		1 x 2 x 3
	Min	66.3	19.3	17.3	4.0		4.0	15.2		4.0	6.6		5.6	4.0		
	Max	473.1	105.0	130.2	61.6		473.1	466.9		466.9	473.1		473.1	466.9		
Total	$\bar{x}$	430.0[a]	227.8[b]	467.0[a]	166.1[c]	<0.001**	273.7	391.3	<0.001**	337.4	308.1	0.678	281.5	363.9	<0.001**	1 x 2 x 3
	± SD	217.6	149.5	230.6	74.7		168.0	262.0		246.2	189.2		194.1	236.0		
	Min	98.0	59.3	145.0	27.6		27.6	84.6		79.0	27.6		27.6	96.6		
	Max	1095.7	1076.6	1039.6	429.1		936.5	1095.7		1095.7	1076.6		1032.4	1095.7		

tidal difference in biomass was observed for the medium-sized zooplankton, with significantly higher value obtained during ebb tide than flood tide (ANOVA, $p < 0.05$; Table 4.8).

There was a significant 3-way interaction effect between moon phase, diel and tide for total zooplankton biomass (ANOVA, $p < 0.01$; Table 4.8), indicating inconsistent diel-tidal pattern among moon phases. Higher total biomass was observed during the 1st quarter night-ebb and 3rd quarter night-ebb and night-flood, respectively (Fig. 4.10). These values were significantly higher than all spring tide combinations (Tukey HSD test, $p < 0.05$; Fig. 4.10; appendix VIa).

Mean biomass of large-sized zooplankton collected during the night was consistently higher than during the day over the dry period except for the new moon. During the new moon, biomass obtained at night-ebb was not significantly different from that obtained at day-ebb and day-flood (Tukey HSD test, $p > 0.05$; Fig. 4.10, appendix VIb). The diel and tidal effects did significantly influence the vertical distribution of large-sized zooplankton biomass as indicated by the 2-way interaction effects between diel and depth and between tide and depth ($p < 0.05$, Table 4.8). Bottom biomass was significantly higher than that of surface during the day but was homogeneous across water column during the night (appendix VIc). Zooplankton biomass at the bottom was also significantly higher than surface biomass at ebb tide but did not significantly differ between depth strata at flood tide (appendix VId).

Unlike large-sized zooplankton, wet biomass of medium-sized zooplankton was more influenced by tidal than by diel effect particularly for samples collected during neap tide. Higher biomass always coincided with ebb tide irrespective of diel cycle during neap tide, but appeared to be similar for ebb and flood tide during spring tide

(Fig. 4.10, appendix VIe). The small-sized zooplankton biomass showed inconsistent diel and tidal patterns over the dry period (appendix VIf).

b. Numerical abundance

Mean total zooplankton abundance was highest during the 3rd quarter followed by 1st quarter, full moon and new moon (ANOVA, $p < 0.001$; Table 4.9). Mean abundance of large-sized zooplankton was significantly least abundant during new moon (ANOVA, $p < 0.001$), while mean values of other three moon phases did not significantly differ from each other (Tukey HSD test, $p > 0.05$; Table 4.9). Medium-sized zooplankton yielded greater numbers during the 3rd quarter whereas other three moon phases were statistically equal in abundance (Table 4.9). Zooplankton abundance over the dry period was highly variable and mainly dominated by medium-sized zooplankton (Fig. 4.11).

Mean total zooplankton abundance at the bottom was significantly higher than at the surface due to higher numbers of medium- and large-sized zooplankton (ANOVA, $p < 0.05$, Table 4.9). However, small-sized zooplankton was equally distributed at surface and bottom waters (ANOVA, $p > 0.05$; Table 4.9). Significant tidal pattern was noted for total and medium-sized zooplankton, with greater abundance obtained during ebb tide than at flood tide (ANOVA, $p < 0.01$). Abundance of small- and large-sized zooplankton was not significantly influenced by tidal cycle (ANOVA, $p > 0.05$, Table 4.9).

Although there was no significant diel pattern in total zooplankton abundance (ANOVA, $p > 0.05$), large size fractions of zooplankton (>250 μm) did significantly differ between diel cycle. Large-sized zooplankton was significantly more abundant

Table 4.9. Zooplankton density: summary results of four-way ANOVA and post-hoc Tukey HSD tests by size fractions in the dry period with respect to moon phase, tide, diel, depth and their interaction. $\bar{x}$ = mean; n = sample size; Min = minimum, Max = maximum; superscripts a, b and c indicate homogeneous groups; * significance at $p < 0.05$, ** significance at $p < 0.01$.

Size fraction		Source of variation														
		Moon phase (1)					Diel (2)			Tide (3)			Depth (4)			Significant interaction effect ($p < 0.05$)
		1st quarter	Full moon	3rd quarter	New moon	p-level	Day	Night	p-level	Ebb	Flood	p-level	Surface	Bottom	p-level	
	n	48	48	48	48		112	80		96	96		96	96		
500 µm	$\bar{x}$	453[a]	417[a]	532[a]	191[b]	<0.001**	370	438	<0.001**	373	423	0.076	305	492	<0.001**	2 x 3, 2 x 4, 1 x 2 x 3
	± SD	437	330	518	129		426	359		398	403		309	456		
	Min	5	45	38	22		5	74		5	34		5	53		
	Max	2668	1375	2098	595		2098	2668		2668	2098		1993	2668		
250 µm	$\bar{x}$	5274[a]	4060[a]	6847[b]	3775[a]	<0.001**	5581	4161	0.001**	5803	4176	0.002**	4477	5501	0.033*	1 x 2 x 3, 2 x 3 x 4
	± SD	3542	2210	5819	1620		4431	2620		4411	2974		3651	3972		
	Min	674	848	1644	1136		927	674		1511	674		1136	674		
	Max	14431	12007	26749	9295		26749	14431		26749	26081		26749	26081		
125 µm	$\bar{x}$	3208[a]	2618[a]	2728[a]	1769[b]	<0.001**	2552	2621	0.456	2759	2402	0.061	2394	2768	0.108	1 x 2 x 3, 1 x 3 x 4
	± SD	1850	1494	1237	993		1544	1469		1561	1444		1352	1639		
	Min	84	705	752	357		84	357		523	84		357	84		
	Max	7551	7717	6740	4151		7717	6695		7551	7717		6740	7717		
Total	$\bar{x}$	8935[a,b,c]	7095[a,b]	10108[c]	5735[d]	<0.001**	8503	7220	0.072	8935	7002	0.002**	7176	8761	0.021*	1 x 2 x 3
	± SD	4978	3235	6306	2472		5330	3770		5392	3855		4315	5092		
	Min	1180	1628	2771	1577		1180	1577		2791	1180		1577	1180		
	Max	20806	17842	31258	13313		31258	20806		31258	29818		31258	29818		

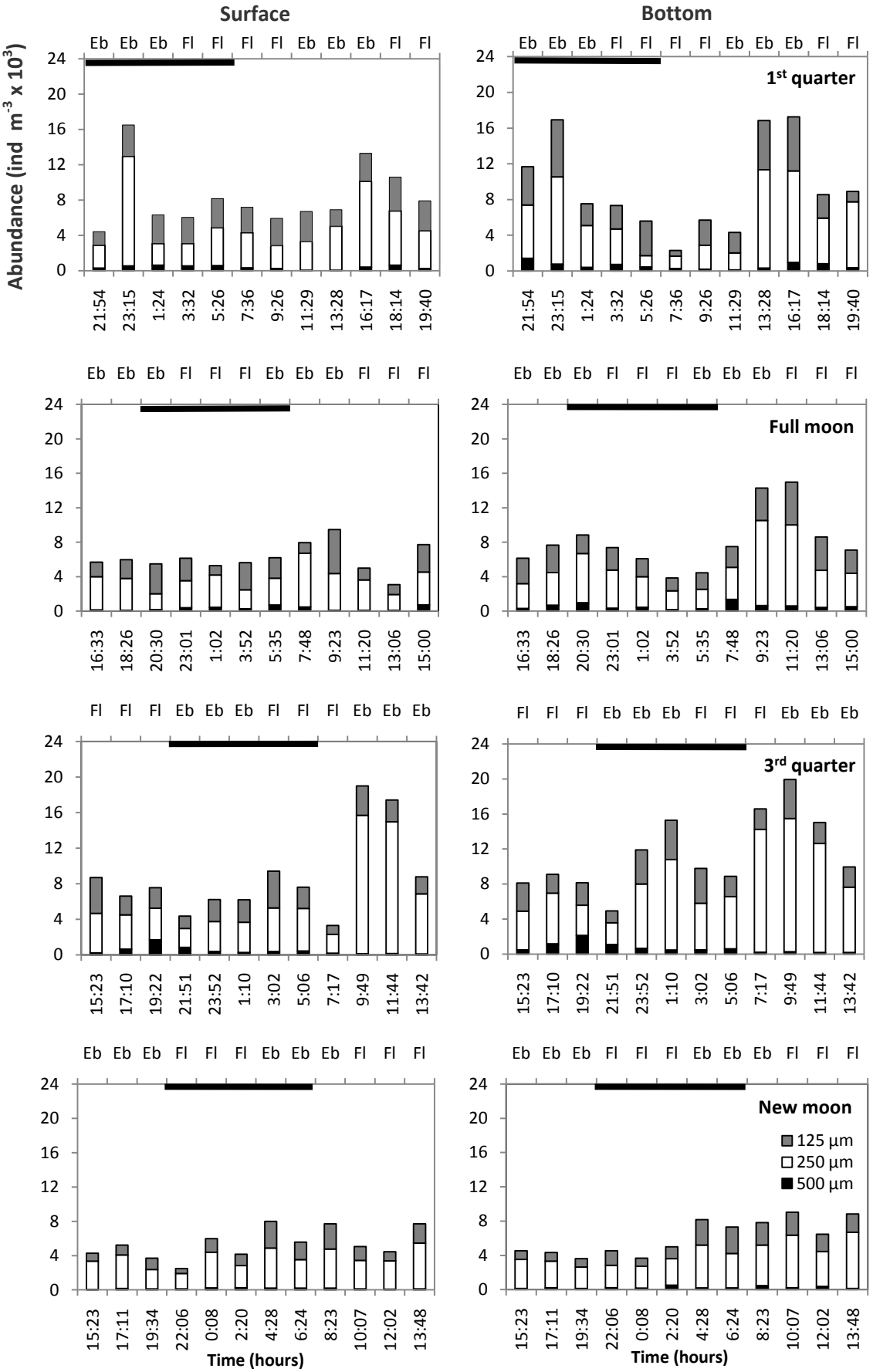


Fig.4.11. Mean surface and bottom zooplankton abundance recorded over 24 hours and four consecutive moon phases in the dry period. Horizontal bar denotes nighttime; Eb = ebb tide, Fl = flood tide. SD not plotted in order to show clearer trend.

during the night than the day (ANOVA, $p < 0.001$), contrasting to medium-sized zooplankton with greater numbers obtained during the day than the night (ANOVA, $p < 0.01$). There was no significant diel pattern for small-sized zooplankton (ANOVA, $p > 0.05$, Table 4.9).

In the dry period, the lowest total zooplankton abundance occurred during the new moon night-flood, leading to a significant 3-way interaction effect between moon phase, diel and tide ($p < 0.01$, Fig. 4.11, appendix VIIa). At each level of moon phase, no significant difference in total abundance was observed for diel and tidal cycles (Tukey HSD test, $p > 0.05$; appendix VIIa). Abundance of each individual size fraction exhibited more significant interaction effects (Table 4.9). Medium-sized zooplankton were in greater numbers particularly during the 3rd quarter day-ebb (Fig. 4.11, appendix VIIb). Large-sized zooplankton, however, exhibited the lowest abundance during neap day-ebb (Fig. 4.11, appendix VIIc). Exceptionally high abundance of large-sized zooplankton during the 3rd quarter day-flood coincided with dusk (1922-hour, Fig. 4.11). Diel vertical variation in abundance of large-sized zooplankton was apparent, with bottom abundance being higher than the surface during the day but became homogeneous across water column during the night (appendix VIId). Abundance patterns of large-sized zooplankton were relatively constant during the period of spring tide (Fig. 4.11). Abundance of small-sized zooplankton was inconsistent over the dry period (Fig. 4.11).

4.1.4.3 Wet period survey

a. Wet biomass

Mean total zooplankton biomass was the highest during the 1st quarter while other three moon phases were not significantly different from each other (Table 4.10).

Table 4.10. Zooplankton wet biomass: summary results of four-way ANOVA and post-hoc Tukey HSD tests by size fractions in the wet period with respect to moon phase, tide, diel, depth and their interaction. $\bar{x}$ = mean; n = sample size; Min = minimum, Max = maximum; superscripts a, b and c indicate homogeneous groups; * significance at $p < 0.05$, ** significance at $p < 0.01$.

Size fraction		Source of variation														
		Moon phase (1)					Diel (2)			Tide (3)			Depth (4)			Significant interaction effect ($p < 0.05$)
		1st quarter	Full moon	3rd quarter	New moon	p-level	Day	Night	p-level	Ebb	Flood	p-level	Surface	Bottom	p-level	
	n	48	48	48	48		104	88		96	96		96	96		
500 µm	$\bar{x}$	824.4 [a]	333.5 [b]	381.0 [b]	386.3 [b]	<0.001**	430.8	541.0	0.097	439.9	522.7	0.011*	502.7	459.9	0.100	
	± SD	976.8	227.8	243.5	346.6		381.8	740.7		643.3	499.3		490.8	651.8		
	Min	100.9	51.0	57.8	36.4		51.0	36.4		36.4	75.1		67.3	36.4		
	Max	6034.8	800.6	1323.2	1720.2		2338.2	6034.8		6034.8	3359.3		3359.3	6034.8		
250 µm	$\bar{x}$	177.9 [a]	105.2 [b]	83.7 [b]	107.5 [c]	<0.001**	138.1	95.4	0.019*	133.7	103.4	0.066	112.1	125.0	0.881	1 x 2, 1 x 3, 2 x 3
	± SD	102.5	57.0	34.1	338.4		240.2	58.4		240.3	91.5		89.4	241.9		
	Min	38.0	38.5	27.9	11.8		33.4	11.8		11.8	23.8		11.8	16.4		
	Max	663.3	259.6	191.1	2395.4		2395.4	293.4		2395.4	663.3		663.3	2395.4		
125 µm	$\bar{x}$	62.0 [a]	68.2 [a,b]	33.8 [b]	44.0 [b]	<0.001**	56.3	46.9	0.624	60.6	43.4	0.095	48.9	55.0	0.263	1 x 2
	± SD	32.1	101.4	15.1	55.8		78.9	30.1		80.8	31.0		51.3	70.6		
	Min	14.6	6.7	10.5	5.4		10.5	5.4		5.4	6.7		5.8	5.4		
	Max	149.8	608.7	77.4	360.4		608.7	136.6		608.7	149.8		419.3	608.7		
Total	$\bar{x}$	1064.2 [a]	506.9 [b]	498.5 [b]	537.8 [b]	<0.001**	625	683	0.257	634	669	0.155	664	640	0.188	2 x 4
	± SD	965.7	261.0	246.8	508.0		488	745		700	527		520	705		
	Min	169.4	132.7	150.2	63.5		133	63		63	125		169	63		
	Max	6122.4	1205.4	1390.7	3046.0		3046	6122		6122	3602		3602	6122		

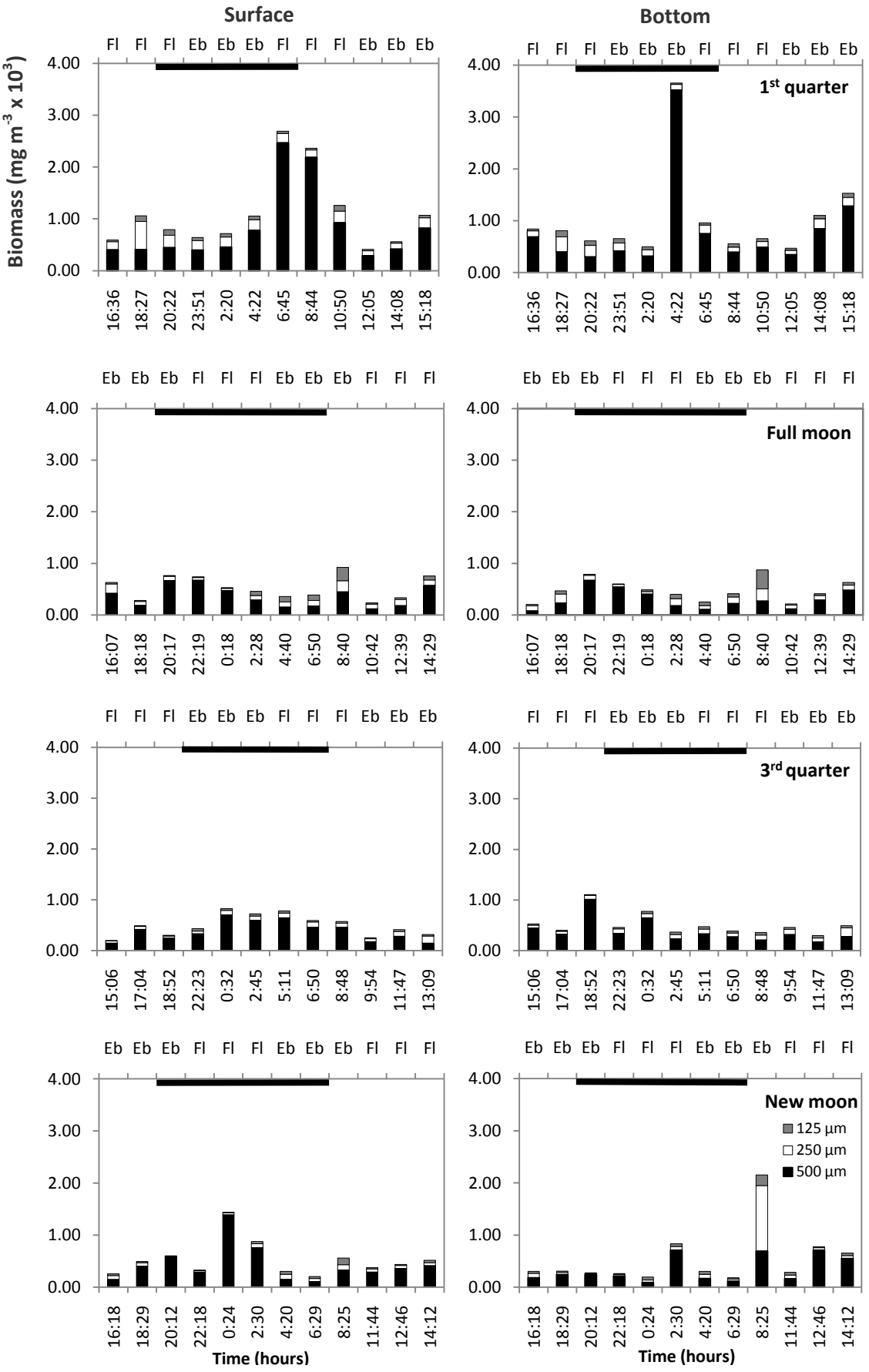


Fig. 4.12. Mean surface and bottom zooplankton wet biomass recorded over 24 hours and four consecutive moon phases in the wet period. Horizontal bar denotes nighttime; Eb = ebb tide, Fl = flood tide. SD not plotted in order to show clearer trend.

Exceptionally high biomass was observed between 0422-hour and 0844-hour during the 1st quarter (Fig. 4.12). In general, large-sized zooplankton contributed the largest proportion of total biomass except for the bottom samples collected at 0825-hour during new moon with medium-sized zooplankton dominating (Fig. 4.12).

There were no significant differences in total zooplankton biomass for the main effects of diel, tide and sampling depth (ANOVA, $p > 0.05$; Table 4.10). The only significant tidal effect was observed for large-sized zooplankton, with higher biomass at flood tide than ebb tide (ANOVA, $p < 0.05$, Table 4.10). Significant diel effect on biomass was observed only for medium-sized zooplankton with greater value obtained during the day than the night (ANOVA, $p < 0.05$, Table 4.10). There was no significant depth effect for all size fractions (ANOVA, $p > 0.05$). There was a significant interaction effect (diel x depth) on total zooplankton biomass ($p < 0.05$), but results of Tukey HSD test did not show any significant interaction effect of diel and tide ($p > 0.05$).

Biomass of medium-sized zooplankton was significantly higher during day-ebb than other diel-tidal combinations (2-way interaction between diel and tide, $p < 0.05$) (appendix VIIIa). The small-sized zooplankton did not show a clear diel pattern in biomass, and the interaction effect between moon phase and diel ($p < 0.05$) showed an inconsistent diel pattern among moon phases (appendix VIIIb). There was no significant interaction effect observed for the large-sized zooplankton (Table 4.10).

b. Numerical abundance

Zooplankton of all size fractions were significantly more abundant during neap than spring tide (ANOVA, $p < 0.001$; Table 4.11). Zooplankton were captured in large quantities during the 1st quarter with maximum abundance at 1827-hour and surface

Table 4.11. Zooplankton density: summary results of four-way ANOVA and post-hoc Tukey HSD tests in the wet period with respect to moon phase, tide, diel, depth and their interaction. $\bar{x}$ = mean; n = sample size; Min = minimum, Max = maximum; superscripts a, b and c indicate homogeneous groups; * significance at $p < 0.05$, ** significance at $p < 0.01$.

Size fraction		Source of variation														
		Moon phase (1)					Diel (2)			Tide (3)			Depth (4)			Significant interaction effect ($p < 0.05$)
		1st quarter	Full moon	3rd quarter	New moon	p-level	Day	Night	p-level	Ebb	Flood	p-level	Surface	Bottom	p-level	
	n	48	48	48	48		104	88		96	96		96	96		
500 µm	$\bar{x}$	2199 [a]	818 [b]	1278 [c]	460 [d]	<0.001**	1304	1053	0.276	1183	1195	0.313	1202	1176	0.573	1 x 3, 2 x 3, 1 x 2 x 3
	± SD	1706	664	709	477		1468	744		1041	1339		1120	1273		
	Min	266	7	163	32		7	58		7	32		43	7		
	Max	9133	4183	3277	1961		9133	3463		5539	9133		5625	9133		
250 µm	$\bar{x}$	7260 [a]	2970 [b]	3824 [a]	1938 [c]	<0.001**	4962	2858	0.001**	3468	4528	0.831	4799	3197	0.085	1 x 3, 2 x 3
	± SD	11513	2219	1383	1007		8190	1683		2086	8521		8477	2093		
	Min	889	904	1758	223		889	223		223	764		223	737		
	Max	68260	12499	7171	4984		68260	7863		12499	68260		68260	13896		
125 µm	$\bar{x}$	2368 [a]	1052 [b]	1684 [a]	1175 [b]	<0.001**	1644	1483	0.932	1744	1396	0.012*	1556	1584	0.660	1 x 2
	± SD	1985	762	871	851		1572	946		1362	1264		1271	1377		
	Min	41	201	176	115		41	176		201	41		41	115		
	Max	9092	4052	4193	3837		9092	4193		8173	9092		9092	8173		
Total	$\bar{x}$	11828 [a]	4840 [b]	6786 [c]	3573 [d]	<0.001**	7910	5394	0.032*	6394	7119	0.260	7557	5957	0.129	1 x 2, 1 x 3
	± SD	12704	2943	1946	2098		9459	2951		3658	9722		9520	4028		
	Min	1591	1645	3124	510		1489	510		510	1268		510	1284		
	Max	77741	14547	11282	9243		77741	14145		18744	77741		77741	20103		

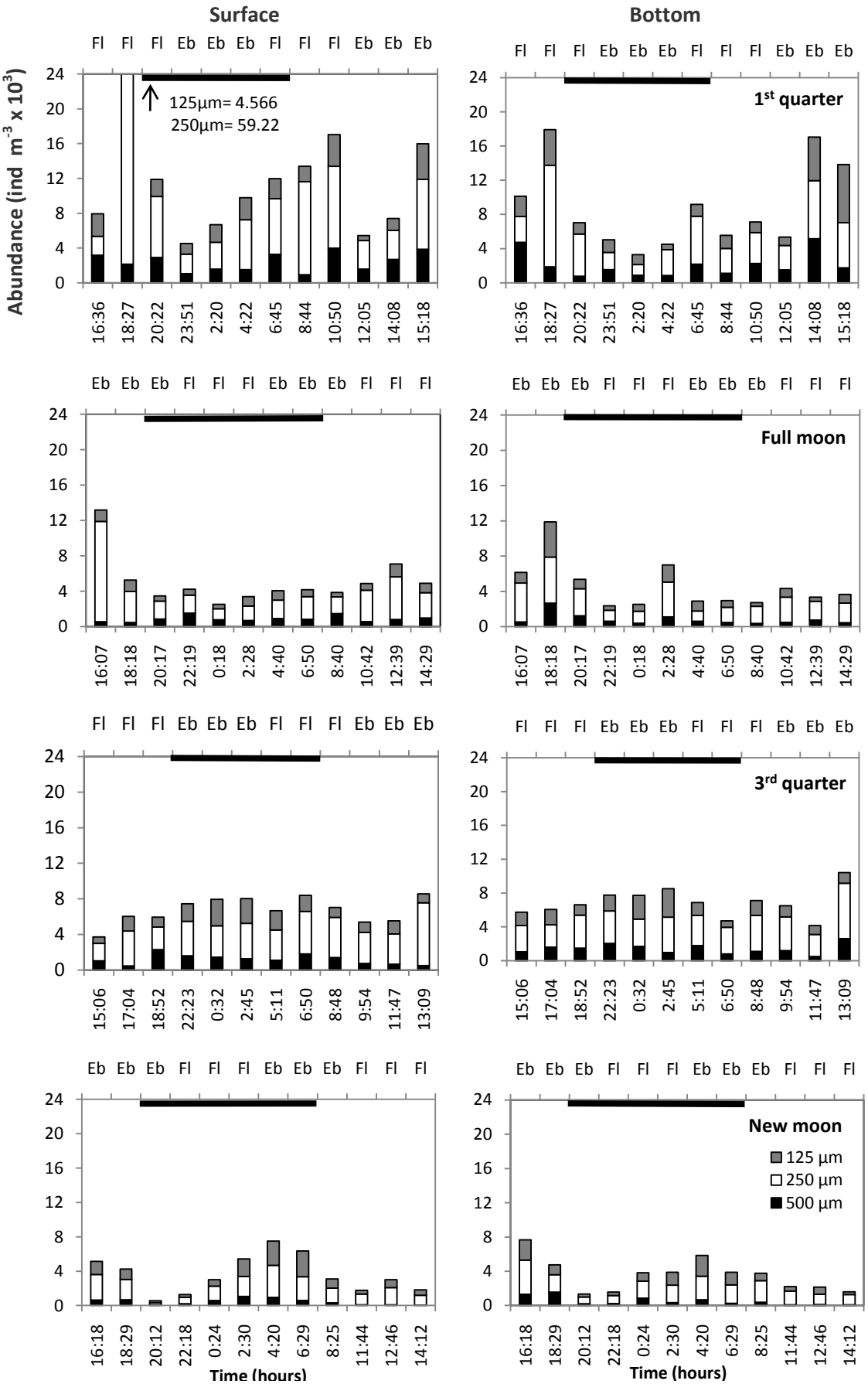


Fig.4.13. Mean surface and bottom zooplankton abundance recorded over 24 hours and four consecutive moon phases in the wet period. Horizontal bar denotes nighttime; Eb = ebb tide, Fl = flood tide. SD not plotted in order to show clearer trend.

water (Fig. 4.13). The abundance patterns during the 1st quarter were highly variable but no marked changes were observed during the 3rd quarter (Fig. 4.13).

Diel effect on abundance was significant for medium-sized and total zooplankton, with higher mean values during the day as compared to the night (ANOVA, $p < 0.001$; Table 4.11). The abundance of small-sized zooplankton was significantly higher during ebb tide as compared to flood tide (ANOVA, $p < 0.05$; Table 4.11). Water depth had no significant effect on zooplankton abundance for all size fractions (ANOVA, $p > 0.05$; Table 4.11).

Four-way ANOVA results indicated various significant interaction effects in zooplankton abundance (Table 4.11). Total zooplankton abundance showed a marginally significant interaction effect between moon phase and diel ($p = 0.0496$). Total zooplankton abundance during spring tide was generally low as compared to neap tide, except for day samples collected at 1607-hour and 1818-hour at full moon (Fig. 4.13). Similar to biomass, abundance of medium-sized zooplankton was highest during day ebb tide (two-way interaction between diel and tide, $p < 0.05$; appendix IXa). The large-sized zooplankton was at minimum abundance during new moon day-flood particularly at 1144- and 1412-hour, when the number of zooplankton recorded during this period was consistently less than 100 ind m^{-3} (Fig. 4.13, appendix IXb).

4.1.4.4 Correlation between zooplankton wet biomass and abundance

In the dry period, the biomass of all size fractions and total zooplankton was significantly positively correlated with their corresponding abundance ($p < 0.05$). Medium- and large-sized zooplankton had stronger correlation between their biomass and abundance ($r > 0.43$, $p < 0.01$) as compared to small-sized zooplankton (Table 4.12). In contrast, significant correlation throughout the wet period was observed only for the medium-sized zooplankton ($p < 0.01$, Table 4.13). There was generally no strong

correlation observed for small- and large-sized zooplankton (Table 4.13). Total zooplankton abundance was significantly correlated with the biomass during neap tide ($p < 0.05$) but not during spring tide ($p > 0.05$, Table 4.13).

Table 4.12. Summary results of Pearson's correlation coefficient (*r*) between wet biomass and numerical abundance for different size fractions and total zooplankton in the dry period. n = sample size; ** significance at $p < 0.01$, * significance at $p < 0.05$.

Moon phase	n	500 µm 48	250 µm 48	125 µm 48	Total 48
1st quarter	*r*	0.84 **	0.58 **	0.47 **	0.62 **
Full moon	*r*	0.61 **	0.59 **	0.29 p = 0.047	0.34 *
3rd quarter	*r*	0.43 **	0.91 **	0.37 *	0.56 **
New moon	*r*	0.54 **	0.73 **	0.53 **	0.48 **

Table 4.13. Summary results of Pearson's correlation coefficient (*r*) between wet biomass and numerical abundance for different size fractions and total zooplankton in the wet period. n = sample size; ** significance at $p < 0.01$, ns no significance.

Moon phase	n	500 µm 48	250 µm 48	125 µm 48	Total 48
1st quarter	*r*	0.23 ns	0.77 **	0.59 **	0.46 **
Full moon	*r*	0.24 ns	0.56 **	0.05 ns	-0.03 ns
3rd quarter	*r*	0.29 p = 0.04	0.73 **	0.27 ns	0.38 **
New moon	*r*	-0.20 ns	0.63 **	0.44 **	-0.11 ns

4.1.5 Zooplankton abundance and composition by taxonomic groups

4.1.5.1 Comparisons between dry and wet period

4.1.5.1.1 General composition and abundance of major taxonomic groups

Copepods were predominantly found in the dry and wet periods, comprising 55 and 71% of the mean total zooplankton abundance, respectively. Cirripede larvae ranked second in abundance (24 and 19%) followed by protozoans (9 and 1%). Each of

the five taxonomic groups (decapods, chaetognaths, polychaetes, gastropods and larvaceans) and unidentified eggs constituted 1 - 3% of the mean total zooplankton abundance in both periods. These groups altogether contributed 8 and 10% of the total zooplankton abundance in the dry and wet periods respectively. Bryozoa larvae represented 2% of the total zooplankton abundance in the dry period but very few larvae were captured in the wet period (<1%). Bivalvia showed an exact opposite pattern to that of Bryozoa larvae. The percentage contribution of Mysidae (0.1%) and Cnidaria (0.3%) were relatively similar in the dry and wet periods. The remaining groups (stomatopods, amphipods, ostracods, isopods, cumaceans, ctenophores, cephalopods, nematodes, ophiopluteus larvae, *Phoronis* larvae and *Lingula* larvae) were always found in low numbers particularly in the wet period (<0.05%, data not shown) (Table 4.14).

Copepod abundances in all samples varied between 621 to 15,792 ind m^{-3} in the dry period and 404 to 15,048 ind m^{-3} in the wet period, respectively. Mean total copepod abundance in the wet period (4,789 ± 3,131 ind m^{-3}) was not significantly different from that in the dry period (4,367 ± 2,474 ind m^{-3}; ANOVA, $p > 0.05$; Table 4.14). Other groups that were not significantly different in abundance between the dry and wet periods include chaetognaths, decapods, gastropods, mysids and cnidarians (ANOVA and Mann-Whitney U test, $p > 0.05$; Table 4.14). Larval stages of cirripede, polychaete and bryozoan together with larvaceans, protozoans and unidentified eggs were significantly more abundant in the dry period than in the wet period (ANOVA and Mann-Whitney U test, $p < 0.05$; Table 4.14).

4.1.5.1.2 Copepods

Copepodid and nauplii stages were always more abundant than adult copepods in both dry and wet periods and constituted 52 and 56% of the mean total copepod abundance respectively. Adult copepods made up 48 and 44% of the zooplankton in the

Table 4.14. Summary results of one-way ANOVA and Mann-Whitney U test (^) on zooplankton major groups between dry and wet period. $\bar{x}$ = mean; % Rel indicates relative abundance; n = sample size; Min = minimum, Max = maximum; ** significance at $p < 0.01$.

Taxon		Period				p-level
		D	% Rel	W	% Rel	
	n	192		192		
Copepoda	$\bar{x}$	4367	55	4789	71	0.401
	± SD	2474		3131		
	Min	621		404		
	Max	15792		15048		
^Cirripedia larvae	$\bar{x}$	1905	24	1300	19	<0.001**
	± SD	2939		5978		
	Min	31		0		
	Max	22298		65667		
Mysidae	$\bar{x}$	4	<1	5	<1	0.163
	± SD	10		24		
	Min	0		0		
	Max	88		272		
Decapoda	$\bar{x}$	105	1	68	1	0.170
	± SD	263		126		
	Min	0		0		
	Max	2619		971		
^Chaetognatha	$\bar{x}$	79	1	104	2	0.709
	± SD	54		115		
	Min	1		0		
	Max	326		824		
Cnidaria	$\bar{x}$	25	<1	24	<1	0.445
	± SD	33		53		
	Min	0		0		
	Max	213		634		
Polychaeta	$\bar{x}$	184	2	62	1	<0.001**
	± SD	276		103		
	Min	0		0		
	Max	1384		560		
Gastropoda	$\bar{x}$	100	1	147	2	0.419
	± SD	119		251		
	Min	0		0		
	Max	881		2130		
Bivalvia	$\bar{x}$	11	<1	57	1	<0.001**
	± SD	15		76		
	Min	0		0		
	Max	91		407		
Bryozoa	$\bar{x}$	127	2	8	<1	<0.001**
	± SD	168		14		
	Min	0		0		
	Max	954		104		
^Larvacea	$\bar{x}$	213	3	95	1	<0.001**
	± SD	214		170		
	Min	0		0		
	Max	1087		1026		
Protozoa	$\bar{x}$	699	9	60	1	<0.001**
	± SD	1218		127		
	Min	0		0		
	Max	6198		941		
Unidentified eggs	$\bar{x}$	131	2	35	1	<0.001**
	± SD	203		86		
	Min	0		0		
	Max	1681		594		

dry and wet periods respectively. The families Acartiidae, Paracalanidae and Oithonidae were predominantly sampled in both periods, comprising >90% of the total copepod abundance (Table 4.15). Although there was no significant difference in total copepod abundance between the dry and wet periods (ANOVA, $p > 0.05$), abundance of the dominant species *Acartia spinicauda*, *Parvocalanus crassirostris*, *Bestiolina similis* and *Oithona simplex* were significantly different between both periods (Table 4.15).

Table 4.15. Mean ($\bar{x}$) and relative abundance (%Rel) of copepods in the dry and wet periods. ^{A} indicates significant test using a one-way ANOVA, $^{\wedge}$ Mann-Whitney U test; '+' present but constituted <0.1% of relative abundance; ** significance at $p < 0.01$, ^{ns} no significance; number of taxa of grouped copepods in parenthesis.

Taxon	Period			
	Dry		Wet	
	$\bar{x}$	%Rel	$\bar{x}$	%Rel
^{A}*P. crassirostris***	1182	27.1	726	15.2
^{A}*A. spinicauda***	224	5.1	625	13.1
^{A}*B. similis***	225	5.1	82	1.7
^{A}*O. simplex***	183	4.2	219	4.6
$^{\wedge}$*Acartia* sp. 1^{ns}	65	1.5	93	1.9
$^{\wedge}$*O. dissimilis***	42	1.0	74	1.5
$^{\wedge}$*E. acutifrons* ^{ns}	48	1.1	82	1.7
$^{\wedge}$*O. aruensis***	43	1.0	30	0.6
T. barbatus	13	0.3	5	0.1
Pseudomacrochiron sp. 1	3	0.1	10	0.2
$^{\wedge}$*P. elegans***	12	0.3	109	2.3
P. trihamatus	5	0.1	6	0.1
P. bowmani	5	0.1	+	+
Kelleria sp. 1	7	0.2	11	0.2
M. norvegica	6	0.1	+	+
C. dorsispinatus	3	0.1	+	+
O. attenuata	5	0.1	+	+
P. aculeatus	8	0.2	+	+
P. annandalei	+	+	6	0.1
Other adults	11(28)	0.3	7(15)	0.2
% of adults		48.0		44.0
Nauplius and copepodid				
^{A}*Acartia* spp. ^{ns}	1123	25.7	1960	40.9
Parvocalanus spp.	531	12.2	508	10.6
Bestiolina sp.	374	8.6	66	1.4
Unidentified nauplii	73	1.7	65	1.3
Tortanus spp.	62	1.4	19	0.4
Pseudodiaptomus spp.	54	1.2	38	0.8
Oithona spp.	27	0.6	29	0.6
Pontellidae spp.	12	0.3	10	0.2
Centropages spp.	14	0.3	+	+
Other copepodids	4	0.1	+	+
% of juveniles		52.0		56.0

Species that were significantly more abundant in the dry period (ANOVA, $p < 0.001$) were *P. crassirostris* and *B. similis*. Abundance of *Bestiolina* copepodids in the dry period was 6 times greater than that in the wet period, but there was no large difference in abundance of *Parvocalanus* copepodids. Species that were more abundant in the wet period included *A. spinicauda* and *O. simplex*. There was no significant difference in abundance of *Acartia* copepodids between the dry and wet periods (ANOVA, $p > 0.05$). However, mean abundance in the wet period was relatively higher than in the dry period (Table 4.15).

The subdominant species (which comprised >1% of the total copepod abundance) *Acartia* sp. 1, *Euterpina acutifrons, Oithona dissimilis* and *Parvocalanus elegans* yielded greater numbers in the wet period than in the dry period. However, the significant difference in abundance between the dry and wet period was only observed for *O. dissimilis* and *P. elegans* (Mann-Whitney U test, $p < 0.001$) but not for *Acartia* sp. 1 and *E. acutifrons* (Mann-Whitney U test, $p > 0.05$). In contrast, *Oithona aruensis* was more numerous in the dry period than in the wet period (Mann-Whitney U test, $p < 0.001$; Table 4.15).

4.1.5.2 Dry period survey

a. Copepods

Mean copepod abundance recorded at surface and bottom waters as well as their mean over the 24 hours is given in Fig. 4.14. Total copepod abundance was significantly different among moon phases (ANOVA, $p < 0.001$), with the lowest mean value obtained during the 1st quarter while the other three moon phases were statistically equal in abundance (Tables 4.16 & 4.17).

Acartia copepodids constituted the most abundant copepod during neap tides (1st quarter = 39%, 3rd quarter = 28%), while *P. crassirostris* dominated the spring tide

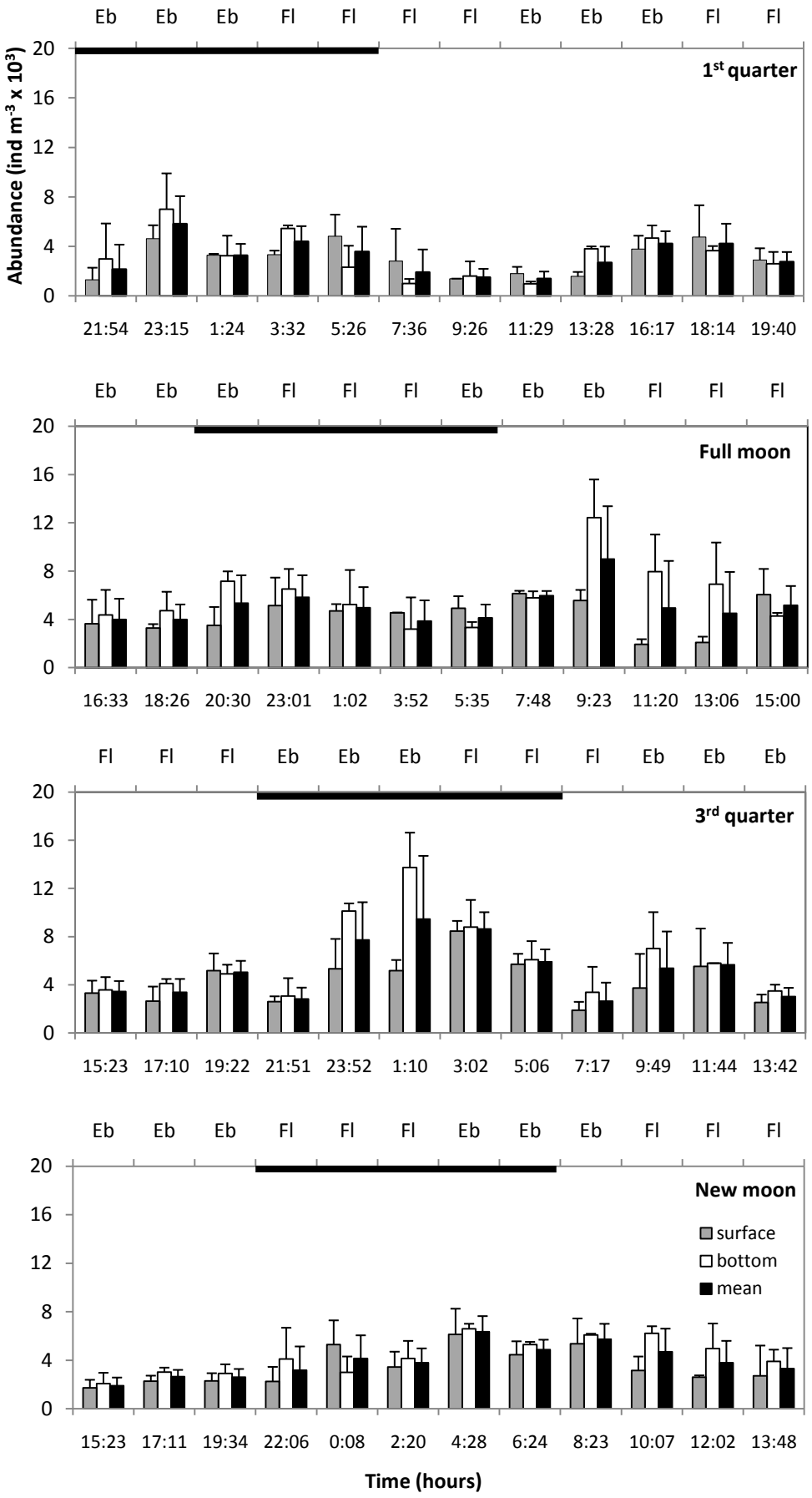


Fig.4.14. Surface, bottom and mean total copepod abundance recorded over 24 hours and four consecutive moon phases in the dry period. Horizontal bar denotes nighttime; Eb = ebb tide, Fl = flood tide.

Table 4.16. Summary results of four-way ANOVA on selected zooplankton groups with respect to moon phase, diel, tide, depth and their interaction in the dry period. Moon phase: Q1 = 1st quarter, FM = full moon, Q3 = 3rd quarter, NM = new moon; Diel: D = day, N = night; Tide: E = ebb, F = flood; Depth: S = surface, B = bottom; superscript a, b and c indicate homogeneous group; ** significance at $p < 0.01$, * significance at $p < 0.05$, ns no significance.

Taxon	Source of variation											
	Moon phase (1)				p-level	Diel (2)	p-level	Tide (3)	p-level	Depth (4)	p-level	Significant interaction effect ($p < 0.05$)
Copepoda												
Total	$Q1^{a}$	FM^{b}	$Q3^{b}$	NM^{b}	<0.001**	D<N	<0.001**	ns	0.559	S<B	<0.01**	1 x 2 x 3
Acartia copepodids	$Q1^{a}$	FM^{a}	$Q3^{a}$	NM^{b}	<0.001**	D>N	<0.001**	ns	0.070	ns	0.052	1 x 2
Acartia spinicauda	ns				0.652	D<N	<0.001**	ns	0.098	S<B	<0.001**	1 x 3, 2 x 4, 1 x 2 x 4
Parvocalanus crassirostris	$Q1^{a}$	FM^{b}	$Q3^{c}$	NM^{c}	<0.001**	D<N	<0.001**	E<F	0.022*	S<B	0.017*	1 x 2, 1 x 3, 1 x 2 x 3, 1 x 2 x 4
Bestiolina similis	$Q1^{a}$	FM^{b}	$Q3^{b}$	NM^{b}	<0.01**	D<N	<0.001**	ns	0.647	ns	0.145	1 x 3
Oithona simplex	$Q1^{a}$	FM^{b}	$Q3^{b}$	$NM^{a,b}$	<0.001**	D<N	<0.001**	ns	0.239	S<B	0.017*	1 x 2
Cirripedia larvae	$Q1^{a}$	FM^{b}	$Q3^{a}$	NM^{b}	<0.001**	D>N	<0.001**	E>F	<0.001**	ns	0.385	1 x 2, 2 x 3, 1 x 2 x 3
Decapoda	$Q1^{a}$	FM^{b}	$Q3^{b}$	NM^{a}	<0.001**	D>N	0.033*	E>F	0.040*	ns	0.837	1 x 2, 1 x 2 x 3
Chaetognatha	$Q1^{a,b}$	FM^{a}	$Q3^{b}$	NM^{a}	<0.001**	ns	0.195	ns	0.480	ns	0.189	1 x 3, 2 x 4
Cnidaria	$Q1^{a}$	FM^{b}	$Q3^{a}$	NM^{b}	<0.001**	ns	0.537	E>F	<0.01**	ns	0.451	1 x 3, 2 x 3, 1 x 2 x 3, 2 x 3 x 4
Polychaeta	$Q1^{a}$	FM^{b}	$Q3^{b}$	NM^{c}	<0.001**	D>N	<0.001**	E>F	<0.001**	ns	0.165	1 x 2, 1 x 2 x 3, 2 x 3 x 4
Gastropoda	$Q1^{a}$	FM^{b}	$Q3^{a}$	NM^{b}	<0.001**	ns	0.674	E>F	<0.01**	ns	0.292	1 x 2, 2 x 4, 1 x 2 x 4, 1 x 3 x 4
Larvacea	ns				0.585	D>N	<0.01**	E>F	<0.01**	ns	0.355	1 x 2
Protozoa	$Q1^{a}$	FM^{b}	$Q3^{c}$	NM^{b}	<0.001**	D>N	<0.01**	ns	0.066	ns	0.282	1 x 2, 1 x 2 x 3
Unidentified eggs	ns				0.641	ns	0.336	E<F	<0.01**	ns	0.114	1 x 2 x 3

Table 4.17. Mean ($\bar{x}$); and relative abundance (%Rel) of copepods with respect to moon phase, diel, tide and depth in the dry period. '+' indicates present but constituted <0.1% of relative abundance, '-' indicates absent; number of taxa of grouped copepods in parenthesis.

Taxon	Moon phase								Diel				Tide				Depth			
	1st quarter		Full moon		3rd quarter		New moon		Day		Night		Ebb		Flood		Surface		Bottom	
	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel
P. crassirostris	615	19	1694	33	1289	25	1131	29	1000	26	1438	29	1116	24	1248	30	1030	27	1335	27
A. spinicauda	203	6	220	4	244	5	228	6	155	4	320	6	215	5	232	6	170	4	278	6
B. similis	155	5	270	5	280	5	195	5	122	3	369	7	234	5	216	5	181	5	269	5
O. simplex	105	3	202	4	276	5	151	4	129	3	260	5	215	5	151	4	156	4	211	4
Acartia sp. 1	66	2	49	1	85	2	59	1	66	2	62	1	61	1	68	2	57	2	72	1
O. dissimilis	63	2	31	1	40	1	33	1	39	1	46	1	38	1	46	1	47	1	36	1
E. acutifrons	40	1	32	1	30	1	90	2	55	1	38	1	53	1	43	1	43	1	53	1
O. aruensis	35	1	22	0.4	92	2	23	1	53	1	29	1	45	1	41	1	44	1	42	1
T. barbatus	12	0.4	5	0.1	33	1	3	0.1	8	0.2	20	0.4	16	0.4	11	0.3	12	0.3	15	0.3
Pseudomacrochiron sp. 1	8	0.2	+	+	5	0.1	-	-	4	0.1	+	+	3	0.1	4	0.1	2	0.1	4	0.1
P. elegans	5	0.1	28	1	5	0.1	11	0.3	3	0.1	25	0.5	8	0.2	17	0.4	10	0.3	15	0.3
P. trihamatus	5	0.1	9	0.2	5	0.1	3	0.1	3	0.1	8	0.2	5	0.1	6	0.1	3	0.1	7	0.1
P. bowmani	4	0.1	9	0.2	7	0.1	+	+	+	+	12	0.2	5	0.1	6	0.1	5	0.1	6	0.1
Kelleria sp. 1	2	0.1	12	0.2	11	0.2	2	0.1	8	0.2	5	0.1	9	0.2	5	0.1	6	0.2	8	0.2
M. norvegica	2	0.1	15	0.3	7	0.1	+	+	6	0.2	7	0.1	10	0.2	3	0.1	6	0.2	6	0.1
C. dorsispinatus	+	+	+	+	8	0.2	+	+	+	+	6	0.1	2	0.1	3	0.1	4	0.1	+	+
O. attenuata	+	+	3	0.1	-	-	18	0.5	5	0.1	7	0.1	8	0.2	3	0.1	5	0.1	6	0.1
P. aculeatus	-	-	30	1	+	+	2	0.1	14	0.3	+	+	16	0.3	+	+	+	+	16	0.3
P. annandalei	-	-	+	+	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Other adults	12	0.3	9	0.2	10	0.2	14	0.3	6	0.2	19	0.4	12	0.3	10	0.2	12	0.3	11	0.2
	(15)		(17)		(12)		(22)		(24)		(24)		(26)		(20)		(24)		(25)	
Nauplius and copepodid																				
Acartia spp.	1232	39	1133	22	1493	28	633	16	1268	32	919	18	1268	28	977	24	1004	27	1241	25
Parvocalanus spp.	236	7	734	14	610	12	545	14	439	11	661	13	549	12	514	12	450	12	613	12
Bestiolina sp.	123	4	397	8	380	7	594	15	285	7	497	10	424	9	323	8	306	8	441	9
Unidentified nauplii	82	3	80	2	88	2	43	1	79	2	66	1	82	2	64	2	67	2	80	2
Tortanus spp.	70	2	41	1	89	2	48	1	70	2	51	1	84	2	40	1	62	2	62	1
Pseudodiaptomus spp.	34	1	40	1	120	2	21	1	32	1	84	2	46	1	61	1	45	1	62	1
Oithona spp.	32	1	31	1	15	0.3	31	1	29	1	24	0.5	25	1	29	1	26	1	29	1
Pontellidae spp.	7	0.2	22	0.4	11	0.2	10	0.3	10	0.3	15	0.3	15	0.3	10	0.2	11	0.3	14	0.3
Centropages spp.	4	0.1	13	0.2	18	0.3	21	1	15	0.4	12	0.2	17	0.4	11	0.3	12	0.3	16	0.3
Other copepodids	8	0.2	+	+	3	0.1	5	0.1	3	0.1	6	0.1	6	0.1	3	0.1	6	0.1	3	0.1

assemblages (full moon = 33%, new moon = 29%). The contribution of *A. spinicauda, O. simplex* and *B. similis* to copepod population was relatively constant among moon phases, constituting 3-6% of the mean total abundance. Copepodids of *Parvocalanus* and *Bestiolina* were also found to be numerically dominant at each moon phase, contributing over 4% of the copepod abundance. Copepods that consistently contributed 1-2% of the total copepod abundance were *Acartia* sp. 1, *Oithona dissimilis* and *Euterpina acutifrons*, while *Tortanus* and *Pseudodiaptomus* were captured mainly as copepodid stages. Three species that were generally encountered in low numbers appeared in higher number during full moon (*P. elegans* and *Paracalanus aculeatus*) and 3rd quarter (*Tortanus barbatus*) (Table 4.17).

Four-way ANOVA performed on the abundant copepod species revealed that the euryhaline copepods *P. crassirostris, O. simplex* and *B. similis* were least abundant during the 1st quarter ($p < 0.001$; Tables 4.16 & 4.17). There were also very few *Parvocalanus* and *Bestiolina* copepodids sampled during this period. Mean abundance of *Acartia* copepodids was significantly lowest during new moon as compared to the other three moon phases (ANOVA, $p < 0.001$) while *A. spinicauda* was statistically equal in abundance among moon phases (ANOVA, $p > 0.05$; Table 4.16).

Mean total copepod abundance during nighttime (5,010 ± 2,599 ind m^{-3}) and at the bottom water (4,950 ± 2,844 ind m^{-3}) was significantly higher than during daytime (3,907 ± 2,282 ind m^{-3}) and at surface water (3,783 ± 1,877 ind m^{-3}) (ANOVA, $p < 0.01$; Table 4.16). Tidal cycle did not significantly affect the total copepod abundance (ANOVA, $p > 0.05$; Table 4.16).

The interaction effect of moon phase, diel and tide in total copepod abundance was marginally significant ($p = 0.045$). Higher abundance of copepods was observed at ebb and flood tides, but in most cases coincided with nighttime except for samples

collected at 0923-hour during full moon (Fig. 4.14). Copepods collected at the bottom were far more abundant than at the surface from 0923-hour to 1306- hour during full moon and 2352-hour to 0110-hour during the 3rd quarter (Fig. 4.14). Out of 48 sampling occasions, only in a few surface samples were copepod numbers more than bottom ones. Higher surface numbers were mostly recorded during the night (e.g. 0525-hour during the 1st quarter, 0352- to 0535-hour during full moon and 0008-hour during new moon) (Fig. 4.14). Results of Tukey HSD test revealed that total copepod abundance was significantly lower during the 1st quarter at daytime particularly from 0736-hour to 1129-hour (Fig. 4.14, appendix Xa).

Generally, *A. spinicauda, P. crassirostris* and *O. simplex* were significantly more numerous during the night than during the day and at the bottom than at the surface water (ANOVA, $p < 0.05$, Table 4.16). The numbers of *B. similis* sampled during the night was also significantly higher than the day (ANOVA, $p < 0.001$), but did not significantly differ with sampling depth (ANOVA, $p > 0.05$; Table 4.16). Only *P. crassirostris* showed significant difference in abundance with tide, being more abundant during flood tide as compared to ebb tide (ANOVA, $p < 0.05$; Table 4.16).

Results of 4-way ANOVA exhibited various interaction effects for *P. crassirostris* due to variable abundance patterns across moon phases (Table 4.16, Fig. 4.15). Diel variation of *P. crassirostris* was significantly different only during the 3rd quarter, with higher abundance obtained during the night than the day at both sampling depths (Fig. 4.15, appendix Xb). The significant tidal effect on *P. crassirostris* abundance was observed only during the 1st quarter. This was mainly due to low number of specimens collected at ebb tide particularly diurnal ebb tide (1129-hour to 1617-hour) (Fig. 4.15, appendix Xb).

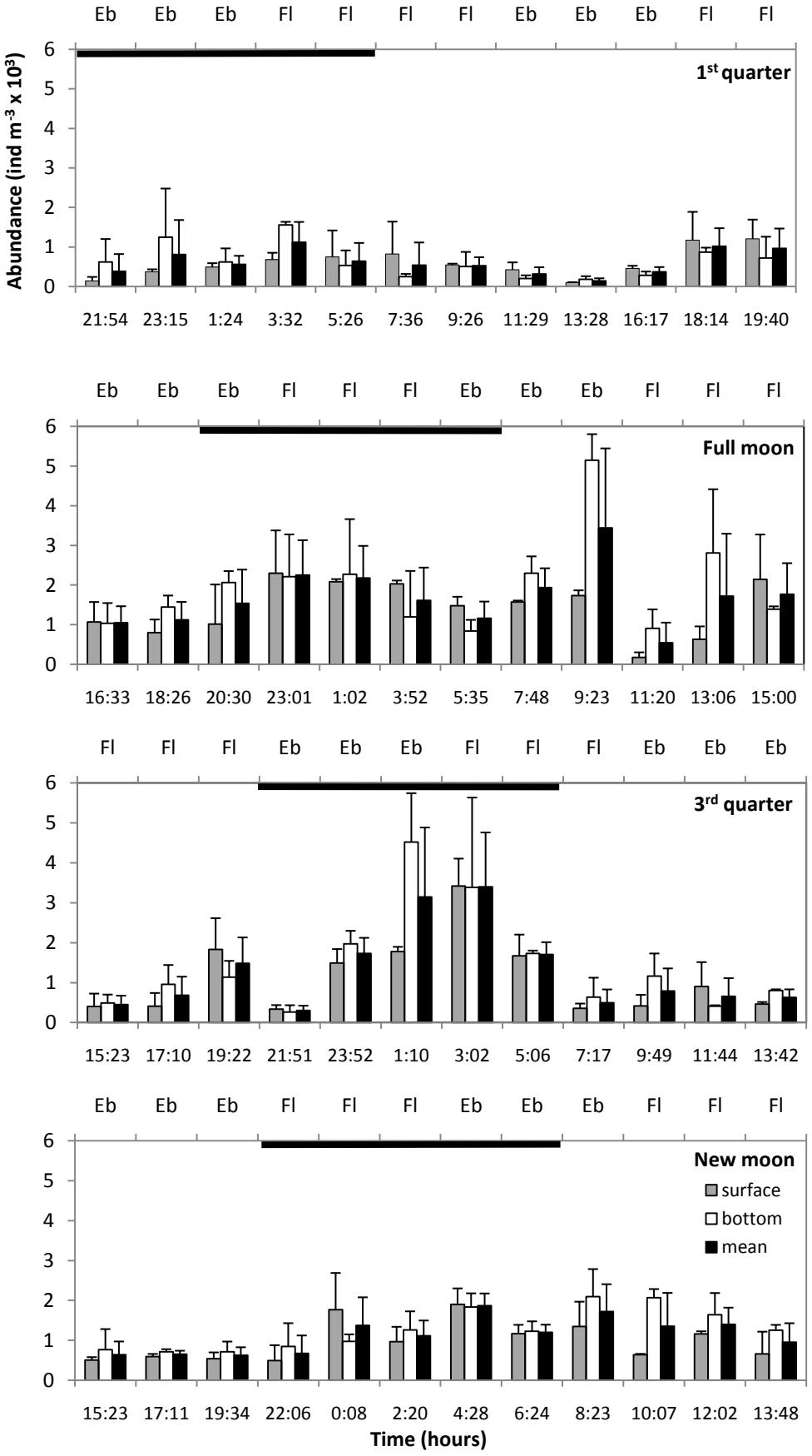


Fig.4.15. Surface, bottom and mean total abundance of *Parvocalanus crassirostris* recorded over 24 hours and four consecutive moon phases in the dry period. Horizontal bar denotes nighttime; Eb = ebb tide, Fl = flood tide.

In general, *P. crassirostris* at the bottom appeared to be more abundant than at surface during spring daytime except for the samples collected at 1500-hour during full moon (Fig. 4.15). There was no large difference in abundance between surface and bottom samples during spring nighttime (Fig 4.15). As mentioned earlier, the significant lower number of *P. crassirostris* during ebb tide was due to fewer specimens collected during the 1st quarter day-ebb. Exceptional higher abundance of *P. crassirostris* in bottom samples at 0923-hour during full moon and 0110-hour during the 3rd quarter corresponded to late ebb tide (Fig 4.15).

The abundance patterns of *B. similis* were relatively similar to that of *P. crassirostris*, suggesting the coexistence of these species. The lower numbers of *B. similis* were observed mainly during neap day-ebb (Fig 4.16). A notable nocturnal increase in abundance of *B. similis* was observed mainly during neap tides (Fig. 4.16). No major peak was observed during nocturnal spring tide (Fig 4.16). Similarly to *P. crassirostris*, an exceptional high (2352-hour and 0110-hour) corresponded to ebb tide (Fig 4.16).

The numbers of *O. simplex* sampled during the 1st quarter were consistently low (Fig. 4.17). Similar to *B. similis*, *O. simplex* was found in higher numbers at 0923-hour during full moon and 2352- and 0110-hour during the 3rd quarter, coinciding with ebb tide. The significant interaction effect between moon phase and tide for *O. simplex* was mainly attributed to these values (appendix Xd).

There was significant interaction effect between diel and depth for *A. spinicauda* abundance ($p < 0.01$; Table 4.16). *A. spinicauda* at the bottom was significantly more abundant than at surface during the day, but was homogeneously distributed across water column during the night (appendix Xe). This pattern was particularly obvious during spring tides as indicated by the 3-way interaction between moon phase, diel and

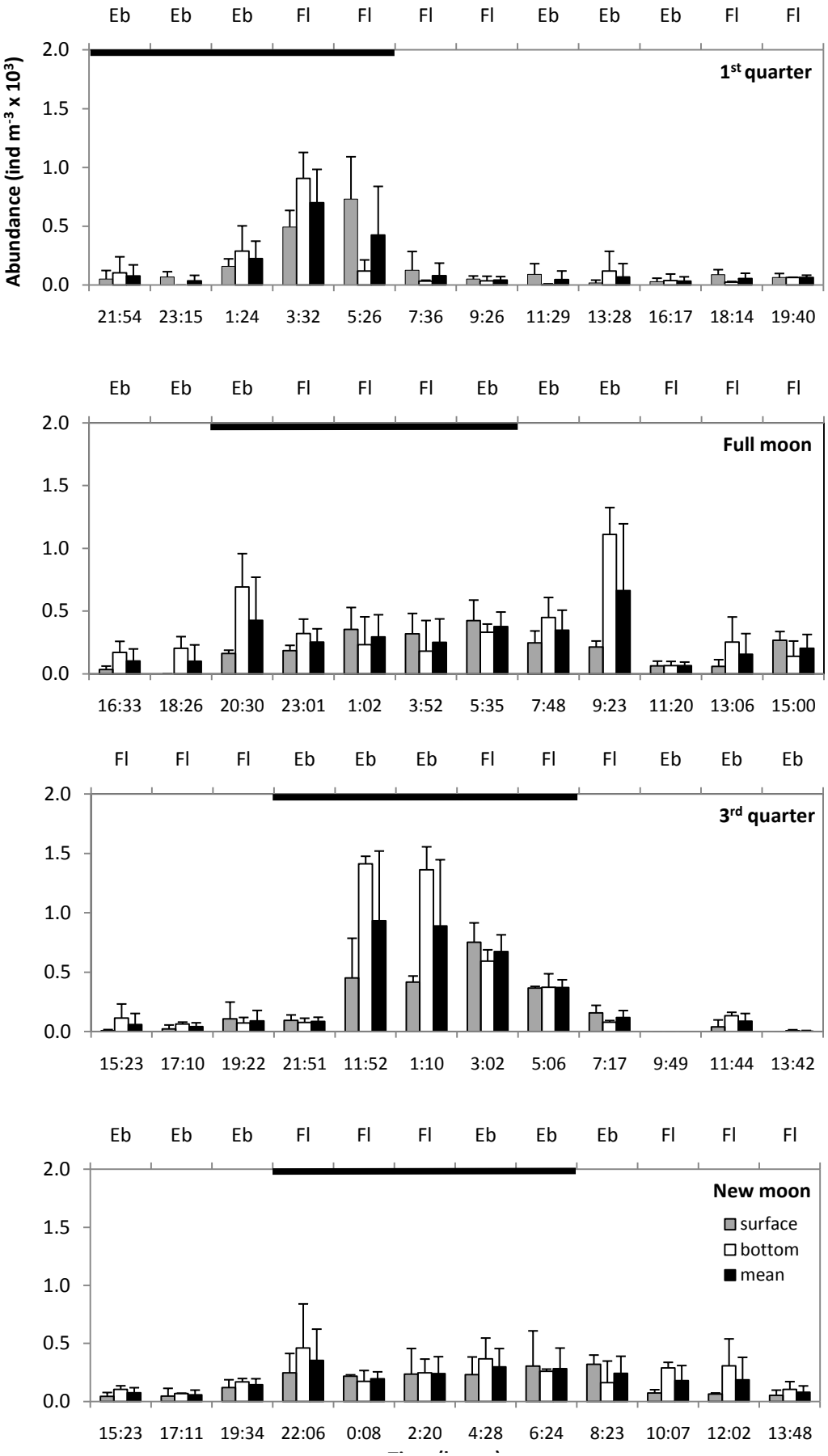


Fig.4.16. Surface, bottom and mean total abundance of *Bestiolina similis* recorded over 24 hours and four consecutive moon phases in the dry period. Horizontal bar denotes nighttime; Eb = ebb tide, Fl = flood tide.

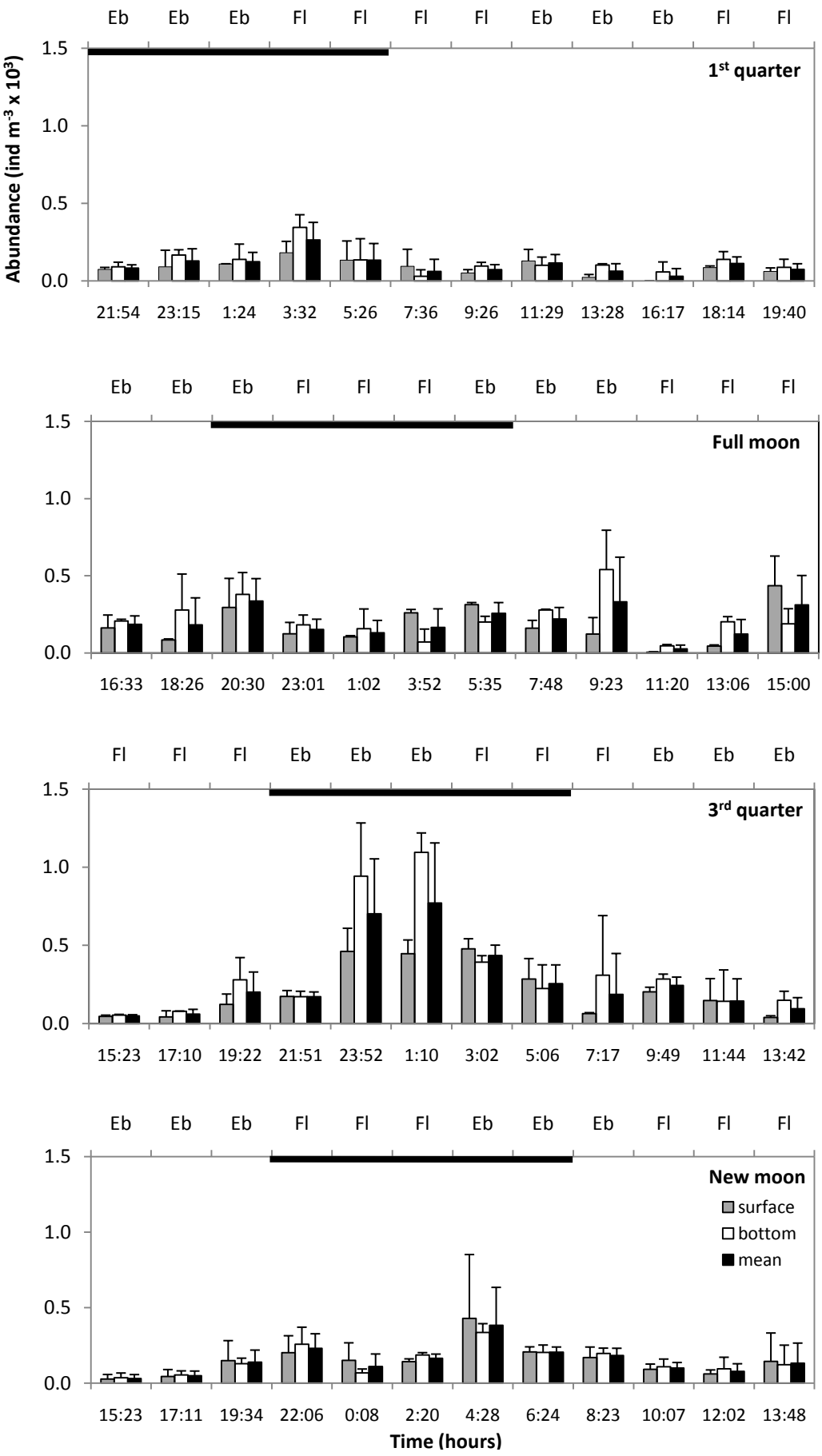


Fig.4.17. Surface, bottom and mean total abundance of *Oithona simplex* recorded over 24 hours and four consecutive moon phases in the dry period. Horizontal bar denotes nighttime; Eb = ebb tide, Fl = flood tide.

depth ($p < 0.05$; appendix Xf). During neap tide, there was no obvious depth but diel pattern for *A. spinicauda*. Abundance at both sampling depths was significantly lower during the day as compared to during the night (Fig. 4.18, appendix Xf).

Acartia copepodids were significantly more abundant during the day compared with the night (ANOVA, $p < 0.001$; Table 4.16). The diel pattern, however, was only significant during full moon and 3rd quarter (Fig. 4.19, appendix Xg). The number of *Acartia* copepodids encountered during new moon was consistently low (Fig. 4.19). The depth variation in *Acartia* copepodids was marginally insignificant (ANOVA, $p = 0.052$) with mean abundance at the bottom (1,241 ± 1,020 ind m^{-3}) being relatively higher than at the surface (1,004 ± 704 ind m^{-3}) (Table 4.16).

b. Cirripede larvae

Cirripede larvae showed a notable neap-spring pattern, with higher numbers of larvae collected during neap tide as compared to spring tide (ANOVA, $p < 0.001$). Mean abundance during daytime and ebb tide was also significantly higher than that of nighttime and flood tide, respectively (ANOVA, $p < 0.001$). Mean abundance at the surface was not significantly different from that of the bottom (ANOVA, $p > 0.05$; Table 4.16).

Cirripede larvae were found in large numbers during neap daytime except for samples collected at 2315-hour during the 1st quarter (Fig. 4.20). Significant lower abundance of cirripede larvae were found during spring night-flood (Fig. 4.20, appendix XIa).

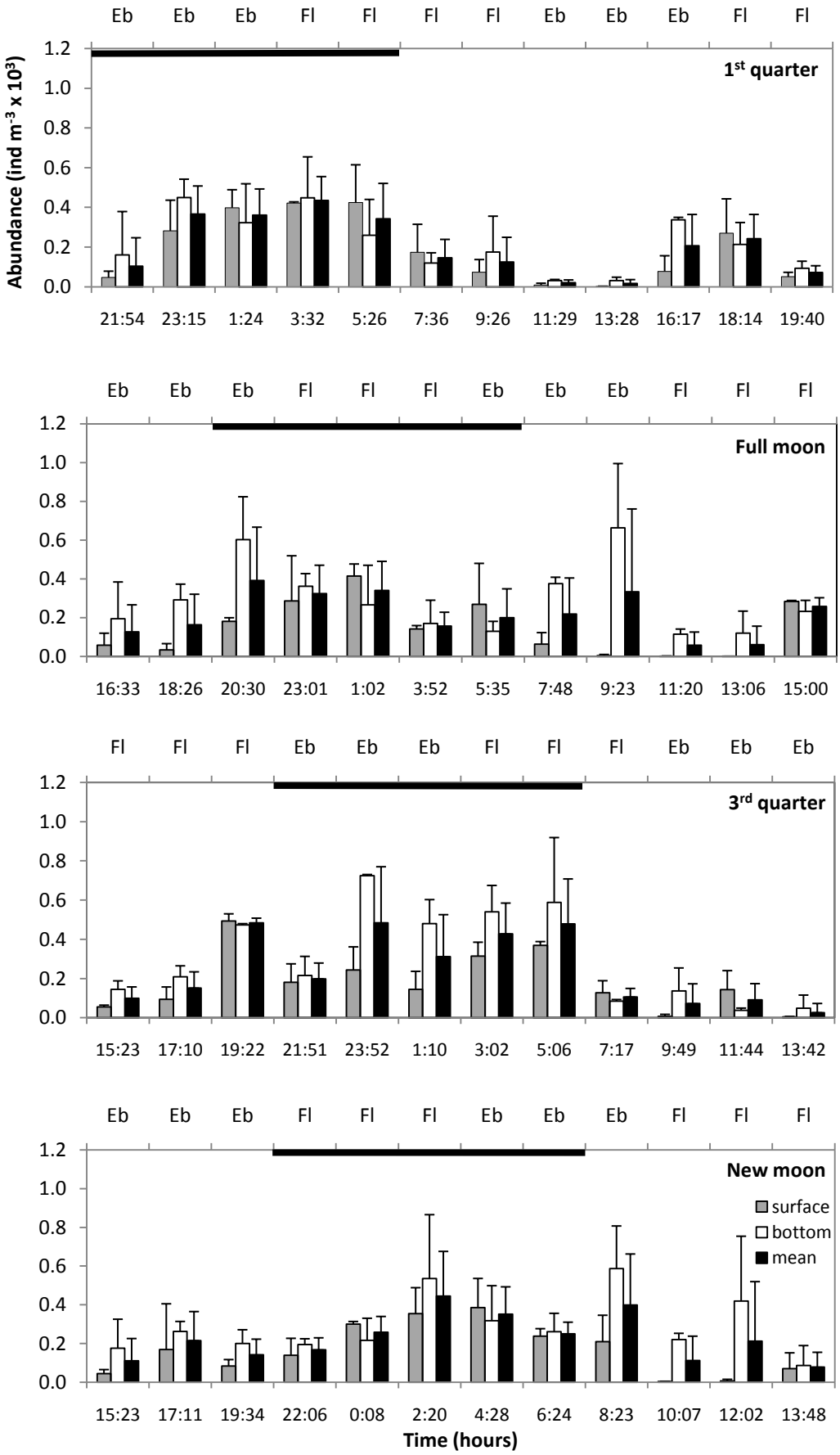


Fig.4.18. Surface, bottom and mean total abundance of *Acartia spinicauda* recorded over 24 hours and four consecutive moon phases in the dry period. Horizontal bar denotes nighttime; Eb = ebb tide, Fl = flood tide.

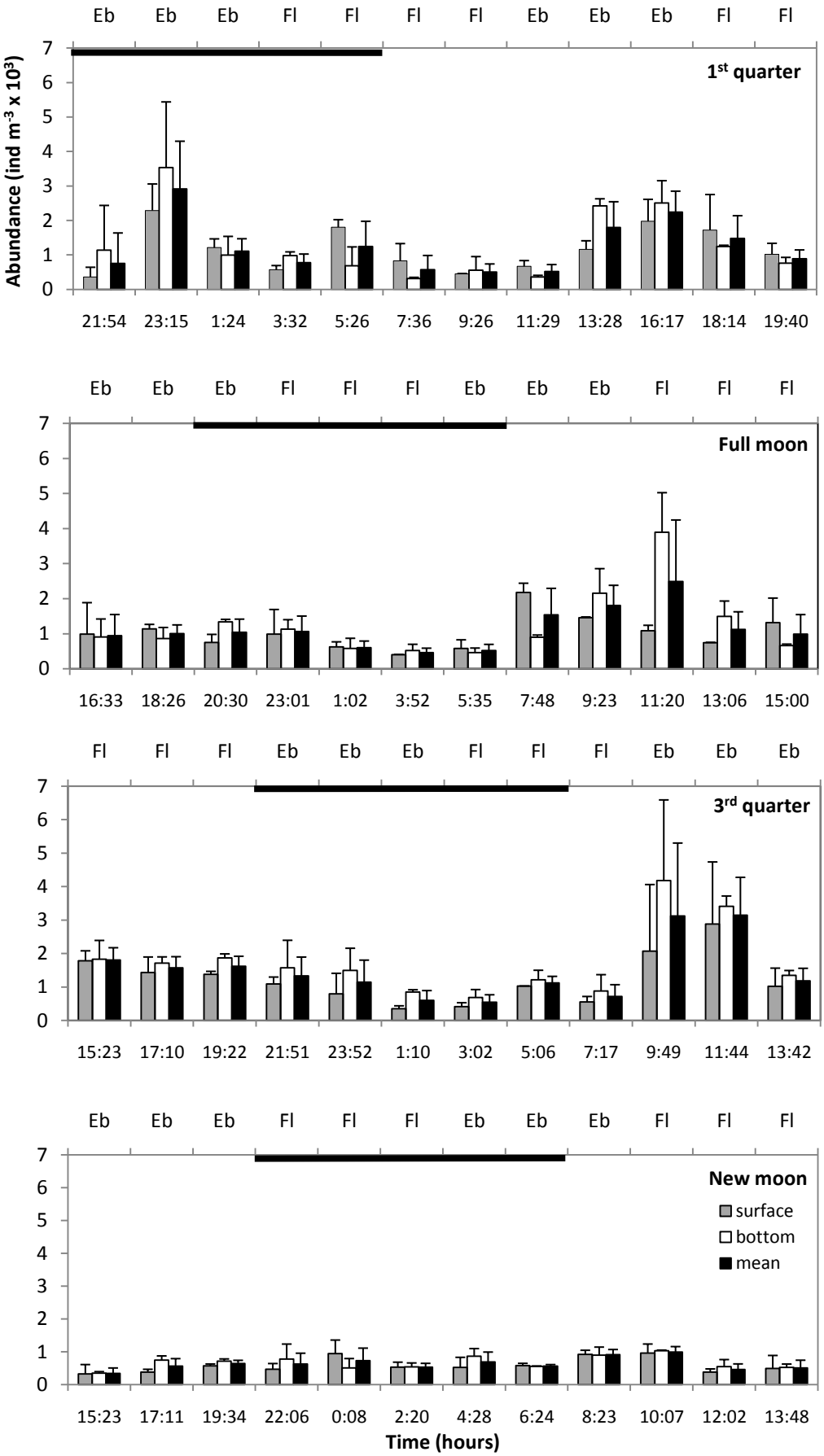


Fig.4.19. Surface, bottom and mean total abundance of *Acartia* copepodids recorded over 24 hours and four consecutive moon phases in the dry period. Horizontal bar denotes nighttime; Eb = ebb tide, Fl = flood tide.

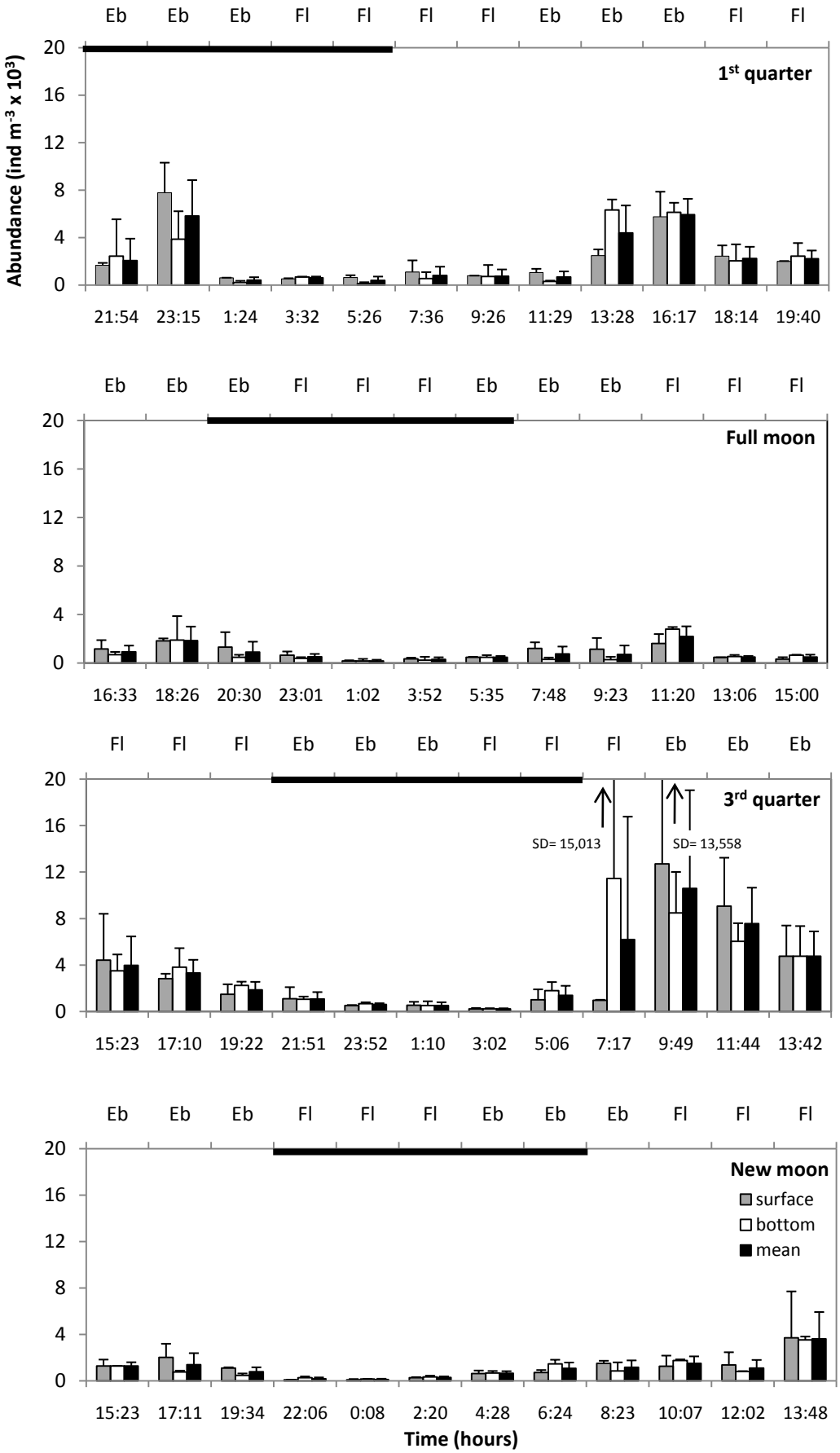


Fig.4.20. Surface, bottom and mean total abundance of Cirripedia larvae recorded over 24 hours and four consecutive moon phases in the dry period. Horizontal bar denotes nighttime; Eb = ebb tide, Fl = flood tide.

c. Decapods

Decapods which comprised of various larval stages were significantly more abundant during full moon and 3rd quarter as compared to 1st quarter and new moon (ANOVA, $p < 0.001$; Tables 4.16 & 4.18). Like cirripede larvae, decapods were more numerous during the day and ebb tide as compared to nighttime and flood tide, respectively (ANOVA, $p < 0.05$). Abundance of decapods was not significantly different between surface and bottom waters (ANOVA, $p > 0.05$; Table 4.16).

The interaction effect between moon phase and diel was marginally significant ($p = 0.047$). There was also significant interaction effect between moon phase, diel and tide ($p < 0.001$). At spring tide, abundance of decapods was significantly lower during night-flood as compared to day-flood (Fig. 4.21, appendix XIb). Nevertheless, it is noted that during spring tide, increase of decapod abundance initially occurred at early ebb tide near dawn through the morning mid- and late ebb tide, and eventually peaked at early flood tide during the day. No major peak was observed thereafter (Fig. 4.21). There was no significant interaction effect between diel and tide during neap tide (Fig. 4.21, appendix XIb).

Zoeae of brachyuran were the most dominant component of decapods during spring tide, representing up to 95% of the total decapod abundance (Table 4.19). Large numbers of brachyuran zoeae were captured during full moon, dominating the decapod assemblages (see Fig. 4.21). Although total decapod abundance was lowest during new moon, brachyuran zoeae were still captured in higher numbers as compared to the period of neap tides (Table 4.19). Very few megalopae and juveniles of brachyuran were collected over the sampling period (<0.2%, Table 4.19). Neap tide decapods were best represented by *Acetes* protozoeae (45 - 71%), while juvenile and adult stages of *Acetes* appeared in low numbers. Mean abundance of the remaining decapod groups was generally higher during neap tide than spring tide (Table 4.19).

Table 4.18. Mean ($\bar{x}$) and relative abundance (%Rel) of major zooplankton groups with respect to moon phase, diel, tide and depth in the dry period. '+' indicates present but constituted <0.1% of relative abundance, number of zooplankton groups in parenthesis.

Taxon	Moon phase								Diel				Tide				Depth			
	1st quarter		Full moon		3rd quarter		New moon		Day		Night		Ebb		Flood		Surface		Bottom	
	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel
Copepoda	3159	35.4	5136	72.4	5253	52.0	3918	68.3	3907	46.0	5010	69.4	4587	51.3	4147	59.2	3783	52.7	4950	56.5
Cirripedia larvae	2201	24.6	807	11.4	3511	34.7	1104	19.2	2630	30.9	891	12.3	2352	26.3	1459	20.8	1899	26.5	1912	21.8
Mysidae	+	+	5	0.1	6	0.1	+	+	+	+	6	0.1	5	0.1	+	+	+	+	5	0.1
Decapoda	54	0.6	256	3.6	70	0.7	42	0.7	129	1.5	72	1.0	102	1.1	109	1.6	89	1.2	122	1.4
Chaetognatha	80	0.9	68	1.0	113	1.1	56	1.0	82	1.0	75	1.0	83	0.9	76	1.1	72	1.0	86	1.0
Cnidaria	37	0.4	21	0.3	24	0.2	19	0.3	26	0.3	24	0.3	31	0.3	20	0.3	23	0.3	28	0.3
Polychaeta	396	4.4	105	1.5	162	1.6	71	1.2	236	2.8	110	1.5	256	2.9	111	1.6	162	2.3	205	2.3
Gastropoda	164	1.8	64	0.9	131	1.3	41	0.7	104	1.2	94	1.3	123	1.4	76	1.1	86	1.2	113	1.3
Bivalvia	14	0.2	10	0.1	12	0.1	8	0.1	10	0.1	13	0.2	12	0.1	10	0.1	8	0.1	14	0.2
Bryozoa	162	1.8	127	1.8	143	1.4	76	1.3	158	1.9	84	1.2	161	1.8	93	1.3	105	1.5	149	1.7
Larvacea	241	2.7	132	1.9	289	2.9	189	3.3	268	3.2	135	1.9	251	2.8	175	2.5	184	2.6	241	2.8
Protozoa	2337	26.2	139	2.0	260	2.6	59	1.0	768	9.0	603	8.3	826	9.2	571	8.2	628	8.8	769	8.8
Unidentified eggs	73	0.8	207	2.9	119	1.2	123	2.2	162	1.9	86	1.2	125	1.4	136	1.9	116	1.6	145	1.7
Others (10)	13	0.1	18	0.3	16	0.2	29	0.5	20	0.2	17	0.2	20	0.2	17	0.2	17	0.2	21	0.2

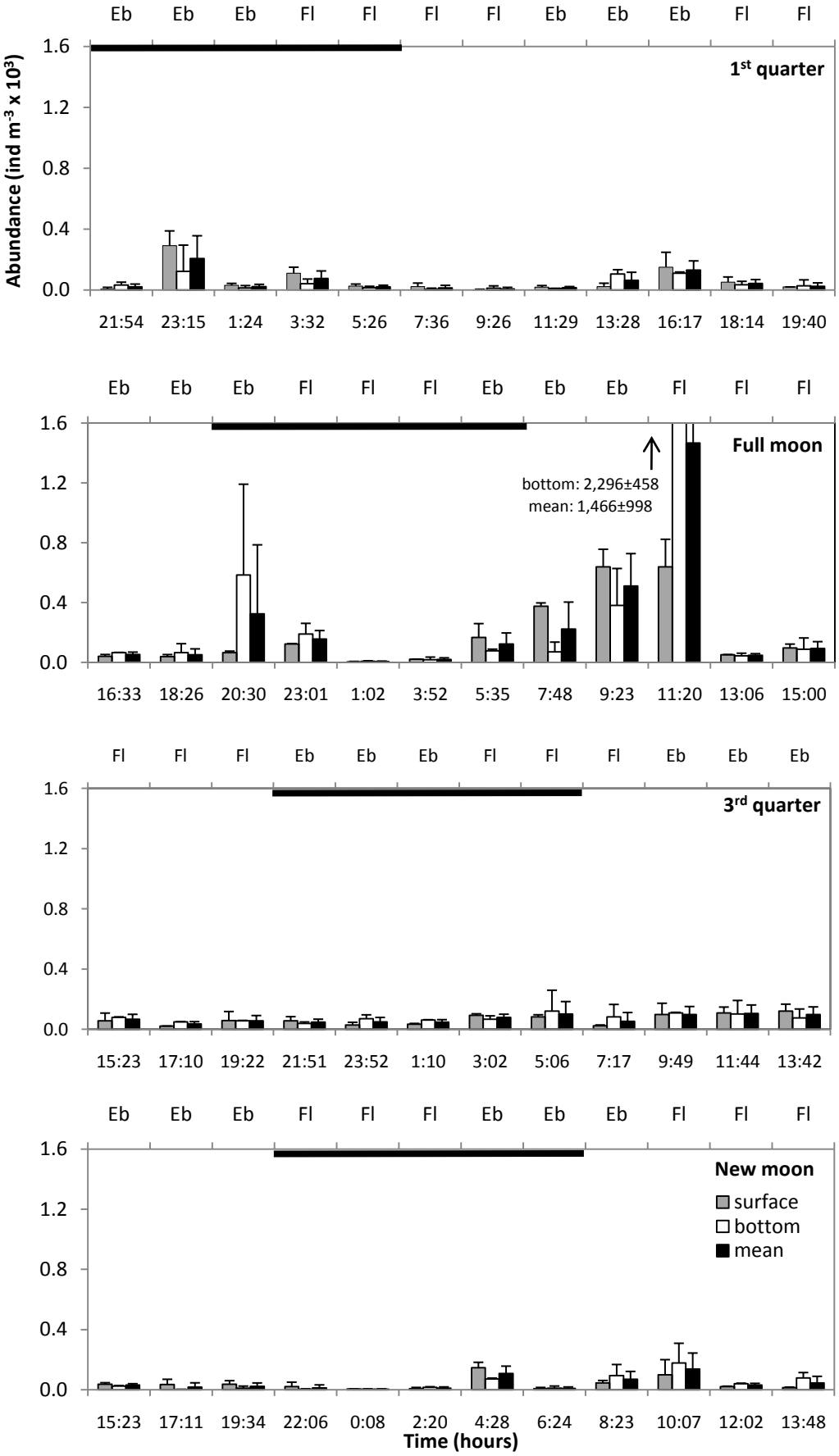


Fig.4.21. Surface, bottom and mean total abundance of decapods recorded over 24 hours and four consecutive moon phases in the dry period. Horizontal bar denotes nighttime; Eb = ebb tide, Fl = flood tide.

Table 4.19. Mean ($\bar{x}$) and relative abundance (%Rel) of different life stages of decapods with respect to moon phase, diel, tide and depth in the dry period. '+' indicates present but constituted <0.1% of relative abundance, '-' indicates absent; number of taxa of grouped decapods in parenthesis.

Taxon	Life stage	Moon phase								Diel				Tide				Depth			
		1st quarter		Full moon		3rd quarter		New moon		Day		Night		Ebb		Flood		Surface		Bottom	
		$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel
Lucifer	Protozoea	-	-	3	1.1	3	4.7	4	9.1	4	2.7	1	1.3	2	2.4	2	2.3	3	3.5	2	1.5
	Juvenile	<1	0.5	<1	0.1	1	0.7	<1	0.2	<1	0.3	<1	0.1	<1	0.4	<1	0.1	<1	0.3	<1	0.2
	Adult	1	1.5	<1	0.2	1	1.7	1	3.0	1	0.8	1	1.0	1	0.8	1	0.9	1	1.1	1	0.7
Acetes	Protozoea	38	70.7	3	1.0	32	45.4	8	19.2	23	17.9	16	21.9	27	26.2	13	12.3	20	22.6	20	16.4
	Juvenile	1	1.6	<1	0.1	1	1.2	<1	0.3	1	0.4	1	0.7	<1	0.3	1	0.7	<1	0.5	1	0.5
Acetes japonicus	Adult	<1	0.1	<1	0.1	<1	0.2	<1	0.8	+	+	<1	0.7	<1	0.1	<1	0.3	<1	0.2	<1	0.2
A. indicus	Adult	+	+	+	+	+	+	<1	0.1	+	+	<1	0.1	+	+	+	+	+	+	+	+
A. sibogae	Adult	+	+	+	+	+	+	+	+	-	-	+	+	+	+	+	+	+	+	+	+
Alpheidae	Zoea	1	1.9	+	+	3	4.8	<1	0.3	1	0.9	1	1.7	1	0.9	1	1.3	1	1.7	1	0.7
	Juvenile	-	-	-	-	-	-	+	+	-	-	+	+	-	-	+	+	-	-	+	+
Palaemonidae	Zoea	<1	0.3	<1	0.1	1	1.7	<1	0.3	<1	0.3	<1	0.6	<1	0.4	<1	0.4	1	0.6	<1	0.2
Penaeidae	Nauplius	8	14.1	5	1.8	17	24.0	3	7.7	5	3.8	12	17.2	8	7.8	8	7.5	7	7.3	10	7.9
	Protozoea	<1	0.1	+	+	+	+	<1	0.1	+	+	+	+	+	+	+	+	<1	0.1		
	Mysis	+	+	+	+	<1	0.2	-	-	+	+	+	+	+	+	<1	0.1	+	+	<1	0.1
	Post-larva	+	+	+	+	<1	0.1	+	+	+	+	<1	0.1	+	+	<1	0.1	<1	0.1	+	+
Brachyura	Zoea	3	6.3	243	95.0	4	6.3	23	55.9	92	71.1	36	50.1	58	57.1	79	72.6	53	59.1	85	69.4
	Megalopa	<1	0.1	<1	0.1	<1	0.2	<1	0.1	<1	0.1	<1	0.3	<1	0.1	<1	0.2	<1	0.1	<1	0.2
	Juvenile	+	+	<1	0.1	<1	0.2	<1	0.1	<1	0.1	<1	0.2	<1	0.1	<1	0.1	<1	0.1	<1	0.1
Diogenidae	Zoea	1	2.3	<1	0.2	2	2.6	1	1.6	1	0.7	1	1.6	2	1.6	<1	0.4	1	0.9	1	1.0
	Juvenile	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Porcellanidae	Zoea	<1	0.3	+	+	2	2.9	<1	0.2	<1	0.1	1	1.8	1	0.6	1	0.6	<1	0.6	1	0.6
Others		+	+	+	+	2	3.0	<1	1.0	1	0.6	<1	0.6	1	1.1	<1	0.1	1	1.2	<1	0.2
		(1)		(3)		(2)		(2)		(2)		(2)		(2)		(3)		(3)		(2)	

d. Mysidae

Non-parametric analysis revealed no significant difference in abundance of Mysidae among moon phases (Kruskal-Wallis ANOVA, $p > 0.05$). Mysidae at each moon phase appeared to be more influenced by the effect of diel rather than tide. All moon phases except for full moon showed a remarkable nocturnal pattern for Mysidae (Mann-Whitney U test, $p < 0.05$, Table 4.20, Fig. 4.22). The tidal effect on Mysidae was significant during the 1st quarter due to almost no specimens collected at 1129 -hour and 1617-hour coinciding with ebb tide (Fig. 4.22). Bottom abundance was significantly higher than at surface (Mann-Whitney U test, $p < 0.05$) during full moon particularly from 1633- to 2030-hour which corresponded to ebb tide (Table 4.20, Fig. 4.22).

Notocanthomysis ranked ahead of Mysidae in abundance (49 - 84%) followed by *Acanthomysis* (14 - 31%) and *Rhopalothalmus* (2 - 21%). *Mesopodosis* was encountered over the dry period but appeared in very few number (<5%). *Erythrop* sp. was rarely captured throughout the sampling period (Table 4.20).

Table 4.20. Summary table of non-parametric Kruskal-Wallis ANOVA (Ψ) and Mann-Whitney U test (^), mean ± SD and relative abundance (in parenthesis) of Mysidae in the dry period. n = sample size; Diel: D = day, N = night; Tide: E = ebb, F = flood; Depth: S = surface, B = bottom; ** significance at $p < 0.01$, * significance at $p < 0.05$, ns no significance.

	1st quarter	Full moon	3rd quarter	New moon
n	48	48	48	48
Main effect				
ΨMoon phase		ns		
^Diel	D<N**	D = N	D<N**	D<N**
^Tide	E>F (p = 0.04)	E = F	E = F	E = F
^Depth	S = B	S<B*	S = B	S = B
Abundance				
Total Mysidae	2 ± 4	5 ± 11	6 ± 15	2 ± 5
Genera				
Acanthomysis sp.	<1 (25)	<1 (14)	1 (21)	<1 (31)
Erythrops sp.	+	-	-	<1 (6)
Mesopodopsis sp.	<1 (5)	+	-	<1 (3)
Notacanthomysis sp.	1 (49)	4 (84)	4 (70)	1 (54)
Rhopalophthalmus sp.	<1 (21)	<1 (2)	<1 (8)	<1 (7)

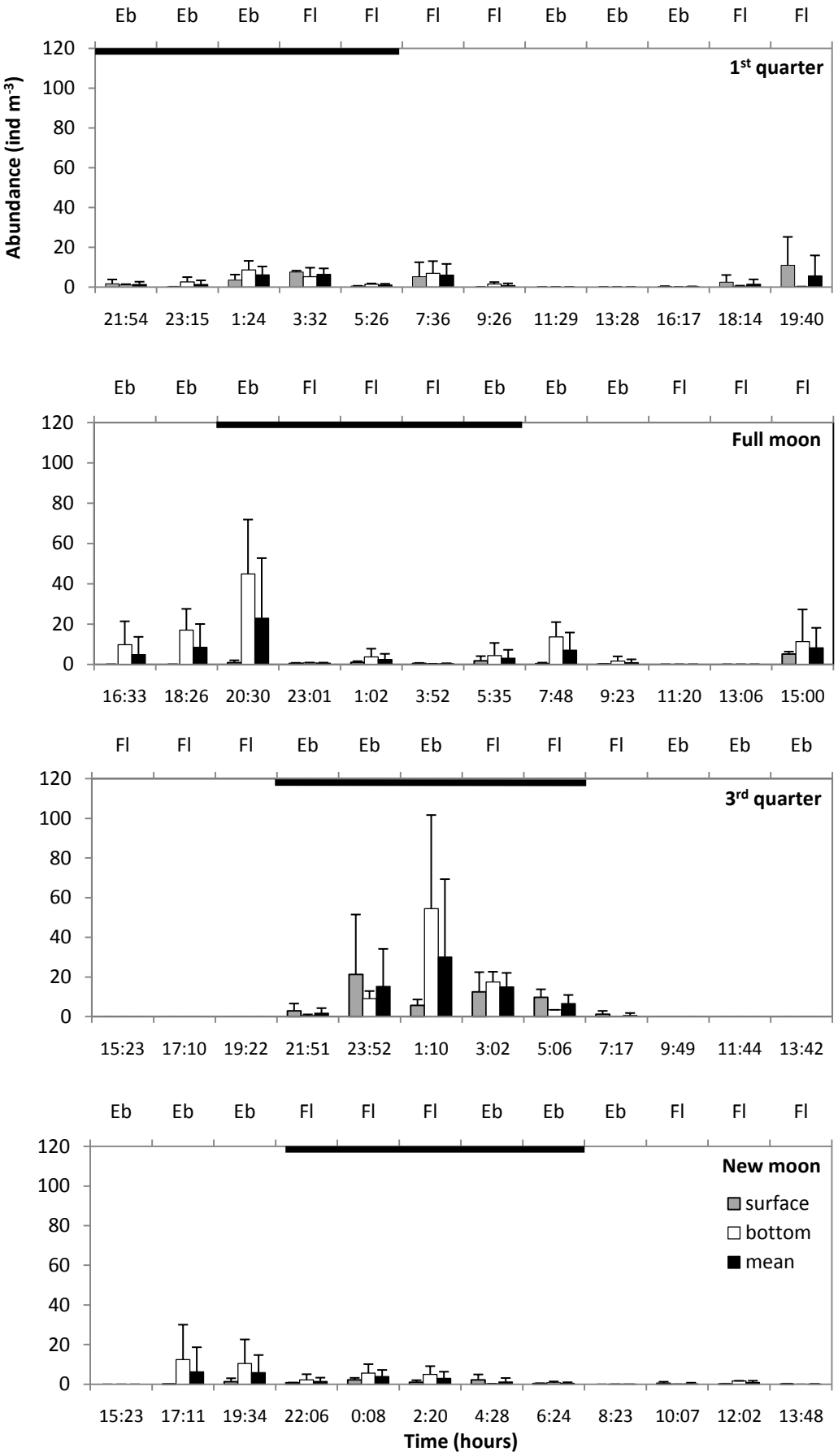


Fig.4.22. Surface, bottom and mean total abundance of Mysidae recorded over 24 hours and four consecutive moon phases in the dry period. Horizontal bar denotes nighttime; Eb = ebb tide, Fl = flood tide.

e. Non-crustacean zooplankton

The non-crustacean zooplankton protozoans, cnidarians and gastropods that were significantly more abundant during neap tide as compared to spring tide (ANOVA, $p < 0.001$; Tables 4.16 & 4.18). Polychaetes comprised largely of larval forms and chaetognaths were also significantly different in abundance among moon phases (ANOVA, $p < 0.001$). Abundance of polychaetes was highest during the 1st quarter and lowest during new moon. Chaetognaths were significantly more abundant during the 3rd quarter while other three moon phases were not significantly different from each other. Abundance of larvaceans was not significantly different among moon phases (ANOVA, $p > 0.05$; Table 4.16). The remaining groups (e.g. bivalves, ctenophores, larvae of echinoderms, bryozoans and *Phoronis* sp.) were not included in the 4-way ANOVA.

On average, polychaetes, gastropods, larvaceans and cnidarians were more abundant at ebb tide as compared to flood tide (ANOVA, $p < 0.01$). Mean abundance of protozoans and chaetognaths was not significantly influenced by tide (ANOVA, $p > 0.05$). Polychaetes, protozoans and larvaceans in day samples were significantly more abundant than night samples (ANOVA, $p < 0.01$). There was no significant diel pattern on abundance of chaetognaths, cnidarians and gastropods (ANOVA, $p > 0.05$; Table 4.16).

Similarly to cirripede larvae, the 3-way interaction effect between moon phase, diel and tide (ANOVA, $p < 0.001$) indicated that the abundance of polychaetes was highest during neap day-ebb, but very few specimens were captured during spring night-flood (Fig. 4.23, appendix XIc). Although there was no significant tidal and depth patterns for chaetognaths, interaction effect between tide and depth showed that this animal was more restricted to the bottom as compared to that of surface during ebb tide, but did not show significant difference between surface and bottom water during flood tide (appendix XId). Interaction effect between factors for other non-crustacean

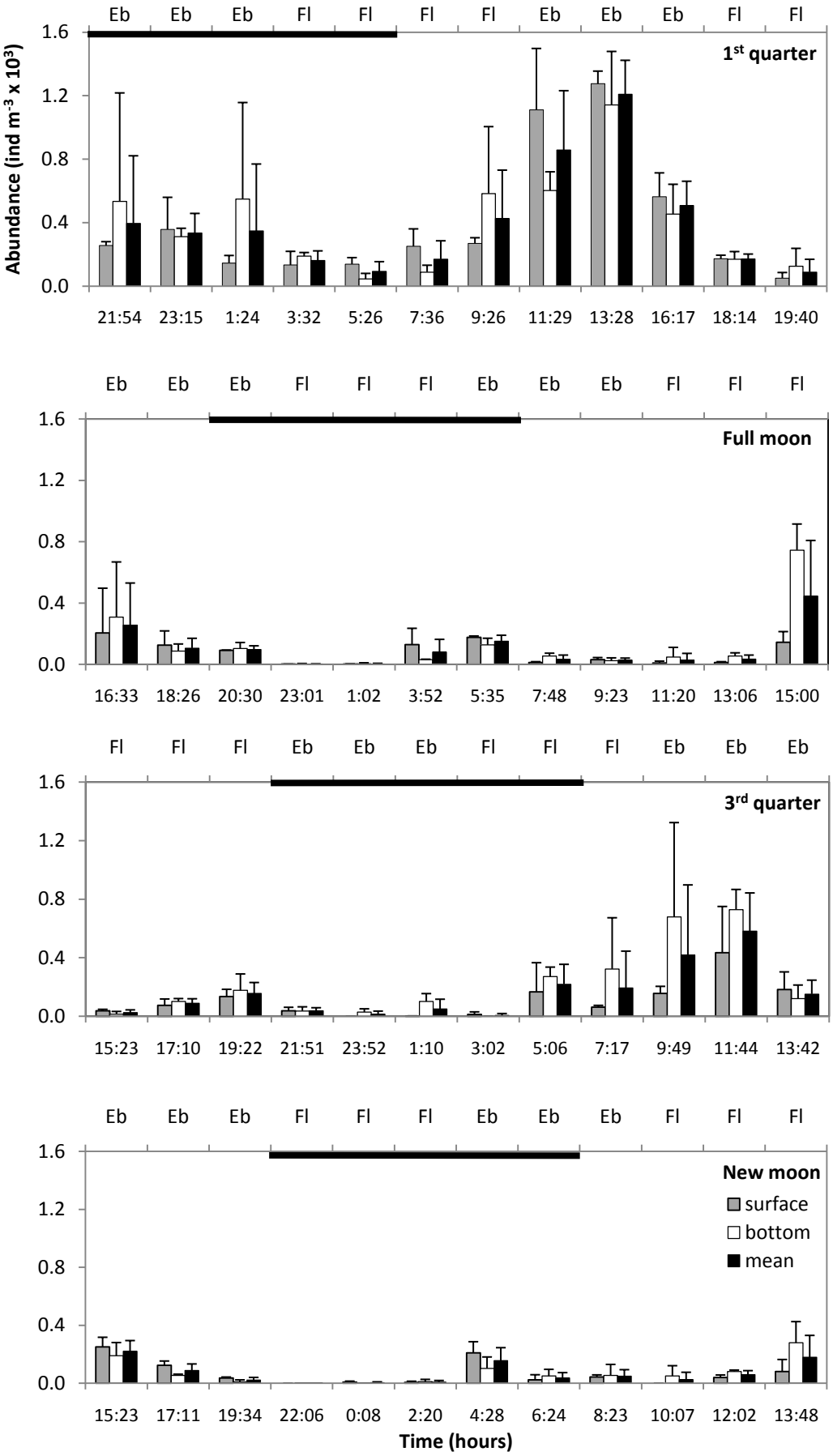


Fig.4.23. Surface, bottom and mean total abundance of polychaetes recorded over 24 hours and four consecutive moon phases in the dry period. Horizontal bar denotes nighttime; Eb = ebb tide, Fl = flood tide.

groups (cnidarians, gastropods, larvaceans and protozoans) are not further addressed here.

4.1.5.3 Wet period survey

a. Copepods

Copepods were significantly more abundant during neap tide than spring tide (ANOVA, $p < 0.001$, Table 4.21, Fig. 4.24). *Acartia* copepodids overwhelmed the neap-tide community, comprising more than 50% of the mean total copepod abundance. *P. crassirostris* outnumbered other copepods during spring tide (26 and 32%). Compared to the dry period, *A. spinicauda* and *O. simplex* exhibited a greater difference in percentage composition among moon phases, ranging from 7 - 16 and 1 - 10% of the total copepod abundance respectively. Species that consistently accounted for 1 to 3% by moon phases were *B. similis*, *Acartia* sp. 1 and *O. dissimilis*. Fewer numbers of *E. acutifrons* (<1%) were found during the 1st quarter and full moon, but the species constituted up to 4% of total copepod abundance during the 3rd quarter. *Parvocalanus elegans* (7%) was the most abundant adult copepod after *P. crassirostris* and *A. spinicauda* during full moon. While very few were captured in most sampling dates, *Pseudodiaptomus annandalei* attained greater abundance (1%) during new moon (Table 4.22).

There was a clear moon phase pattern in abundance of *Acartia* copepodids, with higher abundance during neap tide as compared to spring tide (ANOVA, $p < 0.001$). Fig. 4.25 shows that the variability of *Acartia* copepodids during the 1st quarter was extreme, with abundance ranging from 166 to 13,834 (mean 4,110 ± 3,009 SD) ind m^{-3}. Abundance of *Acartia* copepodids was consistently at low levels during new moon. *A. spinicauda* showed very similar abundance patterns to that of *Acartia* copepodids, with several peaks occurring during the 1st quarter (Fig. 4.26). ANOVA results indicated that

Table 4.21. Summary results of four-way ANOVA on selected zooplankton groups with respect to moon phase, diel, tide, depth and their interaction in the wet period. Moon phase: Q1 = 1st quarter, FM = full moon, Q3 = 3rd quarter, NM = new moon; Diel: D = day, N = night; Tide: E = ebb, F = flood; Depth: S = surface, B = bottom; superscript a, b and c indicate homogeneous group; ** significance at $p < 0.01$, * significance at $p < 0.05$, ns no significance.

Taxon	Source of variation											
	Moon phase (1)				p-level	Diel (2)	p-level	Tide (3)	p-level	Depth (4)	p-level	Significant interaction effect ($p < 0.05$)
Copepoda												
Total	$Q1^{a}$	FM^{b}	$Q3^{a}$	NM^{b}	<0.001**	ns	0.228	ns	0.778	ns	0.228	1 x 2, 1 x 3, 2 x 3, 1 x 2 x 3
Acartia copepodids	$Q1^{a}$	FM^{b}	$Q3^{a}$	NM^{c}	<0.001**	D>N	<0.001**	ns	0.143	ns	0.186	1 x 3, 2 x 3
Acartia spinicauda	$Q1^{a}$	FM^{b}	$Q3^{b}$	NM^{c}	<0.001**	ns	0.516	ns	0.533	ns	0.671	1 x 3, 2 x 3, 1 x 2 x 3
Parvocalanus crassirostris	$Q1^{a}$	FM^{b}	$Q3^{a}$	NM^{b}	<0.001**	ns	0.086	E<F	0.014*	ns	0.97	1 x 2, 1 x 3, 2 x 3, 2 x 4, 1 x 2 x 3
Bestiolina similis	$Q1^{a}$	FM^{a}	$Q3^{b}$	NM^{a}	<0.001**	D<N	<0.001**	ns	0.945	ns	0.675	1 x 2, 2 x 3
Oithona simplex	$Q1^{a}$	$FM^{a,c}$	$Q3^{b}$	$NM^{b,c}$	<0.001**	D<N	<0.001**	E>F	<0.001**	ns	0.477	1 x 2, 1 x 3
Cirripedia larvae	$Q1^{a}$	FM^{b}	$Q3^{a}$	NM^{b}	<0.001**	ns	0.085	E>F	<0.001**	ns	0.445	1 x 2, 1 x 3, 1 x 2 x 3
Decapoda	$Q1^{a}$	FM^{a}	$Q3^{a}$	NM^{b}	<0.001**	ns	0.205	ns	0.060	ns	0.132	1 x 2, 1 x 3, 1 x 2 x 4
Chaetognatha	$Q1^{a}$	FM^{b}	$Q3^{c}$	NM^{d}	<0.001**	ns	0.187	ns	0.197	ns	0.485	1 x 3
Cnidaria	$Q1^{a}$	FM^{b}	$Q3^{a}$	NM^{b}	<0.001**	ns	0.223	E>F	0.034	ns	0.985	2 x 3
Polychaeta	$Q1^{a}$	FM^{b}	$Q3^{c}$	NM^{a}	<0.001**	ns	0.257	E>F	<0.001**	ns	0.597	-
Gastropoda	$Q1^{a}$	FM^{b}	$Q3^{a}$	NM^{b}	<0.001**	ns	0.592	E>F	0.040	ns	0.429	1 x 3
Larvacea	$Q1^{a}$	FM^{b}	$Q3^{a,c}$	$NM^{b,c}$	<0.001**	D<N	0.024	E>F	0.013	ns	0.631	1 x 3
Protozoa	ns				0.517	ns	0.158	E>F	<0.01	ns	0.570	-
Unidentified eggs	$Q1^{a}$	$FM^{a,b}$	$Q3^{b,c}$	NM^{c}	<0.001**	D>N	0.037	ns	0.065	ns	0.294	1 x 2, 2 x 3, 1 x 2 x 3

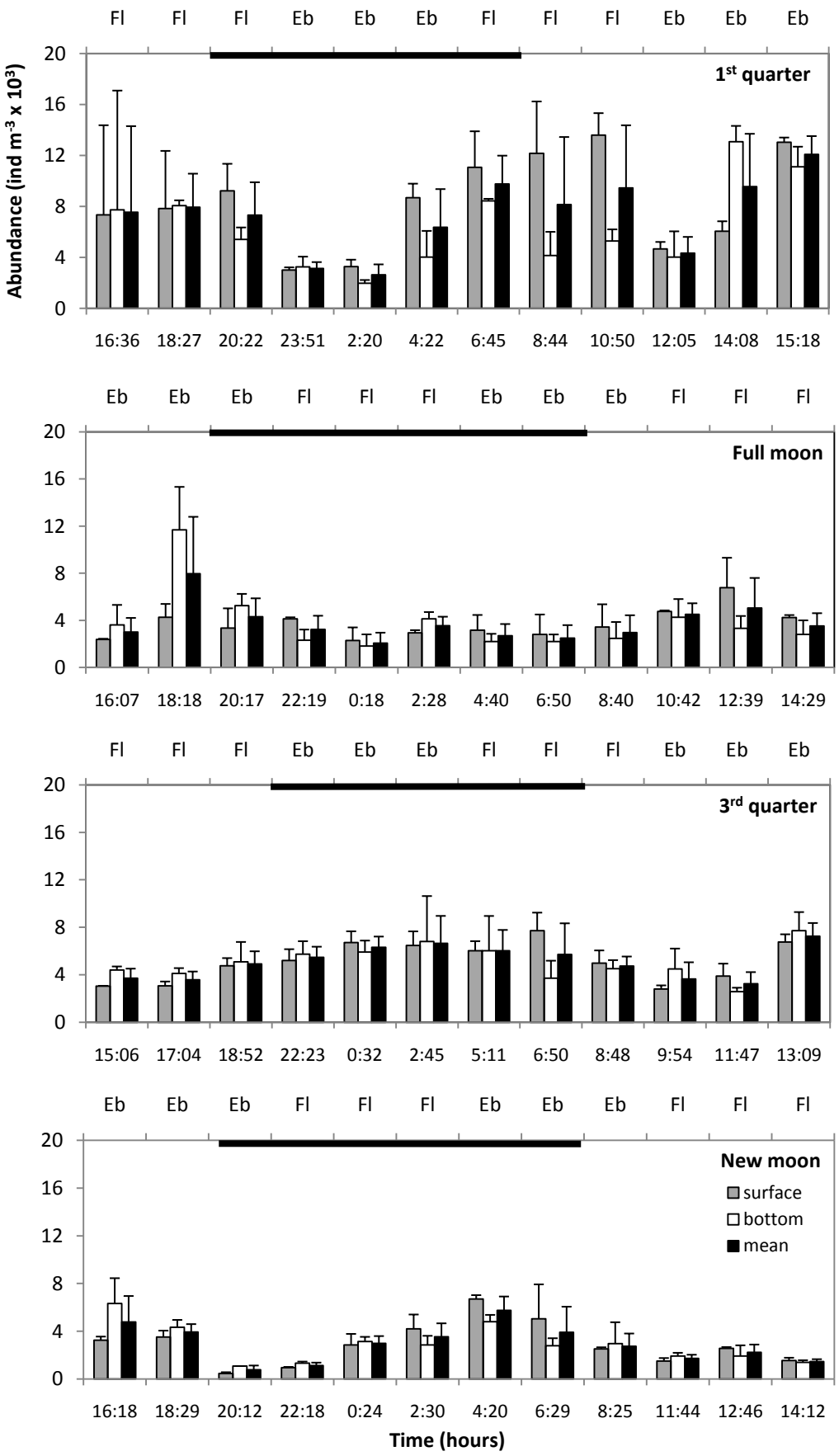


Fig.4.24. Surface, bottom and mean total copepod abundance recorded over 24 hours and four consecutive moon phases in the wet period. Horizontal bar denotes nighttime; Eb = ebb tide, Fl = flood tide.

Table 4.22. Mean ($\bar{x}$) and relative abundance (%Rel) of copepods with respect to moon phase, diel, tide and depth in the wet period. '+' indicates present but constituted <0.1% of relative abundance, '-' indicates absent; number of taxa of grouped copepods in parenthesis.

Taxon	Moon phase								Diel				Tide				Depth			
	1st quarter		Full moon		3rd quarter		New moon		Day		Night		Ebb		Flood		Surface		Bottom	
	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel
P. crassirostris	431	6	997	26	538	11	939	32	757	15	690	16	695	14	757	16	730	15	722	16
A. spinicauda	1207	16	579	15	516	10	199	7	702	14	535	12	614	13	637	13	600	12	651	14
B. similis	137	2	66	2	45	1	80	3	41	1	130	3	113	2	51	1	87	2	77	2
O. simplex	73	1	117	3	390	8	297	10	79	2	385	9	310	6	128	3	221	4	217	5
Acartia sp. 1	203	3	106	3	42	1	19	1	115	2	67	2	83	2	103	2	95	2	91	2
O. dissimilis	126	2	58	2	32	1	81	3	86	2	60	1	46	1	103	2	81	2	67	1
E. acutifrons	21	0.3	16	0.4	205	4	86	3	79	2	86	2	120	2	44	1	74	1	91	2
O. aruensis	77	1	15	0.4	27	1	+	+	27	1	34	1	17	0.4	43	1	41	1	19	0.4
T. barbatus	9	0.1	+	+	8	0.2	2	0.1	3	0.1	8	0.2	7	0.1	3	0.1	6	0.1	4	0.1
Pseudomacrochiron sp. 1	4	0.1	8	0.2	15	0.3	14	0.5	9	0.2	12	0.3	14	0.3	7	0.1	11	0.2	9	0.2
P. elegans	39	1	258	7	50	1	91	3	65	1	162	4	126	3	93	2	105	2	114	2
P. trihamatus	+	+	8	0.2	+	+	14	0.5	7	0.1	5	0.1	3	0.1	10	0.2	6	0.1	7	0.2
P. bowmani	+	+	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Kelleria sp. 1	35	0.5	+	+	5	0.1	4	0.1	10	0.2	12	0.3	16	0.3	6	0.1	13	0.3	9	0.2
M. norvegica	-	-	+	+	+	+	2	0.1	+	+	+	+	+	+	+	+	+	+	+	+
C. dorsispinatus	+	+	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
O. attenuata	+	+	-	-	-	-	-	-	+	+	-	-	-	-	+	+	+	+	-	-
P. aculeatus	+	+	-	-	5	0.1	-	-	-	-	3	0.1	3	0.1	-	-	+	+	2	0.1
P. annandalei	+	+	3	0.1	+	+	19	1	5	0.1	8	0.2	3	0.1	10	0.2	5	0.1	8	0.2
Other adults	11	0.2	3	0.1	8	0.2	8	0.3	4	0.1	11	0.3	9	0.2	5	0.1	7	0.1	7	0.2
	(10)		(9)		(13)		(10)		(11)		(14)		(15)		(12)		(13)		(13)	
Nauplius and copepodid																				
Acartia spp.	4110	56	831	22	2540	50	360	12	2518	49	1301	30	1785	37	2136	45	2204	44	1716	38
Parvocalanus spp.	458	6	546	14	503	10	525	18	458	9	567	13	615	13	401	8	491	10	525	12
Bestiolina sp.	113	2	65	2	17	0.3	70	2	28	1	112	3	90	2	42	1	75	1	58	1
Unidentified nauplii	126	2	26	1	71	1	35	1	62	1	68	2	61	1	68	1	66	1	63	1
Tortanus spp.	18	0.2	19	1	25	0.5	14	0.5	18	0.4	20	0.5	26	1	12	0.3	20	0.4	18	0.4
Pseudodiaptomus spp.	73	1	22	1	31	1	26	1	42	1	33	1	26	1	51	1	41	1	35	1
Oithona spp.	57	1	25	1	11	0.2	23	1	31	1	26	1	31	1	26	1	28	1	30	1
Pontellidae spp.	23	0.3	6	0.2	10	0.2	3	0.1	7	0.1	14	0.3	15	0.3	6	0.1	11	0.2	10	0.2
Centropages spp.	-	-	-	-	-	-	+	+	-	-	+	+	+	+	-	-	+	+	+	+
Other copepodids	+	+	+	+	+	+	3	0.1	+	+	3	0.1	+	+	+	+	+	+	+	+

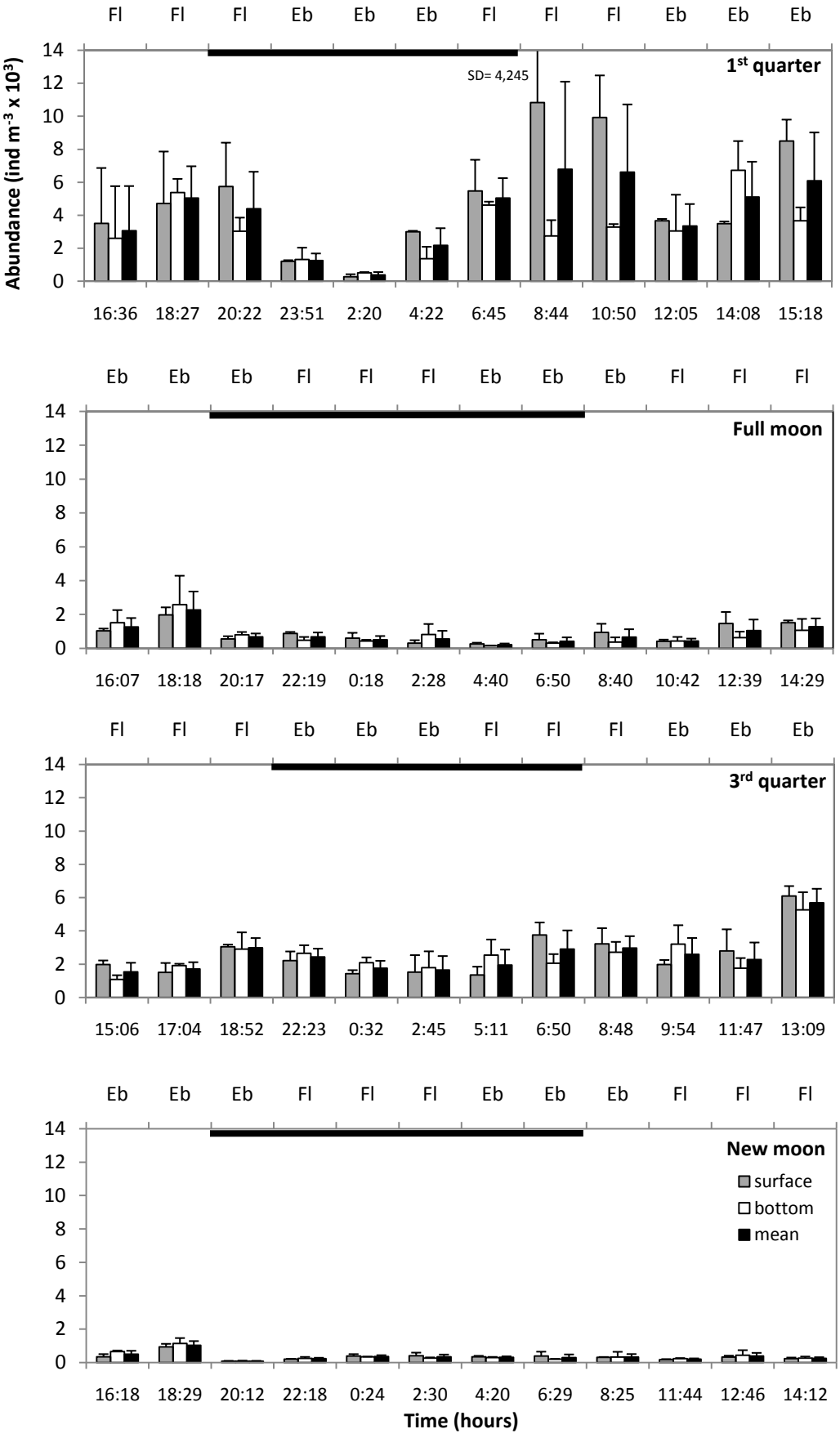


Fig.4.25. Surface, bottom and mean total abundance of *Acartia* copepodids recorded over 24 hours and four consecutive moon phases in the wet period. Horizontal bar denotes nighttime; Eb = ebb tide, Fl = flood tide.

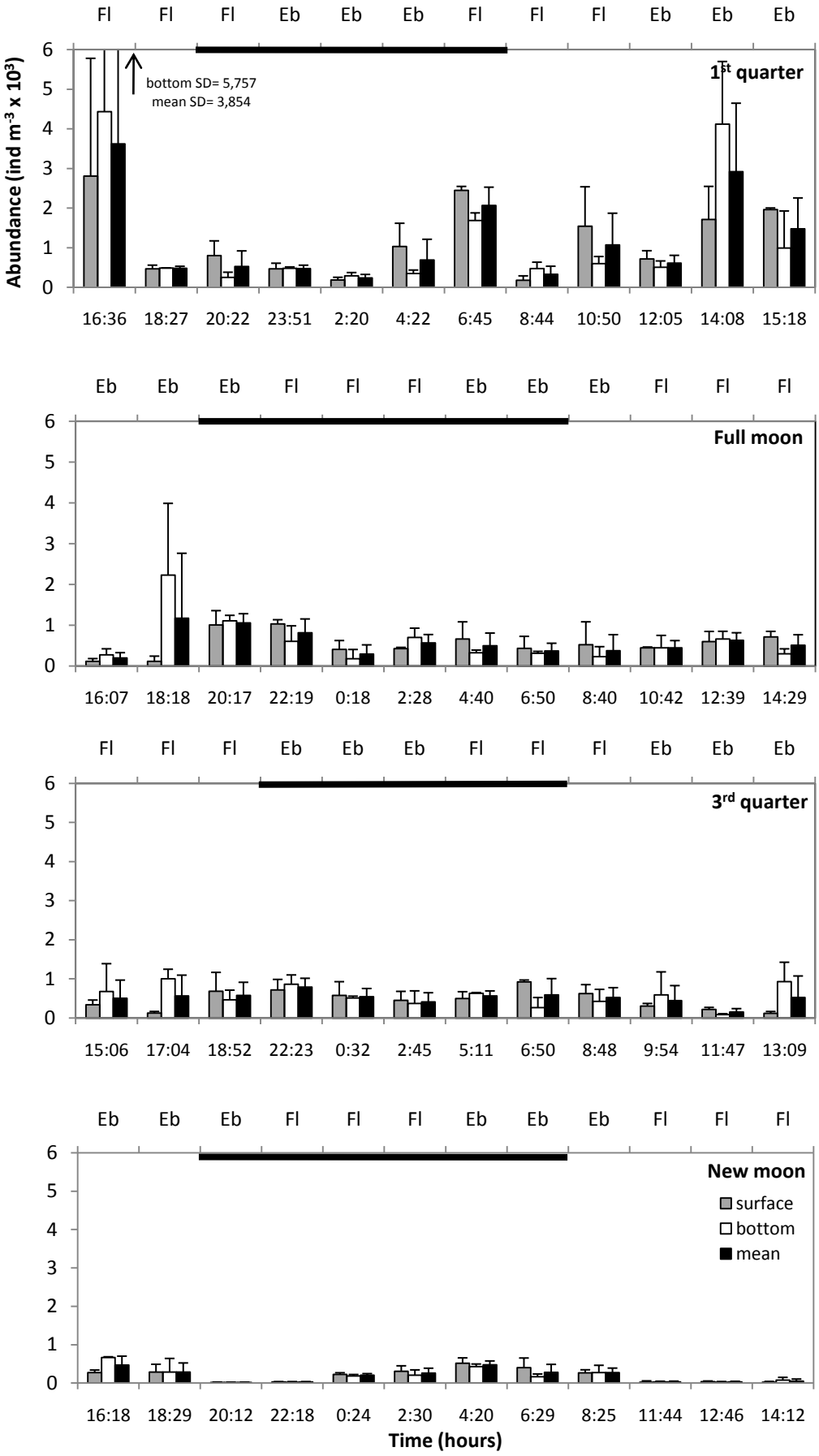


Fig.4.26. Surface, bottom and mean total abundance of *Acartia spinicauda* recorded over 24 hours and four consecutive moon phases in the wet period. Horizontal bar denotes nighttime; Eb = ebb tide, Fl = flood tide.

mean abundance of *A. spinicauda* was highest during the 1st quarter and lowest during new moon particularly at day-flood tide (Fig. 4.26, appendix XIIa). There was no significant difference between full moon and 3rd quarter (Table 4.21). As opposed to *Acartia*, *P. crassirostris* was significantly more abundant during spring tides as compared to neap tides (ANOVA, $p < 0.001$). Abundance of *B. similis* was lowest during the 3rd quarter (ANOVA, $p < 0.001$). The moon phase pattern for *O. simplex* in the wet period was similar to that of dry period, with lowest mean value obtained during the 1st quarter and highest during the 3rd quarter (ANOVA, $p < 0.001$; Table 4.21).

The effects of diel, tide and water depth did not significantly influence the total abundance of copepods (ANOVA, $p > 0.05$; Table 4.21). For *Acartia* copepodids, there was significant diel effect on their total abundance (ANOVA, $p < 0.001$), but not for the effects of tide and water depth (ANOVA, $p > 0.05$; Table 4.21). Total abundance of *Acartia* copepodids was significantly higher during the day (2518 ± 2578 ind m^{-3}) compared to during the night (1301 ± 1498 ind m^{-3}).

The abundance of *A. spinicauda* was not significantly influenced by the main effects of diel, tide and water depth (ANOVA, $p > 0.05$). However, there was significant interaction effect between diel and depth (ANOVA, $p < 0.05$). Although Tukey HSD test reveal insignificant difference among the combinations of diel and water depth, *A. spinicauda* was generally more abundant during the night than the day for surface samples (appendix XIIb). Abundance at the bottom was also relatively higher than at surface during daytime. Similarly, strong peaks were encountered at the bottom particularly during the 1st quarter and full moon daytime despite no significant difference between depth strata (Fig. 4.26).

Abundance of *P. crassirostris* was on average higher during flood tide as compared to ebb tide (ANOVA, $p < 0.05$), but appeared to be not significantly affected

by diel and sampling depth (ANOVA, $p > 0.05$). However, results of 4-way ANOVA displayed various significant interaction effects between the main influencing factors (Table 4.21). Interestingly, only day samples were significantly different in abundance among moon phases, with higher mean value obtained during spring than neap tide. Night samples were constant in abundance among moon phases (appendix XIIc). Surface samples had higher abundance of *P. crassirostris* during the night than the day (Tukey HSD test, $p < 0.05$) whereas bottom samples were not significantly influenced by diel cycle (appendix XIId). Similar to dry period, *P. crassirostris* occurred in lower numbers during day-ebb particularly during the 3rd quarter (Fig. 4.27, appendix XIIe & f).

Diel effect did significantly influence the abundance of *O. simplex* and *B. similis* (ANOVA, $p < 0.001$). Abundance during the night was significantly higher than during the day for both species (Table 4.21). Tide had significant influence on *O. simplex* (ANOVA, $p < 0.001$) but not for *B. similis* (ANOVA, $p > 0.05$). Both species did not significantly differ in abundance between sampling depth (ANOVA, $p > 0.05$; Table 4.21). Fig. 4.28 shows that *B. similis* was consistently found in low numbers during daytime irrespective of tidal cycle. For *O. simplex*, major peak abundance always coincided with night-ebb tide (Fig. 4.29).

b. Cirripede larvae

Cirripede larvae varied greatly in abundance among samples, ranging from no specimen captured during full moon to maximum abundance of 65,667 ind m^{-3} during the 1st quarter (Table 4.14). Strong peak abundance was observed at dusk (1827-hour) during the 1st quarter (Fig. 4.30). Cirripede larvae were significantly more abundant during neap than spring tide (ANOVA, $p < 0.001$; Tables 4.21 & 4.23).

Cirripede larvae were significantly more abundant during ebb tide compared with flood tide (ANOVA, $p < 0.001$) whereas diel and sampling depth had no significant influence on larvae abundance (ANOVA, $p > 0.05$; Table 4.21). Three-way interaction effect between moon phase, diel and tide showed significantly lower number of larvae during spring day-flood tide (Fig. 4.30, appendix XIIIa).

c. Decapods

Although new moon abundance was significantly lower from the other three moon phases (ANOVA, $p < 0.05$), the number of decapods captured during spring tide was comparatively higher than that of neap tide (Tables 4.21 & 4.23). During spring tide, brachyuran zoeae accounted for 56 - 85% of the total decapod abundance, whereas almost no zoeae were captured during the 3rd quarter (Table 4.24). In general, zoeae of brachyura dominated decapod assemblages during spring tide except for samples collected at 1607-hour during full moon where *Acetes* protozoeae were numerically more dominant (Fig. 4.31). During neap tide, *Acetes* was captured mainly as juveniles and represented 14 - 19% of the total decapod abundance. More adults of *Lucifer hanseni* and *Acetes* were sampled in the wet period, accounting for 15 - 18% of the total decapod abundance during neap tide. Zoeae of alphaeids, diogenids and porcellanids were relatively higher in numbers during neap tide (Table 4.24).

Diel and tidal cycles as well as water depth did not significantly affect decapod abundance (ANOVA, $p > 0.05$; Table 4.21). Although there was no significant tidal variation, maximum abundance of decapods during spring tide coincided with ebb tide (Fig. 4.31).

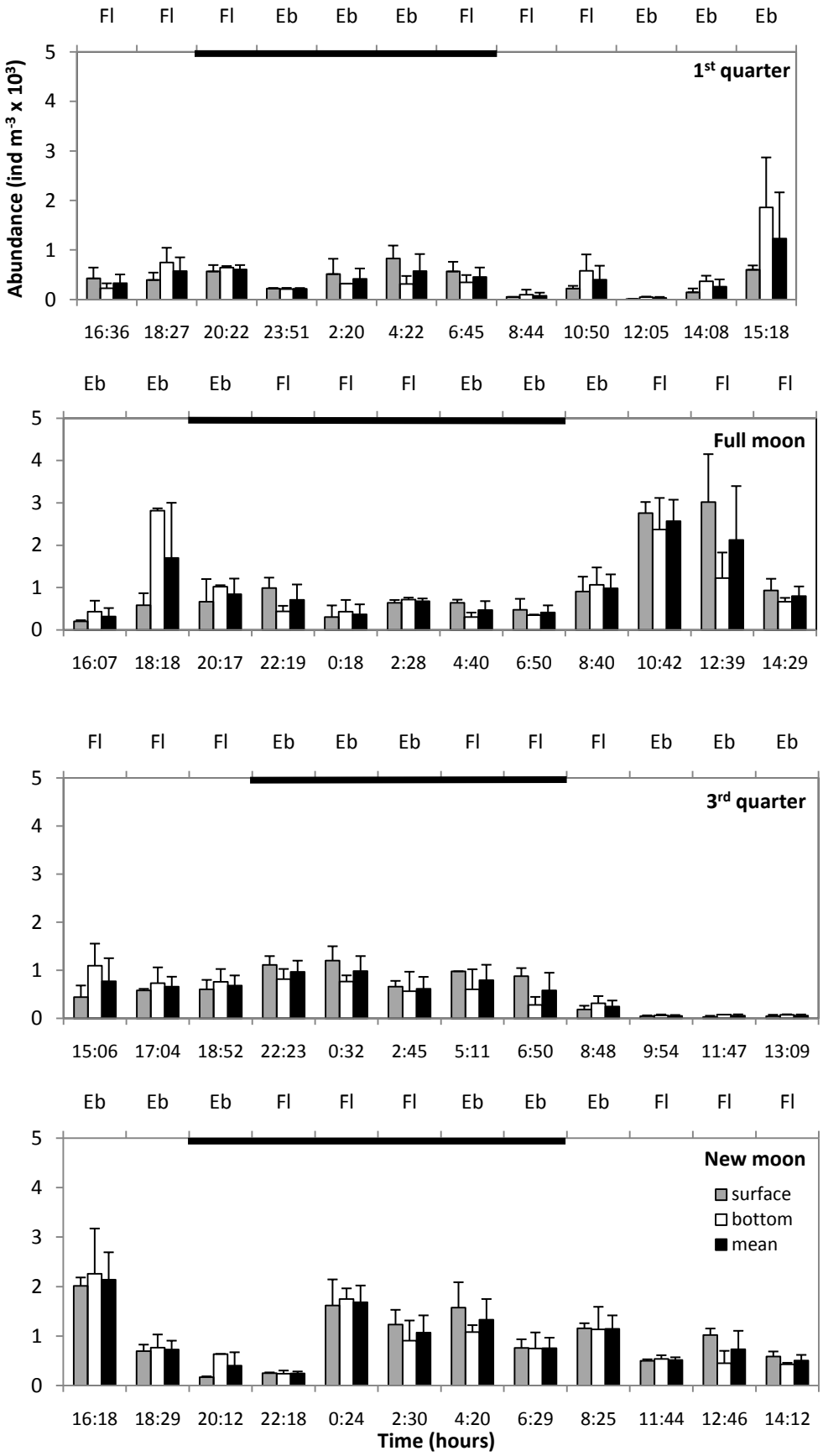


Fig.4.27. Surface, bottom and mean total abundance of *Parvocalanus crassirostris* recorded over 24 hours and four consecutive moon phases in the wet period. Horizontal bar denotes nighttime; Eb = ebb tide, Fl = flood tide.

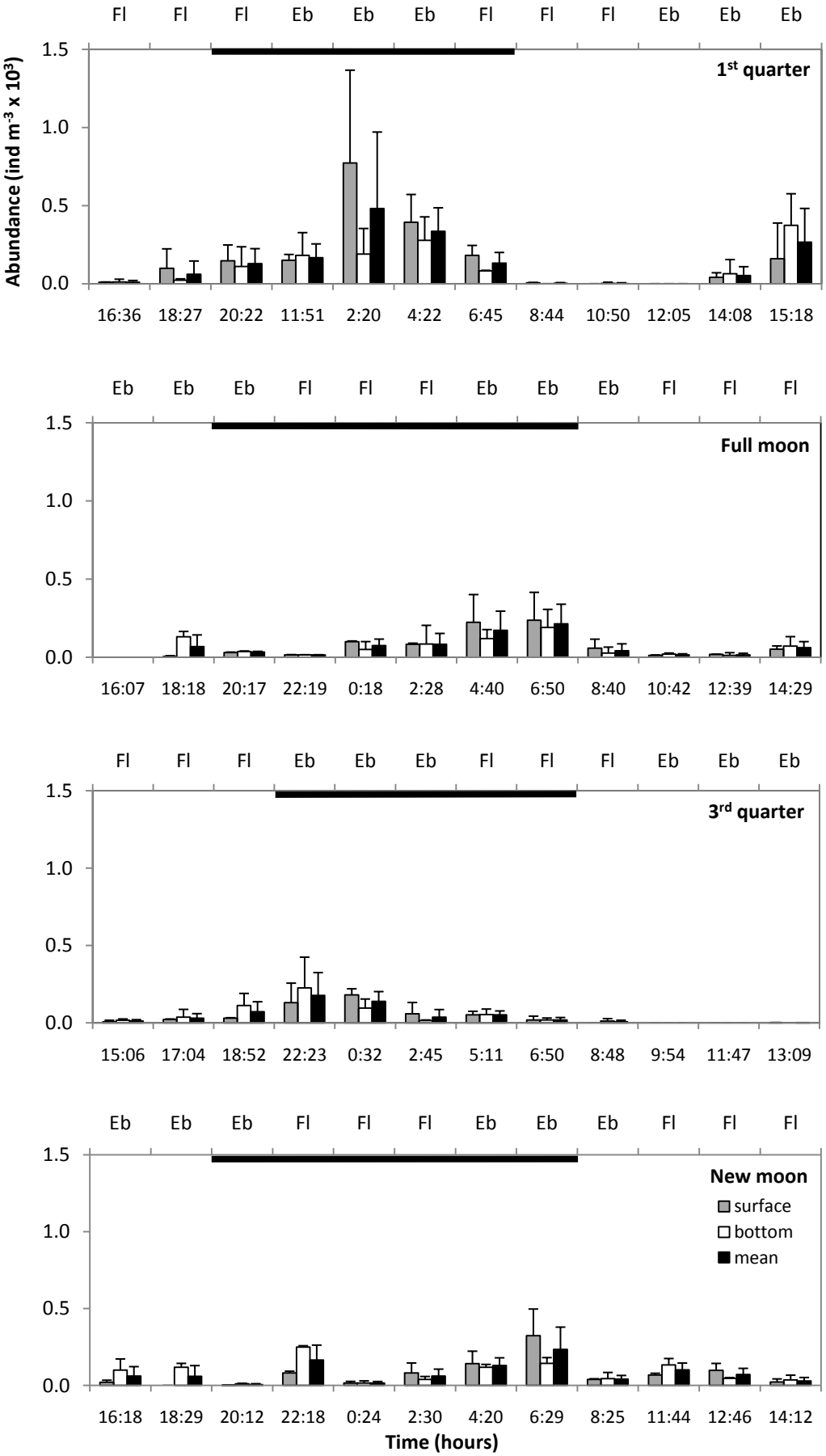


Fig.4.28. Surface, bottom and mean total abundance of *Bestiolina similis* recorded over 24 hours and four consecutive moon phases in the wet period. Horizontal bar denotes nighttime; Eb = ebb tide, Fl = flood tide.

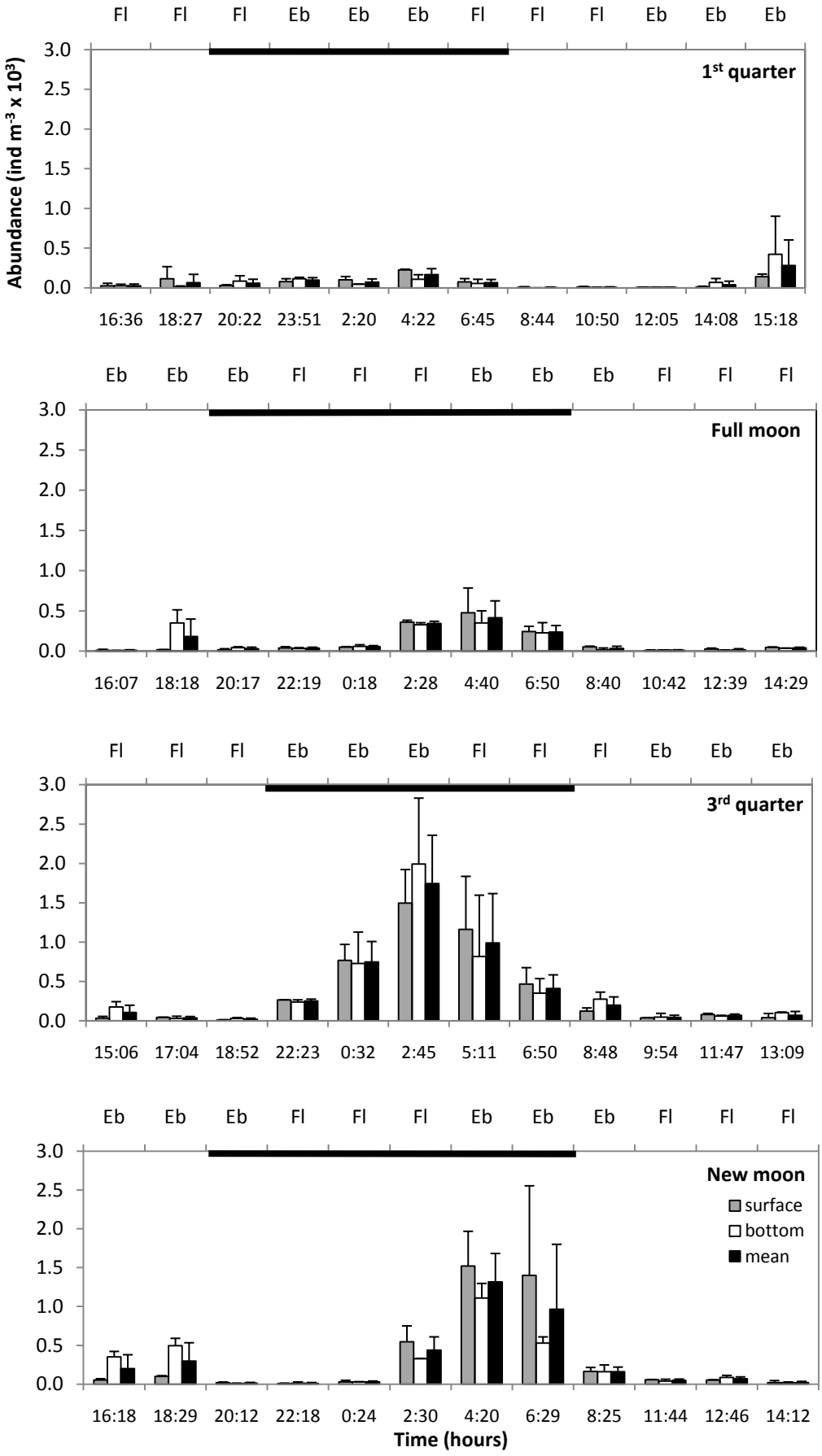


Fig.4.29. Surface, bottom and mean total abundance of *Oithona simplex* recorded over 24 hours and four consecutive moon phases in the wet period. Horizontal bar denotes nighttime; Eb = ebb tide, Fl = flood tide.

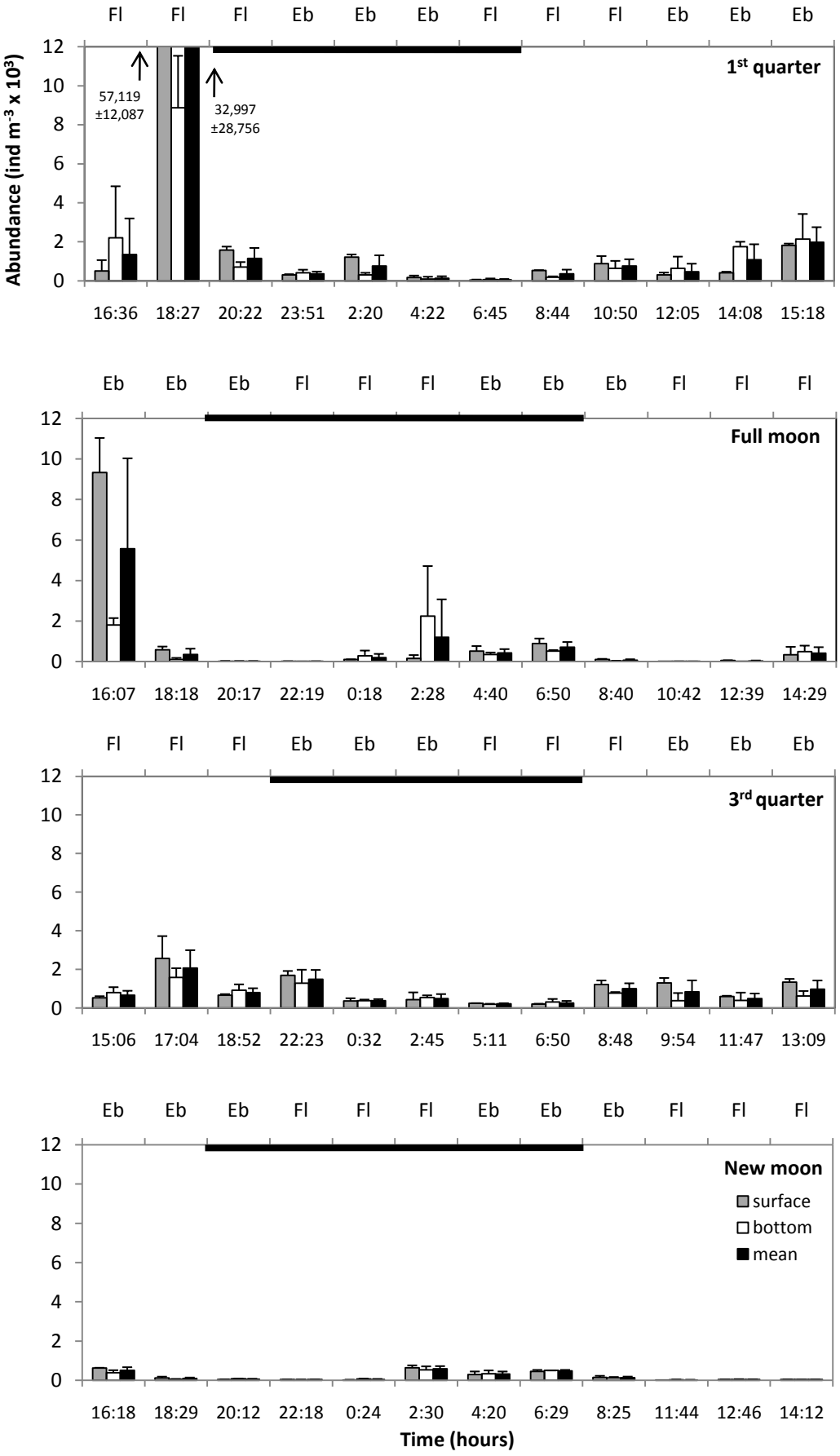


Fig.4.30. Surface, bottom and mean total abundance of Cirripedia larvae recorded over 24 hours and four consecutive moon phases in the wet period. Horizontal bar denotes nighttime; Eb = ebb tide, Fl = flood tide.

Table 4.23. Mean ($\bar{x}$) and relative abundance (%Rel) of major zooplankton groups with respect to moon phase, diel, tide and depth in the wet period. '+' indicates present but constituted <0.1% of relative abundance, number of zooplankton groups in parenthesis.

Taxon	Moon phase								Diel				Tide				Depth			
	1st quarter		Full moon		3rd quarter		New moon		Day		Night		Ebb		Flood		Surface		Bottom	
	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel
Copepoda	7360	62.2	3779	78.1	5099	75.1	2919	81.7	5156	65.2	4356	80.8	4833	75.6	4746	66.7	5024	66.5	4555	76.5
Cirripedia larvae	3452	29.2	752	15.5	804	11.8	192	5.4	2041	25.8	424	7.9	756	11.8	1844	25.9	1887	25.0	713	12.0
Mysidae	14	0.1	+	+	+	+	+	+	6	0.1	3	0.1	+	+	7	0.1	5	0.1	4	0.1
Decapoda	34	0.3	97	2.0	30	0.4	111	3.1	82	1.0	52	1.0	85	1.3	51	0.7	89	1.2	47	0.8
Chaetognatha	227	1.9	46	1.0	113	1.7	29	0.8	108	1.4	99	1.8	105	1.6	102	1.4	102	1.4	105	1.8
Cnidaria	32	0.3	4	0.1	50	0.7	9	0.2	30	0.4	17	0.3	29	0.5	19	0.3	20	0.3	28	0.5
Polychaeta	34	0.3	8	0.2	182	2.7	24	0.7	55	0.7	71	1.3	95	1.5	30	0.4	59	0.8	65	1.1
Gastropoda	298	2.5	44	0.9	166	2.4	79	2.2	166	2.1	124	2.3	189	3.0	105	1.5	131	1.7	162	2.7
Bivalvia	48	0.4	27	0.6	126	1.9	26	0.7	59	0.7	55	1.0	60	0.9	54	0.8	49	0.7	64	1.1
Bryozoa	10	0.1	4	0.1	10	0.2	8	0.2	9	0.1	8	0.1	9	0.1	7	0.1	8	0.1	9	0.1
Larvacea	227	1.9	30	0.6	44	0.6	80	2.2	77	1.0	117	2.2	116	1.8	75	1.1	92	1.2	99	1.7
Protozoa	80	0.7	32	0.7	76	1.1	53	1.5	70	0.9	49	0.9	67	1.1	53	0.7	59	0.8	62	1.0
Unidentified eggs	+	+	14	0.3	81	1.2	38	1.1	48	0.6	19	0.3	45	0.7	24	0.3	28	0.4	41	0.7
Others (10)	+	+	+	+	+	+	4	0.1	4	0.1	+	+	3	0.1	+	+	+	+	+	+

Table 4.24. Mean ($\bar{x}$) and relative abundance (%Rel) of different life stages of decapods with respect to moon phase, diel, tide and depth in the wet period. '+' indicates present but constituted <0.1% of relative abundance, '-' indicates absent; number of taxa of grouped decapods in parenthesis.

Taxon	Life stage	Moon phase								Diel				Tide				Depth			
		1st quarter		Full moon		3rd quarter		New moon		Day		Night		Ebb		Flood		Surface		Bottom	
		$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel	$\bar{x}$	% Rel
Lucifer	Protozoea	3	7.5	<1	0.5	1	4.1	<1	0.2	<1	0.4	2	4.0	2	2.0	1	1.0	2	1.8	1	1.3
	Juvenile	<1	0.5	<1	0.1	<1	1.2	+	+	<1	0.1	<1	0.5	<1	0.4	+	+	<1	0.2	<1	0.3
	Adult	6	18.2	<1	0.3	5	15.2	<1	0.2	3	4.2	2	4.1	3	4.0	2	4.4	2	2.3	4	7.6
Acetes	Protozoea	3	7.6	28	29.2	7	23.2	2	2.2	13	15.6	7	13.4	17	20.2	3	6.0	16	18.4	4	8.0
	Juvenile	6	18.6	1	0.6	4	14.6	2	1.6	3	3.7	4	6.9	2	2.0	5	9.4	3	3.0	4	8.2
Acetes japonicus	Adult	1	2.8	<1	0.2	+	+	2	1.6	1	0.9	1	1.5	<1	0.5	1	2.0	<1	0.6	1	2.1
A. indicus	Adult	1	2.3	1	1.5	-	-	5	4.3	1	1.5	2	4.6	1	1.3	2	4.7	2	1.9	2	3.8
A. sibogae	Adult	<1	0.1	-	-	-	-	+	+	+	+	+	+	-	-	+	+	+	+	+	+
Alpheidae	Zoea	3	10.0	<1	0.3	2	5.5	1	0.7	1	1.7	2	3.2	2	2.0	1	2.7	2	2.3	1	2.1
	Juvenile	-	-	-	-	-	-	+	+	+	+	+	+	-	-	+	+	+	+	+	+
Palaemonidae	zoea	1	3.4	+	+	<1	0.6	+	+	1	0.6	<1	0.2	<1	0.2	<1	0.9	<1	0.4	<1	0.7
Penaeidae	nauplius	<1	0.9	9	9.4	8	25.5	4	3.4	3	3.7	8	15.1	6	7.3	4	8.3	6	6.2	5	10.5
	Protozoea	-	-	+	+	-	-	+	+	+	+	+	+	-	-	+	+	+	+	+	+
	Mysis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Post-larva	<1	0.1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Brachyuran	Zoea	4	11.2	55	56.8	1	4.7	94	85.1	53	64.8	22	42.1	49	58.3	28	54.5	54	60.5	24	50.1
	Megalopa	<1	0.1	<1	0.5	+	+	<1	0.2	<1	0.2	<1	0.3	<1	0.2	<1	0.4	<1	0.1	<1	0.6
	Juvenile	+	+	+	+	<1	0.3	<1	0.2	+	+	<1	0.3	<1	0.1	<1	0.1	<1	0.1	<1	0.2
Diogenidae	Zoea	2	7.2	<1	0.5	1	2.1	<1	0.2	1	1.6	<1	1.0	1	0.7	1	2.6	1	1.2	1	1.6
	Juvenile	<1	0.1	+	+	<1	0.9	<1	0.1	<1	0.2	+	+	<1	0.2	<1	0.1	+	+	<1	0.4
Porcellanidae	Zoea	2	7.3	<1	0.1	<1	0.9	+	+	<1	0.4	1	2.3	<1	0.3	1	2.3	1	0.7	1	1.7
Others		1	2.1	+	+	<1	1.1	<1	0.1	<1	0.4	<1	0.5	<1	0.3	<1	0.6	<1	0.2	<1	0.7
		(1)		(2)		(2)		(2)		(3)		(3)		(2)		(3)		(2)		(3)	

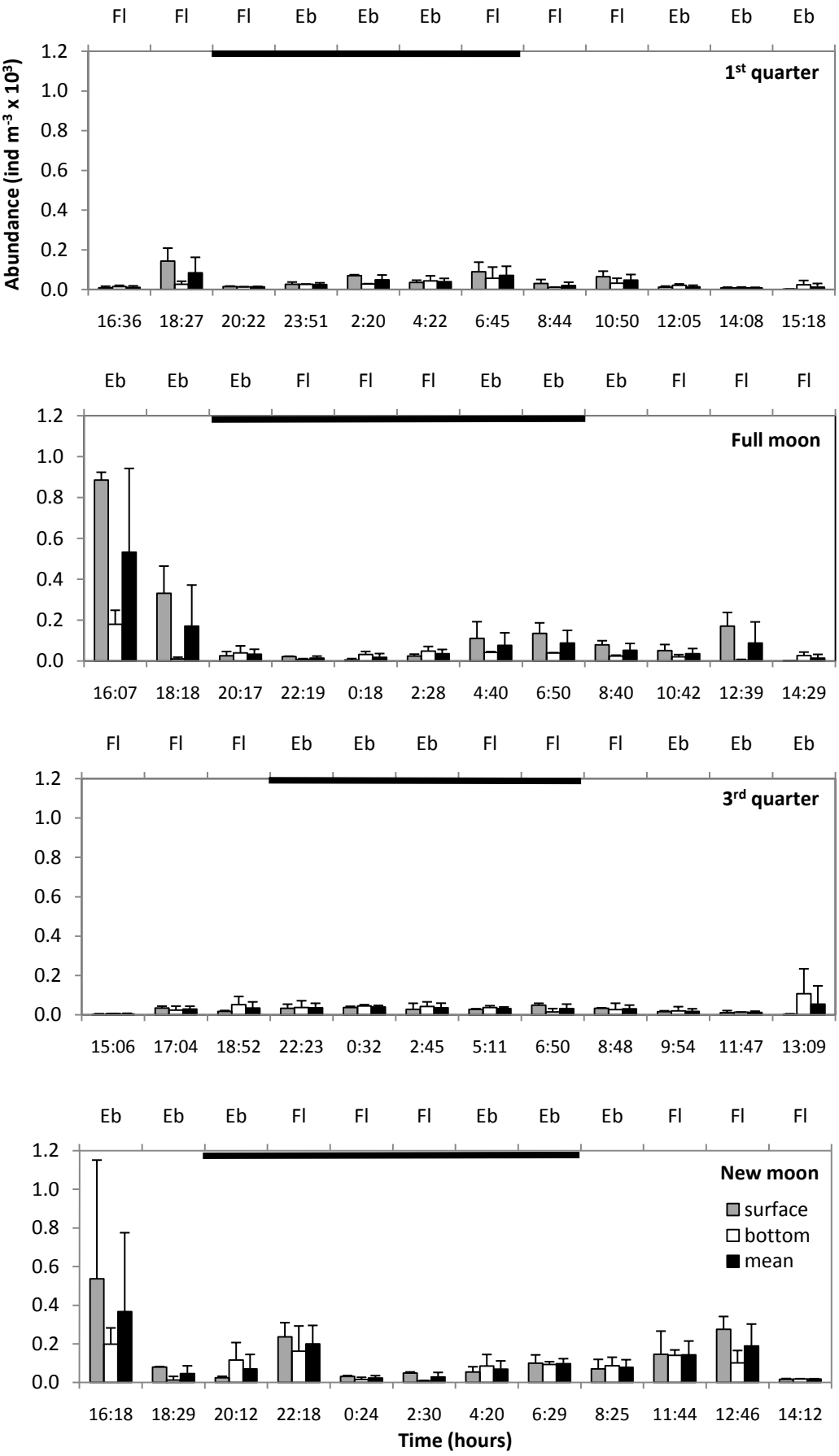


Fig.4.31. Surface, bottom and mean total abundance of decapods recorded over 24 hours and four consecutive moon phases in the wet period. Horizontal bar denotes nighttime; Eb = ebb tide, Fl = flood tide.

d. Mysidae

Mean abundance of Mysidae was highest during the 1st quarter as compared to other three moon phases (Kruskal-Wallis ANOVA and Mann-Whitney U test, $p < 0.05$; Table 4.25) due to strong peak abundance observed at dusk (1827-hour) for both surface and bottom waters (Fig. 4.32). Mysidae was largely represented by *Mesopodosis* sp. (92%) during the 1st quarter whereas *Erythrops* sp. was not present throughout the wet period (Table 4.25).

Table 4.25. Summary table of non-parametric Kruskal-Wallis ANOVA (Ψ) and Mann-Whitney U test (^), mean ± SD and relative abundance (in parenthesis) of Mysidae in the wet period. n= sample size; Diel: D = day, N = night; Tide: E = ebb, F = flood; Depth: S = surface, B = bottom; alphabetic a and b indicate homogeneous group; ** significance at $p < 0.01$, * significance at $p < 0.05$.

	1st quarter	Full moon	3rd quarter	New moon
n	48	48	48	48
Main effect				
ΨMoon phase*	a	a,b	b	b
^Diel	D<N**	D<N**	D<N**	D<N**
^Tide	E = F	E = F	E = F	E = F
^Depth	S = B	S = B	S = B	S = B
Abundance				
Mean abundance	14 ± 46	2 ± 3	2 ± 4	0.5 ± 1
Genera				
Acanthomysis sp.	1 (6)	<1 (45)	<1 (40)	<1 (67)
Erythrops sp.	-	-	-	-
Mesopodopsis sp.	13 (92)	<1 (25)	<1 (0.2)	<1 (1)
Notacanthomysis sp.	<1 (2)	<1 (29)	1 (59)	1 (22)
Rhopalophthalmus sp.	<1 (0.1)	<1 (0.2)	<1 (1)	<1 (10)

Nocturnal increase in Mysidae abundance was apparent in the wet period (Mann-Whitney U Test, $p < 0.01$), while tidal and depth effects did not significantly affect the abundance of Mysidae (Mann-Whitney U Test, $p > 0.05$; Table 4.25; Fig. 4.32).

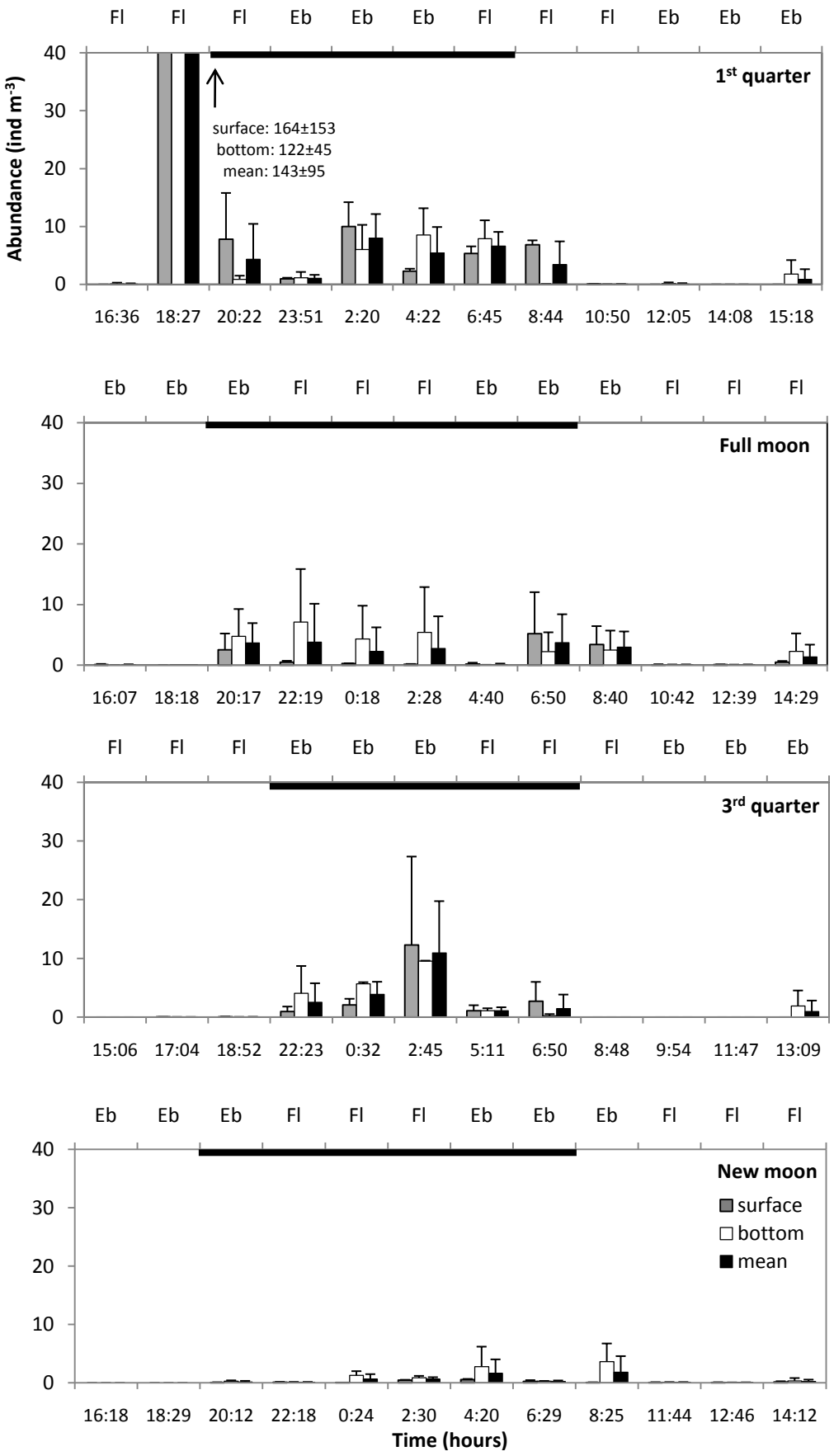


Fig.4.32. Surface, bottom and mean total abundance of Mysidae recorded over 24 hours and four consecutive moon phases in the wet period. Horizontal bar denotes nighttime; Eb = ebb tide, Fl = flood tide.

e. Non-crustacean zooplankton

All selected groups of non-crustacean zooplankton for ANOVA showed a significant difference in abundance among moon phases except for protozoans (Tables 4.21 & 4.23). Almost all selected groups of non-crustacean zooplankton were also significantly influenced by tidal cycle except for chaetognaths, with greater numbers captured at ebb tide as compared to flood tide (ANOVA, $p < 0.05$; Table 4.21). The polychaete larvae were consistently captured in higher numbers during ebb tide particularly during the 3rd quarter (Fig. 4.33). There was no obvious pattern in diel and depth distribution for all non-crustacean zooplankton, with the exception of larvaceans, which were more abundant during nighttime as compared to daytime (ANOVA, $p < 0.05$; Tables 4.21 & 4.23).

4.1.6 Zooplankton community structure

4.1.6.1 Species richness

A total of 108 zooplankton taxa were recorded over the 24-hour sampling period with 47 taxa of copepods, 26 taxa of other crustaceans and 36 taxa of non-crustacean zooplankton. Thirteen taxa identified in the 24-hour sampling period were not recorded in the routine monthly sampling (see Table 3.10). Almost half of these taxa were composed of benthic polychaetes which were rare and mainly occurred in spring tide samples. The numbers of identified zooplankton taxa in the dry period were 104 taxa while the wet period recorded 88 taxa. All 47 copepod species identified for 24-hour sampling were found in the dry period samples whereas wet period samples comprised representatives of 34 species (see Table 3.10).

The numbers of copepod species recorded during the full (34 species) and new moon (40 species) were higher than during the 1st (29 species) and 3rd quarter samples (32 species) in the dry period (Table 4.26). In the wet period, the numbers of copepod

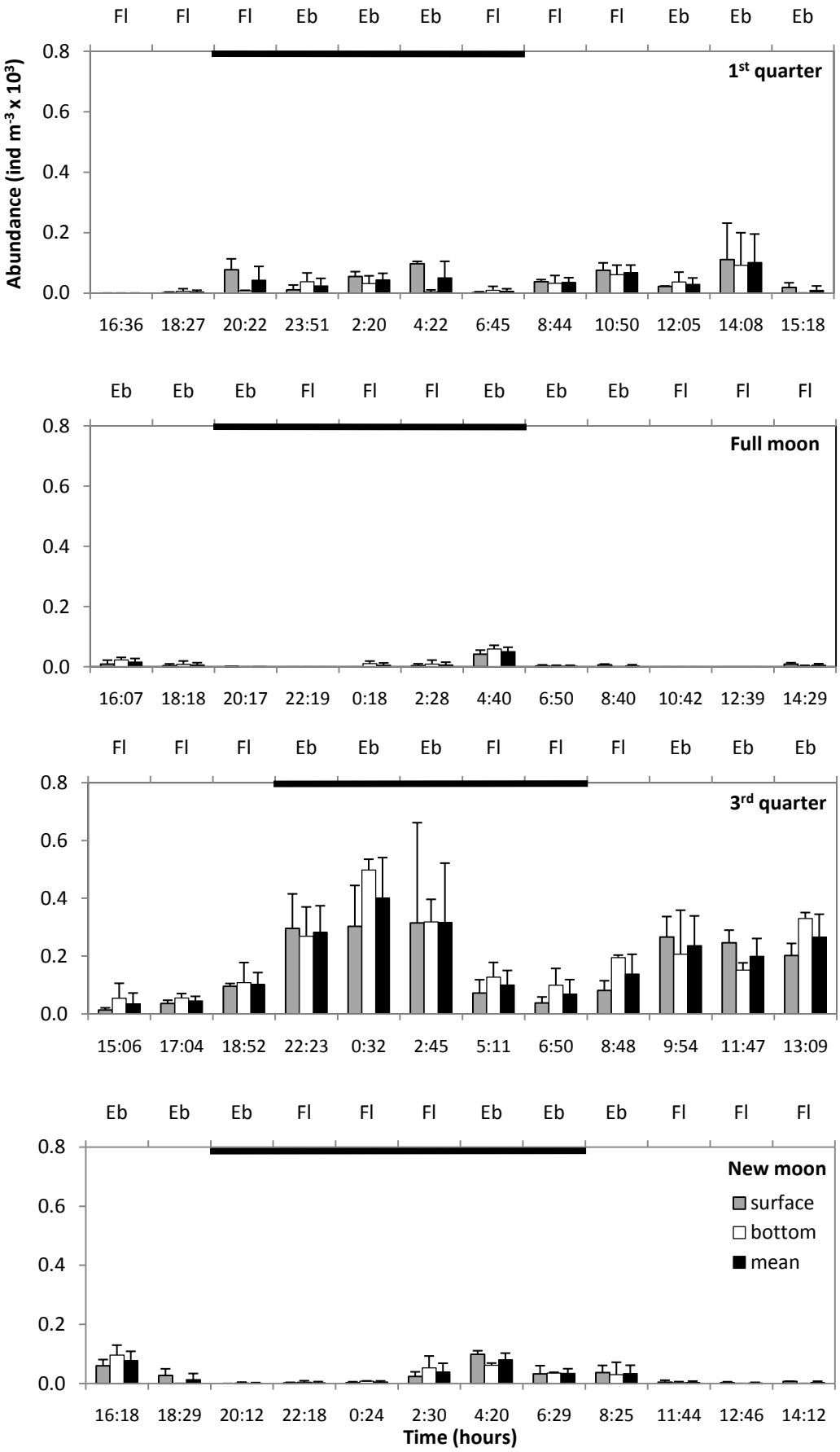


Fig.4.33. Surface, bottom and mean total abundance of polychaetes recorded over 24 hours and four consecutive moon phases in the wet period. Horizontal bar denotes nighttime; Eb = ebb tide, Fl = flood tide.

species recorded were relatively similar among moon phases except for full moon samples which comprised of only 24 species (Table 4.27). The numbers of other zooplankton taxa recorded among moon phases in the dry period were 41 to 54 taxa while in the wet period were 37 to 45 taxa (Tables 4.26 & 4.27).

4.1.6.2 Copepod species diversity

Mean J' and Δ^+ of copepod assemblages were significantly higher in the wet period than the dry period in contrast to Δ^* which was higher in the dry period than the wet period. Mean H' of copepods was not significantly different between dry and wet period (Table 4.28).

In the dry period, mean J', H' and Δ^* values were comparatively higher during neap tide than spring tide (ANOVA, $p < 0.001$), while variation of Δ^+ among moon phases was marginally significant ($p = 0.042$), with lowest value recorded during full moon (Table 4.26). Significant diel pattern was observed for H', Δ^* and Δ^+. Nighttime assemblages had higher H' value than day assemblages, whereas Δ^* and Δ^+ showed an exact opposite pattern (Table 4.26). Δ^* and Δ^+ were at significant lower level during night-flood (appendix XIVa, b). Although J' and H' were significantly higher at ebb than flood tide, tidal effect was more inconsistent among moon phases and diel cycle compared with Δ^* and Δ^+ (appendix XIVc, d). Bottom Δ^* value was significantly lower than that of surface particularly during the period of spring tide (appendix XIVe). Depth pattern was not significantly different for the rest of biological indexes (Table 4.26).

In the wet period, there was no significant moon phase pattern observed for J' and H' (ANOVA, $p > 0.05$; Table 4.27). Diel period did significantly affect J' and H' values, with higher value obtained during the night than the day (ANOVA, $p < 0.05$; Table 4.27). The diel effect, however, was significant only during the 1st quarter or full moon (appendix XVa, b). Tide and depth factors did not significantly affect J' and H'

Table 4.26. Summary results of four-way ANOVA on copepod biodiversity indexes with respect to moon phase, diel, tide, depth and their interaction in the dry period. $\bar{x}$ = mean; n = sample size; biodiversity indexes: S = species richness, J' = Pielou's evenness, H' = Shannon-Wiener diversity indexes, Δ* = average individual taxonomic distinctness and Δ^+ = average specific taxonomic distinctness; homogenous groups indicated by superscripts a, b and c; ** significance at $p < 0.01$, * significance at $p < 0.05$, ns no significance. H' computed on log-base e.

		Source of variation														
		Moon phase (1)					Diel (2)			Tide (3)			Depth (4)			Significant interaction effect ($p < 0.05$)
		1st quarter	Full moon	3rd quarter	New moon	p-level	Day	Night	p-level	Ebb	Flood	p-level	Surface	Bottom	p-level	
	n	48	48	48	48		112	80		96	96		96	96		
Copepods																
S		32	36	29	40											
J'	$\bar{x}$	0.64^{a}	0.49^{b}	0.61^{a}	0.55^{c}	<0.001**	0.58	0.56	ns	0.59	0.55	<0.01**	0.56	0.58	ns	1 x 3, 1 x 2 x 3
	± SD	0.11	0.09	0.11	0.07		0.12	0.10		0.11	0.11		0.12	0.11		
H'	$\bar{x}$	1.54^{a}	1.26^{b}	$1.50^{a,c}$	1.40^{c}	<0.001**	1.36	1.51	<0.001**	1.47	1.38	<0.01**	1.41	1.44	ns	2 x 3, 2 x 4,
	± SD	0.29	0.23	0.26	0.20		0.26	0.26		0.27	0.26		0.29	0.24		1 x 2 x 3
Δ*	$\bar{x}$	82.21^{a}	78.90^{b}	82.62^{a}	81.38^{a}	<0.01**	83.53	78.14	<0.001**	82.80	79.76	<0.001**	82.16	80.40	<0.05*	1 x 3, 1 x 4,
	± SD	4.95	6.74	5.79	5.19		5.76	4.34		5.94	5.36		5.87	5.72		1 x 2 x 3
Δ^+	$\bar{x}$	$84.93^{a,b}$	85.22^{a}	$84.92^{a,b}$	83.76^{b}	0.042*	85.85	83.11	<0.001**	85.15	84.26	<0.001**	84.75	84.66	ns	2 x 3
	± SD	2.46	2.69	2.77	2.93		2.42	2.37		2.52	2.91		2.85	2.66		
Other zooplankton																
S		49	46	41	54											

Table 4.27. Summary results of four-way ANOVA on copepod biodiversity indexes with respect to moon phase, diel, tide, depth and their interaction in the wet period. $\bar{x}$ = mean; n = sample size; biodiversity indexes: S = species richness, J' = Pielou's evenness, H' = Shannon-Wiener diversity indexes, Δ* = average individual taxonomic distinctness and Δ^+ = average specific taxonomic distinctness; homogenous groups indicated by superscripts a, b and c; ** significance at $p < 0.01$, * significance at $p < 0.05$, ns no significance. H' computed on log-base e.

		Source of variation														
		Moon phase (1)					Diel (2)			Tide (3)			Depth (4)			
		1st quarter	Full moon	3rd quarter	New moon	p-level	Day	Night	p-level	Ebb	Flood	p-level	Surface	Bottom	p-level	Significant interaction effect ($p < 0.05$)
	n	48	48	48	48		104	88		96	96		96	96		
Copepods																
S		28	24	30	27											
J'	$\bar{x}$	0.58	0.62	0.62	0.59	ns	0.59	0.62	<0.05*	0.60	0.61	ns	0.60	0.60	ns	1 x 2, 1 x 2 x 3
	± SD	0.15	0.10	0.09	0.11		0.13	0.09		0.11	0.12		0.12	0.11		
H'	$\bar{x}$	1.41	1.44	1.48	1.40	ns	1.32	1.56	<0.001**	1.44	1.42	ns	1.42	1.44	ns	1 x 2, 1 x 2 x 3
	± SD	0.39	0.32	0.25	0.29		0.32	0.26		0.33	0.31		0.32	0.32		
Δ*	$\bar{x}$	74.45[a]	72.18[a]	86.83[b]	82.06[c]	<0.001**	77.96	79.97	0.044*	80.42	77.34	<0.05*	79.00	78.76	ns	1 x 2 x 3
	± SD	8.86	8.99	6.92	6.38		10.77	8.39		10.69	8.55		9.65	9.96		
Δ^+	$\bar{x}$	85.99[a]	82.70[b]	87.45[a]	86.50[a]	<0.001**	86.01	85.25	ns	86.22	85.10	<0.01**	85.75	85.57	ns	1 x 2, 2 x 3, 2 x 4
	± SD	3.48	3.96	2.50	3.37		4.29	3.08		3.70	3.82		3.74	3.87		
Other zooplankton																
S		37	43	43	45											

of copepod assemblages (ANOVA, $p > 0.05$; Table 4.27). Mean Δ^* and Δ^+ were significantly lowest during full moon (ANOVA, $p < 0.001$; Table 4.27). There was a marginally significant difference for Δ^* and no significant difference for Δ^+ between diel cycle. Tide had significant influence on Δ^* and Δ^+ with mean ebb tide value being higher than flood tide value (Table 4.27).

Table 4.28. Copepod biodiversity indexes in the dry and wet periods. $\bar{x}$ = mean; n = sample size; biodiversity indexes: J' = Pielou's evenness, H' = Shannon-Wiener diversity indexes, Δ^* = average individual taxonomic distinctness and Δ^+ = average specific taxonomic distinctness; ** significance at $p < 0.01$, ns no significance. H' computed on log-base e.

		Dry	Wet	p-level
Biodiversity index	n	192	192	
J'	$\bar{x}$	0.57	0.60	<0.01**
	± SD	0.11	0.11	
H'	$\bar{x}$	1.42	1.43	ns
	± SD	0.27	0.32	
Δ^*	$\bar{x}$	81.28	78.88	<0.01**
	± SD	5.85	9.78	
Δ^+	$\bar{x}$	84.71	85.66	<0.01**
	± SD	2.75	3.79	

4.1.6.3 Similarity between zooplankton communities

The cluster analysis and MDS ordination plot show that zooplankton community structure was highly distinct between dry and wet periods (Figs. 4.34 & 4.35). For each period, the neap tide community structure was different from that of spring tide community structure. Two-way crossed ANOSIM between moon phase and diel revealed a significant separation in community structure among moon phases (Global R = 0.87, p = 0.001) and diel (Global R = 0.564, p = 0.001). Pairwise comparisons among moon phases show that the community structure in the dry period was highly distinct from that in the wet period with R values that ranged from 0.8 to 1 (Table 4.29). There was also a strong discrepancy in community structure between neap and spring tide assemblages in each of the sampling period (R values of >0.8). Although the

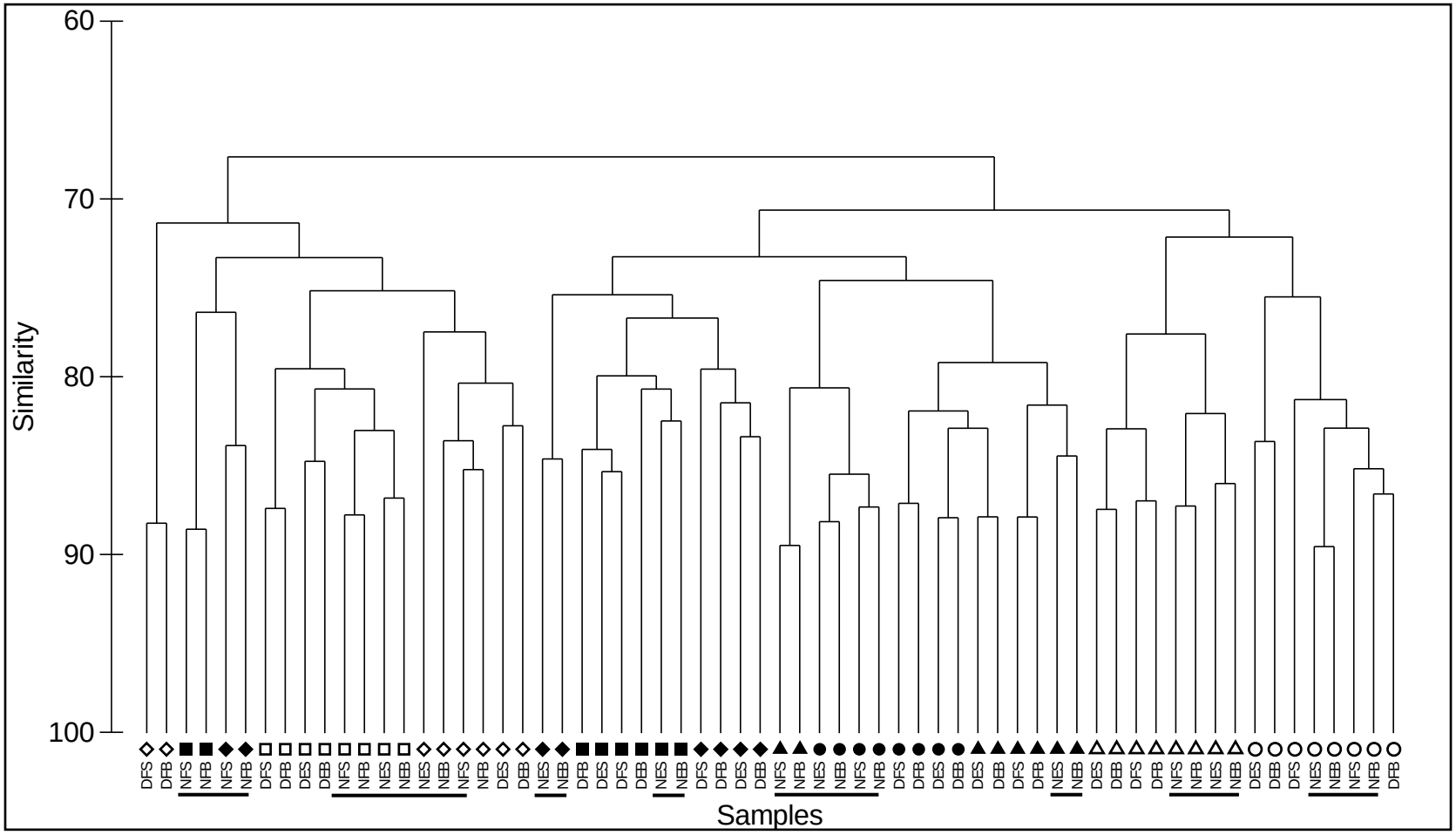


Fig. 4.34. Dendrogram from group average clustering of zooplankton samples based on Bray-Curtis similarity for dry (filled symbol) and wet (open symbol) periods. Triangle indicates 1st quarter; square, full moon; circle, 3rd quarter; diamond, new moon. Three- alphabetic letters: D, day; N, night; E, ebb tide; F, flood tide; S, surface; B, bottom. Horizontal bar indicates nighttime cluster.

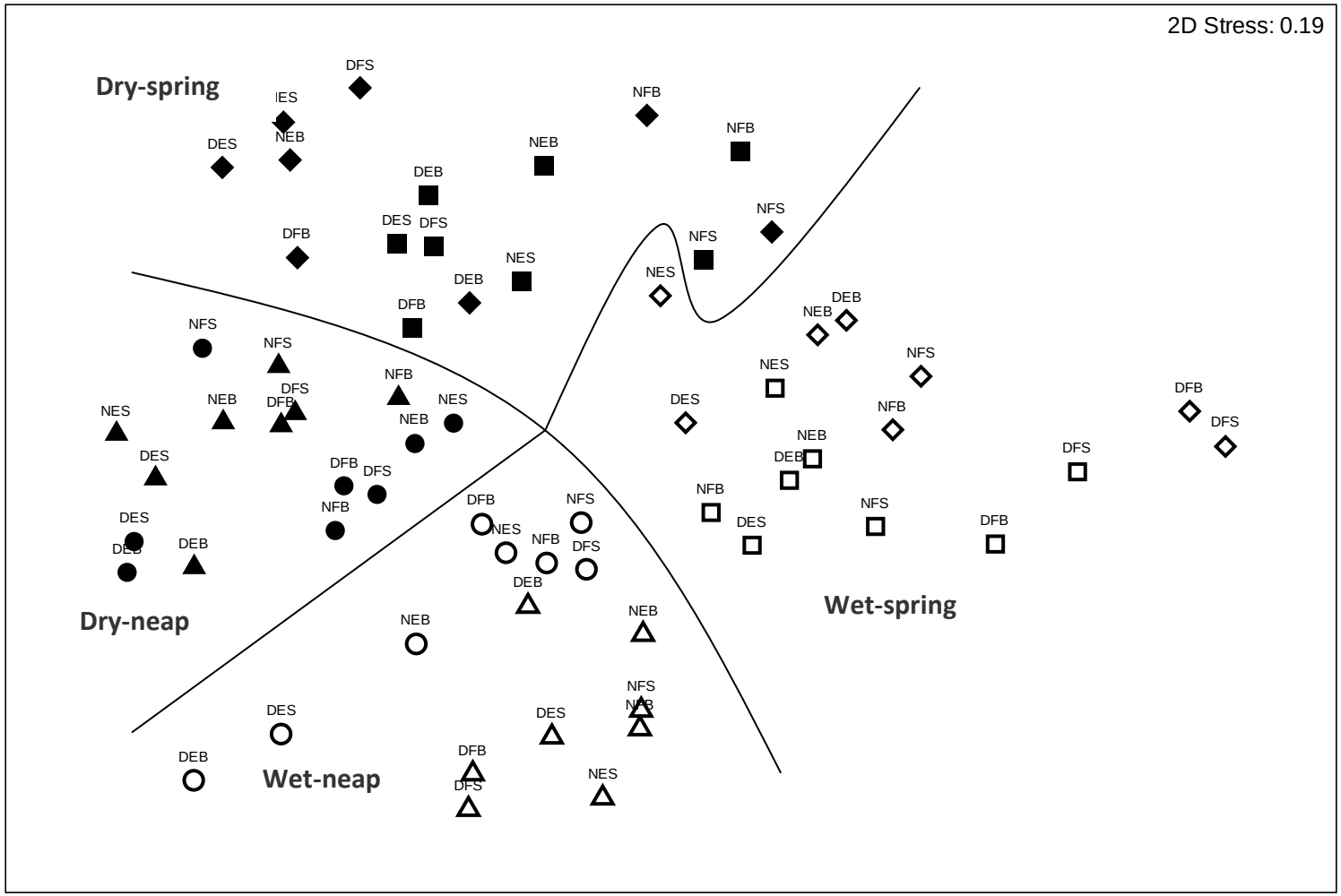


Fig. 4.35. MDS plots of zooplankton assemblages sampled in the dry and wet periods. Symbols and abbreviations as given in Fig. 4.34.

community formed by full moon assemblages was relatively more similar to that of new moon assemblages, their community structure was significantly different (dry period: R = 0.604, p = 0.005; wet period: R = 0.484, p = 0.005) (Table 4.29). Two-way crossed ANOSIM between moon phase and tide and between moon phase and depth indicates that community structure was barely separable by tidal effect (Global R = 0.197, p = 0.007) and not separable by depth effect (R = -0.189, p = 1).

Table 4.29. Results of two-way ANOSIM between moon phase and diel and pairwise comparisons among moon phases. Boldface indicates significance level at $p \leq 0.005$.

Groups	R Statistic	Significance p-level
Moon phase	0.87	0.001
Diel	0.564	0.001

Pairwise tests

Moon phase	Dry period			Wet period			
	1st quarter	Full moon	3rd quarter	New moon	1st quarter	Full moon	3rd quarter
Dry period							
Full moon	**0.984**						
3rd quarter	**0.714**	**0.995**					
New moon	**0.818**	**0.604**	**0.813**				
Wet period							
1st quarter	**1**	**1**	**0.995**	**0.927**			
Full moon	**1**	**1**	**1**	**0.854**	**0.995**		
3rd quarter	**0.969**	**0.984**	**0.927**	**0.938**	**0.943**	**0.948**	
New moon	**0.958**	**0.828**	**0.953**	**0.828**	**0.911**	**0.484**	**0.813**

4.2 Discussion

4.2.1 Hydrographic conditions and phytoplankton

Physical parameters in the Matang mangrove estuaries are altered by the unstable hydrodynamic conditions, which result from the rhythmic tidal movements and climatic factors. Small tidal range during neap tides does not generate substantial turbulence (Chong *et* al., 1999) and the slow tidal current encourages vertical stratification of the water column (Uncles *et* al., 1992). Freshwater inflows and weak vertical mixing in the Matang mangrove estuaries form a temporary salt wedge during neap tide (Sasekumar *et* al., 1994) which can extend over 10 km upstream (see Tanaka & Choo, 2000). At the lower estuary of Sangga Kecil River, a strong stratification was

observed during neap tide in the wet period, but remained vertically homogenous during spring tide. In the dry period, a small extent of stratification in salinity was observed during the 3rd quarter moon phase while salinity was homogenous during the 1st quarter moon phase and spring tide periods. A similar phenomenon was also observed along the west coast of India with vertical stratification during the wet season, but water column became vertically homogenous during drought (Madhupratap, 1987). It is noted that the dry period sampling in this study (July 2003) coincided with strong west to south-westerly winds, which could generate wind mixing currents (see Chapter 3). Therefore, the lack in stratification during dry period neap tide could also be in partly influenced by wind-induced mixing currents. Uncles *et* al. (1992) reported that the vertical stratification was maximized during the peak freshwater runoff in the Merbok mangrove estuary. The estuary is completely vertically well mixed by greater turbulence during spring tide.

Depth variability in temperature and DO level was observed, but not for pH when there was stratification in salinity. Heat absorption from solar irradiance tends to remain at the surface when there is no mixing in the water column. Therefore, surface layer had warmer temperatures than that of the bottom. When the water column was stratified, DO level drops with increasing water depth. Low DO level was also obtained during spring tide. The low oxygen concentration in the water column could be related to the greater oxygen demand owing to microbial activity on the resuspended organic matter (Nelson *et* al., 1994). Turbidity was highly variable in the Matang mangrove estuaries particularly during the spring tide period.

In the same estuaries, Tanaka and Choo (2000) suggested that dissolved inorganic nutrients were higher during spring than neap tide due to outwelling of these nutrients from the mangrove forest and creek. The authors also reported higher chl. *a* concentration during spring tide (up to 80 µg l^{-1}) due to the elevation of dissolved

inorganic nutrients. The nutrient-chl. *a* association, however, was not clear in the present study. Chl. *a* appeared to be light-dependent rather than the influence of nutrient levels. Chl. *a* was consistently at higher levels during the day than the night across moon phases except during the 1st quarter in the wet period (see Fig. 4.9). This could be due to overcast light irradiance by clouds in the rainy day or intense nocturnal grazing by copepods particularly *Acartia* copepodids (see section 4.5.3.1).

4.2.2 Zooplankton composition and community structure

There was no large difference in zooplankton species composition between the routine monthly sampling and the 24-hour sampling (see Table 3.10), but species-specific abundance and distribution patterns of both samplings differed from each other. In particular, the so-called demersal zooplankton such as adults of *P. annandalei* and mysids that were scarcely found throughout the period of routine monthly sampling occurred in considerable numbers in some occasions of the 24-hour sampling period. Although the hyperbenthic shrimps *Acetes* constituted a small percentage composition of zooplankton in terms of numerical abundance, they contributed a large proportion of the zooplankton biomass in the 24-hour study particularly during the wet period. The insignificant correlation between biomass and abundance of large-sized zooplankton in the wet period was in part attributed to this large bodied *Acetes*. The benthic polychaetes that were not observed during the routine monthly sampling were also fairly rare in the present study. These animals were probably captured when they were resuspended by spring tidal currents.

The lower estuary is a unique place where the zooplankton community consists of both estuarine and coastal neritic species. Several marine copepods such as *Canthocalanus pauper, Acrocalanus gibber, Temora turbidata* (Dana), *Oithona brevicornis, Oithona rigida* and some *Corycaeus* species that were never found inside

the mangrove estuaries entered the lower estuary during the dry period (see Table 3.10). These species, however, never occurred in large numbers throughout the sampling period. In fact, most of the zooplankton found at the lower estuary is tolerable to a wide range of salinity although the selective range of salinity preference may vary among species. This is in agreement with Duggan *et* al. (2008)'s observation where zooplankton are mostly marine euryhaline in Darwin Harbour, Australia.

The truly estuarine copepod species suggested by Duggan *et* al. (2008) in Darwin Harbour included several *Pseudodiaptomus* species, *Acartia sinjiensis* Mori and *Oithona nishidai* McKinnon. *Pseudodiaptomus hessei* (Mrázek) and *Acartia clausi* Giesbrecht were similarly reported to dominate the zooplankton community in the tropical brackish lagoon of Ivory Coast particularly during the rainy season (Kouassi *et* al., 2001). Krumme & Liang (2004) also suggested that *Pseudodiaptomus* coexisted with *Acartia* and both were predominantly found in the inner part of the mangrove estuaries of Brazil during the wet period. During the routine monthly sampling of the present study, estuarine copepods consisted of *A. spinicauda, Acartia* sp. 1, *O. aruensis* and *O. dissimilis*, but very few *Pseudodiaptomus* adults were sampled due to neap tide and daytime sampling (see Chapter 3). During the 24-hour sampling, two *Pseudodiaptomus* species, *P. annandalei* and *P. trihamatus* Wright S. were considerably found in the wet-period spring tide (see Table 4.22). Unlike other *Pseudodiaptomus* species found in the Matang mangrove estuaries, *P. annandalei* was rarely sampled at the lower estuary of Matang in the dry period. Its spatial distribution as observed in the routine monthly sampling indicates occurrence at the upper estuary only as compared to other congeneric species, which could be found further downstream (see Table 3.10). Therefore, it is apparent that *P. annandalei* is adapted to low salinity environment compared with other estuarine copepods in the same estuary with greater salinity tolerance. Biomass of *P. hessei* was reported to be higher in a

tropical lagoon in Ivory Coast when salinity was <17 ppt (Kouassi *et* al., 2001), while Chen *et* al. (2003) reported that *Pseudodiaptomus poplesia* (Shen) found in the Pearl River estuary, Hong Kong, has a narrow salinity tolerance of less than 12 ppt. In contrast to *P. annandalei*, *P. bowmani* were mainly found in the more saline coastal waters of Matang. At the lower estuary of Sangga Kecil River, this species was more common in the dry period but rarely occurred in the wet period samples (see Table 3.10). The dominance of *P. annandalei* in stomach contents of the small-sized fishes indicated the importance of this estuarine dweller in the Matang mangrove food web (Chew *et* al., 2007; Then, 2008; see Chapter 5).

Zooplankton community clearly differed among moon phases. Neap tide community was composed of those taxa commonly reported for the routine monthly sampling including most of the meroplanktonic larvae, except for brachyuran. The brachyuran larvae were sampled mainly during spring tide. This was closely linked to the timing of crab larval release, which is discussed in section 4.2.3.

Alldredge & King (1980) reported that the nocturnal emergence of some demersal zooplankters in a tropical reef was inhibited during moonlit period. However, in turbid shallow (Fancett & Kimmerer, 1985; Jacoby & Greenwood, 1989) and deep (Ohlhorst, 1982) waters, nighttime emergence of demersal zooplankters was not affected by moonlight due to poor light penetration through the water column. The distribution of demersal zooplankters in the Matang mangrove estuaries was also unlikely to be much affected by moonlight owing to high water turbidity. The only possible evidence of moonlight effect on zooplankton was observed for mysids during full moon in the dry period, when they were on average more abundant at the bottom than at the surface water as to avoid light illumination (see Table 4.20). For the rest of sampling occasions, mysids were consistently more abundant during the night than the day irrespective of water depth. This suggests that the vertical distribution of mysids in

the water column is more influenced by diel than by moonlight effect. The copepods *P. annandalei* and *P. trihamatus* were distinctly more common during spring tide than during neap tide (see Tables 4.17 & 4.22), implying that the appearance of these organisms may be closely linked to the tidal amplitude.

It has been reported that the demersal copepod *Pseudodiaptomus* stays close to the bottom during the day and migrate into the water column during the night (Fancett & Kimmerer, 1985; Walter, 1987; Jacoby & Greenwood, 1989; Kouassi *et* al., 2001). If *Pseudodiaptomus* performs a regular diel vertical migration, its occurrence and abundance pattern should be relatively similar among moon phases. Nevertheless, *P. annandalei* and *P. trihamatus* were clearly more common during spring than neap tide in this study (see Tables 4.17 & 4.22). In particular, no single specimen of *P. annandalei* was encountered during neap tide in the dry period. This may imply that when tidal condition is less strong, most of these *Pseudodiaptomus* species remain at the bottom even during the night. Interestingly, copepods of this genus can burrow into the sediment or attach to objects or detritus particles during daytime (Hart & Allanson, 1976; Kouassi *et* al., 2001). During spring tide, these species may be swept up by the stronger tidal currents, and therefore become more regularly sampled by net tow. Since *P. annandalei* is believed to be a strongly estuarine, they may have been horizontally transported downstream by spring tidal currents and thus caught during spring tide.

Also, since *Pseudodiaptomus* species were mainly consumed by small-sized fishes in the study area (see Table 5.3), it cannot be ruled out that they could perform behavioral vertical migration during spring tide, when turbidity is high and their visibility by visual predators becomes reduced. Then (2008) reported that fish abundance sampled during spring tide was comparatively lower than that in neap tide. Her results were however preliminary since they were based on surveys conducted during one spring and one neap tide. Therefore, further research is required to test the

hypothesis that tidal current, predation pressure or both have an effect on the abundance and variability of estuarine *Pseudodiaptomus* species during the different moon phases.

Previous studies categorized amphipods, cumaceans, isopods and ostracods as primary benthic dwellers (Emery, 1968; Robertson & Howard, 1978; Jacoby & Greenwood, 1989). It was suggested that a small proportion of these taxa would nocturnally emerge into the water column for mating, dispersal or ecdysis (Foxon, 1936; Mills, 1967; Anger & Valentine, 1976; Robertson & Howard, 1978; Ambrose, 1986), whereas the remaining proportion spend most of the time at the bottom (Jacoby & Greenwood, 1989). Therefore, these animals are often captured in low numbers by tow-net even during the night (Jacoby & Greenwood, 1989). Results of the present study are in agreement with Jacoby & Greenwood (1989). These taxa never occurred in large numbers in tow-net samples although they were more common during the 24-hour sampling (see Table 3.10). Amphipods and ostracods were occasionally consumed in large quantities by the small-sized fishes found in the same estuaries (see Chapter 5; Then, 2008), implying that these animals are at risk of visual predation by fish.

4.2.3 Zooplankton abundance and biomass

As mentioned earlier, the large-sized zooplankton constituted the largest proportion of zooplankton biomass particularly in the wet period. An exceptional high biomass of medium-sized zooplankton during new moon in the wet period was largely due to the contamination of mangrove detritus in bottom samples (see Fig. 4.12). However, the significant positive correlation between biomass and abundance for the medium-sized zooplankton during this period (r = 0.63, see Table 4.13) indicates that the contamination of mangrove detritus did not severely result a large difference in zooplankton distribution between abundance and biomass.

The mesh size of plankton net used in this study was 160 µm. Some of the small-sized zooplankton may have passed through the plankton net. This explains the irregular abundance of small-sized zooplankton in the present work. Although not entirely consistent across moon phases, abundance and biomass of medium- and large-sized zooplankton were in part influenced by diel and tidal effect. Since each of the fractionated components was composed of various zooplankton taxa and individually different in body size, the distribution pattern in biomass may not necessarily reflect the abundance distribution pattern, which was indicated by a weak correlation coefficient. This discrepancy could be avoided by using an alternative method based on a length-weight regression, whereby biomass is measured in individual carbon weight (Uye, 1982).

4.2.3.1 Diel effect

Fulton (1984) documented that most of the copepods found in the estuary tended to remain near to the bottom during the day, and their abundance at the surface increased significantly during the night. In shallow waters of Maizuru Bay, Japan, Ueda (1987) reported that the dominant coastal copepods were ontogenetically distributed at different layers of the water column, where the early developmental stages generally resided in the upper layer and older copepodids and adults stayed in deeper waters. The ontogenetic vertical distribution was not observed during the night as older developmental stages performed a nocturnal upward migration into the water column. Using a net tow, Jacoby & Greenwood (1989) did not observe a notable diel pattern in abundance of *Acartia* and *Parvocalanus* but did observe for *Oithona* spp. in Moreton Bay, Australia. Although the adults of the four dominant copepod species considered in the present study could be frequently sampled through the water column during the day,

the adult population of these species was clearly more abundant during the night than during the day.

It is noteworthy that *A. spinicauda* was able to maintain its vertical position at lower layers of the water column even during diurnal spring tide (see section 4.1.5.2a). A strong nocturnal migrating behavior under the condition of strong tidal currents was also previously documented for *Acartia tonsa* in temperate estuary (Fulton, 1984). Among the dominant copepods found in the Maizuru Bay, *Acartia* showed the greatest diel vertical migration (Ueda, 1987). However, *A. sinjiensis* was distributed homogeneously through the water column in the well-mixed Haughton River estuary, Australia (McKinnon & Klumpp, 1998a).

Aggregation at the bottom during the day and dispersal during nighttime are common features observed for several species of *Acartia* and *Oithona* in various marine ecosystems including coral reefs, seagrass beds, coastal embayment and mangroves (Emery, 1968; Hamner & Carleton, 1979; Ohlhorst; 1982; Omori & Hamner, 1982; Ueda *et* al., 1983; Ambler *et* al., 1991; Buskey *et* al., 1996). The copepod aggregations were composed predominantly of adults (Hamner & Carleton, 1979; Ueda *et* al., 1983; Ambler, 2002), and generally occurred a few cm above the substrate (Ueda *et* al., 1983; Fulton, 1984; Ambler, 2002). Although there was no direct attempt to observe copepod aggregation in the Matang mangrove estuaries, it is likely that *A. spinicauda* aggregated at the bottom below the depth of plankton net tow during diurnal neap tide. Because of the difficulty to sample immediately above the sediment using a tow-net, the bottom samples of the present study were collected at ca. 50 cm above the sediment bottom. Therefore, copepod aggregations that formed immediately above the sediment would be largely undersampled by the plankton net. This explains why there was no marked variation in the vertical distribution of *A. spinicauda* during diurnal neap tide. Fulton (1984) reported that the numbers of *A. tonsa* collected by pump sampler at the bottom

during the day did not significantly differ from those collected by vertical and surface tow-nets in the water column during the night. Cohen and Forward (2005) speculated that low abundance of shallow water copepod *Calanopia americana* Dahl F. in the water column of Newport River estuary during the day resulted from the tendency of the copepod living on the sediment during daytime. Similar speculation was also suggested for other zooplankton in tropical waters (Kouassi *et* al., 2001; Pagano *et* al., 2006).

Jacoby and Greenwood (1989) classified *Oithona* spp. in Moreton Bay as demersal zooplankters since they were found to be very close to the substrate during the day. McKinnon & Klumpp (1998a) indicated that the adults of oithonids were found to be more abundant at the bottom as compared to surface water in subtropical mangrove estuary, albeit a strong tidal condition. Results of the present study are generally in agreement with the above studies, where the most dominant cyclopoid *O. simplex* tended to avoid hovering in the water column during the day. Although small in body size, *O. simplex* showed a clear diel pattern in abundance particularly during spring tide in the wet period (see Fig. 4.29). However, *P. crassirostris* with a relatively similar body size did not exhibit such a diel pattern, but was rather homogeneously distributed. This discrepancy could be related to different behavioral responses to turbulence, since *O. simplex* may possess stronger swimming mode than *P. crassirostris* to overcome turbulent diffusion. Buskey *et* al. (1996) suggested that *Oithona oculata* Farran could swim up to 25 body length s^{-1} to maintain its position within the swarm that formed between the mangrove prop roots during daylight. This swimming speed was much higher than most of the other planktonic organisms with swimming speed of <5 body length s^{-1}.

Previous studies conducted in tropical Australian estuaries indicated no diel vertical migration of *P. crassirostris* and *B. similis* (Kimmerer & McKinnon, 1987;

McKinnon & Klumpp, 1998a). The closely related species *P. crassirostris* and *Paracalanus parvus* (Claus) did not show a clear diel vertical migration during summer, while the distribution of these species at deeper water layer during the day in winter was influenced by *Noctiluca scintillans* (Macartney) Kofoid & Swezy bloom (Tang *et* al., 1994). Ueda (1987) reported that diel vertical migration was markedly observed for adult males of *P. crassirostris* but not for adult females. The author showed disproportionate number of adult male and female during the day but they occurred in about equal numbers during the night. The number of adult copepods was not partial to any sex in the present work. Nevertheless, the present study showed a significant diel difference in total abundance of adult *P. crassirostris* and *B. similis*, respectively. Similar to *A. spinicauda*, *P. crassirostris* and *B. similis* may have aggregated very close to the sediment bottom during diurnal neap tide particularly during ebb tide; consequently, a large proportion of the adult population was undersampled by tow-net. Although not as abundant as *A. spinicauda*, the number of *P. crassirostris* collected at the bottom was comparatively higher than that of surface water during diurnal spring tide in the dry period. This pattern, however, did not persist in the wet period. This could be related to excessive turbulence caused by spring tidal currents augmented by intense freshwater discharge. This assumption, however, needs further investigation as current velocities were not measured in the present study.

As discussed earlier, *P. annandalei* and *P. trihamatus* were clearly more abundant during spring tide but very few specimens were collected during neap tide even during the night. These two species constituted the most important diets of the small-sized fishes found in the Matang mangrove estuaries. It was suggested that intra- and inter-specific variability in diel vertical migration of copepods was largely due to body characteristic such as body size and morphology, pigmentation and lipid content (Bollens & Frost, 1991a; Hays, 1994, 1995; Hays *et* al., 2001). Individuals with higher

lipid content did not display extensive diel vertical migrating behavior compared with those of low lipid content (Hays *et* al., 2001). Also, female copepods with egg sacs did not undergo diel vertical migration and consistently remained at the sediment bottom as a means of avoiding visual predators (Bollens & Frost, 1991a). Given that adult female *Pseudodiaptomus* had high lipid content (Fancett & Kimmerer, 1985), more pigmented and large in body size, the observations by Hays (1995), Hays *et* al. (2001) and Bollens and Frost (1991a) may be the case in the present study.

Although some developmental stages of copepods may have passed through the plankton tow-net, the numbers of juvenile copepods sampled in this study were higher than the numbers of adult copepods. Copepodids of *Acartia* constituted the largest proportion of the juvenile copepod population. As expected, a nocturnal increase in abundance was not observed for *Acartia* copepodids but they did reside at deeper water layer. This was due to the catch that mostly comprised of older copepodids. The lack of nocturnal migration behavior in copepodids may be due to less predation pressure by fish, which feed selectively on large bodied prey items (Fulton, 1984).

Other than copepods, mysids also constituted a major food source for Matang mangrove fishes, implying that these animals are at high risk of visual predation. Diel vertical migration of these animals is primarily cued by light changes (Gal *et* al., 1999). Emergence of these animals in the coral reefs occurred after midnight (Ohlhorst, 1982) and the presence of moonlight sufficiently deterred their vertical migration (Alldredge & King, 1980). This has drawn a verdict that mysids are highly photosensitive (Kouassi *et* al., 2006). In Merbok mangrove estuary, Malaysia, mysids were found to aggregate at the edge of mangrove channels during the day (Hanamura *et* al., 2008). In other tropical estuaries, mysids were found to be just above the sediment surface during daytime and migrating into the water column after sunset (Kouassi *et* al., 2006). In the present study, mysids clearly exhibited a strong migratory behavior on a diel basis. The obscured diel

pattern that occurred with significant depth variability during full moon in the dry period may indicate that the extent of nocturnal upward migration of mysids could be reduced but not completely prevented by moonlight. This was not the case in the wet period when moonlight was overcast by clouds. An aberrant high abundance of mysids obtained at dusk during the 1st quarter in the wet period (see Fig. 4.32) could be related to an association between the animal's behavior and hydrodynamic processes.

In order to increase the chances of larval survival and maintain the population, several reproductive adaptations have been adopted by the estuarine organisms with planktonic larvae. One of these adaptations is to release larvae at night when visual predator abundance is believed to be minimal. Meroplanktonic larvae that were documented to be more abundant during the night included cirripede larvae in the Senegal River estuary (Pagano *et* al., 2006), polychaete larvae in Goa mangrove estuary, India (Goswami, 1984) and crab larvae in some tropical and temperate estuaries (review by Forward, 1987). However, studies have also documented a reverse diel timing of larval release in cirripedes (e.g. Macho *et* al., 2005) and brachyurans (e.g. Macintosh, 1979). With few exceptions, abundance of young larval stages of cirripedes, polychaetes and brachyurans often was found to be higher during the day than the night in the Matang mangrove estuaries. This may suggest that visual predation pressure is not a crucial factor controlling the timing of larval release in these turbid mangrove systems. Based on the fish stomach contents analysis, cirripede nauplius and polychaete larvae were not as important as adult copepods and other demersal zooplankters in fish diets (see Chapter 5). These larvae may not have to bear intense risk of visual predation as encountered by adult copepods and other demersal zooplankters. Furthermore, the presence of light can induce photosensitive larvae such as cirripedes to form swarms that may reduce larval mortality by predation (Macho *et* al., 2005). For crabs, larval release occurred mainly during spring tide, which was previously documented to have

low fish abundance in the Matamg mangrove estuaries (Singh & Sasekumar, 1994; Then, 2008). Increased turbidity undoubtedly reduces predatory fish vision and makes crab larvae less conspicuous. Perhaps of the above-mentioned possibilities, predation avoidance may be a less important selective factor on the timing of larval release. This may explain why larval release of these organisms could have occurred during daytime in the Matang mangrove estuaries. Indeed, release of these larvae was more precisely timed by tidal than by diel rhythm (see section 4.2.3.2).

4.2.3.2 Tidal effect

Since the zooplankton community structure in the estuary is clearly distinct from that of adjacent coastal waters, some mechanisms prevail which prevents the estuarine population from being washed out to the adjacent coastal waters or vice versa for the stenohaline zooplankton. The effects of tides are regarded as an extremely important factor controlling zooplankton dynamics in the estuaries (Grindley, 1984; Marques *et* al., 2006). Several mechanisms have been proposed to explain estuarine zooplankton advection by tidal flushing. These mechanisms include high reproductive potential to compensate the loss rate (Ketchum 1954; Gupta *et* al. 1994), physical entrapment (Castel & Veiga., 1990; Morgan *et* al., 1997; Roman *et* al., 2001) and adaptive behavior through tidally induced vertical migration, which has been observed for a wide range of zooplankton including copepods (Trinast, 1975; Wooldridge & Erasmus, 1980; Kimmerer & McKinnon, 1987; Hough & Naylor, 1991, 1992; Morgan *et* al., 1997; Ueda *et* al., 2010), crab larvae (Cronin & Forward, 1979), mysids (Wooldridge & Erasmus, 1980; Orsi, 1986; Kimmerer *et* al., 1998), chaetognaths (Cohen & Forward, 2005) and fish larvae (Fortier & Leggett, 1983). It was also suggested that zooplankton could horizontally migrate to calmer areas to avoid export by diffusive turbulence (Cronin *et* al. 1962; De Pauw, 1973; Wooldridge & Erasmus, 1980; Roddie *et* al. 1984).

Among the behavioral adaptations of zooplankton population retention, tidal vertical migration (TVM) is the most commonly reported mechanism for estuarine zooplankton. It is generally accepted that upper layer flow is comparatively greater than deep layer flow due to bottom friction. Also, tidal currents in mangrove estuaries are asymmetrical, being stronger during ebb tide than flood tide (Wolanski *et* al., 1980; Woodroffe, 1985a, b; Roman *et* al., 2001). Therefore, estuarine zooplankton by remaining at the river bottom on ebb flow would avoid net-export whereas migrating into the water column on flood flow would give an opposite effect (Wooldridge & Erasmus, 1980; Kimmerer & McKinnon, 1987; Hough & Naylor, 1991, 1992; Morgan *et* al., 1997; Ueda *et* al., 2010). Advection of copepods near surface water can be several orders of magnitude greater than copepods near the bottom (Manning & Bucklin, 2005). Nevertheless, tidally induced vertical migration is a complex mechanism involving the animal's response to tidal changes which may differ with its position along the estuary (Hough & Naylor, 1991, 1992; Ueda *et* al., 2010). Additionally, the effectiveness of tidally induced vertical migration is dependent not only upon animal's swimming behavior, but also upon localized hydrodynamic conditions such as horizontal and vertical current speed and water depth (Ueda *et* al., 2010).

In the present study, TVM of zooplankton can be shown by a significant interaction effect between tide and sampling depth. This was not detected for most of the taxa except for chaetognaths. For size fractionated zooplankton, only the combined large-sized zooplankton in the dry period indicated a significance of this interaction effect. These results contrast with Kimmerer *et* al. (1998)'s results which documented TVM for almost all of the common zooplankton found in the estuary including copepods. The less striking TVM of estuarine copepod *A. spinicauda* in the present study could be obscured by stronger diel vertical migration. Its population within the Matang mangrove estuaries could also be maintained by other mechanisms such as

strong swimming ability, lateral migration, onshore currents and nearshore frictional effects. *A. spinicauda* did not significantly differ in abundance among moon phases in the dry period. This may indicate the maintenance of its population in the lower estuary perhaps through strong swimming ability associated with the above-mentioned physical processes, but rule out the possibility of lateral migration to slow current areas. Hough and Naylor (1991) did not find significant differences in abundance of *Eurytemora affinis* (Poppe) between the middle and edge of a river channel, and suggested that the swimming speed of this copepod is strong enough to override the seaward current speed.

In the present study, moon phase variation of *A. spinicauda* in the wet period was more dramatic with very high abundance during the 1st quarter and very low abundance during new moon. The extremely high abundance could be related to its reproductive proliferation period, while extreme low abundance could either be due to tidal response to avoid tidal flushing or predation. Copepods may laterally swim to calmer areas at the banks to avoid tidal flushing. Avoidance of predation by mangrove fish larvae is possible since gobiid larvae are particularly abundant during the same sampling occasion (Ooi, in preparation). There was a marked drop in abundance of *Acartia* copepodids during spring tide in both dry and wet period. *Acartia* copepodids with weaker swimming ability and lower salinity tolerance did not undergo diel vertical migration as exhibited by their adults. Thus, it is possible that they laterally migrate to calmer areas among the mangrove prop roots or into the inundated mangrove forest to reduce the risk of being exported by strong spring tidal currents. Therefore, abundance of copepodids at the lower estuary abruptly dropped during the period of spring tide.

Abundance of *P. crassirostris* was significantly higher during spring tide compared with neap tide. The moon phase variation in abundance appeared to result from the animals residing close to the bottom during diurnal neap tide and their resuspension into the water column during spring tide. As a matter of fact, weekly

abundance of this copepod was consistent and thus precluded the possibility of net seaward advection. Since the small copepod is comparatively a weak swimmer, the population of *P. crassirostris* at the lower estuary of Matang may have been due to other adaptive mechanisms such as rapid growth (Kimmerer & McKinnon, 1987) and higher salinity tolerance of the copepod. *P. crassirostris* was found to be equally and abundantly distributed from the upper estuary of Matang to adjacent coastal waters (see Chapter 3, Chew & Chong, 2011). Although *B. similis* and *O. simplex* were found to congregate with *P. crassirostris* at the bottom at or close to low slack water in the dry period, there was no apparent tidal response from these species. An exceptionally low abundance of the three species during the 1st quarter in the dry period was unlikely due to tidal effect, but rather two plausible reasons. First, the abundance of the dinoflagellate *Noctiluca* was found to be highest during this sampling date (see Table 4.18). Therefore, bioluminescence transmitted by a dense population of *Noctiluca* may have a significant impact on copepod distribution during the night (e.g. Buskey *et* al., 1983). Second, the unusually high turbidity recorded at daytime (see Fig. 4.5) possibly indicated an irregular environmental disturbance which potentially influenced the distribution and abundance of these copepods. However, the precise cause of the unusually high turbidity event was undetermined. Noteworthy, during spring tide in the wet period, nocturnal increase in abundance of *O. simplex* only occurred on ebb but not flood tide. This may be one of the adaptive strategies of *O. simplex* to avoid upstream transport by flood tidal currents since low salinity is unfavourable to it.

In comparison to diel effect, larval release is often timed to synchronize with tidal rhythms. As opposed to population retention mechanisms, larvae of estuarine meroplankton have been suggested to utilize a reverse TVM and thus enhancing a net seaward transport (Drake & Arias, 1991; Zeng & Naylor, 1996a, c; Queiroga *et* al., 1997). Larval export with the aid of ebb tidal currents has been commonly observed for

estuarine crab species (e.g. Dittel & Epifanio, 1990; Dittel *et* al., 1991; Queiroga *et* al., 1994). In the present study, abundance of cirripede nauplii, polychaete larvae and brachyuran zoeae was consistently at higher concentrations on ebb than on flood tide. Although the exact timing of larval release by the ovigerous females of these organisms has not been empirically quantified for the Matang mangrove estuaries, it is believed that females endogenously timed their release of larvae at maximum flood tide so that the newly hatched larvae can utilize the following ebb tidal currents for seaward transport. This contention is supported by laboratory observations of several mangrove *Uca* species (Macintosh, 1984). It has been reported that nearshore waters provide an optimal salinity for the dominant meroplanktonic larvae found in this mangrove system, while the upper estuary with lower salinity recorded low numbers of larvae (see Chapter 3). Therefore, synchronous larval release with ebb tidal currents is also a function to prevent larvae from being transported upstream. Decapod larvae in a typical estuarine system are susceptible to prolonged, very low salinity condition (Vernberg *et* al., 1974; Christy, 1982; Forward, 1987).

The timing of larval release as related to moon phase depends on the shore level which determines the settlement and distribution of intertidal animals. Cirripedes from the upper intertidal zone release larvae mainly during spring high tide, whereas in the lower intertidal zone where animals are inundated by seawater for most of the time, larval release can occur at low tide (Macho *et* al., 2005). Luckens (1970) similarly reported that cirripedes at the upper intertidal zone released larvae during spring tide and storm but no larval release was observed during neap tide and calm weather even though the fertilized females are ready to do so. For littoral and supralittoral crab species, larvae are generally released during spring tide and no such semilunar or lunar timing was observed for most of the sublittoral species (Christy, 1986). In tropical mangrove estuaries, larval release by crab species found in the forested areas occurs

mainly during spring tide (Macintosh, 1984). In the present study, brachyuran zoeae were more abundant during spring tide while cirripede and polychaete larvae were more abundant during neap tide. Presumably this variation was attributed to their adult population that was distributed at different shore level. Larvae of the crab species found on the mangrove forest floor require greater tidal amplitude for seaward transport. Therefore, larval release that is timed at spring tide would enhance export to coastal waters. For cirripedes and polychaetes that are distributed at the lower shore or below tide level, neap-ebb tidal currents are sufficient for larval dispersion. However, spawning during the extreme spring tide conditions may have detrimental effects on these relatively small sized larvae. This explains why there were almost no larvae of these organisms captured during spring tide particularly on flood tide.

In contrast to the export mechanism, larval stages that are ready for settlement would utilize onshore currents for recruiting back to their parental habitat, especially during the night. This reinvasion mechanism has been previously documented for megalopae (Dittel & Epifanio, 1990; Zeng & Naylor, 1996b; Queiroga, 1998; Ross, 2001) and cyprids (Shanks, 1986). However, megalopae and cyprids were scarcely found in the present study although the latter were occasionally consumed in large quantities by the Matang mangrove fishes (Then, 2008). Drake *et* al. (1998) also showed similar results for megalopae in the inlet water of Bay of Cádiz, SW Spain. The low abundance of these larvae was mainly due to the sampling procedure which may have undersampled the onshore migrating larvae that reside very close to the bottom or attach to the drifting mangrove leaves (Wehrtmann & Dittel, 1990). Onshore migrating larvae can also be under represented if reinvasion occurs at the intermediate period of spring and neap tide.

4.2.4 Adaptive significance of diel and tidal responses

Diel vertical migration (DVM) of zooplankton has been well documented for a wide range of organisms from freshwater systems to deep oceans. DVM has been hypothesized to be an adaptive behavior for metabolic conservation (e.g. Enright, 1977) and predator avoidance (Hobson & Chess, 1976; Zaret & Suffern, 1976; Robertson & Howard, 1978). However, the metabolic conservation hypothesis was tested to be disadvantageous for animals that undergo DVM (Lampert, 1989; Aksnes & Giske, 1990). On the other hand, predator avoidance as a selective pressure of DVM was empirically supported by some evidence for both freshwater and marine zooplankton (Stich & Lampert, 1981; Fancett & Kimmerer, 1985; Gliwicz, 1986; Bollens & Frost, 1989, 1991b; Bollens *et* al., 1992; Hays, 1994; Boscarino *et* al., 2007). Although there were no concomitant fish data for the present study, diel fish assemblages obtained on another sampling occasion by Then (2008) implicates fish predation as a selective pressure resulting in DVM of zooplankton. She recorded significantly higher fish abundance during diurnal neap tide. In particular, the dominant zooplanktivorous ambassid and engraulids captured during the day displayed higher gut fullness than those captured during the night. This timing of high gut fullness of fish was corresponded to low abundance of dominant adult copepods and almost near absence of demersal zooplankters in the water column. Presumably the prey animals reside at the bottom where there is minimum risk of fish predation.

The four dominant adult copepods (*A. spinicauda*, *P. crassirostris*, *B. similis* and *O. simplex*) and mysids showed a notable diel pattern in abundance but the larger copepods, *P. annandalei* and *P. trihamatus*, and pericarid zooplankters lacked this pattern. The last three demersal zooplankters are postulated to spend more time at the bottom especially during neap tide when tidal condition is less turbulent. This raises the question of why there is a necessity for some organisms to migrate into the water

column during the night if remaining at the bottom should reduce the risk of predation. As suggested by Robertson & Howard (1978), there must be an equivalent important advantage to induce this adaptive migratory behavior. Feeding and reproduction are the best reasons to explain this scenario. The stable isotope analysis indicated mysids as a carnivorous zooplankton that depends on primary zooplankton consumers, while *P. annandalei* is a herbivore which forages mainly on microalgae. These results are in agreement with comparable species based on gut contents analysis (Kouassi *et* al., 2001, 2006). Studies suggest that mysids are active nocturnal feeders of animal prey, while *P. hessei* does not show a clear diel feeding rhythm because this copepod could ingest microphytobenthos during the day when it remains benthic or hyperbenthic. Presumably, the primary zooplankton consumers are more abundant in the water column. Therefore, mysids have to undergo more extensive nocturnal migration into the water column to feed than herbivorous *P. annandalei*.

Although it cannot be ruled out that the four dominant adult copepods can feed on microphytobenthos in shallow waters, diel vertical migration appears more regular for these copepods compared to *P. annandalei*. This however could be related to the differences in reproductive strategies among these copepods. Reproduction during nocturnal upward migration has been demonstrated for *Acartia* (Pagano et al., 2004), *P. crassirostris* (Ueda, 1987), *Oithona* (Ambler, 2002) and amphipods (Mills, 1967; Robertson & Howard, 1978). The three calanoid copepods (*A. spinicauda*, *P. crassirostris* and *B. similis*) are known broadcast spawners (McKinnon & Klumpp, 1998b). Nocturnal migration would confer greater safety under cover of darkness for broadcast spawners when they mate and reproduce in the water column. On the other hand, egg sac spawners such as oithoniids release and disperse their eggs in the water column during dusk to hatch (Ambler, 2002). Perhaps due to intense predation by fish in Matang waters (Chapter 5), *P. annandalei*, which is also an egg sac spawner, may not

adopt a similar migration and spawning strategy as oithoniids. This may explain the more pronounced nocturnal migration observed for *O. simplex* than *P. annandalei* in the present study. It would be interesting to determine the spawning strategy adopted by *P. annandalei* in future study.

It is noted that there was a considerable number of dominant adult copepods caught during diurnal neap tide although many were surmised to reside at the bottom. Huntley and Brooks (1982) gave a compelling explanation based on the food availability, suggesting that individuals that do not feed to satiation during the night would remain in the water column, a behavior that often occurs when food is scare. It has been reported that copepods generally feed during the night when the risk of predation is minimum (review by Mauchline, 1998). Therefore, the abrupt drop in chl. *a* as observed during night in the present study is likely related to intense grazing by herbivorous zooplankton in the water column. The starving individuals will remain in the water column to feed despite being exposed to high risk of predation.

As mentioned earlier in the Matang mangrove estuaries, the release of newly hatched meroplanktonic larvae were more synchronized to tidal than diel rhythm. Seaward export of meroplanktonic larvae has been reported as a selective adaptation to avoid fish predation (review by Morgan, 1986). However, this may not be the case in the Matang mangrove estuaries since predation pressure is not the most important factor that controls the timing of larval release. Therefore, the most plausible trigger for larval export is the high availability of diatoms in nearshore waters, which are preferentially foraged by meroplanktonic larvae such as cirripede and brachyuran larvae (Turner *et* al., 2001; Schwamborn *et* al., 2006).

Conclusion

The present investigation shows variable patterns of zooplankton abundance in relation to small temporal changes in environmental conditions. The most dominant adult copepods tend to avoid active swimming in the water column during daytime but this behavior is not observed for copepodids. Spring tidal currents tend to swirl up the copepods from the bottom into the water column, while individuals with strong swimming ability (e.g. *A. spinicauda*) could maintain their vertical position at the bottom of the water column. If spring tidal flow becomes too excessive, estuarine copepods may seek refuge in the calmer areas to avoid export from the estuaries, but this is not evident for the euryhaline species *P. crassirostris*. As opposed to estuarine residence, the coastal copepods with higher salinity preference may utilize adaptive mechanisms to avoid upstream advection, in particular, during the wet period when low salinity becomes lethal to coastal species. Mysids exhibit nocturnal vertical migration, while such movement among other demersal zooplankters is generally transient being more common during spring tide. Release of meroplanktonic larvae follows a tidal rather than diel rhythm.

The present study did not consider the possibility of physical processes such as estuarine turbidity maximum and frontal river plume, which were reported to have significant impact on zooplankton population dynamics in the estuaries (e.g. Roman *et* al., 2001; Morgan *et* al., 2005). Therefore, future research should also include these physical processes.

CHAPTER 5

TROPHIC STRUCTURE IN MATANG MANGROVE ESTUARIES AND ADJACENT COASTAL WATERS: ROLE OF ZOOPLANKTON AS FOOD FOR SMALL-SIZED FISHES

5.1 Results

5.1.1 Fish stomach contents analysis

5.1.1.1 Percentage of stomach fullness

A total of 2521 juvenile and small-bodied fishes of standard length 1.5 - 18 cm, belonging to 26 species and collected from June 2003 to June 2004 in the Matang mangrove estuaries were analyzed for their stomach contents. Seventy-two percent of the fish examined had full and gorged stomachs whereas fish with empty stomachs made up only 13% (Fig. 5.1). All estuaries had higher numbers of fish with full stomachs except Sangga Besar River, where 36% of the stomachs examined were empty (Fig. 5.2).

All the common fish species had relatively high percent of stomachs with food except the leiognathid *Eubleekeria splendens* (Cuvier) with vacuity index (VI) of 63 (Table 5.1). The percentage of full and gorged stomachs combined was more than 50% for all ariids, *Arius maculatus*, *A. venosus* Valenciennes, *Cryptarius truncatus* (Valenciennes) and *Ketengus typus* Bleeker, the clupeid *Anodontostoma chacunda* (Hamilton), the scat *Scatophagus argus* (Linnaeus), the lutjanid *Lutjanus johnii* (Bloch), the carangid and the sciaenid *Pennahia anea* (Bloch) (Table 5.1). All stomachs of *Eleutheronema tetradactylum* (Shaw) and *P. anea* had food (VI = 0) (Table 5.1).

5.1.1.2 Dietary composition and frequency of occurrence

A total of 57 types of food items were identified in 2183 stomachs that contained food. The food types were pooled into 27 smaller groups as listed in Table 5.2. The fish diet composed of both planktonic and benthic animals as well as plant

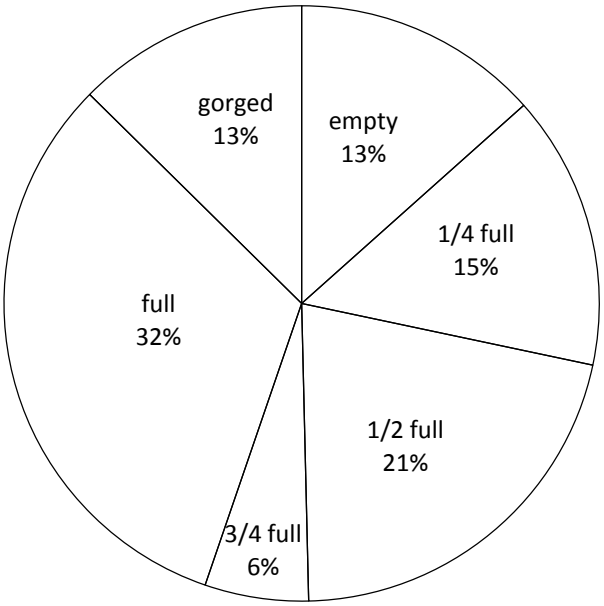


Fig. 5.1. Percentage stomach fullness of 2,521 fish (all species combined) in Matang mangrove estuaries from June 2003 to June 2004.

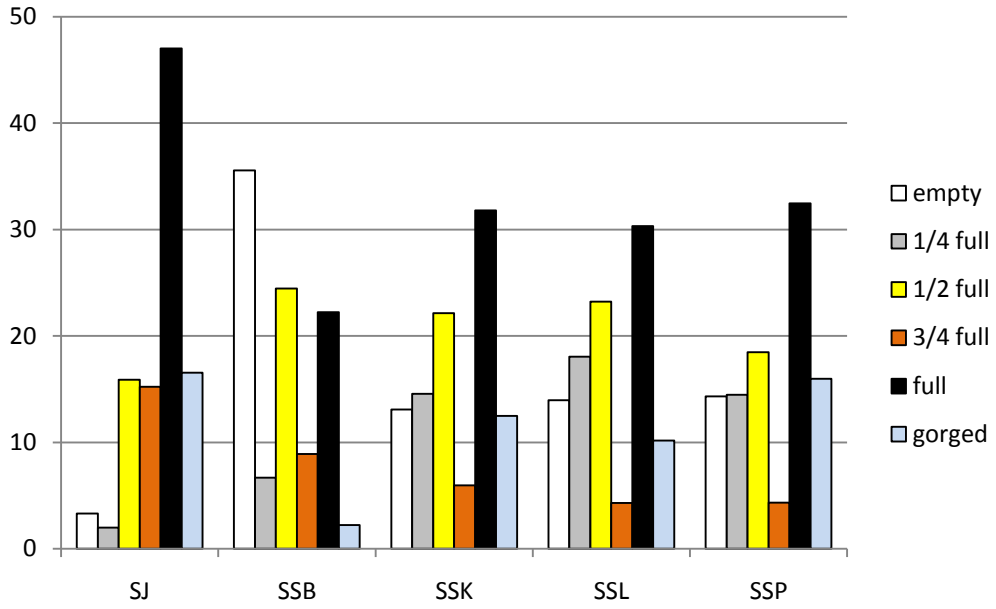


Fig. 5.2. Percentage stomach fullness of fish sampled in different water channels of Matang mangrove estuaries. Sampling rivers: SJ = Jaha River; SB = Sangga Besar River; SK = Sangga Kecil River; SL = Selinsing River; and SP = Sepetang River.

Table 5.1. Percentage stomach fullness of 26 common fish species found in Matang mangrove estuaries. n = sample size, VI = vacuity index, Abbr. = abbreviation of fish species used in PCA.

Fish species	Abbr.	n	Percentage stomach fullness					
			empty (VI)	1/4 full	1/2 full	3/4 full	full	gorged
Ambassis gymnocephalus (Lacepède)	Agym	205	17	19	16	5	36	8
Arius maculatus (Thunberg)	Amac	255	2	4	16	6	43	29
Cryptarius truncatus (Valenciennes)	Atrun	64	13	6	22	8	45	6
Arius venosus Valenciennes	Aveno	62	3	5	3	5	47	37
Ketengus typus Bleeker	Ktyp	30	10	3	23	7	50	7
Carangidae sp.	Caran	19	5	5	11	0	21	58
Anodontostoma chacunda (Hamilton)	Acha	70	9	6	17	10	59	0
Ilisha melastoma (Bloch & Schneider)	Imela	48	17	10	19	8	27	19
Butis koilomatodon (Bleeker)	Pkoil	9	22	22	33	0	11	11
Stolephorus baganensis Hardenberg	Sbaga	368	15	19	21	6	29	10
Thryssa kammalensis (Bleeker)	Tkamm	154	14	17	26	8	23	12
Gerres erythrourus (Bloch)	Gabbr	9	22	11	11	11	44	0
Gerres filamentosus Cuvier	Gfila	14	36	21	7	7	29	0
Glossogobius giuris (Hamilton)	Ggiur	87	25	16	23	3	28	5
Pomadasys kaakan (Cuvier)	Pkaa	182	11	14	20	7	34	14
Leiognathus brevirostris (Valenciennes)	Lbrev	136	18	13	29	2	35	2
Eubleekeria splendens (Cuvier)	Lspl	22	64	5	14	0	18	0
Lutjanus johnii (Bloch)	Ljoh	39	13	23	13	0	38	13
Upeneus sulphureus Cuvier	Usulp	17	12	12	29	0	47	0
Eleutheronema tetradactylum (Shaw)	Etetra	10	0	20	30	10	10	30
Scatophagus argus (Linnaeus)	Sarg	145	3	3	14	5	48	26
Dendrophysa russelii (Cuvier)	Druss	32	3	25	34	6	25	6
Johnius borneensis (Bleeker)	Jvog	46	22	13	24	17	24	0
Johnius belangerii (Cuvier)	Jbel	36	14	19	8	11	25	22
Johnius weberi Hardenberg	Jweb	378	17	24	32	4	17	6
Pennahia anea (Bloch)	Pmacr	14	0	7	7	14	50	21

Table 5.2. List of food items identified from the fish stomachs, and their pooled grouping. 'Abbr' indicates abbreviation of food items used in multivariate analysis (PCA), '-' not included in the PCA.

Food item	Abbr	Taxa grouping
Acartia sp.	Acar	Copepoda
Acartia spinicauda	Aspi	Copepoda
Parvocalanus crassirostris	Pcras	Copepoda
Pseudodiaptomus annandelei	Panan	Copepoda
Pseudodiaptomus trihamatus	Ptri	Copepoda
Calanopia thompsoni	Cthom	Copepoda
Labidocera pectinata	Lpec	Copepoda
Tortanus barbatus	Tbarb	Copepoda
Oithona sp.	Oitho	Copepoda
Euterpina acutifrons	Eacu	Copepoda
Harpacticoida	Har	Copepoda
Unidentified copepods	Unidcope	Copepoda
Other copepods	Cope	Copepoda
Cirripede nauplius	Cirrnau	Cirripedia
Cirripede cypris	Cirricy	Cirripedia
Mysidae	Mysid	Mysidae
Acetes spp.	Acet	Acetes
Lucifer hanseni	Luci	Other decapods
Caridean zoea	Cari	Other decapods
Caridean prawn		Other decapods
Palaemonidae prawn	Palae	Other decapods
Penaeidae prawn	Penaid	Other decapods
Sesarmid crab		Other decapods
Grapsid crab		Other decapods
Brachyura zoea	Bra	Other decapods
Brachyura megalopa		Other decapods
Brachyura juvenile		Other decapods
Diogenidae	Dio	Other decapods
Porcellanidae zoea	-	Other decapods
Unidentified prawn fragments	Unidpra	Other decapods
Unidentified crab fragments	Unidcrab	Other decapods
Other decapods	Deca	Other decapods
Stomatopoda	Sto	Stomatopoda
Amphipoda		Amphipoda
Gammaridae	Amphi	Amphipoda
Hyperiidae		Amphipoda
Isopoda	Isop	Isopoda
Ostracoda	Ost	Ostracoda
Cumacea	Cum	Cumacea
Unidentied crustacean fragments	Unidcrust	Unidentified crustaceans
Chaetognatha	Chae	Chaetognatha
Polychaeta	Poly	Polychaeta
Gastropod	Ga	Gastropoda
Bivalvia	Biv	Bivalvia
Echinodermata	Echi	Echinodemata
Protozoa	Pro	Protozoa
Hydrozoa	Hyd	Cnidaria
Bryozoa	Bry	Bryozoa
Nematoda	Nema	Nematoda
Teleost	Tele	Teleost
Fish scales	Fscale	Fish scales
Unidentified eggs	Unideggs	Unidentified eggs
Diatom	Dia	Diatom
Detritus	Detri	Detritus
Sediment	Sedi	Sediment
Larvacea		
Sipuncula	-	Others
Unidentified material		

materials and sediment. Crustaceans made up the largest component among prey items, of which 11 taxa were copepods. Other decapods consumed consisted of different life stages. The plant materials composed mainly of benthic microalgae and mangrove detritus. Two taxa, that is, larvaceans and peanut worm *Phascolosoma arcuatum* (Gray) were volumetrically less important. These taxa were grouped together with unidentified materials as 'others' (Table 5.2).

Copepods were the most common prey items consumed by the juvenile and small bodied fishes caught in Matang mangrove estuaries, with 52% of occurrence followed by plant detritus (40%) and *Acetes* (16%) (Fig. 5.3). Food items that constituted 5 - 10% of occurrence were cirripede larvae (4%), mysids (7%), other decapods (10%), amphipods (6%), polychaetes (5%), gastropods (6%) and sediment (7%). In terms of volumetric composition, copepods contributed 36% of the diets for juvenile and small fishes, while *Acetes* and detritus each contributed 12% (Fig. 5.4). Mysids (5%) and other decapods (7%) also contributed a considerable volume to dietary composition of fish. The remaining groups altogether contributed 29% to volumetric composition (Fig. 5.4).

Tables 5.3 and 5.4 show the percentage of mean volumetric composition and frequency of occurrence of 26 common fish species found in Matang mangrove estuaries. *Ambassis gymnocephalus* (Lacepède) and *A. maculatus* appeared to depend largely on copepods, with mean volumetric composition and occurrence of over 70 and 90% respectively. Other fish species that frequently consumed the copepods (50 - 85% occurrence and 20 - 60% mean volumetric composition) were the ariid *A. venosus*, leiognathids *Leiognathus brevirostris* and *E. splendens*, engraulids *Stolephorus baganensis* and *Thryssa kammalensis*, gerreid *Gerres erythrourus* (Bloch), and sciaenids *Dendrophysa russelii* (Cuvier), *Johnius borneensis* (Bleeker) and *Johnius weberi*.

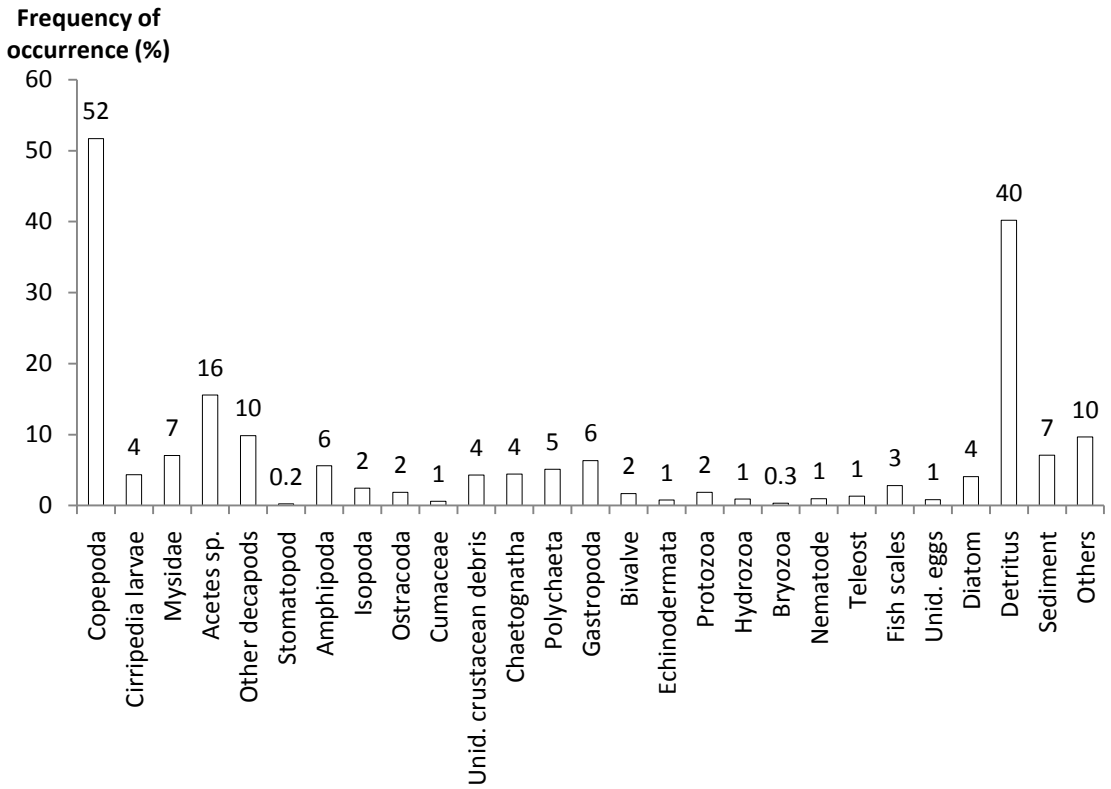


Fig. 5.3. The percentage of occurrence (%) of food items found in 2183 small-sized (1.5 to 18 cm) mangrove fish with filled stomachs in Matang waters, June 2003 to June 2004.

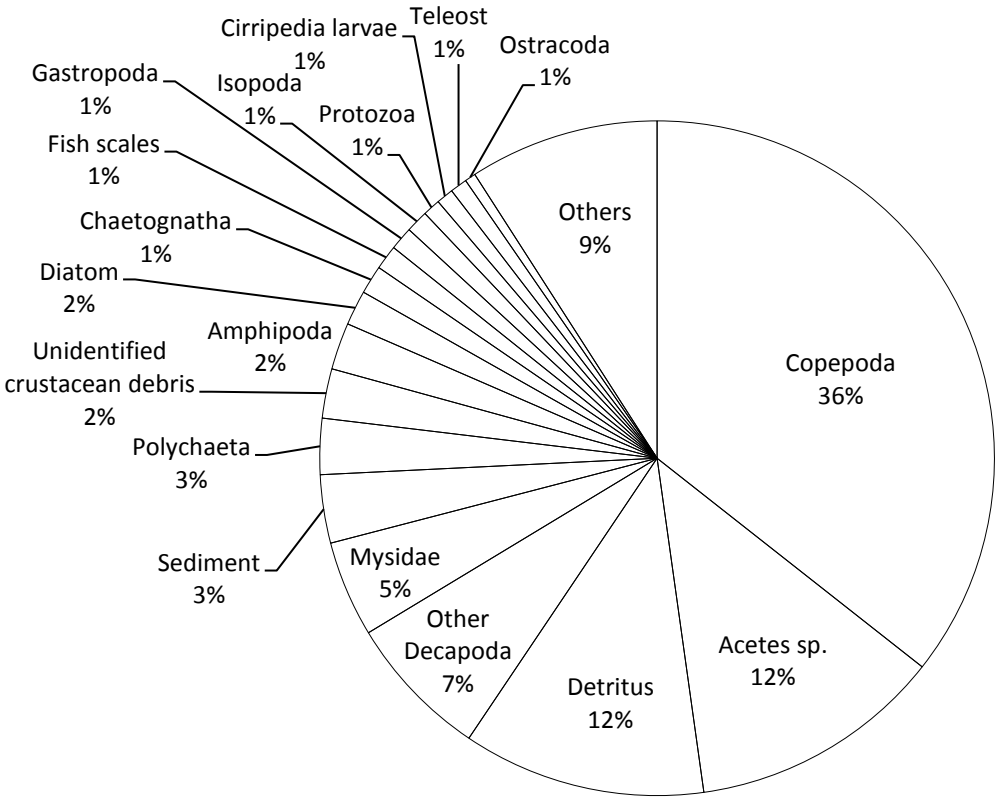


Fig.5.4. Mean volumetric composition (%) of food items fed by small-sized mangrove fish (1.5 to 18 cm) in Matang waters.

Table 5.3. Mean volumetric composition (%) of food items of small-sized fishes in Matang Mangrove estuaries, Malaysia. Min-Max minimum and maximum standard length, n number of stomachs with food, Bs dietary niche breadth.

Fish species	*Ambassis gymnocephalus*	*Arius maculatus*	*Cryptarius truncatus*	*Arius venosus*	*Ketengus typus*	Carangidae sp	*Anodontostoma chacunda*	*Ilisha melastoma*	*Butis koilomatodon*	*Stolephorus baganensis*	*Thryssa kammalensis*	*Gerres erythrourus*	*Gerres filamentous*	*Glossogobius giuris*	*Pomadasys kaakan*	*Leiognathus brevirostris*	*Eubleekeria splendens*	*Lutjanus johnii*	*Upeneus sulphureus*	*Eleutheronema tetradactylum*	*Scatophagus argus*	*Dendrophysa russelli*	*Johnius borneensis*	*Johnius belangerii*	*Johnius weberi*	*Pennahia anea*
Mean standard length (cm)	3.5	7.9	8.0	8.5	6.1	8.0	5.6	5.2	4.7	5.6	6.4	4.6	6.5	6.3	6.5	3.3	4.0	8.1	6.1	7.1	5.3	5.8	7.0	5.5	7.1	4.2
±SD	0.4	2.3	2.1	2.4	1.9	0.9	0.9	1.3	0.6	1.0	1.2	0.8	2.0	1.2	1.6	0.6	1.1	2.1	0.7	0.8	1.3	1.9	1.5	2.4	1.8	0.8
Min-Max	2.2-5.4	3.2-12.4	4.4-12.9	3.5-13.5	2.8-10.2	6.4-9	3.5-7.5	3.2-8.1	4-5.5	3.5-7.7	4.2-8.9	3.5-5.7	3.3-10	3.6-8.5	3-12.3	1.5-4.7	3-6.4	5.5-14	5-7	6.3-8.9	2.1-8.5	3-12.6	5-13	2.6-9.5	3.3-14	3.3-5.7
n	170	249	56	60	27	18	64	40	7	311	132	7	9	65	162	111	8	34	15	10	141	31	36	31	315	14
Bs	0.02	0.03	0.20	0.24	0.07	0.04	0.07	0.12	0.08	0.09	0.09	0.11	0.17	0.26	0.20	0.08	0.07	0.07	0.13	0.04	0.03	0.19	0.14	0.25	0.21	0.05
Food items																										
Acartia sp.	6.7	<1	-	-	-	-	-	-	-	2.1	4.0	-	-	-	-	4.0	-	-	-	-	-	-	-	-	-	-
Acartia spinicauda	9.9	<1	-	<1	-	-	-	<1	-	3.0	1.0	-	-	<1	-	2.5	-	-	-	-	-	<1	-	<1	<1	-
Parvocalanus crassirostris	7.2	<1	-	<1	-	-	<1	-	-	2.4	<1	-	-	-	-	1.0	-	-	-	-	-	-	-		-	-
Pseudodiaptomus annandalei	14.2	60.4	7.6	16.6	<1	-	-	2.5	1.4	21.4	23.9	7.9	11.4	10.9	1.7	15.6	38.6	-	1.6	-	-	17.0	34.1	7.3	24.5	-
Pseudodiaptomus trihamatus	2.9	8.8	<1	3.4	-	-	-	<1	-	5.8	3.3	-	-	<1	-	<1	-	-	<1	-	<1	9.6	1.1	1.3	1.2	-
Calanopia thompsoni	-	<1	-	-	-	-	-	<1	-	-	<1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Labidocera pectinata	<1	-	-	-	-	-	-	2.5	-	<1	<1	-	-	-	-	<1	-	-	-	-	-	-	-	-	-	-
Tortanus barbatus	<1	-	-	-	-	-	-	<1	-	<1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oithona sp.	2.4	<1	-	<1	-	-	-	-	-	<1	<1	-	-	-	-	<1	1.6	-	-	-	-	-	-	-	<1	-
Euterpina acutifrons	<1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	<1	-	-	-	-	-	-	-	-	-	-
Harpacticoid	<1	1.8	2.7	<1	-	-	-	-	-	<1	<1	29.0	<1	<1	<1	19.0	10.9	-	<1	-	<1	2.4	-	2.1	1.3	-
Unid. copepods	39.3	1.8	<1	<1	-	-	-	2.0	-	14.7	7.0	-	-	6.8	-	9.3	7.0	-	-	-	<1	<1	-	-	1.6	-
Total Copepoda	83.2	73.0	10.3	21.7	<1	-	<1	8.8	1.4	50.0	40.1	36.9	12.0	18.3	1.7	52.7	58.1	-	1.9	-	<1	30.4	35.3	10.9	29.0	-
Cirripede larvae	2.8	<1	-	<1	-	-	-	<1	-	2.8	<1	-	-	-	-	1.6	12.8	-	-	-	<1	-	-	-	<1	-
Mysidae	<1	<1	-	<1	-	-	-	44.0	-	3.5	4.1	-	-	12.6	14.9	<1	-	6.8	37.1	-	-	12.4	7.9	12.1	1.0	57.1
Acetes sp.	1.4	1.8	3.1	5.4	-	57.8	-	10.5	10.0	18.5	37.7	-	10.2	21.1	27.8	<1	-	38.5	20.0	60.0	-	18.5	23.8	17.8	7.3	28.6
Miscellaneous decapods	<1	1.8	3.7	9.2	<1	36.1	-	5.0	5.7	8.2	4.9	-	-	9.1	19.1	-	-	45.8	20.1	40.0	-	10.6	14.9	8.2	7.5	-
Stomatopoda	-	-	<1	-	-	-	-	-	-	-	<1	-	-	-	<1	-	-	-	2.2	-	-	-	-	-	-	-
Amphipoda	<1	<1	<1	<1	-	-	-	<1	53.3	<1	<1	1.1	-	2.3	1.6	-	-	2.9	-	-	<1	6.8	<1	11.2	8.6	-
Isopoda	<1	<1	-	1.6	<1	-	-	<1	14.6	-	-	-	11.1	1.2	2.2	-	3.8	-	-	-	-	1.3	<1	18.0	2.5	-
Ostracoda	-	<1	-	1.1	1.1	-	-	-	4.3	<1	<1	-	-	-	<1	<1	-	-	1.3	-	-	-	-	-	2.6	-
Cumacea	-	-	-	-	-	-	-	-	-	-	-	-	-	<1	<1	-	-	-	1.3	-	-	<1	-	-	<1	-
Unid. crustacean debris	1.5	3.6	2.1	4.8	2.8	-	-	<1	-	2.3	3.3	-	-	10.5	4.9	<1	3.8	1.5	1.3	-	-	-	<1	<1	1.6	-
Chaetognatha	3.7	<1	-	<1	-	-	-	12.4	-	3.9	1.2	25.7	-	-	-	<1	-	-	-	-	-	-	3.8	-	<1	-
Polychaeta	<1	4.3	26.8	9.9	2.2	-	-	2.5	7.9	<1	-	-	-	-	1.9	<1	-	<1	-	-	-	-	5.8	-	4.2	7.1
Gastropoda	<1	<1	3.0	<1	-	-	-	-	-	3.5	<1	-	-	<1	-	3.4	<1	-	-	-	<1	-	<1	-	1.0	-
Bivalvia	-	<1	<1	<1	-	-	<1	-	-	<1	-	-	22.2	-	1.4	-	-	-	-	-	-	-	-	-	<1	-
Echinodermata	-	-	-	-	-	-	-	-	-	<1	-	-	-	-	<1	-	-	-	-	-	-	-	-	3.0	2.0	-
Protozoa	<1	-	-	-	-	-	-	-	-	-	-	-	-	<1	-	-	3.8	-	-	-	12.6	-	-	-	-	-
Hydrozoa	-	<1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4.4	-	-	-	-	-
Bryozoa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.5	-	-	-	-	-

Table 5.3, continued

Fish species	*Ambassis gymnocephalus*	*Arius maculatus*	*Cryptarius truncatus*	*Arius venosus*	*Ketengus typus*	Carangidae sp	*Anodontostoma chacunda*	*Ilisha melastoma*	*Butis koilomatodon*	*Stolephorus baganensis*	*Thryssa kammalensis*	*Gerres erythrourus*	*Gerres filamentous*	*Glossogobius giuris*	*Pomadasys kaakan*	*Leiognathus brevirostris*	*Eubleekeria splendens*	*Lutjanus johnii*	*Upeneus sulphureus*	*Eleutheronema tetradactylum*	*Scatophagus argus*	*Dendrophysa russelli*	*Johnius borneensis*	*Johnius belangerii*	*Johnius weberi*	*Pennahia anea*
Mean standard length (cm)	3.5	7.9	8.0	8.5	6.1	8.0	5.6	5.2	4.7	5.6	6.4	4.6	6.5	6.3	6.5	3.3	4.0	8.1	6.1	7.1	5.3	5.8	7.0	5.5	7.1	4.2
±SD	0.4	2.3	2.1	2.4	1.9	0.9	0.9	1.3	0.6	1.0	1.2	0.8	2.0	1.2	1.6	0.6	1.1	2.1	0.7	0.8	1.3	1.9	1.5	2.4	1.8	0.8
Min-Max	2.2-5.4	3.2-12.4	4.4-12.9	3.5-13.5	2.8-10.2	6.4-9	3.5-7.5	3.2-8.1	4-5.5	3.5-7.7	4.2-8.9	3.5-5.7	3.3-10	3.6-8.5	3-12.3	1.5-4.7	3-6.4	5.5-14	5-7	6.3-8.9	2.1-8.5	3-12.6	5-13	2.6-9.5	3.3-14	3.3-5.7
n	170	249	56	60	27	18	64	40	7	311	132	7	9	65	162	111	8	34	15	10	141	31	36	31	315	14
Bs	0.02	0.03	0.20	0.24	0.07	0.04	0.07	0.12	0.08	0.09	0.09	0.11	0.17	0.26	0.20	0.08	0.07	0.07	0.13	0.04	0.03	0.19	0.14	0.25	0.21	0.05
Food items																										
Nematoda	-	<1	-	<1	-	-	<1	-	-	-	-	-	1.1	<1	<1	1.6	-	-	-	-	-	-	-	<1	<1	-
Teleost	-	<1	<1	1.5	-	<1	-	-	-	<1	-	11.3	-	4.9	1.3	-	-	-	-	-	-	3.2	4.4	-	1.0	-
Fish scales	-	<1	<1	2.0	50.0	-	-	-	-	<1	<1	-	-	-	1.6	<1	-	<1	4.7	-	-	1.9	-	1.3	<1	-
Unid. eggs	-	-	-	<1	-	-	-	-	-	<1	<1	-	-	-	-	4.1	-	-	-	-	-	-	-	-	-	-
Benthic microalgae	-	<1	-	-	-	-	38.5	-	-	-	-	-	-	1.4	-	-	2.5	-	-	-	4.7	-	-	-	<1	-
Detritus	1.4	6.3	16.8	18.4	27.6	-	37.7	4.5	2.9	2.1	2.7	5.0	19.4	5.2	4.3	17.2	10.0	<1	-	-	71.5	10.5	3.4	2.2	8.9	-
Sediment	-	2.7	17.1	16.4	1.5	-	22.5	-	-	<1	<1	-	-	1.5	3.2	9.6	-	-	-	-	3.8	-	-	-	1.7	-
Others	2.9	2.0	14.4	6.2	13.3	5.6	<1	9.8	-	2.9	2.8	20.0	23.9	10.4	12.8	6.3	5.0	2.9	10.0	-	1.4	4.2	-	13.9	19.9	7.1

Table 5.4. Frequency of occurrence (%) of food items of small-sized fish species in Matang mangrove estuaries, Malaysia.

Fish species	*Ambassis gymnocephalus*	*Arius maculatus*	*Cryptarius truncatus*	*Arius venosus*	*Ketengus typus*	Carangidae sp	*Anodontostoma chacunda*	*Ilisha melastoma*	*Butis koilomatodon*	*Stolephorus baganensis*	*Thryssa kammalensis*	*Gerres erythrourus*	*Gerres filamentous*	*Glossogobius giuris*	*Pomadasys kaakan*	*Leiognathus brevirostris*	*Eubleekeria splendens*	*Lutjanus johnii*	*Upeneus sulphureus*	*Eleutheronema tetradactylum*	*Scatophagus argus*	*Dendrophysa russelli*	*Johnius borneensis*	*Johnius belangerii*	*Johnius weberi*	*Pennahia anea*
Mean standard length (cm)	3.5	7.9	8.0	8.5	6.1	8.0	5.6	5.2	4.7	5.6	6.4	4.6	6.5	6.3	6.5	3.3	4.0	8.1	6.1	7.1	5.3	5.8	7.0	5.5	7.1	4.2
Min-Max	2.2-5.4	3.2-12.4	4.4-12.9	3.5-13.5	2.8-10.2	6.4-9	3.5-7.5	3.2-8.1	4-5.5	3.5-7.7	4.2-8.9	3.5-5.7	3.3-10	3.6-8.5	3-12.3	1.5-4.7	3-6.4	5.5-14	5-7	6.3-8.9	2.1-8.5	3-12.6	5-13	2.6-9.5	3.3-14	3.3-5.7
n	170	249	56	60	27	18	64	40	7	311	132	7	9	65	162	111	8	34	15	10	141	31	36	31	315	14
Food items																										
Acartia sp.	11.8	1.6	-	-	-	-	-	-	-	4.8	6.1	-	-	-	-	6.3	-	-	-	-	-	-	-	-	-	-
Acartia spinicauda	20.0	2.8	-	10.0	-	-	-	5.0	-	8.7	4.5	-	-	1.5	-	5.4	-	-	-	-	-	3.2	-	3.2	<1	-
Parvocalanus crassirostris	18.8	<1	-	11.7	-	-	1.6	-	-	3.2	3.0	-	-	-	-	3.6	-	-	-	-	-	-	-	-	-	-
Pseudodiaptomus annandalei	24.1	85.9	25.0	68.3	3.7	-	-	10.0	14.3	35.0	38.6	28.6	22.2	24.6	6.8	34.2	75.0	-	33.3	-	-	51.6	50.0	22.6	43.8	-
Pseudodiaptomus trihamatus	12.4	54.6	1.8	33.3	-	-	-	5.0	-	22.8	18.2	-	-	3.1	-	9.0	-	-	13.3	-	<1	35.5	16.7	9.7	6.0	-
Calanopia thompsoni	-	<1	-	-	-	-	-	5.0	-	-	<1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Labidocera pectinata	1.8	-	-	-	-	-	-	5.0	-	2.6	<1	-	-	-	-	<1	-	-	-	-	-	-	-	-	-	-
Tortanus barbatus	<1	-	-	-	-	-	-	5.0	-	<1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oithona sp.	12.9	<1	-	1.7	-	-	-	-	-	<1	2.3	-	-	-	-	4.5	37.5	-	-	-	-	-	-	-	<1	-
Euterpina acutifrons	9.4	39.4	12.5	20.0	-	-	-	-	-	1.3	8.3	42.9	11.1	3.1	<1	46.8	62.5	-	6.7	-	<1	19.4	-	12.9	10.5	-
Harpacticoid	9.4	39.4	12.5	20.0	-	-	-	-	-	1.3	8.3	42.9	11.1	3.1	<1	46.8	62.5	-	6.7	-	<1	19.4	-	12.9	10.5	-
Unid. copepods	51.8	6.4	1.8	1.7	-	-	-	5.0	-	23.8	9.8	-	-	10.8	-	18.0	37.5	-	-	-	<1	3.2	-	-	3.8	-
*Copepoda	94.7	91.2	28.6	68.3	3.7	-	1.6	22.5	14.3	68.5	57.6	71.4	33.3	27.7	6.8	85.6	75.0	-	40.0	-	2.1	61.3	50.0	32.3	50.5	-
Cirripede larvae	17.6	2.0	-	3.3	-	-	-	2.5	-	12.2	<1	-	-	-	-	11.7	25.0	-	-	-	<1	-	-	-	<1	-
Mysidae	1.2	<1	-	1.7	-	-	-	52.5	-	6.1	9.8	-	-	16.9	20.4	<1	-	11.8	46.7	-	-	32.3	11.1	16.1	2.2	57.1
Acetes sp.	1.8	5.6	5.4	11.7	-	61.1	-	20.0	14.3	21.5	41.7	-	11.1	26.2	35.2	1.8	-	50.0	20.0	60.0	-	25.8	41.7	29.0	9.2	28.6
Miscellaneous decapods	1.8	6.4	7.1	15.0	3.7	38.9	-	5.0	14.3	11.3	5.3	-	-	10.8	25.9	-	-	58.8	33.3	40.0	-	9.7	16.7	9.7	13.0	-
Stomatopoda	-	-	1.8	-	-	-	-	-	-	-	<1	-	-	-	1.2	-	-	-	6.7	-	-	-	-	-	-	-
Amphipoda	<1	1.6	7.1	8.3	-	-	-	5.0	57.1	1.0	1.5	14.3	-	6.2	8.0	-	-	2.9	-	-	<1	9.7	2.8	22.6	18.7	-
Isopoda	<1	<1	-	5.0	3.7	-	-	2.5	28.6	-	-	-	11.1	3.1	6.8	-	12.5	-	-	-	-	3.2	2.8	29.0	5.1	-
Ostracoda	-	1.2	-	15.0	3.7	-	-	-	14.3	2.3	3.8	-	-	-	<1	2.7	-	-	6.7	-	-	-	-	-	3.2	-
Cumacea	-	-	-	-	-	-	-	-	-	-	-	-	-	4.6	<1	-	-	-	6.7	-	-	6.5	-	-	1.6	-
Unid. crustacean debris	1.8	10.4	3.6	15.0	7.4	-	-	2.5	-	3.2	3.8	-	-	12.3	6.2	<1	12.5	2.9	6.7	-	-	-	2.8	3.2	2.9	-
Chaetognatha	15.9	1.6	-	1.7	-	-	-	12.5	-	13.2	6.1	28.6	-	-	-	1.8	-	-	-	-	-	-	13.9	-	<1	-
Polychaeta	<1	12.4	32.1	25.0	3.7	-	-	5.0	28.6	1.3	-	-	-	-	3.7	1.8	-	2.9	-	-	-	-	8.3	-	7.3	7.1
Gastropoda	6.5	7.2	17.9	1.7	-	-	-	-	-	17.0	7.6	-	-	4.6	-	12.6	12.5	-	-	-	<1	-	5.6	-	3.5	-
Bivalvia	-	3.6	1.8	3.3	-	-	3.1	-	-	4.8	-	-	22.2	-	1.9	-	-	-	-	-	-	-	-	-	<1	-
Echinodermata	-	-	-	-	-	-	-	-	-	<1	-	-	-	-	<1	-	-	-	-	-	-	-	-	12.9	3.5	-
Protozoa	4.7	-	-	-	-	-	-	-	-	-	-	-	-	1.5	-	-	12.5	-	-	-	22.0	-	-	-	-	-
Hydrozoa	-	1.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12.1	-	-	-	-	-
Bryozoa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5.0	-	-	-	-	-
Nematoda	-	1.2	-	1.7	-	-	3.1	-	-	-	-	-	11.1	1.5	<1	5.4	-	-	-	-	-	-	-	3.2	1.3	-
Teleost	-	1.2	1.8	1.7	-	5.6	-	-	-	<1	-	14.3	-	6.2	3.1	-	-	-	-	-	-	3.2	5.6	-	1.3	-

Table 5.4. Frequency of occurrence (%) of food items of small-sized fish species in Matang mangrove estuaries, Malaysia.

Fish species	*Ambassis gymnocephalus*	*Arius maculatus*	*Cryptarius truncatus*	*Arius venosus*	*Ketengus typus*	Carangidae sp	*Anodontostoma chacunda*	*Ilisha melastoma*	*Butis koilomatodon*	*Stolephorus baganensis*	*Thryssa kammalensis*	*Gerres erythrourus*	*Gerres filamentous*	*Glossogobius giuris*	*Pomadasys kaakan*	*Leiognathus brevirostris*	*Eubleekeria splendens*	*Lutjanus johnii*	*Upeneus sulphureus*	*Eleutheronema tetradactylum*	*Scatophagus argus*	*Dendrophysa russelli*	*Johnius borneensis*	*Johnius belangerii*	*Johnius weberi*	*Pennahia anea*
Mean standard length (cm)	3.5	7.9	8.0	8.5	6.1	8.0	5.6	5.2	4.7	5.6	6.4	4.6	6.5	6.3	6.5	3.3	4.0	8.1	6.1	7.1	5.3	5.8	7.0	5.5	7.1	4.2
Min-Max	2.2-5.4	3.2-12.4	4.4-12.9	3.5-13.5	2.8-10.2	6.4-9	3.5-7.5	3.2-8.1	4-5.5	3.5-7.7	4.2-8.9	3.5-5.7	3.3-10	3.6-8.5	3-12.3	1.5-4.7	3-6.4	5.5-14	5-7	6.3-8.9	2.1-8.5	3-12.6	5-13	2.6-9.5	3.3-14	3.3-5.7
n	170	249	56	60	27	18	64	40	7	311	132	7	9	65	162	111	8	34	15	10	141	31	36	31	315	14
Food items																										
Fish scales	-	3.6	3.6	11.7	74.1	-	-	-	-	<1	<1	-	-	-	3.1	<1	-	2.9	13.3	-	-	3.2	-	3.2	2.2	-
Unid. eggs	-	-	-	1.7	-	-	-	-	-	2.3	2.3	-	-	-	-	6.3	-	-	-	-	-	-	-	-	-	-
Benthic microalgae	-	<1	-	-	-	-	93.8	-	-	-	-	-	-	1.5	-	-	12.5	-	-	-	12.8	-	-	-	<1	-
Detritus	6.5	55.8	71.4	88.3	77.8	-	90.6	20.0	14.3	20.3	27.3	42.9	44.4	15.4	25.3	55.0	25.0	2.9	-	-	97.2	41.9	33.3	29.0	43.5	-
Sediment	-	7.2	32.1	31.7	3.7	-	71.9	-	-	<1	<1	-	-	1.5	6.2	13.5	-	-	-	-	8.5	-	-	-	2.5	-
Others	4.1	4.0	19.6	10.0	22.2	5.6	1.6	12.5	-	3.5	3.8	28.6	33.3	12.3	15.4	8.1	12.5	2.9	13.3	-	2.8	9.7	-	16.1	25.4	7.1

* denotes percentage of total fish examined which content prey from similar group.

The most important copepod species *Pseudodiaptomus annandalei* was mainly consumed by the ariids, *A. maculatus* (85% occurrence) and *A. venosus* (68% occurrence), all sciaenids except *P. anea* (22 - 52% occurrence), engraulids (35 - 39% occurrence) and leiognathids (34 - 75% occurrence). The congener of *P. annandalei*, *Pseudodiaptomus trihamatus* was also frequently consumed by *A. maculatus* with over 50% of occurrence (Table 5.4). The dominant mangrove copepod species *Acartia spinicauda, Parvocalanus crassirostris* and *Oithona* spp. were observed in the diets of ambassid, engraulids and leiognathids but their contribution never exceeded 10% of the mean volumetric composition (Table 5.3). Other copepod species *Calanopia thompsoni* Scott A., *Labidocera pectinata* Thompson I.C. & Scott A., *Tortanus barbatus* and *Euterpina acutifrons* were rarely encountered and not ingested by most of the fish species. The harpacticoid copepods formed a considerable volume to the diets of gerreid *G. erythrourus* and leiognathids, with mean volumetric composition that ranged from 10 - 30% (Table 5.3).

Sergestid shrimps (*Acetes* spp.) were the major food source after copepods, being consumed by various economically-important or common fish species such as carangid, threadfin, snapper, grunter, anchovies, sciaenids and gobiid with mean volumetric composition ranging from 7 - 60% (Table 5.3). Except the mainly resident gobiid and sciaenid fishes, most of these fishes are migrant species coming into the mangrove estuaries to feed at the juvenile phase. Mysids were mainly eaten by clupeid *Ilisha melastoma* (Bloch & Schneider), sciaenid *P. anea*, mullid *Upeneus sulphureus* and gobiid *Glossogobius giuris* (Hamilton). Four fish species *L. johnii, E. tetradactylum, P. anea* and Carangidae sp. did not feed on copepods but all four depended on hyperbenthic shrimps, while one eleotrid species *Butis koilomatodon* (Bleeker) fed on large quantities of amphipods (58% of volumetric composition) and to a lesser extent isopods (15%) (Table 5.3).

Three fish species *S. argus*, *K. typus* and *A. chacunda* which had <5% occurrence of copepod food did not feed on pelagic shrimp, but frequently fed on mangrove detritus (75 - 97% occurrence) (Table 5.4). Benthic microalgae and sediment also formed a large proportion of the diet of *A. chacunda*, contributing over 60% of the volumetric composition (Table 5.3). Fish scales made up over 50% of the dietary volume of the stomach of *K. typus* (Table 5.3).

The fish species that depended on benthic animals included the ariids, *C. truncatus* and *A. venosus*, and gerrid, *Gerres filamentosus* Cuvier. The sedentary polychaetes were mainly consumed by the ariids with mean volumetric composition that ranged from 10 - 27%, while the gerrid fed on bivalves with 22% composition (Table 5.3). Large quantities of detritus were also encountered in their stomachs.

Chaetognaths and cirripede larvae were supplementary food of some copepod feeders in the estuaries. For example, chaetognaths contributed 12% and 26% of the dietary composition of clupeid, *I. melastoma* and gerrid, *G. erythrourus* respectively. Cirripede larvae were ingested by the leiognathid *E. splendens* with volumetric composition of 13% (Table 5.3). Benthic protozoans, bryozoans, hydrozoans and nematodes were never ingested in large quantities by most of the fish species except the scat, with 13% of its diets made by protozoan tintinnids (Table 5.3).

5.1.1.3 Multivariate analysis and food specialization

The relative importance of food items for 26 common fish species found in Matang mangrove estuaries is captured by the PCA ordination biplot in Fig. 5.5. The first two axes derived from PCA explained approximately 44% of the total percentage variance of the dietary data (Table 5.5). The factor loadings or eigen vectors indicate that the first axis was closely associated with *Acetes*, mysids and unidentified prawns in the negative direction while the contribution of detritus increases in the positive

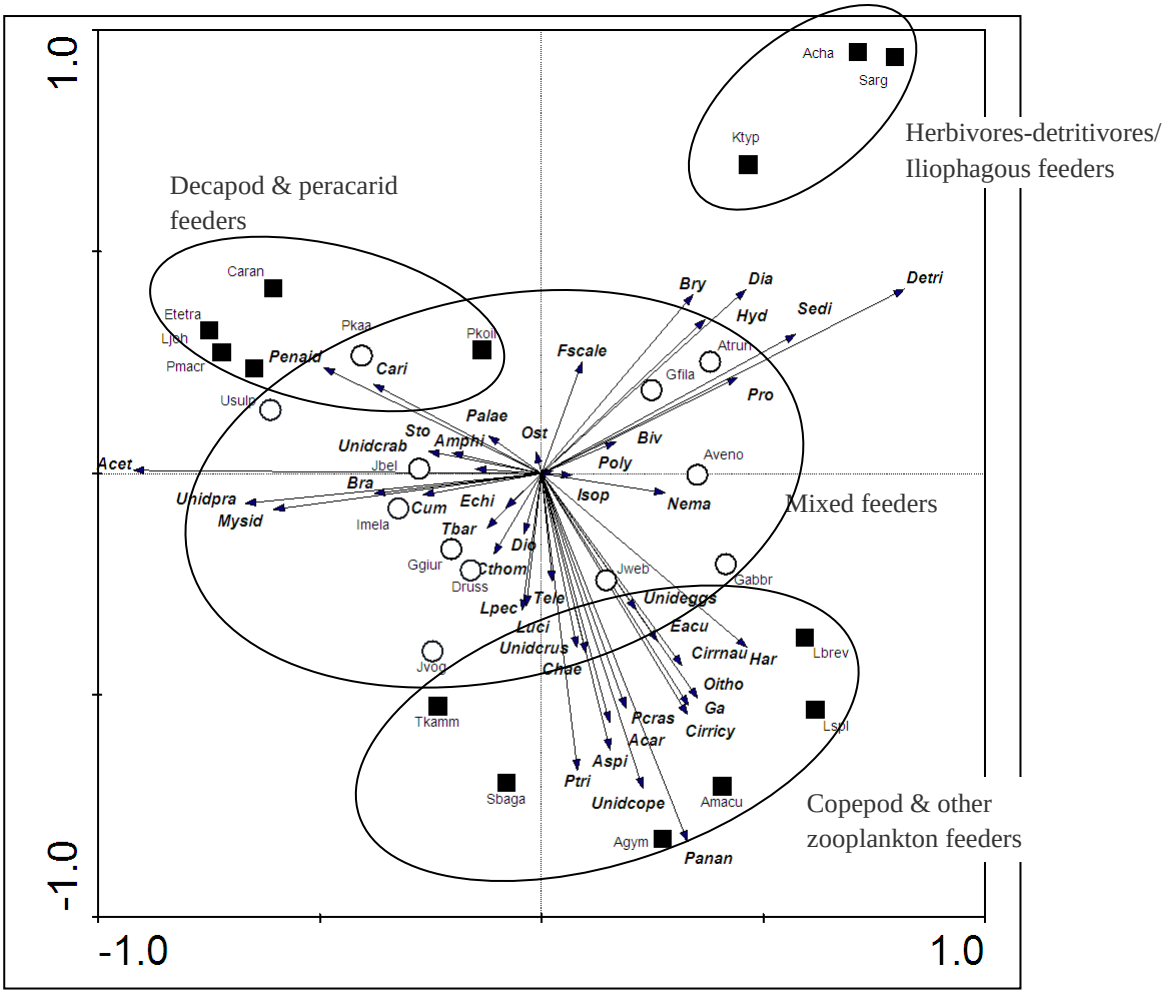


Fig. 5.5. PCA biplots based on the dietary composition of 26 small-sized fish species found in Matang mangrove estuaries. Arrows denote food items, symbols denote fish species; abbreviations for food items and fish species are given in Tables 5.2 and 5.3 respectively; ■ Dietary niche breadth <0.1, ○ dietary niche breadth >0.1.

direction. For the second axis, consumption of *P. annandalei* and *P. trihamatus* increases in the negative direction.

The PCA ordination biplot shows that the 26 fish species can be generally divided into four categories based on their dietary composition. The first category or copepods/zooplankton feeders consists of fish species that fed on copepods (including the benthic harpacticoids) and other planktonic organisms such as chaetognaths, cirripede larvae, small teleost and unidentified eggs. Fish species belonging to this category included *A. gymnocephalus, S. baganensis, T. kammalensis, A. maculatus, L.*

brevirostris and *E. splendens*, which had a narrow dietary niche breadth of <0.1. Their diet was mainly contributed by copepods (Fig. 5.5, see Table 5.3).

Table 5.5. Eigenvalues and factor loadings of the first four axes derived from PCA, based on the dietary composition data of 26 fish species found in Matang mangrove estuaries. Full names of dietary composition are given in Table 5.2.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.28	0.159	0.09	0.081
Cumulative variance (%)	28	43.9	52.9	61
Dietary composition				
Acar	0.1535	-0.5618	-0.2541	0.3483
Aspi	0.1542	-0.623	-0.244	0.2129
Pcras	0.1897	-0.5293	-0.2468	0.3265
Panan	0.329	-0.8301	0.2082	-0.0931
Ptri	0.0806	-0.6694	0.0634	-0.1007
Cthom	-0.1084	-0.1826	-0.3166	-0.25
Lpec	-0.0441	-0.3087	-0.4624	-0.094
Tbarb	-0.1234	-0.1233	-0.4077	-0.2392
Oitho	0.3314	-0.5239	-0.151	0.2487
Eacu	0.2611	-0.3781	-0.2607	0.2445
Har	0.4628	-0.3922	-0.0206	0.0237
Unidcope	0.2284	-0.7102	-0.2609	0.2556
Acet	-0.9205	0.0075	0.1255	0.2701
Luci	-0.0341	-0.2995	-0.0787	0.1546
Mysid	-0.6051	-0.081	-0.559	-0.5333
Cari	-0.3794	0.2015	-0.0114	0.3275
Penaid	-0.4922	0.2383	0.2353	0.6443
Palae	-0.1196	0.0847	0.1814	-0.0255
Unidpra	-0.6692	-0.0674	0.2861	-0.0196
Bra	-0.3783	-0.0454	0.0785	-0.0135
Dio	-0.0404	-0.1366	0.2417	-0.124
Unidcrab	-0.2024	0.0469	0.0789	-0.3655
Cirrnau	0.3163	-0.4334	-0.0702	0.1767
Cirricy	0.3288	-0.5448	-0.3016	0.2026
Sto	-0.2556	0.0494	-0.172	-0.1247
Amphi	-0.1501	0.0108	0.6775	-0.4598
Isop	0.0252	0.0063	0.5642	-0.4241
Ost	-0.0132	0.049	0.4623	-0.3799
Cum	-0.268	-0.0479	-0.1193	-0.24
Unidcrus	0.08	-0.3931	0.0161	-0.1305
Chae	0.1002	-0.4058	-0.2936	-0.0356
Poly	0.0689	-0.0041	0.2385	-0.4394
Ga	0.3519	-0.5073	-0.0511	0.1927
Biv	0.1676	0.0713	0.1995	0.0385
Echi	-0.0812	-0.0788	0.2752	-0.2642
Pro	0.4427	0.2165	-0.1645	0.14
Hyd	0.3688	0.3469	-0.1348	0.0772
Bry	0.3412	0.403	-0.1598	0.0897
Nema	0.279	-0.0444	0.1078	-0.0422
Tele	0.0244	-0.244	0.1299	-0.0982
Fscale	0.0912	0.2512	0.0043	-0.2583
Unideggs	0.2131	-0.308	-0.1723	0.1868
Dia	0.46	0.4146	-0.1884	0.1484
Detr i	0.8183	0.4159	-0.0351	-0.066
Sedi	0.574	0.3138	-0.0053	-0.0118

Five species of the second category or decapod/peracarid feeders forms a distinct group on the upper-left of the biplots (Fig. 5.5) and fed exclusively on decapods and peracarids. Fish species of this category included Carangidae, *E. tetradactylum, L. johnii, P, anea* and *B. koilomatodon,* with dietary niche breadths of less than 0.1.

Fish species that fall in the third category consumed mainly plant materials, benthic organisms such as polychaetes, protozoans, hydrozoans, bryozoans, and nematodes, fish scales and sediment (Fig. 5.5). Three species *A. chacunda*, *K. typus* and *S. argus* were of this category and also had dietary niche breadths of less than 0.1 (see Table 5.3). The contribution of copepods to their diet never exceeded 1% volumetrically.

The fourth category or mixed feeders had a relatively broader range of food items (dietary niche breadths >0.1). At least 2% of their dietary volume was contributed by copepods (see Table 5.3). Seven out of twelve species in this category (*G. giuris, I. melastoma, P. kaakan, D. russelii, Johnius belangerii* (Cuvier), *J. borneensis* and *U. sulphureus*) relied on a mixture of food items that consisted of copepods, decapods and peracarids. Five species (*G. erythrourus, G. filamentosus, A. venosus* and *C. truncatus* and *J. weberi*) that exploited food items such as zooplankton, plant materials and benthic animals were plotted on the positive direction of axis 1. As the fish species in the forth category were composed of fish with a wide range of body length, their broad dietary niche breadths could be attributed to ontogenetic diet shifts.

5.1.1.4 Ontogenetic shifts in dietary composition

Copepods contributed over 48% volumetric composition of the food of ariids combined (except *K. typus*) across all size classes (Table 5.6, Fig. 5.6). Nevertheless, the ariids displayed some changes in their dietary composition with body length. *Acetes* appeared to be an important food item after copepods in the smallest size class (Fig. 5.6). The contribution of *Acetes* as a supplementary food was substituted by polychaetes

when the fish size class increased. Other decapods that were not ingested by the individuals in the smallest size class appeared to be consumed by the individuals in the larger size classes (Fig. 5.6). Dietary niche breadths calculated for all size classes were ≤0.1 (Table 5.6).

Table 5.6. Mean volumetric composition (%) of food items of all ariids (excluding *K. typus*) according to five size classes. Bs dietary niche breadth.

Size Class	1	2	3	4	5
Length interval (cm)	(3 - 4.9)	(5 - 6.9)	(7 - 8.9)	(9 - 10.9)	(11 - 14)
Mean standard length (cm)	4.15	6.07	7.90	9.81	11.52
± SD	0.55	0.53	0.58	0.54	0.63
n	42	75	106	101	41
Bs	0.09	0.07	0.06	0.10	0.07
Acartia spinicauda	<1	<1	<1	<1	-
Pseudodiaptomus annandalei	38.2	47.1	48.6	42.6	45.6
Pseudodiaptomus trihamatus	5.0	8.9	6.6	4.4	8.8
Harpacticoid	5.3	2.4	1.9	<1	<1
Unid. copepods	<1	<1	2.4	<1	-
Total Copepoda	49.0	59.0	59.8	48.3	57.7
Cirripede larvae	<1	<1	<1	<1	<1
Mysidae	-	<1	<1	<1	-
Acetes sp.	6.2	2.4	2.3	1.7	2.3
Other Decapoda	<1	2.4	3.5	4.4	4.7
Stomatopoda	-	-	-	<1	-
Amphipoda	-	<1	<1	<1	<1
Isopoda	-	1.1	<1	<1	1.2
Ostracoda	-	<1	<1	<1	<1
Cumacea	-	-	-	-	-
Unid. crustacean debris	5.8	2.3	3.6	4.1	2.2
Chaetognatha	<1	<1	-	-	-
Polychaeta	2.5	4.3	6.6	14.9	12.9
Gastropoda	1.0	1.9	<1	<1	<1
Bivalvia	-	1.2	<1	<1	2.1
Echinodermata	-	-	-	-	-
Protozoa	-	-	-	-	-
Hydrozoa	-	<1	<1	<1	-
Bryozoa	-	-	-	-	-
Nematoda	<1	<1	<1	-	-
Teleost	1.2	<1	1.7	<1	-
Fish scales	<1	<1	<1	<1	<1
Unid. eggs	-	-	-	<1	-
Diatom	2.4	-	-	-	-
Detritus	20.6	9.0	6.7	9.5	10.1
Sediment	5.2	8.8	5.5	10.3	3.1
Others	4.3	4.6	6.6	3.3	2.5

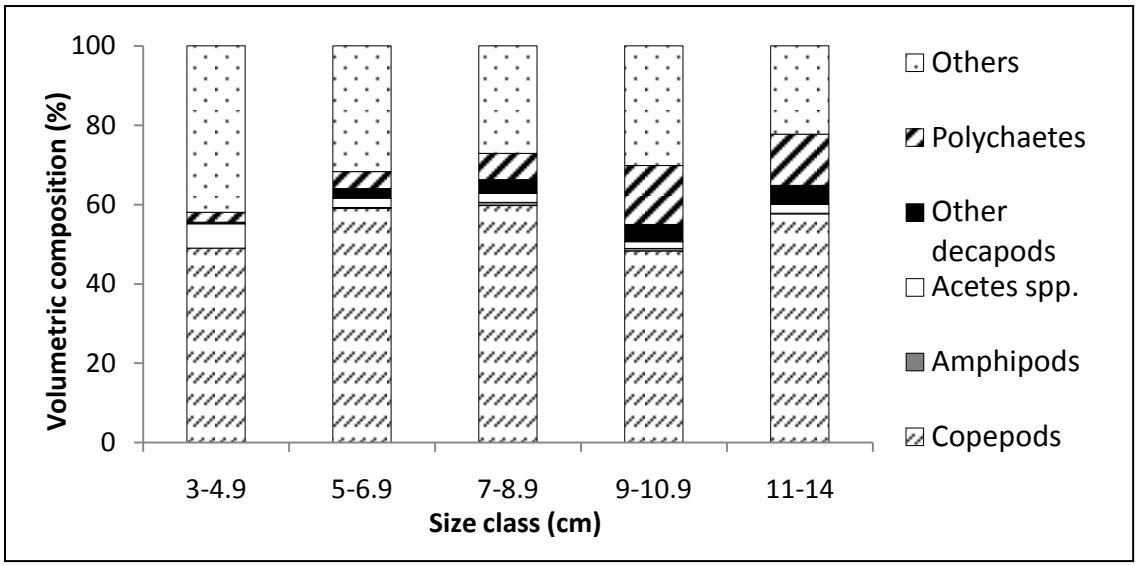


Fig. 5.6. Mean volumetric composition (%) of food items for combined ariids by size classes.

The marine migrant fish *P. kaakan* exhibited a distinct ontogenetic shift in dietary composition across size classes. Individuals in the smallest size class fed primary on *Acetes* spp. and mysids, and to a lesser extent copepods and polychaetes (Table 5.7, Fig. 5.7). The contribution of *Acetes* and mysids progressively decreased when size class increased, while other decapods became volumetrically important in the larger size classes. Copepods were not ingested by any individuals with standard length >7cm, whereas bivalves and teleost made up approximately 20% of the volumetric composition in the largest size class (Table 5.7, Fig. 5.7). The smallest size class had lowest dietary niche breadth (0.09) while 7 - 8.9 cm size class had the broadest (0.2) (Table 5.7).

Copepods were ingested by all size classes of combined sciaenids (excluding *P. anea*) except the largest size class (12 - 14cm). The contributions of copepods to the diet of sciaenids however decreased progressively with increasing body length of fish (Fig. 5.8). In contrast, the volume of ingested other decapods increased when fish length increased. *Acetes* spp. and amphipods were consumed by the individuals of all size classes, while mysids were mainly fed by smaller size classes as supplementary food. The sciaenids had dietary niche breadths ranging from 0.11 - 0.28. Individuals in the 6 -

7.9 and 8 - 9.9 cm size classes appeared to feed on a wide range of food items with dietary niche breath of >0.2 (Table 5.8).

Table 5.7. Mean volumetric composition (%) of food items of *P. kaakan* according to four size classes. Bs dietary niche breadth.

Size Class	1	2	3	4
Length interval (cm)	(3 - 4.9)	(5 - 6.9)	(7 - 8.9)	(9 - 13)
Mean standard length (cm)	4.00	5.92	7.80	9.83
± SD	0.58	0.51	0.61	1.08
n	21	76	56	9
Bs	0.09	0.19	0.20	0.16
Acartia spinicauda	-	-	-	-
Pseudodiaptomus annandalei	6.1	1.9	<1	-
Pseudodiaptomus trihamatus	-	-	-	-
Harpacticoid	<1	-	-	-
Unid. copepods	-	-	-	-
Total Copepoda	6.3	1.9	<1	-
Cirripede larvae	-	-	-	-
Mysidae	33.9	15.9	7.2	11.1
Acetes spp.	41.4	29.8	22.6	11.1
Other Decapoda	-	16.5	27.8	32.2
Stomatopoda	-	-	<1	4.4
Amphipoda	-	2.3	1.3	1.7
Isopoda	-	2.6	2.8	1.1
Ostracoda	-	-	<1	-
Cumacea	-	-	<1	-
Unid. crustacean debris	4.8	5.3	5.4	-
Chaetognatha	-	-	-	-
Polychaeta	4.8	<1	3.0	-
Gastropoda	-	-	-	-
Bivalvia	-	<1	1.8	11.1
Echinodermata	-	-	<1	-
Protozoa	-	-	-	-
Hydrozoa	-	-	-	-
Bryozoa	-	-	-	-
Nematoda	-	<1	-	-
Teleost	-	2.1	-	5.0
Fish scales	<1	1.6	2.4	-
Unid. eggs	-	-	-	-
Diatom	-	-	-	-
Detritus	1.5	5.9	3.7	1.1
Sediment	2.4	1.2	6.7	-
Others	4.8	13.7	13.2	21.1

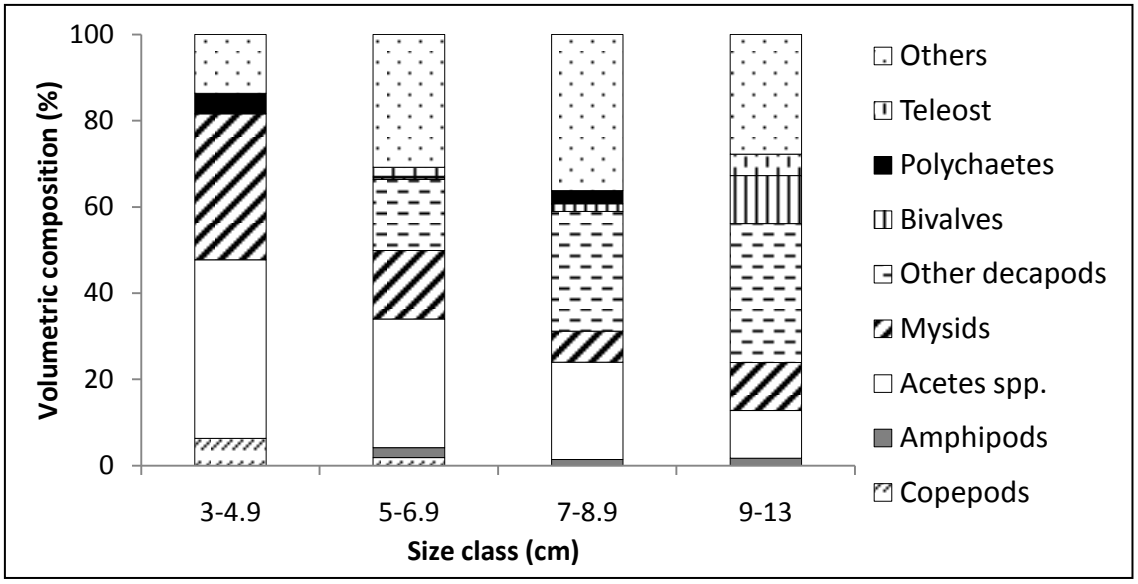


Fig. 5.7. Mean volumetric composition (%) of food items for *P. kaakan* by size classes.

Table 5.8. Mean volumetric composition (%) of food items of all sciaenids (excluding *P. anea*) according to six size classes. Bs dietary niche breadth.

Size Class	1	2	3	4	5	6
Length interval (cm)	(2 - 3.9)	(4 - 5.9)	(6 - 7.9)	(8 - 9.9)	(10 - 11.9)	(12 - 14)
Mean standard length (cm)	3.4	5.1	7.0	8.6	10.7	12.9
± SD	0.4	0.6	0.5	0.5	0.4	0.7
n	28	97	181	82	17	7
Bs	0.11	0.11	0.23	0.28	0.15	0.13
Acartia spinicauda	3.1	<1	-	-	-	-
Pseudodiaptomus annandalei	23.1	39.1	21.8	14.7	5.6	-
Pseudodiaptomus trihamatus	4.8	3.6	1.6	<1	-	-
Harpacticoid	10.1	1.2	<1	<1	-	-
Other copepods	3.4	1.9	1.4	<1	-	-
Total Copepoda	44.6	46.2	25.3	15.8	5.6	-
Cirripede larvae	-	-	-	<1	-	-
Mysidae	18.9	3.0	3.0	-	-	-
Acetes spp.	8.3	4.4	12.2	15.2	5.9	7.1
Other Decapoda	3.2	8.3	4.7	10.4	36.5	37.9
Stomatopoda	-	-	-	-	-	-
Amphipoda	9.3	11.5	6.4	4.2	13.8	21.4
Isopoda	<1	3.2	3.8	4.9	-	-
Ostracoda	-	-	2.5	4.4	-	-
Cumacea	<1	<1	<1	<1	2.35	-
Unid. crustacean debris	<1	<1	1.88	2.0	-	-
Chaetognatha	-	1.19	<1	-	-	-
Polychaeta	<1	2.68	6.33	1.5	-	-
Gastropoda	-	<1	<1	1.2	2.4	-
Bivalvia	-	-	<1	-	-	-
Echinodermata	-	-	1.7	3.8	-	-
Protozoa	-	-	-	-	-	-
Hydrozoa	-	-	-	-	-	-
Bryozoa	-	-	-	-	-	-
Nematoda	<1	<1	<1	-	-	-
Teleost	1.8	-	1.0	3.5	-	7.1
Fish scales	1.4	<1	<1	0.79	1.8	4.3
Unid. eggs	-	-	-	-	-	-
Diatom	-	<1	-	-	-	-
Detritus	<1	6.77	9.28	10.2	4.7	7.9
Sediment	-	<1	<1	1.3	15.3	14.3
Others	10.5	10.7	20.0	20.3	11.8	-

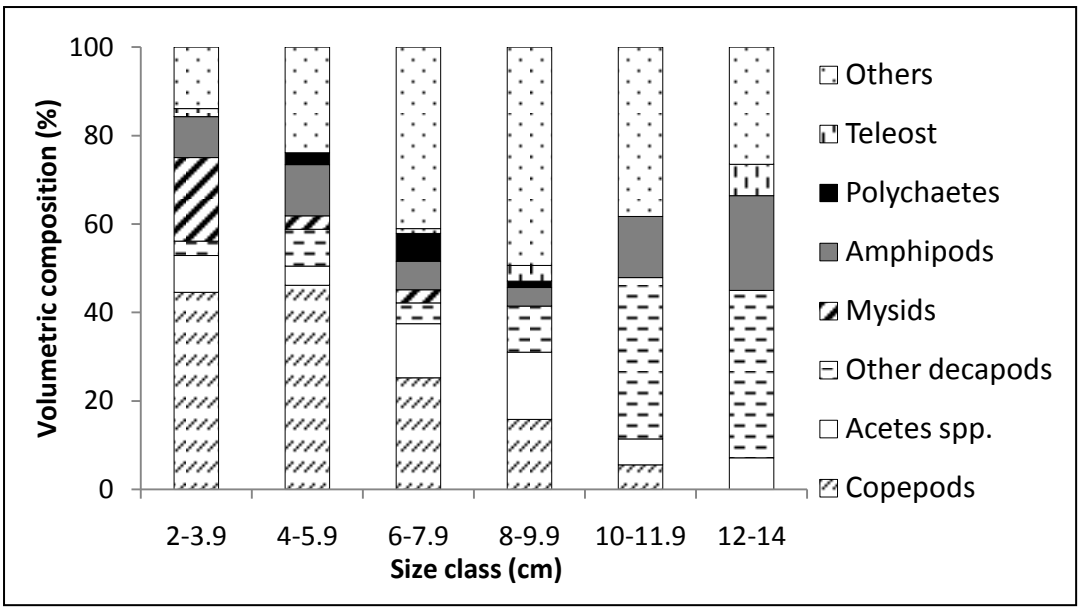


Fig. 5.8. Mean volumetric composition (%) of food items for combined sciaenids by size classes.

The PCA ordination biplots in Fig. 5.9 illustrate the ontogenetic shifts in dietary composition of ariids, *P. kaakan* and sciaenids. The first two axes of PCA explained 65% of the cumulative variance of the size-related dietary data (Table 5.9). The eigen vectors or factor loadings indicate that the percentage volumetric composition of *P. annandalei*, *P. trihamatus*, other copepods and sedentary polychaetes increased in the negative direction of axis 1, while the utilization of *Acetes* and unidentified prawns increased in the positive direction of axis 1. Axis 2 is primarily a descriptor of mysids in the positive direction and sediments, *Diogenes*, amphipods and unidentified prawns in the negative direction.

The plots show marked ontogenetic diet shifts for sciaenids and *P. kaakan*. Smaller prey items such as copepods and mysids were mainly consumed by the younger fish while larger prey items such as prawns and crabs were eaten by larger grown fish. Although there was some evidence of ontogenetic diet shifts for ariids, all size classes of ariids were close to each other on the plots.

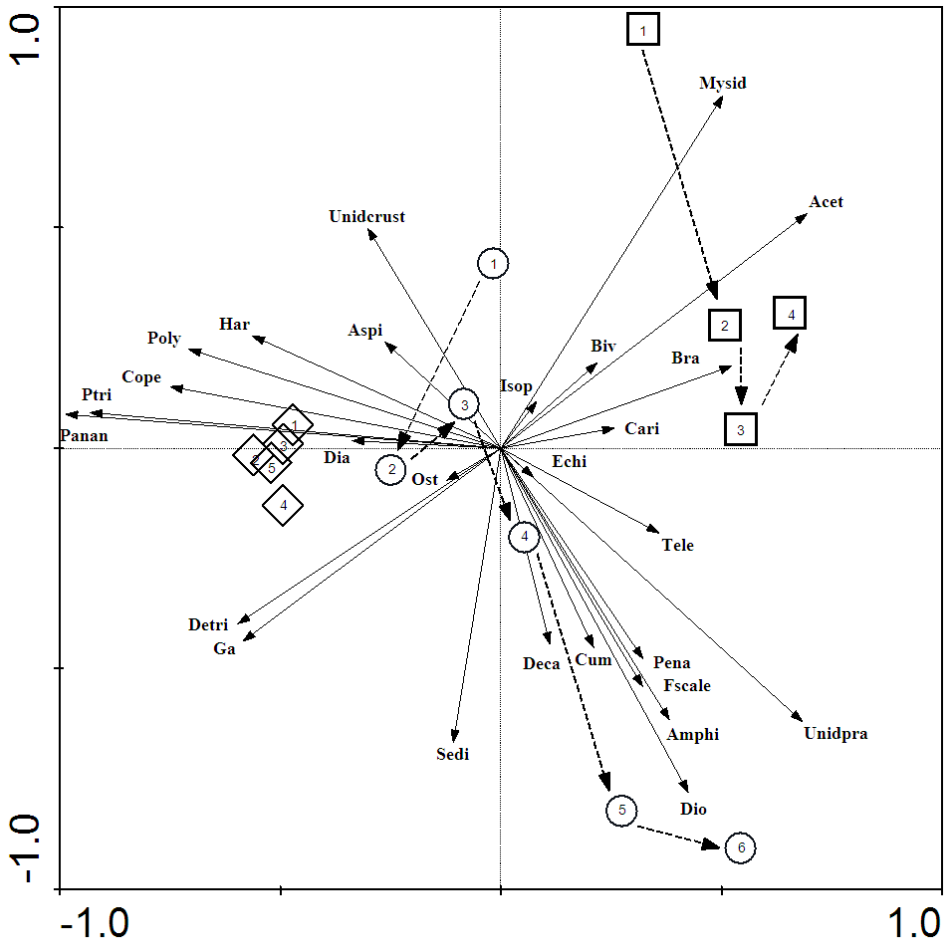


Fig. 5.9. PCA biplots of ontogenetic shift in dietary composition of estuarine, euryhaline and marine fishes with respect to size class. Solid arrows denote food items, dashed arrows denote diet shifts, numbers denote size class as given in Tables 5.6, 5.7 and 5.8 for ariids, *P. kaakan* and sciaenids respectively; abbreviations for food items are given in Table 5.2; ◊ Ariids, □ *P. kaakan*, ○ Sciaenids.

Table 5.9. Eigenvalues and factor loadings derived from PCA based on the dietary composition of ariids, *P. kaakan* and sciaenids, data according to size class. Full names of dietary composition are given in Table 5.2.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.442	0.209	0.095	0.079
Cumulative variance (%)	44.2	65.1	74.6	82.6
Dietary composition				
Aspi	-0.2628	0.2405	0.7425	-0.2664
Pana	-0.9874	0.0767	0.0797	-0.0509
Ptri	-0.9318	0.0803	0.2062	0.1045
Har	-0.564	0.2544	0.5244	-0.2243
Cope	-0.7497	0.139	0.4428	-0.0492
Amp	0.382	-0.6162	0.5461	-0.3131
Mysid	0.5031	0.7992	0.1597	-0.2006
Ace	0.6938	0.5317	-0.304	-0.322
Cari	0.2573	0.046	-0.5266	0.0041
Pena	0.3214	-0.4774	-0.251	-0.2422
Unidpra	0.683	-0.6197	0.2	0.0917
Brajuv	0.5238	0.1863	0.0657	0.7949
Dio	0.4245	-0.7802	-0.1526	-0.2047
Deca	0.1103	-0.4456	-0.4571	-0.0669
Iso	0.0808	0.1058	-0.0559	0.2079
Ost	-0.1236	-0.0733	-0.2829	0.0481
Cum	0.2099	-0.4522	0.0172	-0.2946
Unidcrus	-0.3027	0.4984	-0.6466	-0.1717
Gas	-0.5852	-0.4377	-0.1793	-0.0225
Bv	0.2182	0.1938	-0.0483	0.9196
Poly	-0.7082	0.2249	-0.4824	0.0951
Echi	0.0732	-0.065	-0.1666	-0.0562
Tele	0.3583	-0.1924	0.4013	0.2057
Fscale	0.3205	-0.5407	-0.1378	-0.4041
Dia	-0.3379	0.0172	0.0703	-0.0404
Detri	-0.5966	-0.3985	-0.3367	-0.0136
Sedi	-0.1085	-0.6666	-0.4822	-0.1433

5.1.2 Stable isotopes analysis

5.1.2.1 Mangrove leaves and seston

Fallen senescent leaves of three mangrove species *Bruguiera parviflora* (Roxb.) Wight & Arn. ex Griff., *Rhizophora mucronata* Lam. and *Rhizophora apiculata* showed little variation in $\delta^{13}C$ values, with mean of -29.0 (± 0.8), -28.0 (± 1.2) and -27.9 (± 0.9) ‰ respectively (Table 5.10). However, there were greater differences in $\delta^{15}N$ values, ranging from 2.3 ‰ for *R. apiculata* to 6.3 ‰ for *R. mucronata*. The mean C/N ratios of mangrove leaves were substantially high with values that ranged from 115.4 to 214.0.

Table 5.10. Mean values of $\delta^{13}C$, $\delta^{15}N$ and C/N ratios for samples collected in the Matang mangrove estuaries, adjacent coastal waters, Malaysia. n = sample size; number within parentheses = number of individuals pooled for analysis; '-' data not available. Sampling sites are referred to Fig. 2.3.

Species/type	Site	n	Size category SL = standard length	$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)		C/N	
				Mean	± SD	Mean	± SD	Mean	± SD
Scenescent mangrove leaf									
Rhizophora mucronata	SK1	2		-28.0	1.2	6.3	0.5	115.4	42.4
Rhizophora apiculata	SK2	2		-27.9	0.9	2.3	0.0	116.2	2.9
Bruguiera parviflora	SK3	2		-29.0	0.8	3.8	0.5	214.0	9.3
Mean				-28.3	0.9	4.1	1.8	148.5	54.4
Seston	SP1	3	<63 µm	-26.6	0.5	4.1	1.0	8.1	0.3
Seston	SK3	3	<63 µm	-22.8	0.6	7.5	0.7	7.9	0.1
Seston	NS1	3	<63 µm	-18.8	2.2	4.9	1.2	8.3	0.3
Seston	OS1	3	<63 µm	-22.7	0.4	8.5	0.1	7.7	1.0
Copepoda									
Acartia spinicauda	SK1	2	>500 µm	-22.3	0.2	8.8	0.1	5.3	0.2
A. spinicauda	SK3	2	>500 µm	-20.6	0.5	9.0	0.3	5.7	0.2
Centropages dorsispinatus	SK3	2	>500 µm	-20.0	0.4	8.1	0.3	5.5	0.2
C. dorsispinatus	OS	2	>500 µm	-17.6	0.1	8.1	0.1	5.0	0.1
Pseudiaptomus spp.	SK1	2	>500 µm	-21.5	0.4	7.8	0.1	5.4	0.1
Pseudiaptomus spp.	SK3	2	>500 µm	-20.1	0.1	8.1	0.1	5.6	0.1
Pseudiaptomus spp.	OS	2	>500 µm	-17.8	0.1	7.0	0.1	5.1	0.2
Tortanus spp.	SK1	2	>500 µm	-22.7	0.0	10.2	0.4	5.2	0.2
Tortanus spp.	SK3	2	>500 µm	-20.6	0.6	8.9	0.2	5.7	0.1
Tortanus spp.	OS	2	>500 µm	-18.1	0.1	9.0	0.4	4.9	0.0
Decapoda									
Acetes spp.	SK1	2	>500 µm	-20.0	0.5	9.9	0.7	5.1	0.6
Acetes spp.	NS4	2	>500 µm	-16.1	0.1	9.6	0.7	4.6	0.2
Brachyuran zoeae	SK3	2	>500 µm	-20.0	1.1	5.8	0.1	9.3	0.5
Brachyuran zoeae	NS4	2	>500 µm	-19.2	0.0	4.3	0.2	12.3	0.9
Caridean zoeae	SK3	2	>500 µm	-20.3	0.9	8.2	0.0	5.9	0.1
Diogenidae zoeae	OS	2	>500 µm	-18.0	0.4	8.5	0.5	6.8	0.3
Lucifer hanseni	OS	3	>500 µm	-17.7	0.4	8.4	0.1	5.8	0.3
Porcellanidae zoeae	SK1	3	>500 µm	-19.0	0.1	8.6	0.1	6.2	0.3
Porcellanidae zoeae	NS4	3	>500 µm	-15.1	0.2	7.7	0.1	6.5	0.3
Other zooplankton									
Mysidae	SK1	2	>500 µm	-20.5	0.4	10.8	0.2	4.7	0.3
Mysidae	NS4	2	>500 µm	-16.5	0.6	10.5	0.3	4.8	0.3
Ostracoda	SK1	2	>500 µm	-18.2	1.3	8.9	0.1	9.4	0.4
Stomatopoda larvae	SK1	2	>500 µm	-21.2	0.1	11.0	0.1	6.0	0.3
Stomatopoda larvae	NS4	2	>500 µm	-17.3	0.2	9.1	0.2	5.9	0.5
Chaetognatha	SK1	3	>500 µm	-23.4	0.1	11.7	0.1	11.7	0.3
Chaetognatha	OS	2	>500 µm	-18.9	0.4	11.3	0.1	7.4	0.7
Fish									
Arius maculatus	SL2	2 (6,2)	6.6-10.1 cm SL	-23.8	0.0	12.7	0.1	-	-
Johnius weberi	NS2	2 (3,3)	8.4-9.3 cm SL	-18.0	1.4	12.8	0.1	-	-
J. weberi	SK3	2 (3,3)	7.5-9.0 cm SL	-20.7	2.4	13.0	0.2	-	-
J. weberi	SL3	2 (2,2)	7.1-9.5 cm SL	-24.5	1.0	12.6	0.4	-	-
J. weberi	SL1	2 (3,2)	6.2-8.8 cm SL	-23.3	1.9	13.7	0.5	-	-
Leiognathus brevirostris	SK2	2 (4,4)	4.0-4.5 cm SL	-24.1	0.4	13.6	0.2	-	-
L. brevirostris	SL2	2 (7,6)	3.1-4.9 cm SL	-24.8	0.3	12.6	0.5	-	-
L. brevirostris	SL1	2 (5,5)	3.8-4.5 cm SL	-24.8	0.1	14.2	0.0	-	-
Stolephorus baganensis	NS2	2 (5,4)	5.2-6.9 cm SL	-16.7	0.6	13.2	0.0	-	-
S. baganensis	SK2	2 (5,6)	4.5-6.8 cm SL	-20.6	0.9	14.7	0.4	-	-
S. baganensis	SL3	2 (1,1)	5.1-6.3 cm SL	-21.8	0.3	13.3	0.5	-	-
Thryssa kammalensis	NS3	2 (2,3)	6.0-6.5 cm SL	-17.7	1.3	13.6	0.6	-	-
T. kammalensis	SK2	2 (4,1)	4.3-8.2 cm SL	-19.0	0.1	13.9	0.2	-	-
T. kammalensis	SL3	2 (1,1)	5.3-5.5 cm SL	-22.9	1.4	13.1	0.1	-	-
T. kammalensis	SL1	2 (3,3)	4.6-9.2 cm SL	-20.4	0.2	14.7	0.1	-	-
Upeneus sulphureus	NS3	2 (4,2)	5.5-6.5 cm SL	-15.8	0.1	11.7	0.1	-	-

The overall mean values of senescent mangrove leaves were -28.3 (± 0.9) ‰ for $\delta^{13}C$, 4.1 (± 1.8) ‰ for $\delta^{15}N$ and 148.5 (± 54.4) for C/N ratio (Table 5.10).

The surface seston samples collected at four different stations showed large variations in $\delta^{13}C$, with overall values ranging between -27.2 ‰ at the lower reaches of Sepetang River (SP1) and -16.3 ‰ in nearshore waters (NS1). Seston samples of <63 µm size fraction had the lowest mean $\delta^{13}C$ value at SP1 (-26.6 ± 0.5 ‰), close to mangrove carbon signature. Non-parametric Mann-Whitney U test revealed marginally significant difference between $\delta^{13}C$ of senescent mangrove leaves and seston collected at SP1 ($p = 0.039$, Table 5.11). The mean seston $\delta^{13}C$ values (-22.8 ± 0.6 ‰) at the lower reaches of Sangga Kecil River (SK3) and nearshore waters (-18.8 ± 2.2 ‰) were

Table 5.11. Results of non-parametric Mann-Whitney U test, comparing $\delta^{13}C$ of senescent mangrove leaves with seston. n = sample size; * significance at $p < 0.05$. Sampling station: SP1 = lower reaches of Sepetang River; SK3 = lower reaches of Sangga Kecil River; NS1 = nearshore waters; and OS1 = 55 km offshore.

	n	Mean	± SD	p-level
Senescent mangrove leaves	6	-28.3	0.9	
Seston				
Station				
SP1	3	-26.6	0.5	0.039*
SK3	3	-22.8	0.6	0.020*
NS1	3	-18.8	2.2	0.020*
OS1	3	-22.7	0.4	0.020*

significantly more enriched relative to seston samples collected at SP1 (Kruskal-Wallis test, $p < 0.05$; Table 5.12). The surface seston samples collected at 55 km offshore (OS1) had mean $\delta^{13}C$ value of -22.7 (± 0.4) ‰. This value is highly reflective of phytoplankton, assuming that there was no significant mixing of terrestrial plant detritus.

Table 5.12. Results of Kruskal-Wallis test on seston $\delta^{13}C$ and $\delta^{15}N$, with comparisons among stations. n = sample size; homogenous groups indicated by superscripts a, b and c; * significance at $p < 0.05$. Sampling station: SP1 = lower reaches of Sepetang River; SK3 = lower reaches of Sangga Kecil River; NS1 = nearshore waters; and OS1 = 55 km offshore.

Station	n	Mean	± SD	H	p-level
$\delta^{13}C$					
SP1	3	-26.6[a]	0.5	9.5	0.024*
SK3	3	-22.8[b]	0.6		
NS1	3	-18.8[c]	2.2		
OS1	3	-22.7[b]	0.4		
$\delta^{15}N$					
SP1	3	4.1[a]	1.0	9.7	0.022*
SK3	3	7.5[b]	0.7		
NS1	3	4.9[a]	1.2		
OS1	3	8.5[b]	0.1		

The seston $\delta^{15}N$ values were significantly lower at SP1 (4.1 ± 1 ‰) and nearshore waters (4.9 ± 1.2 ‰) as compared to those at SK3 (7.5 ± 0.7 ‰) and OS1 (8.5 ± 0.1 ‰) (Kruskal-Wallis test, $p < 0.05$; Table 5.12). The C/N ratios for all seston samples were very much lower than the senescent mangrove leaves, with mean values of 8.1 (± 0.3) at SP1, 7.9 (± 0.1) at SK3, 8.3 (± 0.3) at nearshore waters and 7.7 (± 1.0) at OS1 (Table 5.10).

5.1.2.2 Carbon isotopic ratios of animals

The 14 selected zooplankton taxa had mean $\delta^{13}C$ values ranging from -23.4 ‰ for chaetognaths at the upper reaches of Sangga Kecil River (SK1) to -15.15 ‰ for porcellanid zoeae at nearshore waters (Table 5.10). If the phytoplankton $\delta^{13}C$ value in the study area was -22.7 ‰, all zooplankton taxa were generally enriched in ^{13}C relative to phytoplankton, except for chaetognaths (-23.4 ‰) and copepod *Tortanus* (-22.7 ‰) at upper reaches of Sangga Kecil River (Table 5.10). The remaining taxa from the same station were enriched in ^{13}C relative to phytoplankton by 0.5 ‰ to 4.6 ‰. Ostracods (-18.2 ± 1.3 ‰) and porcellanid zoeae (-19.0 ± 0.1 ‰) had the highest mean $\delta^{13}C$ values at this station (Table 5.10). Thus, the contribution of mangrove carbon as compared to

phytoplankton to zooplankton nutrition at upper reaches of Sangga Kecil River was negligible.

At the lower reaches of Sangga Kecil River (SK3), the mean zooplankton $\delta^{13}C$ values fell within a narrow range of -21 and -20 ‰, and again showed no evidence of mangrove carbon in their tissues but showed high dependency on phytoplankton (Table 5.10, Fig. 5.10). As similar to seston samples, zooplankton were most enriched in ^{13}C in nearshore waters, with mean $\delta^{13}C$ values that ranged from -19.2 ‰ for brachyuran zoeae to -15.1 ‰ for porcellanid zoeae (Table 5.10, Fig. 5.10). Zooplankton collected at the station 18 km offshore (OS) had mean $\delta^{13}C$ values intermediate between lower reaches of Sangga Kecil River and nearshore waters, ranging between -18.9 and -17.6 ‰ (-18.0 ± 0.5 ‰) (Table 5.10, Fig. 5.10). After pooling the data, $\delta^{13}C$ values of zooplankton were significantly most enriched in nearshore waters (Kruskal-Wallis test, $p < 0.01$; Table 5.13).

Table 5.13. Results of Kruskal-Wallis test on zooplankton $\delta^{13}C$ and $\delta^{15}N$ values with comparisons among stations. Zooplankton data were pooled based on their trophic positions. n = sample size; homogenous groups indicated by superscripts a, b and c; * significance at $p < 0.05$, ** significance at $p < 0.01$. Sampling station: SK1 = upper reaches of Sangga Kecil River; SK3 = lower reaches of Sangga Kecil River; NS4 = nearshore waters; and OS = 18 km offshore.

Zooplankton	Station	n	Mean	± SD	H	p-level
$\delta^{13}C$						
Herbivores & omnivores	SK1	9	-20.1[a]	1.8	18.7	<0.001**
	SK3	8	-20.3[a]	0.5		
	NS4	3	-15.1[b]	0.2		
	OS	9	-17.7[c]	0.3		
Carnivores	SK1	11	-21.7[a]	1.4	18	<0.001**
	SK3	2	-20.6[a,c]	0.6		
	NS4	6	-16.6[b]	0.6		
	OS	4	-18.5[c]	0.5		
$\delta^{15}N$						
Herbivores & omnivores	SK1	9	8.5[a]	0.4	8.2	0.042*
	SK3	8	8.4[a]	0.4		
	NS4	3	7.7[b]	0.1		
	OS	9	8.0[a,b]	0.6		
Carnivores	SK1	11	10.8[a]	0.7	8.5	0.037*
	SK3	2	8.9[b]	0.2		
	NS4	6	9.7[b]	0.7		
	OS	4	10.2[a,b]	1.3		

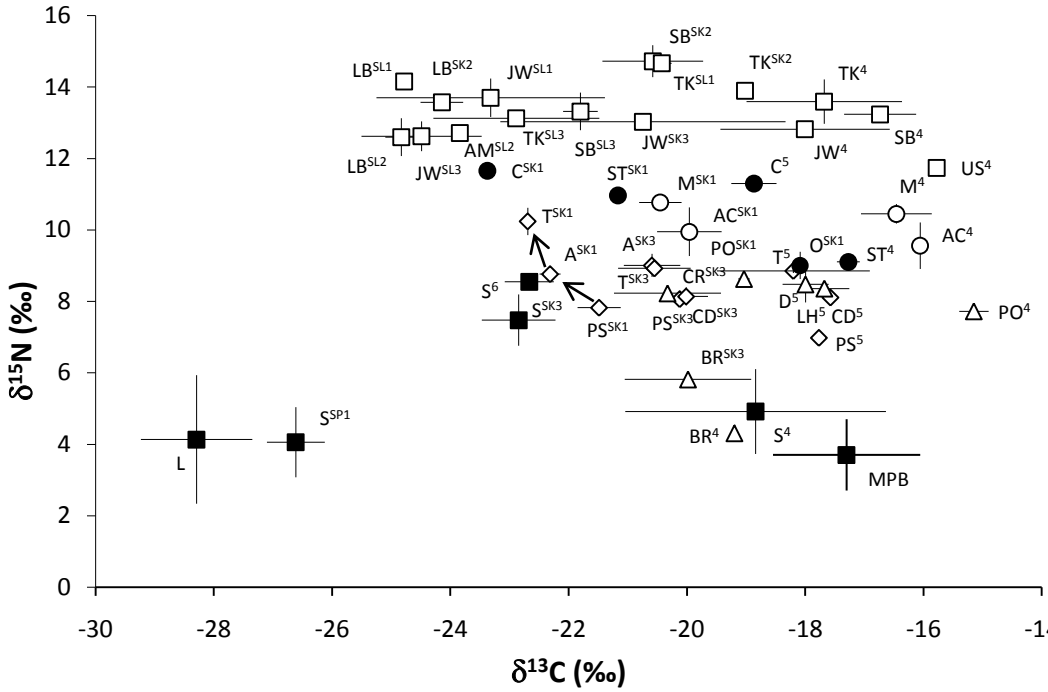


Fig. 5.10. $\delta^{13}C$ and $\delta^{15}N$ values of different primary producers, zooplankton and fish in the Matang mangrove estuaries and adjacent coastal waters. Arrows indicate change in $\delta^{15}N$ values (trophic positions) from herbivorous through omnivorous to carnivorous copepods, error bars indicate ± SD. Primary producers (■): L = senescent mangrove leaves, S = seston, MPB = benthic microalgae (Tanaka *et* al., 2011). Consumers: copepods (◊), A = *Acartia spinicauda*, CD = *Centropages dorsispinatus*, PS = *Pseudodiaptomus* spp., T = *Tortanus* spp.; decapods (Δ), BR = brachyuran zoeae, CR = caridean zoeae, D = diogenid zoeae, LH = *Lucifer hanseni*, PO = Porcellanidae zoeae; hyperbenthic shrimps (○), AC = *Acetes* spp., M = Mysidae; other zooplankton (●), C = Chaetognatha, O = Ostracoda, ST = Stomatopoda larvae; fish (□), AM = *Arius maculatus*, LB = *Leiognathus brevirostris*, JW = *Johnius weberi*, SB = *Stolephorus baganensis*, TK = *Thryssa kammalensis*, US = *Upeneus sulphureus*. Superscripts indicate locations as in Fig. 2.3.

The small-sized fishes of the five abundant species *A. maculatus, J. weberi, L. brevirostris, S. baganensis* and *T. kammalensis* in Matang mangrove estuaries had mean $\delta^{13}C$ values that ranged from -24.8 to -16.7 ‰ (Table 5.10). The leiognathid *L. brevirostris* had the most depleted $\delta^{13}C$ values among the selected fish species (ranged from -24.8 to -24.1 ‰). The ariid *A. maculatus* was also depleted in ^{13}C relative to phytoplankton, with mean $\delta^{13}C$ value of -23.84 (± 0.05) ‰. Both species were more confined in the estuarine waters. The sciaenid *J. weberi* collected along a gradient from mangrove to nearshore waters had a wide range of $\delta^{13}C$ values, ranging from the most negative or depleted value (-24.5 ± 1.0 ‰) at the upper reaches of Selinsing River (SL1)

to the most enriched value in nearshore waters (-18 ± 1.4 ‰). The engraulids *S. baganensis* and *T. kammalensis* had $\delta^{13}C$ values that ranged from -22.9 (± 1.4) to -16.73 (± 0.6) ‰. The coastal species *U. sulphureus* found in nearshore waters had mean $\delta^{13}C$ value of -15.77 (± 0.09) ‰ (Table 5.10, Fig. 5.10).

5.1.2.3 Nitrogen isotopic ratios of animals and trophic levels

Except for the brachyuran zoeae, all animals collected from mangrove and adjacent coastal waters showed $\delta^{15}N$ values that ranged from 7.0 (± 0.1) ‰ for the copepod *Pseudodiaptomus* to 14.7 (± 0.9) ‰ for *S. baganensis* (Fig.5.10). The mean $\delta^{15}N$ values of brachyuran zoeae recorded at the lower reaches of Sangga Kecil River (5.82 ‰) and in nearshore waters (4.31 ‰) were much lower than other animals (Fig. 5.10). Three trophic levels were identified for consumers in the food webs. The mean $\delta^{15}N$ values of *Pseudodiaptomus* at different stations were consistently the lowest (except brachyuran zoeae). Thus, in this study the mean $\delta^{15}N$ value (7.6 ± 0.5 ‰) of this taxon was taken as the representative baseline for primary consumers in the food web. The overall difference in $\delta^{15}N$ values between zooplankton taxa was 4.7 ‰ (ranged from 7.0 to 11.7 ‰). If trophic fractionation for $\delta^{15}N$ is 3 ‰ (review by Peterson & Fry, 1987), zooplankton formed two tropic levels in the Matang food web (see Fig. 5.10, Table 5.14).

Interestingly, three copepod genera (*Pseudodiaptomus, Acartia* and *Tortanus*) represented three trophic levels at the upper reaches of Sangga Kecil River (Fig. 5.10). Based on previous studies, *Acartia* and *Tortanus* were considered as omnivores and carnivores, respectively (Lonsdale *et* al., 1979; Ohtsuka *et* al., 1987). These taxa had higher trophic position than *Pseudodiaptomus*, which reinforces the idea that *Pseudodiaptomus* is herbivorous. Other than *Tortanus*, the carnivorous zooplankton

included the chaetognaths, *Acetes*, mysids and stomatopod larvae. The $\delta^{15}N$ values of these carnivorous zooplankton ranged between 8.9 to 11.7 ‰ with an average of 10.2 (± 1) ‰ (Fig. 5.10). The decapod larvae, adult of *Lucifer hanseni*, copepod *Centropages dorsispinatus* and ostracods had $\delta^{15}N$ values (ranged from 7.7 to 8.9 ‰) close to *A. spinicauda* and intermediate between *Pseudodiaptomus* and carnivorous zooplankton, suggesting that these taxa were omnivorous. The omnivorous zooplankton had overall mean $\delta^{15}N$ values of 8.4 (± 0.4) ‰, closer to *Pseudodiaptomus* than carnivorous zooplankton.

In contrast to $\delta^{13}C$, the differences in $\delta^{15}N$ between stations for pooled zooplankton data were significant (Kruskal-Wallis test, $p = 0.04$; Table 5.13). If samples of herbivorous and omnivorous zooplankton at nearshore waters and carnivorous zooplankton at lower reaches of Sangga Kecil River were excluded from the analysis, the spatial differences in $\delta^{15}N$ for zooplankton were not significantly different.

The six fish species had greater $\delta^{15}N$ values than those of zooplankton, ranging from 11.73 to 14.72 ‰. The mean $\delta^{15}N$ value of all fish combined (13.3 ± 0.8 ‰) was 3.1 ‰ and 5.7 ‰ higher than the carnivorous and herbivorous zooplankton, respectively (Fig. 5.10). This is in agreement with the $\delta^{15}N$ fractionation per trophic level as suggested by previous studies.

Table 5.14. Trophic position of zooplankton (except brachyuran zoeae), fish and penaeid prawns from various studies conducted in the Matang mangrove estuaries and adjacent coastal water. *Pseudodiaptomus* spp. is assigned as representative baseline at second trophic level.

Taxon	Mean $\delta^{15}N$	Estimated isotopic trophic position	Assigned trophic level	Source
Zooplankton				
Herbivore-omnivores				
Pseudodiaptomus spp.	7.6	2.0	2	this study
Centropages dorsispinatus	8.1	2.2	2	this study
Porcellanidae zoeae	8.2	2.2	2	this study
Caridean zoeae	8.2	2.2	2	this study
Lucifer hanseni	8.4	2.2	2	this study
Diogenidae zoeae	8.5	2.3	2	this study
Ostracoda	8.9	2.4	2	this study
Acartia spinicauda	8.9	2.4	2	this study
Carnivores				
Tortanus spp.	9.6	2.7	3	this study
Acetes spp.	9.8	2.7	3	this study
Stomatopoda larvae	10.0	2.8	3	this study
Mysidae	10.6	3.0	3	this study
Chaetognatha	11.5	3.3	3	this study
Fish larvae				
Carangidae	7.2	1.9	2	Ooi (unpbl. data)
Engraulidae	8.8	2.4	2	Ooi (unpbl. data)
Carangidae 1	10.8	3.0	3	Ooi (unpbl. data)
Gobiidae	11.1	3.2	3	Ooi (unpbl. data)
Engraulidae 1	11.5	3.3	3	Ooi (unpbl. data)
Blenidae	12.0	3.5	3	Ooi (unpbl. data)
Fish				
Liza melinoptera	9.5	2.6	3	Then, 2008
Anodontostoma chacunda	9.7	2.7	3	Hayase *et* al., 1999
Scathophagus argus	10.8	3.1	3	Then, 2008
Upeneus sulphureus	11.7	3.4	3	this study
Ambassis gymnocephalus	11.7	3.4	3	Hayase *et* al., 1999
Plotosus canius	11.9	3.4	3	Then, 2008
Lutjanus vitta	11.9	3.4	3	Hayase *et* al., 1999
Pomadasys kaakan	12.1	3.5	3	Then, 2008
Tetraodon fluviatilis	12.6	3.7	4	Then, 2008
Arius maculatus	13.0	3.8	4	Then, 2008; this study
Johnius weberi	13.0	3.8	4	this study
Johnius borneensis	13.2	3.8	4	Then, 2008; Hayase *et* al., 1999
Leiognathus brevirostris	13.4	3.9	4	this study
Stolephorus insularis	13.5	3.9	4	Hayase *et* al., 1999
Lutjanus johnii	13.6	4.0	4	Then, 2008
Stolephorus commersonnii	13.6	4.0	4	Hayase *et* al., 1999
Stolephorus baganenesis	13.8	4.0	4	this study
Thryssa kammalensis	13.9	4.1	4	Then, 2008; this study
Epinephelus coioides	14.5	4.3	4	Then, 2008
Thryssa hamiltonii	14.6	4.3	4	Then, 2008
Penaeid prawns				
Parapenaeopsis hardwickii	8.4	2.3	2	Chong *et* al., 2001
Parapenaeopsis sculptilis	9.5	2.6	3	Chong *et* al., 2001
Metapenaeus brevicornis	9.7	2.7	3	Chong *et* al., 2001
Peneus merguinensis	9.9	2.8	3	Chong *et* al., 2001
Parapenaeopsis coromandelica	10.3	2.9	3	Chong *et* al., 2001
Metapenaeus lysianassa	10.4	2.9	3	Chong *et* al., 2001

5.2 Discussion

5.2.1 Mangrove habitat as feeding ground for juvenile fish

Most of the fish captured in the mangrove estuaries were predominantly juveniles or sexually immature (Chong *et* al., 1990; Sasekumar *et* al. 1994), whereas very few were adults or large-sized fish (Hajisamae *et* al., 2006). Several hypotheses have been advanced to explain why mangrove habitats are so attractive to juvenile fish. One of these hypotheses is the food availability hypothesis in the mangrove estuaries (Nagelkerken *et* al., 2000; Laegdsgaard & Johnson, 2001; Chong, 2007). This hypothesis is supported by the greater zooplankton abundance in Matang mangrove estuaries and nearshore waters (Chew & Chong, 2011; see Chapter 3), where zooplankton are the potential food source for juvenile and small fishes. Other studies further suggested that high fish densities in nursery or feeding areas corresponded to high densities of both planktonic and benthic animals (e.g. Jacoby & Greenwood, 1989; Edgar & Shaw, 1995).

In the present study, most of the fish examined (>70%) had full stomachs, implying active feeding when they were caught. A similar study in the same estuaries also recorded high percentage of full stomachs (Then, 2008). Laegdsgaard & Johnson (2001) reported that the high feeding rate of juvenile fish in the mangrove estuaries was attributed to higher food supply in the estuaries compared with adjacent mudflat and seagrass habitats. Therefore, the greater stomach fullness of fish in Matang mangrove estuaries could be related to high abundance of zooplankton in the estuaries.

Ooi and Chong (2011) showed that most of the existing fish families in Matang mangrove estuaries spawn in offshore marine waters, and enter the estuaries as late larval or juvenile stage. These larger forms are possibly adapted for feeding on the dense population of zooplankton in the mangrove estuaries (Laegdsgaard & Johnson,

2001; Ooi & Chong, 2011). This explains why most of the migrant fish species recorded higher percent of gut fullness.

5.2.2 Interspecific feeding patterns and ontogenetic diet shifts

With such high densities of zooplankton in Matang mangrove estuaries, it is not surprising that most of the juvenile of the common fish species captured depended to a large extent on zooplankton as food. Except for the three herbivores-detritivores species, all other fish species examined consumed the mesozooplankton that ranged in size from 0.2 - 20 mm. The dietary composition differed among individuals. The small-sized ambassid, engraulids and leiognathids consumed a large proportion of copepods (>40%, see Table 5.3). However, their feeding patterns were variable in that the secondary food items of ambassid and engraulids were composed of planktonic organisms, while the leiognathids consumed detritus and benthic organisms such as harpacticoids, which were rarely captured by the plankton net (see Fig. 5.5). Blaber (1997) had categorized ambassids and engraulids as plankton feeders and leiognathids as meiofauna feeders. Copepods consistently dominated the diet of the above-mentioned fishes, therefore their dietary niche breadths were <0.1.

The four commercially important species *E. tetradactylum*, *L. johnii*, *P. anea* and the unidentified carangid did not feed on smaller zooplankton such as copepods, but were highly dependent on larger shrimps and prawns. These species are marine migrants which entered the estuaries at the juvenile stage (Blaber, 1997; Then, 2008). The smallest size specimen examined for these species ranged from 3.3 to 6.4 cm (see Table 5.3), which were relatively larger in size than mysids, *Acetes* and juvenile prawns. Moreover, the mouth dimensions of these species were relatively larger than the copepod feeders for the same body length. Thus, the larger prey items such as shrimps and prawns were preferred by these species compared to smaller copepods. The diet of

L. johnii in the present study was similar to that reported by Then (2008) with no copepods consumed. However, Kiso and Mahyam (2003) showed the consumption of copepods by small juveniles of *L. johnii*, indicating the importance of copepods at their early juvenile stage. The narrow dietary niche breadths (<0.1) of the above four fishes are related to the fact that there was less apparent ontogenetic diet shift, a result from the limited numbers of samples examined.

Species with broader dietary niche breadths (>0.1) were likely to undergo ontogenetic diet shift. For example, all sciaenids (except *P. anea*) had greater dietary niche breadths (>0.14) consuming a wide range of prey items, ranging from copepods to other decapods and benthic animals (see Table 5.3). The diets of sciaenids combined (except *P. anea*) clearly reflected the size-related ontogenetic shift. Thus small individuals fed on small prey such as copepods and mysids and larger individuals fed on larger prey such as *Acetes*, other decapods and benthic organisms. Although species within the same family may show similarities in dietary composition due to similar in mouth gape and feeding behavior (Platell & Potter, 2001), *J. weberi* appeared to be different in dietary composition from those of other family members as indicated by the PCA biplots (see Fig. 5.5). The variability may be related to the consumption of bivalves, benthic microalgae and sediment, which were not found in the diet of other sciaenid members (see Table 5.3).

The ariids *A. venosus* (0.24) and *C. truncatus* (0.2) had broader dietary niche breaths compared with *A. maculatus* (0.03), implying that the latter is more specialized in feeding on certain prey items at the juvenile stage. This is the fact that the dietary composition of juvenile *A. maculatus* was almost exclusively contributed by the copepods namely *P. annandalei*. *Arius venosus* and *C. truncatus* also depended on *P. annandalei* but to a lesser extent than *A. maculatus*. Apart from copepods, benthic polychaetes and plant detritus were also consumed by *A. venosus* and *C. truncatus*. The

diet differences within family could be a feeding strategy to partition food resources so as to reduce interspecific competition (Platell & Potter, 2001). The ontogenetic diet shift of all ariids (except for *K. typus*) showed reliance on copepods across all size classes (3 - 14 cm). Nevertheless, small sized fish switched their secondary food source of *Acetes* to polychaetes and prawns when they grow larger. This is in agreement with Singh (2003) that larger ariids in Matang mangrove estuaries relied on polychaetes, penaeids and other macrobenthos as food sources.

The juvenile grunter *P. kaakan* across all size classes utilized a wide range of food items in Matang mangrove estuaries, with an overall dietary niche breadth of 0.2; it is thus a generalist. Then (2008) showed that this species could utilize up to 30 food categories in Matang mangrove estuaries, the highest among the fish species examined. However, the small size class (3 - 4.9 cm) had a low dietary niche breadth as *Acetes* and mysids dominated its food composition (75%) (see Table 5.7).

It is particularly noteworthy that three species including two leiognathids and *G. erythrourus* fed considerable numbers of benthic harpacticoids (>10% volumetric composition, see Table 5.3). This could be related to the similarity of their mouth morphology, where the protrusible mouth enables them to consume the benthic animals including the meiofauna that inhabits on or beneath the sediments (Cyrus & Blaber, 1982).

5.2.3 Prey selectivity and availability

Similar to other mangrove estuaries, copepods were consistently the most abundant component of zooplankton in Matang (see Chapter 4; Chew & Chong, 2011). *P. annandalei*, which is known to be benthic or demersal at day time and migrate into the water column at night (Fancett & Kimmerer, 1985; Jacoby & Greenwood, 1989; Walter, 1987; Kouassi *et* al., 2001) was an important prey item for juvenile fish in

Matang mangrove estuaries. Although *Acartia*, *Parvocalanus* and *Oithona* were reported to be more abundant in the Matang mangrove estuaries (Chew & Chong, 2011), *P. annandalei* was ingested by most of the young juvenile fish in Matang mangrove estuaries. Based on an experimental study, the planktivorous yellow-eye mullet appeared to feed heavily on *Pseudodiaptomus cornutus* Nicholls and *Pseudodiaptomus colefaxi* Bayly rather than the abundant copepod *Acartia tranteri* Bradford (Fancett & Kimmerer, 1985). The food selection of juvenile fish could be related to size and lipid content of copepods. Juvenile fish preferentially feed on large copepods particularly the female with egg sacs which is more vulnerable due to slower swimming (Rajasilta & Vuorinen, 1983). Fancett and Kimmerer (1985) found that the lipid storage of female *Pseudodiaptomus* was about two times greater than *A. tranteri*. Therefore, juvenile and small fish preferred to feed on the lipid-laden and cumbersome *P. annandalei* rather than the smaller and more mobile copepods in Matang mangrove estuaries.

The planktonic shrimps such as *Acetes* and mysids appear to be important as intermediate prey items between copepods and larger decapods and other benthic animals for young juvenile fish in Matang mangrove estuaries. The abundance of food appears to regulate food selection by fishes. The euryhaline *Acetes* and mysids were reported to occur year round and showed no seasonality in Matang mangrove estuaries (Hanamura *et* al., 2007, 2008). The mysids were also abundant in mangrove estuaries than sandy shore without mangrove (Hanamura *et* al, 2008). The *Acetes* shrimps were significantly more abundant than penaeid prawns in Sementa mangrove estuaries (Mariana, 1993). Although *Acetes* adults were more common in nighttime samples in this study, high abundance of larval stages of *Acetes* occurred year-round (see Chapter 4). Similarly, mysid abundance was not significantly different between the dry and wet

periods (see Chapter 4). Hence, *Acetes* and mysid shrimps are always readily available to juvenile fish in Matang mangrove estuaries.

In contrast to copepods and hyperbenthic shrimps, the hydromedusae and ctenophores were never found in the stomachs of fishes examined, although the gelatinous zooplankton were commonly found in the Matang mangrove estuaries (see Chapter 3). The species-specific study on anchovy's diet showed that hydromedusae were avoided possibly related to low nutritional value and presence of nematocysts which might be detrimental to predatory fish (Johnson *et* al., 1990). On the other hand, the hydromedusae and ctenophores if consumed may be quickly digested except possibly their nematocysts. Nevertheless, examination for these organelles was never attempted in the present study. Coull *et* al. (1995) emphasized that the direct examination of stomach contents might be imprecise due to rapid digestion of non-chitinous animals. However, other gelatinous zooplankton such as chaetognaths and polychaetes were occasionally observed in Matang fish diets.

Although copepods, mysids and *Acetes* were important food items to juvenile fish in Matang mangrove estuaries, other foods such as amphipods, isopods and ostracods were occasionally consumed in larger quantities than copepods and hyperbenthic shrimps. For example, *J. weberi* which generally did not feed on ostracods appeared to feed heavily on them in February 2004 (Chew *et* al., 2007). The eleotrid *B. koilomatodon* depended largely on amphipods (90% volumetric composition) in July 2003, while other sampling occasions showed a mixture of various food items (data not shown). Cirripede cyprids which were never found in large quantities in fish diet appeared to be substantially high in August and October 2004 in Matang mangrove estuaries (Then, 2008). Such irregularities are likely due to opportunistic feeding when preferred prey foods are scarce. Schafer *et* al. (2002) suggested that the fish that are

abundantly found in a particular habitat are adapted to feed opportunistically on prey that are readily available in the habitat at that time.

Short-term tidal and diel variations are known to have an influence on zooplankton community and thus the availability of potential prey for juvenile fish. The anchovies *Anchoa mitchilli* (Valenciennes) found in the American North Inlet Estuary fed primarily on larger crab megalopae, shrimps zoeae and amphipods during the night and smaller copepods, crab zoeae and barnacle cyprids during the day (Johnson *et* al., 1990). Robertson & Howard (1978) also demonstrated diet switch of zooplanktivorous fish from copepods and decapod larvae during the day to amphipods during the night in an Australian eelgrass meadow and adjoining mudflat. Although the present diet study was conducted during day and neap tide (except for two during spring tide), the fishes found in Matang mangrove estuaries were able to feed opportunistically on known nocturnal animals such as amphipods, isopods and ostracods (see Table 5.3). These animals were more common during the night but were never sampled in large numbers by plankton net in Matang mangrove estuaries, possibly due to their adaptive behavior to avoid intense predation risk (see Chapter 4). Nevertheless, any predation on brachyuran zoeae by juvenile fish was not obvious in the present study probably due to the mass spawning of crab larvae that occurred during spring tide (see Chapter 4), while the fish samplings were conducted mostly during neap tide.

5.2.4 Food web structure

5.2.4.1 Primary producers

Mean $\delta^{13}C$ values (-28.3 ± 0.9 ‰) of senescent mangrove leaves (*B. parviflora, R. mucronata* and *R. apiculata* combined) was within the range reported for young mangrove leaves (-28.7 to -26.71 ‰) in Matang mangrove estuaries (Hayase *et* al., 1999), and drifted mangrove leaves in Selangor coastal waters (Newell *et* al., 1995), ca.

200 km south of the present study site. These are typical values within the range of C_3 plant (-30 to -24 ‰) (see review by Bouillon *et* al., 2008). Zieman *et* al. (1984) and Dehairs *et* al. (2000) found insignificant difference in $\delta^{13}C$ values between fresh and senescent mangrove leaves after about 6 weeks of decomposition.

The fresh and senescent mangrove leaves were reported to have lower nitrogen as compared to fresh seagrasses (Zieman *et* al., 1984) and macroalgae (Lee, 2000). The overall mean $\delta^{15}N$ value of senescent mangrove leaves in the present study was 4.1 ‰, which is comparable to those previously reported in Malaysian mangrove estuaries (Hayase *et* al., 1999; Newell *et* al. 1995). Because of low nitrogen but high carbon content, the C/N ratios of senescent leaves in the present study were substantially higher (mean = 149) as compared to the C/N ratios of 50 in fresh mangrove leaves (Bouillon *et* al., 2000). Lee (2005) suggested that the C/N ratios of mangrove leaves of poor nutritional value (such as during senescence) could be greater than 100.

The Matang mangrove estuaries are characterized by turbid waters, with mean maximum turbidity of up to 197 NTU during spring tide (see Table 4.3). Limited colonization of macroalgae occurred on fish cages (Madin *et* al., 2009) and no seagrasses were observed within the vicinity of estuaries. Prominent macrophytes and seagrasses were similarly not found in turbid mangrove estuaries of India (Dehairs *et* al., 2000). Therefore, mangroves and both planktonic and benthic microalgae are the major carbon sources in the Matang mangrove estuaries (Chong *et* al., 2001).

As in other estuarine systems, the seston $\delta^{13}C$ values in Matang followed a typical trend, with the most negative signal recorded at lower reaches of Sepetang River (-26.6 ‰) to least negative signal in nearshore waters (-18.8 ‰). Station at lower reaches of Sangga Kecil River had a mean $\delta^{13}C$ value (-22.8 ‰) intermediate between Sepetang River and nearshore waters (see Table 5.10). The seston $\delta^{13}C$ values at 10 km

off Matang mangrove estuaries were -21.0 ‰ and -20.4 ‰ (Chong *et* al., 2001). A similar spatial pattern of $\delta^{13}C$ values in the offshore direction has been reported by Hayase *et* al. (1999) in the same estuaries, with a comparable range of -25.6 to -17.9 ‰.

It is technically difficult to isolate bulk phytoplankton from the water samples. Hence, the seston $\delta^{13}C$ values that ranged between -23 and -17 ‰ have been accepted as tropical marine phytoplankton values (review by Bouillon *et* al., 2008), with an average of -22 ‰ (France, 1995). Benthic microalgae were on the average 5 ‰ enriched in $\delta^{13}C$ value relative to phytoplankton (France, 1995). Although stable isotope compositions of benthic microalgae were not analyzed in the present study, a recent investigation by other workers showed mean $\delta^{13}C$ value of -17.3 ‰ (ranged from -18.5 ‰ to -16.1 ‰) for benthic microalgae isolated from the mudflat sediment of Matang (Okamura *et* al., 2010). The mean value was comparable to the reported values of cultured samples of benthic diatoms (-17.8 ‰) reported by Rodelli *et* al. (1984) and field samples collected from tropical mangrove sediment (-17.3 ‰) by Bouillon *et* al. (2002).

Surface seston collected at 55 km offshore (OS1) had mean $\delta^{13}C$ value of -22.7 ‰ and C/N ratio of 7.7. The typical C/N ratios for phytoplankton were reported to range between 6.6 and 8.7 (Redfield *et* al., 1963). The C/N ratios would be more than 12 if the seston samples consisted largely of terrestrial plant detritus (Faganeli *et* al., 1988; Cifuentes *et* al., 1996). Rau *et* al. (1990) also suggested no significant contribution of terrestrial plant detritus in seston samples with C/N ratios <10. Based on the above assumptions, the offshore seston therefore was composed mainly of phytoplankton. Although near to mangrove forest, seston samples collected at the lower reaches of the estuary (station SK3) had a mean $\delta^{13}C$ value (-22.8 ‰) which was almost similar to that of the far offshore station, and its mean C/N ratio (8.3) indicates no

substantial mixing of phytoplankton with terrestrial plant detritus. The seston $\delta^{13}C$ value (ca. -22 ‰) was also recorded at the lower reaches of Sangga Besar River (Hayase *et* al., 1999).

The mean depth of nearshore waters was around 3.3 m (Chew & Chong, 2011) and was somewhat near to an extensive mudflat area (see Fig. 2.1). Nearshore seston appeared to be more variable in $\delta^{13}C$ values as compared to other samples, ranging from -20.3 to -16.3 ‰ (-18.8 ± 2.2 ‰). Compared with the lower reaches of Sangga Kecil River, nearshore seston was on the average enriched in ^{13}C by 4 ‰, possibly indicating a mixture of phytoplankton and resuspended benthic microalgae. Chai *et* al. (2011) reported high abundance of benthic diatoms in the mudflat sediment that were resuspended into the water column during high tide. Therefore, it is possible to sample a mixture of phytoplankton and benthic diatoms from the water column. However, the ^{13}C enrichment of seston as a result of high growth rates of the centric diatom *Coscinodiscus* must also be taken into account in this study. Albeit limited examination of phytoplankton samples in the study area, centric diatoms that were incidentally sampled by zooplankton net seemed to be more abundant in nearshore waters than mangrove estuaries. It was reported that high growth rates of *Coscinodiscus* would ultimately enrich its $\delta^{13}C$ value up to -15 ‰ (Fry & Wainright, 1991). Because of the overlap in $\delta^{13}C$ values between benthic microalgae and fast growing *Coscinodiscus*, it is difficult to draw a conclusion whether the fast growing planktonic diatoms or benthic microalgae are the ones responsible for seston ^{13}C enrichment.

According to Hayase *et* al. (1999) and Primavera (1996), the depleted $\delta^{13}C$ values of seston in the mangrove estuaries were attributed to a large proportion of suspended detrital mangrove material. The mean $\delta^{13}C$ value of seston at lower reaches of Sepetang River was -26.6 ‰, a value close to mangrove signature (-28.3 ‰). The

previous study also recorded a comparable $\delta^{13}C$ value (-25.6 ‰) for seston at the lower reaches of Sepetang River although C/N ratio was not available in their study (Hayase *et* al., 1999). As discussed earlier, the C/N ratios for suspended detrital mangrove was 12.1 (Cifuentes *et* al., 1996). For the mangrove leaves, the C/N ratio declined to 24 after 1.5 month of decomposition (Dehairs *et* al., 2000). If the estuarine seston was composed of largely detrital mangrove, a higher C/N ratio (probably >12) would be expected. However, the mean seston C/N ratio at the lower reaches of Sepetang River (mean = 8.1) was much lower than the suspended detrital mangrove i.e. within the C/N range for phytoplankton. A similar phenomenon was also observed in tropical Indian mangrove estuaries (Bouillon *et* al., 2000; Dehairs *et* al., 2000). These authors suggested that the depleted $\delta^{13}C$ value but low C/N ratio for seston were attributable to estuarine phytoplankton being depleted in $\delta^{13}C$ value. This depletion is due to carbon uptake from a ^{13}C-depleted DIC pool, as a result of microbial respiration during decomposition of mangrove detritus. Therefore, the assumption of a large proportion of mangrove detritus in estuarine seston (from 10 µm to 63 µm) may be too simplistic if based on the $\delta^{13}C$ values alone, which are close to the mangrove signal. In fact, direct measurement on $\delta^{13}C$ of DIC pool indicated highly variable values in tropical mangrove estuaries, with more depleted values generally obtained in the upper reaches and tidal creek areas of the estuaries as compared to coastal waters (Bouillon *et* al., 2000; 2004).

The $\delta^{15}N$ values of marine phytoplankton were reported to range from 3 to 12 ‰ (Mariotti et al., 1984; Owens *et* al., 1988) with an average of 8.7 ‰ (Peterson & Howarth, 1987). Although spatially different, the seston $\delta^{15}N$ values recorded in this study fell within the range of marine phytoplankton. The mean seston $\delta^{15}N$ value at 55 km offshore (8.5 ‰) was almost similar to the average suggested by Peterson and

Howarth (1987). The isotopic compositions for seston at this offshore station were assumed to have the least terrestrial and anthropogenic influences.

The enrichment in ^{15}N for estuarine and coastal seston has always been linked to the anthropogenic sewages, which composed of ^{15}N-enriched organic matter (Dehairs *et* al., 2000; Lee, 2000). The input of ^{15}N-enriched pollutants was likely to be minor in the Matang mangrove estuaries, as $\delta^{15}N$ values recorded for seston in this study were comparatively lower (<8 ‰) than those of highly urbanized mangrove estuaries (e.g. Dehairs *et* al., 2000; Lee, 2000; Newell *et* al., 1995).

The mean $\delta^{15}N$ value obtained for seston at the lower reaches of Sangga Kecil River (7.9 ‰) was close to that of the station at 55 km offshore. However, seston samples collected at the lower reaches of Sepetang River and nearshore waters had depleted $\delta^{15}N$ values relative to the station at the lower reaches of Sangga Kecil River. The low $\delta^{15}N$ value of seston in Sepetang River may be due to the excess of ambient DIN inside the mangrove estuaries, allowing the uptake of low $\delta^{15}N$ values of DIN by phytoplankton (see Cifuentes *et* al., 1988; Wainright & Fry, 1994). In nearshore waters, the low $\delta^{15}N$ value of seston may be due to the mixture of benthic microalgae and fast growing centric diatoms depleted in ^{15}N. However, the determination of seston $\delta^{15}N$ has always been difficult due to multiple nitrogen sources and limited $\delta^{15}N$ data from coastal microalgae.

5.2.4.2 Potential carbon pathways

Although the mangrove forest reserve supplies about 10 t C of mangrove litter ha^{-1} yr^{-1} to Matang mangrove estuaries (Ong & Gong, 2004), all selected zooplankton taxa (>500 µm) in the present study had $\delta^{13}C$ values closer to that of phytoplankton or benthic microalgae, rather than mangrove detritus. This indicates that zooplankton had

higher selectivity for microalgae than mangrove-based detritus. Compared to invertebrate and fish studies from Malaysian mangrove habitats (Rodelli *et* al., 1984; Newell *et* al., 1995; Chong *et* al., 2001), the present study showed a narrower range of $\delta^{13}C$ values for zooplankton which followed a general trend where more negative values were observed in the estuaries than those of the adjacent coastal waters. These authors were in agreement that the ^{13}C enrichment of animal tissues in adjacent coastal waters was possibly related to the contribution of a combination of phytoplankton and benthic microalgae, whereas tissue ^{13}C depletion was attributed to mangrove carbon assimilation in the mangrove estuaries. However, care must be taken before making conclusion as to which carbon source is more important to zooplankton nutrition because estuarine phytoplankton have a wide range of $\delta^{13}C$ values that may overlap those of mangrove or benthic microalgae, as discussed earlier.

The present study showed that the contribution of mangrove-based carbon to zooplankton nutrition was insignificant in the mangrove estuaries and adjacent coastal waters. The results were consistent to those reported for mangrove decapod larvae and other zooplankton (Schwamborn *et* al., 2002). In contrast, Chong *et* al. (2001) reported the substantial contribution of mangrove carbon to penaeid prawns' nutrition in the upper Matang mangrove estuaries, amounting up to 80%, though the authors did not consider the existence of ^{13}C-depleted estuarine phytoplankton. Nevertheless, if it does exist in Matang waters, $\delta^{13}C$-depleted phytoplankton may be considered as an important link between mangrove and zooplankton as a result of phytoplankton uptake of mangrove ^{13}C released into the DIC pool with the aid of bacterial decomposition. Thus, mangrove may contribute a considerable part of the phytoplanktom carbon in the mangrove system.

Zooplankton at stations SK1 and SK3 derived their nutrition directly or via intermediaries from phytoplankton. A mixture of phytoplankton and benthic microalgae

perhaps in various degrees is likely to support the zooplankton community in the nearshore coastal waters, particularly over or adjacent to mudflats. Enriched $\delta^{13}C$ of zooplankton in adjacent coastal waters could be related to their assimilation of heavier ^{13}C in fast growing diatoms or/and benthic microalgae. The higher selectivity of zooplankton for microalgae over mangrove detritus could be explained by the fact that mangrove plant detritus is low in nutritional value and less palatable due to its refractory compounds as compared to microalgae (Rodelli *et* al., 1984; DeMott, 1988; Robertson *et* al., 1992). Several experimental studies reinforce the food-selection hypothesis for zooplankton, where copepods prefer to feed on microalgae over vascular plant detritus (DeMott, 1988), while the vascular plant detritus potentially retards the growth of postlarval penaeid prawns (Gleason, 1986).

Only the chaetognaths and copepod *Tortanus* at station SK1 did not show enrichment in ^{13}C relative to typical phytoplankton. This may be related to the assimilation of ^{13}C depleted food source from the estuaries, which could be of mangrove origin or ^{13}C depleted estuarine phytoplankton. Lower or depleted $\delta^{13}C$ values of zooplankton in upstream and fresh waters are common in tropical and temperate estuaries (del Giorgio & France, 1996; Dehairs *et* al., 2000; Bouillon *et* al., 2000). Since the chaetognaths and copepod *Tortanus* mainly feed on smaller zooplankton, their lower $\delta^{13}C$ values indicated the presence of ^{13}C depleted zooplankton in the estuaries. Unfortunately, since zooplankton samples were collected from the coastal water until 7 km upstream of Sangga Besar River in the present study, the degree of ^{13}C depletion in upper stream zooplankton remained unknown.

The porcellanid zoeae from nearshore waters had the most enriched $\delta^{13}C$ value (-15 ‰), suggesting the utilization of heavier ^{13}C microalgae. If $\delta^{13}C$ value of benthic microalgae in the study area is around -17 ‰ (Okamura *et* al., 2010), the $\delta^{13}C$ value of

porcellanid zoeae is enriched by about 2 ‰ relative to benthic microalgae. The $\delta^{13}C$ enrichment was much higher than the typical trophic fractionation value of 0 – 1 ‰. This may suggest that porcellanid zoeae utilized more the heavier ^{13}C planktonic centric diatoms than benthic microalgae. However, further investigation is needed to confirm the exact contributor of ^{13}C enrichment of decapod larvae in coastal waters because cyanobacteria could also be the potential ^{13}C-enriched source in marine habitats (Cura, 1987).

The selected fish species *A. maculatus*, *L. brevirostris* and *J. weberi* that were encountered along the Selinsing Rivers and upper reaches of Sangga Kecil River had $\delta^{13}C$ values intermediate between mangrove and typical marine phytoplankton. Other fish species such as *P. kaakan*, *Plotosus canius* Hamilton, *Tetraodon fluviatilis* Hamilton, *A. gymnocephalus*, *Stolephorus commersonnii* Lacepède and *Stolephorus insularis* Hardenberg and penaeid prawns generally found in the upper Matang mangrove estuaries also exhibited relatively similar $\delta^{13}C$ values (Hayase *et* al., 1999; Chong *et* al., 2001; Then, 2008). These authors suggested that these animals derived their energy source mainly from mangrove-based carbon. As discussed earlier, the intermediate $\delta^{13}C$ values could also be due to the assimilation of ^{13}C depleted estuarine phytoplankton. With the presence of ^{13}C-depleted estuarine phytoplankton, the identification of carbon pathways in the mangrove food webs is clearly more complicated than previously assumed.

Chong (2007) reported seven pelagic fishes including the zooplanktivores *A. gymnocephalus*, *S. commersonnii* and *S. insularis* that assimilated mangrove carbon to as much as 80%. This indirectly indicated that the zooplankton consumed by zooplanktivores were considerably dependent on mangrove-based carbon. However, some studies suggested that the large spatial variation of $\delta^{13}C$ values in zooplankton is

attributed to their selective feeding on phytoplankton over other seston components (see del Giorgio & France, 1996; Bouillon *et* al., 2000). If ^{13}C-depleted estuarine zooplankton in the upper estuary of Matang is due to selection of ^{13}C-depleted estuarine phytoplankton, then assimilation of phytoplankton carbon is more important than mangrove carbon. For instance, both stomach contents and δ^{13}C value of *A. gymnocephalus* provide some evidence of ^{13}C-depleted estuarine phytoplankton assimilation. *A. gymnocephalus* in the upper part of Sangga Besar River fed exclusively on calanoid copepods (see Table 5.3) and yet had a mean δ^{13}C value of -24 ‰ (Hayase *et* al., 1999). Assuming a maximum trophic fractionation of 1 ‰ between the ambassid and its prey item, the δ^{13}C value of calanoid copepods would be estimated at -25 ‰. This value is quite close to the δ^{13}C value of the seston (-26.6 ‰) located within the same area of fish collection (see Table 5.10). However, further research is needed to confirm selective feeding of phytoplankton and other seston components by calanoid copepods since microheterotrophs found on mangrove detritus could also be a potential food source for zooplankton.

The harpacticoids were mainly consumed by leiognathids, while polychaetes and bivalves were common in the diet of ariids, sciaenids and *P. kaakan*. To date, the stable isotopic composition of benthic harpacticoids in tropical mangrove estuaries has not been reported. These copepods are likely to depend on the microheterotrophs found on deposited microalgal or mangrove detritus. It was suggested that the meiofauna consumed the microorganisms on detritus (Lillebo *et* al., 1999; Montagna, 1995). Hence, both mangrove and phytoplankton are potential carbon sources assimilated by benthic harpacticoids via microheterotrophs as intermediaries, and in turn utilized by predatory fish such as gerrids and leiognathids (see Table 5.3).

Unlike benthic harpacticoids, there are relatively more stable isotope data reported for macrobenthos in tropical mangrove estuaries (e.g. Rodelli *et* al., 1984; Newell *et* al., 1995; Bouillon *et* al., 2002; Demopoulos *et* al., 2007; Abrantes & Sheaves, 2009). In Matang, particularly Sangga Besar and Selinsing estuaries, the macrobenthos were composed largely of molluscs, crustaceans and polychaetes (Muhammad Ali, 2004). The $\delta^{13}C$ values of bivalve suspension feeders in the mangrove estuaries generally fall between mangrove and typical marine phytoplankton, suggesting a combination of both carbon sources in their tissues (Rodelli *et* al., 1984; Newell *et* al., 1995; Demopoulos *et* al., 2007; Abrantes & Sheaves, 2009). These values could also result from assimilation of ^{13}C-depleted estuarine phytoplankton (Abrantes & Sheaves, 2009). Therefore, the intermediate $\delta^{13}C$ values of Matang juvenile fish that rely on both zooplankton and benthic animals indicate the assimilation of both mangrove and phytoplankton carbon in the food web.

Inside the estuaries, *S. baganensis* and *T. kammalensis* (this study) had enriched $\delta^{13}C$ values relative to their congeneric species *S. commersonnii* and *S. insularis* (Hayase *et* al., 1999). Then (2008) also reported higher $\delta^{13}C$ values for engraulids caught in Sepetang estuary. The stomach content analysis showed that these sympatric species consumed relatively similar prey items such as hyperbenthic shrimps (see Table 5.3; Hayase *et* al., 1999; Then, 2008), whereby the variation in $\delta^{13}C$ values may be due to the mobility of animals, suggesting that the fish with higher $\delta^{13}C$ values might feed at the lower part of the estuaries before moving further upstream. As expected, fish samples collected at the lower estuary and nearshore waters showed high dependency on phytoplankton and benthic microalgae, with *Upeneus sulphureus* having the most enriched $\delta^{13}C$ value (see Table 5.10). This species feeds exclusively on *Acetes* and mysids (see Table 5.3).

5.4.2.3 Trophic levels of organisms

The trophic positions of consumers were determined based on the mean $\delta^{15}N$ value of *Pseudodiaptomus* as representative of primary consumers in the Matang mangrove estuaries (Table 5.14). Although the $\delta^{13}C$ values of zooplankton primary consumers showed high dependency on phytoplankton at the upper and lower reaches of Sangga Kecil River, there was little difference between $\delta^{15}N$ values of primary consumers and seston in the estuaries (see Fig. 5.10). Overlap in $\delta^{15}N$ between primary consumers and seston was also reported in Southern Ocean pelagic food webs (Richoux & Froneman, 2009). This may be related to the fact that zooplankton primary consumers not only ingest the phytoplankton but also the microorganisms found on the microalgal detritus such as N_2-fixing bacteria, with relatively decreased $\delta^{15}N$ value (Currin *et* al., 1995). Nevertheless, the average enrichment of around 3 ‰ per trophic level for consumers was in agreement with the $\delta^{15}N$ trophic fractionation. If the primary producers are included, the food web structure of Matang mangrove estuaries and adjacent coastal waters will consist at least of four trophic levels (Table 5.14), but likely to be five if piscivores are included.

Most of the copepods and decapod larvae at the trophic level of primary consumers are generally omnivorous, showing the ability to feed on a mixture of phytoplankton and smaller zooplankton (Kleppel, 1993; Schwamborn *et* al., 2002). Therefore, it is not surprising that zooplankton taxa examined in the present study were mainly omnivores (trophic positions of >2, see Table 5.14). However, the average $\delta^{15}N$ value of omnivorous zooplankton was closer to the herbivore *Pseudodiaptomus* than carnivorous zooplankton, suggesting that the omnivorous zooplankton may ingest more plant than animal foods. In an experimental study, crab zoeae were found to forage higher amounts of centric diatoms than fauna due to their limited ability to capture active prey (Schwamborn *et* al., 2006). Thus, it appears that phytoplankton are easier to

access than highly mobile animals by small size omnivorous zooplankton. To resolve the problem of exactly what kinds of food items were consumed by the omnivorous zooplankton, direct examination on their gut contents should be conducted in future research.

The chaetognaths that depend largely on copepods (Tönnesson & Tiselius, 2005) are assigned at trophic level higher than copepods (Table 5.14). The higher trophic position of chaetognaths has been reported for the pelagic food web of the Southern Ocean (Richoux & Froneman, 2009). The stomach contents analysis of mysids (Winkler *et* al., 2007) and *Acetes* (Chiou *et* al., 2005) revealed the extent of omnivorous feeding. In the present study, *Acetes* and mysids were highly carnivorous and are placed at the third trophic level above the zooplankton primary consumers at the second trophic level (see Fig. 5.10). The high abundance of zooplankton particularly copepods in Matang mangrove estuaries and nearshore waters (see Chapter 4; Chew & Chong, 2011) may explain the high degree of carnivory for *Acetes* and mysids.

During embryogenesis, the $\delta^{15}N$ value of decapod larvae could decrease by up to 2.3 ‰ (Schwamborn *et* al., 2002). This may explain why the $\delta^{15}N$ values of brachyuran zoeae were comparatively lower than other zooplankton in this study. The higher C/N ratios of brachyuran zoeae (>9.3, see Table 5.10) compared to other decapods may suggest high lipid content in larval tissues (Schwamborn *et* al., 2002).

Larval and small size fishes found in Matang and nearshore waters are assigned at the second to fourth trophic levels, while penaeid prawns are at the second and third trophic levels (Table 5.14). The prey food items consumed by fish and prawns were generally consistent with their trophic positions. There were no strict herbivores observed for the selected fish and prawns. *A. chacunda* and *L. melinoptera*, categorized as phytodetritivores, had $\delta^{15}N$ values somewhat close to omnivorous zooplankton.

Stomach content analysis revealed that copepods, protozoans and fungal spores formed a part of their diet other than benthic diatoms (present study; Then, 2008). This indicates that the phytodetrivores are able to assimilate nitrogen from plant and animal foods.

In general, fish at the higher trophic level have greater size than those at the lower trophic level. Fish larvae collected in this study area are assigned to the second and third trophic levels compared with larger sized fishes at the fourth trophic level (Table 5.14). The ontogenetic diet shifts were particularly apparent for engraulids, with larval fish at lower trophic level relying on small planktonic prey but switching to carnivorous feeding at the juvenile and adult stages at higher trophic levels.

Although both *A. gymnocephalus* and *L. brevirostris* fed largely on copepods, yet the trophic position of the former was comparatively lower than the latter (Table 5.14). This discrepancy may be due to *L. brevirostris* consuming benthic harpacticoids which likely fed on microheterotrophs with enriched ^{15}N. Microheterotrophs in sediment have been suggested to assimilate enriched ^{15}N from DIN pool (Demopoulus *et* al., 2007).

5.3 Conclusion

This study shows that zooplankton especially copepods and hyperbenthic shrimps (such as mysids and *Acetes*) constituted the prey for juvenile and small size fishes in Matang mangrove estuaries. Although these fishes preferentially feed on these taxa, they are also adapted to feed opportunistically on other prey items which are readily available in the mangrove estuaries. Ontogenetic diet shift is apparent for large species. The copepod *Pseudodiaptomus annandalei* and mysids are mainly fed by young and juvenile fish, while decapods (shrimps and crabs), polychaetes and bivalves are particularly important to the nutrition of older juvenile and subadult fish.

Results of carbon isotopic ratios indicate that phytoplankton are an important energy source for zooplankton in open mangrove channels in spite of mangrove detritus forming a large proportion of the suspended particulate organic matter. In nearshore waters, zooplankton are likely to derive their energy source from a combination of phytoplankton and benthic microalgae. However, it is difficult to identify the exact carbon source assimilated by the consumers particularly in nearshore waters and in the more enclosed upper estuaries, where $\delta^{13}C$ values of phytoplankton may overlap with those of benthic microalgal and mangrove signatures. Therefore, the contribution of energy from primary producers and its flow through the food web of Matang mangrove estuaries is more complex than previously thought.

The $\delta^{15}N$ values reflected correctly the trophic positions of consumers, suggesting at least four trophic levels for Matang mangrove estuaries and coastal food webs. Carbon or energy source from primary producer is mainly transferred via zooplankton at the second and third trophic levels to predatory fish at higher trophic levels.

CHAPTER 6

GENERAL DISCUSSION AND CONCLUSION

6.1. Role of zooplankton in the mangrove food web

Fig. 6.1 shows a conceptual food web structure of Matang mangrove estuaries based on the results of stomach contents and stable isotope analyses. There were 98 fish species recorded in mangrove estuaries of Matang, but the 26 fish species considered in the present study comprised a large proportion of fish composition in terms of biomass (62%) and density (87%) (Then, 2008). Therefore, it can be concluded that most of the young and small bodied fishes (both residents and marine migrants) in these estuaries rely mainly on zooplankton as energy source. Noteworthy, the ariid *Arius maculatus*, which constituted the highest biomass among fish in these estuaries (Then, 2008), fed largely on the estuarine copepods (e.g. *Pseudodiaptomus annandalei*) at the juvenile stage. Although the stomach contents of fish larvae were not examined in the present study, the abundance of fish larvae that were positioned at the third trophic level (see Table 5.14) was strongly correlated to zooplankton abundance (Ooi & Chong, 2011) indicating the importance of zooplankton to larval fish nutrition in the mangrove estuaries. In view of high dependency of larval and juvenile fish on estuarine zooplankton, the present study supports the premise that mangrove estuaries provide zooplankton food for fish, including those of economically important species.

Stable isotope analysis in the present study corroborates the trophic role of zooplankton as intermediaries which link primary producers to juvenile and small bodied fishes in the mangrove food web. Although zooplankton $\delta^{13}C$ values of the present study displayed strong reliance on microalgal carbon source, other consumers, some of which are zooplankton feeders, showed variable and site-dependent $\delta^{13}C$ values in the mangrove estuaries. In order to give a better picture of site-dependent $\delta^{13}C$ values of consumers, these values of present and previous studies in Matang mangrove

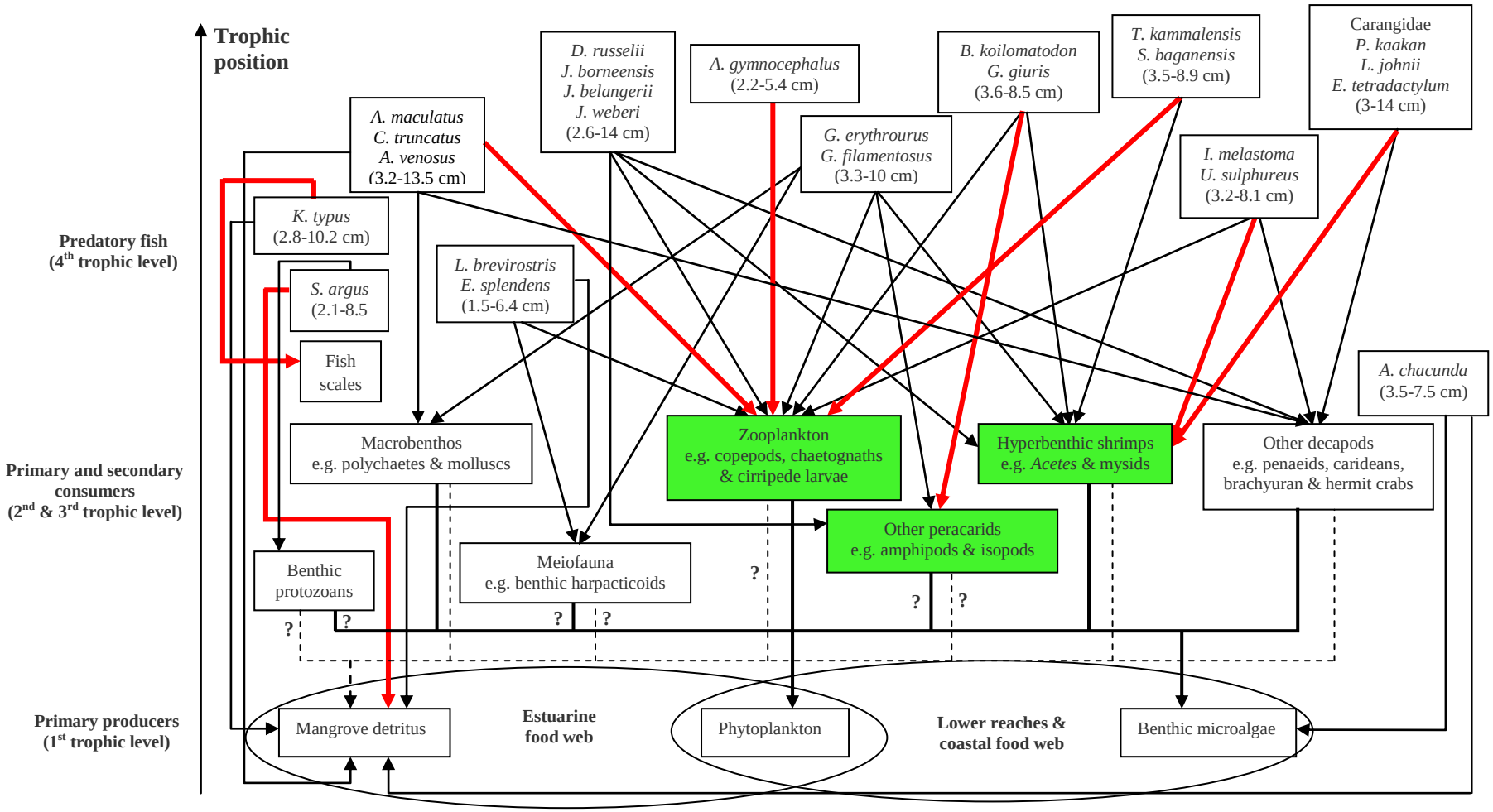


Fig. 6.1. Schematic trophic relationships (not to scale) of the 26 common fish species and their prey items in the Matang mangrove food webs. Darker arrows indicate microalgae-based (phytoplankton + benthic microalgae) food chain and dotted arrows indicate mangrove-based food chain. '?' indicates trophic links that have yet to be reported in the Malaysian mangrove estuaries. Major food items that contributed more than 50% of fish dietary composition are indicated by thick arrows in red, while food items that contributed 10% to 50% of dietary composition are indicated by thin arrows. Prey items with dietary composition of less than 10% not shown. Animals in green boxes are categorized as zooplankton in the present study. Values in parenthesis indicate range of fish standard length examined.

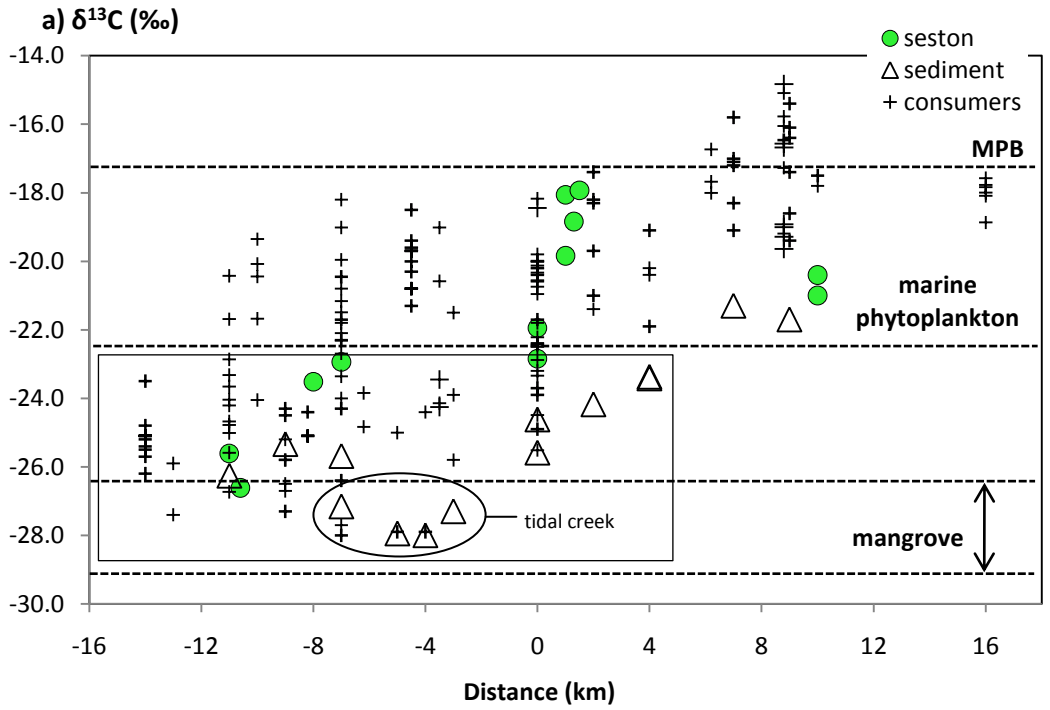


Fig. 6.2. Compilation of $\delta^{13}C$ values of organisms and sediments in the Matang mangrove estuaries and adjacent coastal waters from the present and previous studies (Hayase *et* al., 1999; Chong *et* al., 2001; Then, 2008; Okamura *et* al., 2010; Tanaka *et* al., 2011; Ooi, unpublished data). Dashed lines indicate $\delta^{13}C$ values of primary producers, MPB indicates microphytobenthos; samples within rectangular box were depleted in ^{13}C relative to typical marine phytoplankton, and samples collected from the tidal creek were within ellipse. 0 km indicates lower estuary, positive indicates seaward direction and negative indicates towards upstream direction.

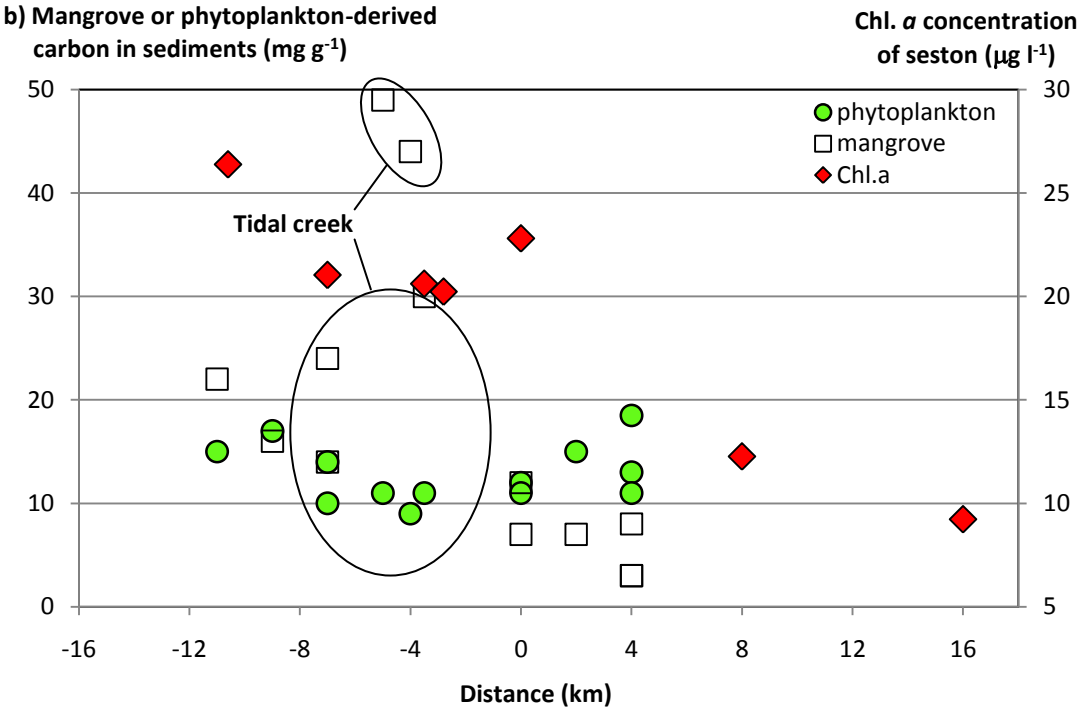


Fig. 6.3. Compilation of mangrove- and phytoplankton-derived carbon in sediments (left vertical axis) and chlorophyll *a* concentration of seston (right vertical axis) in the Matang mangrove estuaries and adjacent coastal waters (Okamura *et* al., 2010; Chew, data not reported). Samples collected from the tidal creek were within ellipses. 0 km indicates lower estuary, positive indicates seaward direction and negative indicates towards upstream direction.

estuaries were compiled, collated and presented in Fig. 6.2. The estimated mangrove and phytoplankton derived carbon in sediments as well as chlorophyll *a* concentration of seston in Fig. 6.3 would provide information on the availability and variability of primary producers along the estuarine gradient.

All consumers at nearshore and offshore waters showed high dependency on phytoplankton and benthic microalgal carbon (present study; Chong *et* al., 2001; Chong *et* al., 2011), although outwelled mangrove carbon was evident in nearshore sediments (Okamura *et* al., 2010). Consumers from the estuaries, on the other hand, showed variable $\delta^{13}C$ values. About half of these values were depleted in ^{13}C relative to typical marine phytoplankton signature (see Fig. 6.2). Distinctively depleted $\delta^{13}C$ values of consumers were mainly encountered in tidal creek and upper estuarine areas (Chong *et* al., 2001; Tanaka *et* al., 2011).

While mangrove-derived carbon in the sediments was significantly higher in tidal creek and upper reach areas compared to lower reaches and adjacent coastal waters of Matang (Okamura *et* al., 2010), phytoplankton-derived carbon in sediments and chlorophyll *a* concentration of seston were not lower upstream or tidal creek areas (see Fig. 6.3; Hayase *et* al., 1999; Tanaka & Choo, 2000; Okamura *et* al., 2010). Indeed, the estimated chlorophyll *a* concentration of seston was rather high in the region of about 10 km upstream (see Fig. 6.3) or tidal creek (see Tanaka & Choo, 2000) waters. This implies that phytoplankton abundance is not limited in the tidal creek and upper reach areas compared to more marine influenced mangrove waters. Moreover, the rough estimation of energy flow from primary to secondary production indicated excess phytoplankton to support the entire mesozooplankton nutrition in the Matang mangrove estuaries (Tarutani *et* al., 2007). Apart from zooplankton utilization, the excess phytoplankton energy source is believed to support the sessile filter feeders on the mangrove substrates (e.g. barnacles, mussels and oysters) or eventually decomposed in

the water column if not utilized (Tarutani et al., 2007). Assuming there is no severe eutrophication in the Matang mangrove waters (Alongi *et* al., 2003), the contribution of phytoplankton in the mangrove food web may be more important than previously thought.

6.2. Matang copepod community in comparison to other tropical water communities

From the routine monthly and 24-hour samplings, a total of 112 zooplankton taxa were recorded, with 51 copepod species (see Table 3.10). Amongst the copepods, 14 species were rarely sampled (occurrence of <13%) throughout the study period. Eight of them were truly stenohaline, which occurred only at the lower estuary and stations towards offshore. These included *Canthocalanus pauper*, *Acrocalanus gracilis* Giesbrecht, *Labidocera euchaeta* Giesbrecht, *Pontella* sp. 1, *Temora discaudata* Giesbrecht, *T. turbidata*, *Corycaeus dahli* Tanaka and *Macrosetella gracilis* (Dana) (see Table 3.10). Almost all these species have been previously reported in the Straits of Malacca (Rezai *et* al., 2004). Three species namely *A. gracilis*, *T. discaudata* and *M. gracilis* were found in offshore waters located 55 km from the coast of Matang (see Table 3.14). *M. gracilis* was found in considerable numbers in this location (>100 ind m^{-3}). Rezai *et* al. (2004) collected copepods along the north-south transect of the Straits of Malacca. They found that *M. gracilis* was more abundant in the more oceanic northern region of the straits as compared to the central and southern regions, and during the drier southwest monsoon period (July - August) as compared to during the wetter northeast monsoon period (November - December). This suggests its preference for more oceanic conditions. As Matang mangrove estuaries are an open estuarine system and often subject to extensive freshwater flushing, the oceanic copepod species had never occurred in large numbers throughout the study period. Duggan *et* al. (2008)

similarly reported low number of oceanic copepod species in the Darwin Harbour, Australia.

Other rare representatives of copepods include three species of benthic harpacticoids (Adenopleurellidae sp., Ectinosomatidae sp. and *Longepedia* sp.), two species of symbiotic copepods (*Paramacrochiron amboinense* Mulyadi and *Caligus* sp.) and a species of epipelagic copepods (*Clytemnestra scutellata* Dana) (see Table 3.10). Although the benthic harpacticoids were rarely sampled in the water column, they can be numerically abundant in the sediments of mangrove estuaries (Boxshall & Halsey, 2004). This was evident in the stomach contents of some mangrove fishes such as the leiognathids and gerrids, which fed considerably on benthic harpacticoids (see Chapter 5). Sasekumar (1994) investigated the meiofauna community at different shore levels of the mangrove in Selangor, Malaysia. He found that the benthic harpacticoids constituted the most abundant component of meiofauna after the nematodes, and were mainly distributed at the lower shore of *Avicennia* zone, where the forest floor was frequently inundated. The symbiotic copepod *Paramacrochiron* is a common associate that lives on their cnidarian hosts including hydrozoans and scyphozoans, while the copepod *Caligus* is a common parasite found on their fish hosts (Boxshall & Halsey, 2004). Adults of both symbiotic copepods can be accidentally caught by plankton tow net when they occur temporarily as plankton to search for their new host.

Habitat niche partitioning amongst zooplankton is believed to reduce interspecific competition for space and resources. In the marine environment, the habitat niche partitioning of zooplankton can occur in the horizontal or vertical plane. Ueda (1987) investigated the distribution of two copepod species from the same subgenus *Acartiura* (*Acartia omorii* Bradford and *Acartia hudsonica* Pinhey) in the Maizuru Bay, Japan. He found that the recruitment time of both species appeared to be closely synchronous but their distribution was separated in the offshore axis. *A.*

hudsonica was more restricted to the inner part of the bay than *A. omorii.* The restriction of *A. hudsonica* to inlet waters or estuaries was observed in the Pacific regions but not in the Atlantic regions. This could be related to the co-existence of the subgenus species of *Acartia* in the Pacific waters whereas this case was not observed in the Atlantic waters (Ueda, 1987). *Acartia* species belonging to different subgenera, on the other hand, appeared to be separated in time than in space (Ueda, 1987). This was observed in two species, *Acartia californiensis* and *Acartia clausi* in the San Francisco Bay (Ambler *et* al., 1985). The seasonal succession of *A. californiensis* occurred during the dry-warm season, but was replaced by *A. clausi* during the wet-cold season.

For vertical habitat-partitioning, Ambler and Miller (1987) found that copepod congeners were distributed at different depths of the water column. Although there was an overlap in distribution among zooplankton in the present study, the congeneric copepod species exhibited segregation along the offshore axis. Both *A. spinicauda* and *A. erythraea* in the same subgenus *Odontacartia* were spatially segregated. Segregation among the congeners of copepods was also observed for other genera such as *Pseudodiaptomus* and *Oithona* (see Table 3.10).

In tropical mangrove estuaries, the estuarine species of copepods are mainly from the families Acartiidae, Pseudodiaptomidae and Oithonidae. There were 10 species of *Acartia* and 10 species of *Pseudodiaptomus* reported in the Cochin backwaters and adjacent coastal waters, India (Madhupratap, 1987). This number was much higher than that in the Matang mangrove estuaries, which recorded only three species of *Acartia* and four species of *Pseudodiaptomus* (see Table 3.10). The truly estuarine copepods such as *Acartia centrura* Giesbrecht, *A. bowmani* Abraham, *A. bilobata* Abraham, *A. plumosa* Scott T. and *Acartiella keralensis* (Wellershaus) contributed approximately 62% to the total copepod population in the Cochin backwaters, and some species were found to be spatially or temporally segregated from

the others. However, all these estuarine species were not sampled in the Matang mangrove estuaries. *A. spinicauda* was also reported in the Cochin backwaters, but occurred in fewer number compared to Matang mangrove estuaries. The absence of other more successful congeners may be the factor that leads to the dominance of *A. spinicauda* in the Matang mangrove estuaries.

Although the number of species in *Pseudodiaptomus* was comparable to that of *Acartia* in the Cochin backwaters, the numerical proportion accounted for *Pseudodiaptomus* species was much lower than the *Acartia* species (Madhupratap, 1987). This was also the case in the Matang mangrove estuaries. However, both *Acartia* and *Pseudodiaptomus* species can be equally important in terms of abundance in other tropical estuaries such as Furo do Meio, northern Brazil (Krumme & Liang, 2004) and coastal lagoon of Ivory Coast (cited by Robertson & Blaber, 1992). In Furo do Meio, species of *Acartia* were mainly represented by *A. tonsa* and *A. lilljeborgii* Giesbrecht, while *Pseudodiaptomus* were represented by *P. marshi* Wright S. and *P. Richardi* Dahl F. (Krumme & Liang, 2004). These four species altogether contributed over 90% to the total abundance of zooplankton. In the coastal lagoon of Ivory Coast, zooplankton community was dominated by *A. clausi* and *P. hessei* (cited by Robertson & Blaber, 1992). Duggan *et* al. (2008) reported four species of *Acartia* (*A. sinjiensis, A. pacifica, A. erythraea* and *A. fossae* Gurney) and three species of *Pseudodiaptomus* (*P. mertoni* Früchtl, *P. annandalei* and *P. griggae* Walter) in the Darwin Harbour. All *Acartia* species were more abundant in the inner part of the estuary, and *A. sinjiensis* were predominant among the acartiids. For *Pseudodiaptomus*, only *P. mertoni* was considerably found in the Darwin Harbour, whereas *P. annandalei* and *P griggae* were scarce. Unlike Darwin Harbour, *A. erythraea* did not intrude into the Matang mangrove estuaries throughout the study period, while *P. annandalei* constituted the most important pseudodiaptomids (Chapters 4 & 5).

Oithona hebes Giesbrecht was reported to be an important cyclopoid found in the Furo do Meio. This species also occurred in the estuaries of Mandovi and Zuari, India (Dalal & Goswami, 2001), but was absent in the Malaysian and Australian mangrove estuaries (McKinnon & Klumpp, 1998a; Duggan *et* al., 2008; Chew & Chong, 2011). *O. aruensis, O. nishidai, O. simplex*, *O. robertsoni* McKinnon, *O. attenuata, O. brevicornis*, *O. rigida*, *O. nana* and *O. fallax* Farran were among the oithonids reported in the tropical Australian mangrove estuaries (McKinnon & Klumpp, 1998a; McKinnon, 2000; Duggan *et* al., 2008). *O. aruensis* and *O. nishidai* appeared to be estuarine and constituted the most abundant oithonids in the Darwin Harbour (Duggan *et* al., 2008).

A total of six species of oithonids were recorded in the Matang mangrove estuaries and adjacent coastal waters (see Table 3.10). *O. dissimilis* which was more restricted within the Matang mangrove estuaries was not reported in the Australian mangrove estuaries. *O. aruensis* was also commonly found in the Matang mangrove estuaries, and its distribution could be extended to nearshore water as compared to *O. dissimilis*. *O. attenuata, O. brevicornis* and *O. rigida* which are neritic species but rarely entered the estuaries (Chew & Chong, 2011). *O. simplex* was widespread from the upper reaches to offshore water and constituted the most dominant oithonids in the Matang mangrove estuaries (see Chapters 3 & 4; Chew & Chong, 2011). Although some species of *Acartia, Pseudodiaptomus* and *Oithona* are regionally widespread, species composition in these genera is distinctly different among estuaries of different geographic zones.

6.3. Tidal responses of copepods: estuarine versus neritic species

This section is to highlight some points which are not discussed in the previous chapters. As mentioned in Chapter 4, tidal vertical migration (TVM) of estuarine copepods is position-dependent in the estuary (Hough & Naylor, 1991, 1992; Ueda *et* al., 2010) in order to maintain their position within the optimal range of salinity. This ultimately results in the accumulation of estuarine copepods in the middle part of the estuaries (see Hough & Naylor, 1991, 1992). The adaptive TVM also allows higher accumulation of estuarine copepods in the upper estuary during spring tide as compared to neap tide (Hough & Naylor, 1991) perhaps to minimize population loss due to seaward advection. Based on the results of both routine monthly and 24-hour samplings, it is likely that the estuarine copepod *A. spinicauda* adopts similar adaptive position-dependent TVM in the Matang mangrove estuaries. The evidence to support this postulation includes higher abundance of both *Acartia* adults and copepodids at mid-estuary (see Table 3.7) and the significantly lower abundance of these copepods at the lower estuary during spring than neap tide (see Tables 4.17, 4.22; Fig. 4.26). These distributional patterns were not observed for marine euryhaline species such as *P. crassirostris, B. similis* and *O. simplex*. The preceding suppositions, however, did not take into account the possibility of losses from offshore advection and predation, which could also have significant impact on the abundance of copepods.

The process of tidal mixing can potentially import a significant amount of neritic zooplankton into the estuaries (Heip *et* al., 1995). However, the neritic zooplankton that are brought into the estuaries are usually unable to live successfully in most estuaries thereby leading to a net degradation of their abundance (Kimmerer & McKinnon, 1987; Soetaert & Herman, 1994). The net mortality of neritic zooplankton in the estuaries has been estimated to be on average 5% per day, and the value could be up to 40% per day for certain species. About 1,500 metric tonnes of the total annual dry weight of neritic

mesozooplankton have been reported to enter and degrade in the Westerschelde estuary, Netherlands (Soetaert & Herman, 1994). Therefore, it is apparent that estuaries function as sinks rather than as sources of neritic zooplankton. Since salinity stress is often a key factor responsible for the mortality of neritic zooplankton in the estuaries, it is interesting to know whether similar adaptive tidal-related migration as observed in estuarine copepods are also developed in neritic copepods to avoid over dispersion into the estuaries. According to Kimmerer & McKinnon (1987) and Soetaert & Herman (1994), it is unlikely that such a behavioural adaptation occurred in neritic zooplankton because of their wide geographical range. Moreover, the efficiency of their vertical swimming activity is poor to prevent their entry into the estuaries (Soetaert & Herman, 1994).

In the present study, most of the copepod species encountered are those that thrive in neritic waters except for some truly estuarine and euryhaline species (see Chapter 3). The stenohaline species that are commonly found in the adjacent coastal waters (e.g. *A. erythraea*, *Centropages* spp., *Eucalanus subcrassus* Giesbrecht, *O. attenuata* and *C. andrewsi*) were scantily or not sampled inside the Matang mangrove estuaries. As the number of neritic copepod species were higher than the estuarine ones, the consistently higher copepod taxonomic distinctness (Δ^* and Δ^+) at the lower estuary during ebb than flood tide (Chapter 4) indicates that most neritic copepod species at the lower estuary occurred mainly during ebb tide, but they avoided this area during flood tide. The upward nocturnal migration of *O. simplex* during the wet spring tide also occurred at ebb tide but not at flood tide (see Chapter 4).

In view of these findings, the question arises as to why such a distribution pattern could occur if the neritic copepods do not possess tidally-induced adaptation to prevent them from entering the estuaries. Therefore, in contrast to the previous findings, it is concluded that tidally-induced migration of neritic copepods does occur in adjacent

coastal waters of Matang although this hypothesis awaits further research for confirmation.

6.4. Limitations of the study and future perspectives

Monthly and weekly variations in abundance and distribution of zooplankton as well as their trophic role in the food web are quite conclusively depicted in the present study except for some aspects, which still remain uncertain due to limitations of the sampling procedure. However, these uncertainties have invoked several hypotheses which deserve to be tested in future research.

Since high mangrove-derived carbon and distinctive depleted $\delta^{13}C$ values of consumers (e.g. fish and penaeid prawns) were mainly encountered in tidal creeks and upper reach areas of Matang (Chong *et* al., 2001; Okamura *et* al., 2010; Tanaka *et* al., 2011), where zooplankton has yet to be studied, future research pertaining to mangrove zooplankton trophodynamics should focus in these areas. In view that zooplankton are selective feeders, the hypothesis to be tested is that depleted $\delta^{13}C$ values of zooplankton in tidal creeks and upper reaches of turbid mangrove waters are due to the assimilation of depleted ^{13}C phytoplankton and not mangrove carbon due to depleted ^{13}C of DIC pool. The incorporation of mass balance method (e.g. ECOPATH) in future mangrove trophodynamics study is needed to quantitatively picture the energy flow from primary producers to higher trophic levels. Importantly, this method would reveal whether phytoplankton production alone is sufficient to support the zooplankton in turbid mangrove waters.

It is also interesting to test the hypothesis that the tidally-induced vertical migrations of the estuarine copepods are site-dependent along the estuaries. Estuarine copepods found at the lower estuary are thought to retain themselves in the estuaries by ascending during flood tide and descending during the ebb tide. A reverse behavioral

response is likely to be taken by copepods in the upper estuary. The scale of TVM for lower estuarine copepods is expected to be greatest during the wet spring tide when tidal current is stronger, and therefore leading them to horizontal displacement either towards upstream or into the mangrove forest. It would be interesting to investigate if the estuarine copepods take refuge among the mangrove prop roots or at the inundated forest floor when tidal currents are extreme. The exact opposite adaptive TVM found in estuarine copepods at the lower estuary is postulated to be practiced by the neritic copepods. Fig. 6.4 illustrates a schematic diagram of position-dependent TVM of copepods in the estuaries and nearshore waters. It was reported that the adaptive TVM could even occur in naupliar and early copepodid stages (Ueda *et* al., 2010). Further studies should thus consider the different ontogenetic stages of copepods in TVM.

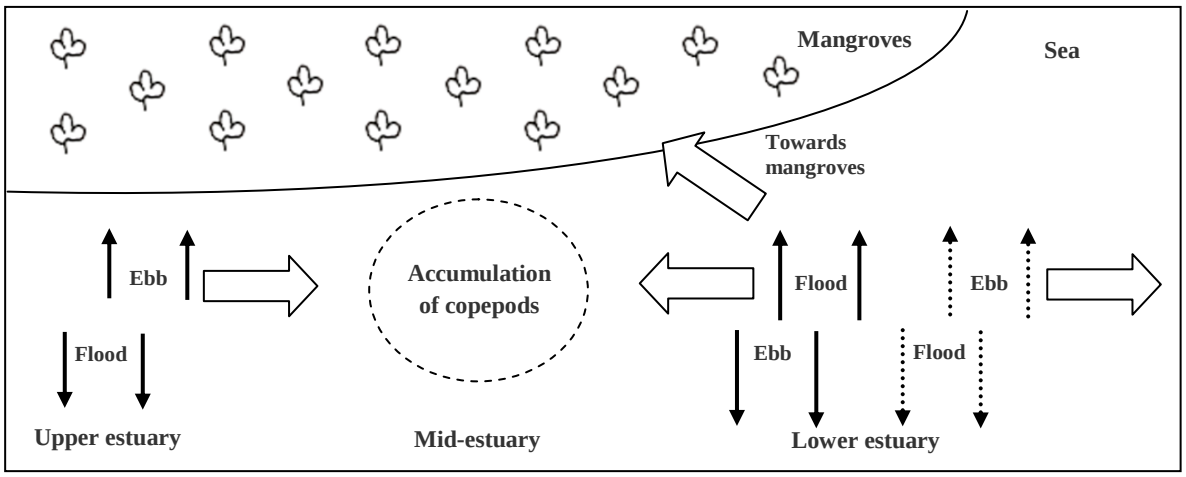


Fig. 6.4. Schematic diagram (not to scale) of the proposed adaptive position-dependent TVM. The solid arrows indicate estuarine copepods, thin dashed arrows indicate neritic copepods, and thick arrows indicate net horizontal movement.

Although an extensive zooplankton collection was made in the present study, knowledge on the distribution pattern of the demersal copepod *P. annandalei* is still lacking and less conclusive due to the sampling limitations of the present study. *P. annandalei* especially its adult stage was sampled in considerable numbers only during the wet spring tide at the lower estuary (Chapter 4). This distribution pattern merits further study to test the hypothesis that *P. annandalei* is restricted to the low salinity

region such as the upper reaches of Matang. Because of intense predation pressure by fish, the amplitude of its diel vertical migration may not be as extensive as other dominant copepod species in the same estuaries. The study should also include a test to determine whether the estuarine turbidity maximum as observed in other estuarine systems (e.g. Roman *et* al., 2001) also occurs in the Matang mangrove estuaries and has any significant impact on the vertical migration of *P. annandalei*.

It has been reported that the zooplankton including copepods, decapod larvae and fish larvae accumulate at frontal zone of the estuary formed by convergent current flows (e.g. Epifanio, 1987; Govoni & Grimes, 1992; Russell *et* al., 1999). Increased standing stocks of zooplankton in this region offer bountiful food sources to a variety of zooplanktivorous fish in the estuarine system (Morgan *et* al., 2005). The lateral boundary layer formed by two different water masses (see Wolanski *et* al., 1992) does occur in the Matang mangrove estuaries during the period of wet spring tides (personal observation). However, its impact on zooplankton community was not evaluated in the present study. Therefore, it is interesting to know whether such physical processes can affect zooplankton community structure and composition, and thus the trophic interactions in mangrove estuaries.

Pagano *et* al. (2006) investigated diel feeding rhythms of mesozooplankton in the tropical estuary of Senegal and found that the dominant zooplankton taxa such as larvae of cirripede and calanoid copepods had maximal gut florescence at night. This suggests that feeding activity of zooplankton peaked at nighttime. In the present study, there was a substantial drop in chl. *a* during the night, but increase in the abundance of dominant adult copepods. As diel vertical migration does occur in the community of microalgae, it cannot be ascertained whether a significant drop in chl. *a* was associated with intense grazing pressure by herbivorous zooplankton or nocturnal sinking of

microalgae, until further studies are conducted to determine the diel feeding behaviour of zooplankton or nocturnal sinking of microalgae.

6.5 Conclusion

The present study can be considered as the first comprehensive ecological study on mangrove and nearshore zooplankton community in Malaysia. The study has fulfilled all the three major objectives that were set out. Two main findings of the present study including the highly dynamic zooplankton community (objective 1) which appears sensitive to the changes in environmental factors (objective 2), and the crucial role played by zooplankton in the estuarine food web (objective 3) support the two hypotheses tested in the present study. The findings suggest that any anthropogenic disturbance on the zooplankton populations crucial to the nutrition of juvenile fish in nursery areas could have an impact on coastal fisheries. Therefore, the present study has not only contributed to the existing knowledge on tropical zooplankton and mangrove ecology, but also to fundamental knowledge pertinent to coastal fishery management. Zooplankton assessment appears be a valuable tool to evaluate the importance of fish nursery areas as well as in environmental impact assessments. Although the present study did not show substantial contribution of mangrove-derived carbon to the nutrition of zooplankton and small-sized fish, the mangrove ecosystem is known to function as sink and source for various organic and inorganic nutrients, which are essentially important for phytoplankton production. Moreover, the complex mangrove root system and surface sediments that are covered by mangrove leaf litter and detritus would serve as refugia for the variety of fish and other aquatic animals.

SUMMARY

1. Climate of the study area is dictated by monsoon seasons, with SW monsoon commencing from May to September, and NE monsoon from November to March. The transition between SW and NE monsoons, called the intermonsoon (IN period), occurs in April and October. The SW monsoon is generally characterized by lower rainfall, while the IN period and NE monsoon generally bring heavy rainfall.
2. The spatial and temporal variability in environmental parameters of the Matang mangrove estuaries and adjacent coastal waters was primarily influenced by the extent of freshwater input and tidal mixing. Generally, there was a gradual increase in salinity, pH and DO level from the upper estuary to offshore waters. Turbidity, dissolved inorganic nitrogen and chl. *a* did not show similar changes, but lower values were often recorded in offshore waters. Mean temperature and PO_4^{3-} appeared to be spatially constant.
3. During the NE and IN periods, salinity and pH were markedly depressed by substantial freshwater input, and values of both parameters increased during low rainfall. Unlike salinity and pH, freshwater input generally increased the DO level and dissolved inorganic nutrients. Peak chl. *a* was observed with a lag period after the estuaries were replete with dissolved inorganic nutrients. A notable drop in DO level, however, appeared to coincide with maximal chl. *a* probably due to high microbial activity. These findings were observed during the IN period and NE monsoon.
4. There were generally no marked changes in environmental parameters during the SW monsoon except for the months of strong winds in August 2002 and July 2003. Perhaps due to wind-induced horizontal tidal mixing, salinity was found to be spatially homogenous during the months coinciding with strong winds. Monthly

chl. *a* during the period of SW monsoon was at low level except for the months that coincided with strong winds when chl. *a* was above overall mean. Temperature did not vary significantly between monsoon seasons.

5. A strong stratification in salinity, pH, DO level and temperature was observed during the wet neap tides. The scale of stratification for these physical parameters appeared to be smaller during the dry neap tides. All these parameters became vertically well mixed across the water column during spring tides. Chl. *a* often peaked during daytime and dropped abruptly during the night.
6. Total zooplankton biomass and density of monthly samples ranged from 46.1 mg m^{-3} to 2718.9 mg m^{-3} and 3,425 ind m^{-3} to 469,666 ind m^{-3}, respectively. Average standing stocks increased progressively from the upper estuary through mid- and lower estuary to nearshore water and decreased in further offshore. Zooplankton community was predominated by copepods which contributed 62% of the overall mean total zooplankton abundance, followed by cirripede larvae (18%) and polychaete larvae (4%). Protozoans, decapods, gastropods, chaetognaths, larvaceans and bryozoan larvae each contributed 1 to 3%.
7. The most dominant copepod species were *P. crassirostris, A. spinicauda, O. simplex, B. similis* and *E. acutifrons*, while the subdominant species were *P. elegans, O. aruensis, O. dissimilis* and *O. attenuata*. Copepodids of *Tortanus, Pseudodiaptomus* and pontellids were also frequently sampled but not their adults. Almost all cirripede larvae were captured at the naupliar stages. Larvae of sergestids, luciferids, diogenids and brachyurans dominated the decapod community, while sabellariids and spionids dominated the polychaetes.
8. Monthly mean abundance of copepods at five sampling stations ranged from 3,030 to 62,650 ind m^{-3}. Although the abundance of copepods was generally highest at nearshore waters (20,311 ± 12,892 ind m^{-3}), the seasonal maximum of

copepod abundance of 62,650 ind m^{-3} was obtained at the upper estuary. The pooled copepod abundance was significantly higher during the IN period and NE monsoon as compared to SW monsoon, suggesting that copepod abundance was closely linked to the rainfall pattern. Three dominant copepod species *A. spinicauda*, *P. crassirostris* and *O. simplex* were significantly more abundant during the IN period and NE monsoon, while abundance of *B. similis* and *E. acutifrons* did not significantly differ between monsoon seasons.

9. Cirripede larvae occurred all year round, with an exceptionally peak abundance in October 2002. Cirripede larvae were found to be more numerous than copepods on some sampling occasions (July 2002, May and October 2003) at the lower estuary and nearshore waters. Polychaete larvae were significantly more abundant during the SW monsoon as compared to during the IN period and NE monsoon. The variability in abundance of polychaete larvae between monsoons occurred mainly at the mid- and lower estuary. Polychaete larvae were found to be more abundant than copepods in June 2003 at the lower estuary.
10. A total of 99 zooplankton taxa from routine monthly sampling were identified. Fourty-eight taxa were representatives of the Copepoda. Species richness of zooplankton and copepods were highest at nearshore waters (zooplankton: 82 taxa, copepods: 42 taxa) followed by offshore (78, 39), lower estuary (72, 34), mid-estuary (66, 29) and upper estuary (61, 25). Copepod community inside the mangrove estuaries was characterized by low diversity but high dominance, whereas the lower estuary and adjacent coastal waters showed the opposite.
11. There were gradual changes in zooplankton community structure from the upper estuary to offshore waters. Zooplankton taxa that were more confined within the estuaries included *A. spinicauda*, *Acartia* sp. 1, *O. dissimilis* and *O. aruensis*. Nearshore and offshore waters composed of various neritic copepod species (e.g.

Centropages spp., *A. erythraea, P. aculeatus, A. gibber*, *Corycaeus* spp., *Tortanus* spp., *Oithona* spp. etc), most meroplanktonic larvae and larvaceans. The euryhaline zooplankton such as the copepods *P crassirostris*, *P. elegans*, *O. simplex* and *B. similis*, the protozoans, and the chaetognaths were common in both estuarine and coastal waters. Seasonal shift in community structure occurred at the lower estuary, where the estuarine zooplankton were predominant during the IN period and NE monsoon, whereas the stenohaline and euryhaline zooplankton were predominant during the SW monsoon.

12. Total zooplankton biomass and abundance in all samples collected during the 24-hour sampling ranged from 27.6 to 6122.4 mg m^{-3} and 510 to 77,741 ind m^{-3}, respectively. Large-sized zooplankton (>500 µm) displayed diel and tidal vertical distribution particularly in the dry period. Abundance was higher at the bottom than at the surface during the day and ebb tide, and became homogeneously distributed across the water column during the night and flood tide. These patterns were not observed for zooplankton from the smaller size fractions (<500 µm).
13. Generally, the four most dominant copepod species *A. spinicauda, P. crassirostris, B. similis* and *O. simplex* and mysids exhibited a clear diel pattern, with higher abundance during night than day. Abundance of the dominant copepod species was also found to be higher at the bottom than surface, especially during daytime. Meroplanktonic larvae such as cirripedes, polychaetes and brachyurans did not display a significant diel but tidal pattern. Abundance of these larvae was consistently higher during ebb tide than during flood tide. There was no clear depth pattern observed for these meroplanktonic larvae.
14. The neap tide community during the dry period was composed of various neritic copepods (e.g. *C. dorsispinatus* and *T. barbatus*) and meroplanktonic larvae. The neap tide community during the wet period was characterized by the estuarine

copepod *A. spinicauda*, while the demersal copepod *P. annandalei* occurred in greater number during the wet spring tide. *P. crassirostris*, brachyuran zoeae and some peracarids occurred in equal numbers during both dry and wet period, but were consistently more abundant during spring than neap tide. *B. similis*, *O. dissimilis*, *O. simplex* and *E. acutifrons* did not show a clear lunar pattern in abundance.

15. The feeding preference of the 26 common fish species found in the Matang mangrove estuaries can be categorized into four major groups: 1) copepod and other zooplankton feeders, 2) decapod and peracarid feeders, 3) herbivores-detritivores or iliophagous feeders, and 4) mixed feeders. Copepods were the most important food source, with 52% of the fish feeding on these animals. Five to 16% of fish consumed *Acetes*, mysids, cirripede larvae and amphipods. *P. annandalei* was the most important copepod species consumed by most juvenile and small-sized mangrove fishes. The dominant copepods *Acartia* and *P. crassirostris* were mainly exploited by ambassids and engraulids. The hyperbenthic shrimps *Acetes* and mysids were fed by various economically-important fish species such as carangids, snappers, threadfins and grunters.
16. Stable isotope analysis indicated that zooplankton relied primarily on phytoplankton and benthic microalgae, whereas the contribution of mangrove-based carbon to zooplankton nutrition was negligible. Phytoplankton and benthic microalgae were assimilated by fish species via intermediaries at the lower reaches and coastal waters. It was still unclear whether fish species found in the more enclosed upper reaches utilized a mixture of carbon from mangrove and phytoplankton or ^{13}C-depleted estuarine phytoplankton.
17. The range of $\delta^{15}N$ values indicated at least four trophic levels in the Matang mangrove food web. The piscivores at the fifth trophic level were few.

Zooplankton were at the second and third trophic levels. The findings of both stomach content and stable isotope analyses corroborate the importance of zooplankton to mangrove fish nutrition and support that phytoplankton are important food source for zooplankton in open turbid waters of Matang mangrove estuaries.

18. Despite some sampling limitations, the present study has given rise to several hypotheses which deserve further testings and research.