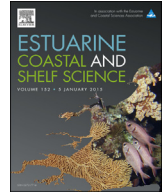




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Vertical migration and positioning behavior of copepods in a mangrove estuary: Interactions between tidal, diel light and lunar cycles

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ABSTRACT

Two-hourly zooplankton samplings encompassing tidal (semi-diurnal), diel (24 h), and lunar (4 phases) cycles during the dry (July 2003) and wet (November 2003) monsoon periods were conducted in the Matang estuary to investigate the vertical distribution and behavior of five different groups of copepods (estuarine, euryhaline, marine euryhaline, stenohaline and nocturnal pontellids) in response to the tidal and light regime. Diel vertical migration (DVM) was evident for all copepod groups but the observed patterns differed among species and sampling period (wet or dry and neap or spring tide). Tidally-induced vertical migration (TVM), superimposed by DVM, was observed for estuarine, marine euryhaline and stenohaline copepods but not for euryhaline and nocturnal pontellid copepods. Estuarine copepods tended to ascend during night-flood tide and descent to the bottom during day-ebb tide; this suggests a selective mechanism to penetrate upstream and maintain position in the estuary. In contrast, the marine euryhaline and stenohaline copepods remained at the bottom especially during day-flood tide and ascended into the water column during night-ebb tide; this suggests a selective mechanism to avoid upstream transport. Euryhaline copepods did not respond to tidal advection probably due to their wide range of salinity tolerance, while the large nocturnal pontellid copepods have strong swimming ability. Adaptive vertical migration appears to be a major factor structuring the copepod community in tropical estuaries, and its occurrence in most copepods suggests that neritic marine zooplankton tidally-advected into estuaries and nearshore waters can survive better than previously thought.

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1. Introduction

Estuarine copepods have evolved adaptive mechanisms to compensate for their loss in numbers due to the strong bi-directional tidal-river flow, large salinity fluctuations and intense predation pressure. Among the hypothesized adaptive mechanisms, such as high reproductive rate (Ketchum, 1954; Kimmerer and McKinnon, 1987; Gupta et al., 1994), passive accumulation in the turbidity maximum zone (Castel and Veiga, 1990; Morgan et al., 1997; Roman et al., 2001),

behavioral responses that involve vertical (e.g. Zaret and Suffern, 1976; Wooldridge and Erasmus, 1980) and horizontal (Cronin et al., 1962; Wooldridge and Erasmus, 1980; Roddie et al., 1984) migrations are the most studied. Studies have shown that copepods can sustain their population numbers in estuaries through a combination of these mechanisms (Ueda et al., 2010; Schmitt et al., 2011).

Behavioral responses with respect to diel and tidally-induced vertical migrations are mediated by several factors. Light is a major environmental cue regulating diel vertical migration (DVM) observed in marine copepods (Forward, 1988; Cohen and Forward, 2009). Predator avoidance is a prime selective force for DVM since strong evidence shows that large marine copepods move down below the surface layer to avoid visual predators during daytime (e.g. Bollens et al., 1992; Hays, 1994). While large adult copepods ascend the water column during night, small or young copepods may adopt a reverse migrating behavior as their adults to evade

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non-visual, nocturnal predators (Ohman, 1990). In contrast, tidally-induced vertical migration (TVM) of copepods as observed in estuaries is strongly controlled by tidal flow (e.g. Hough and Naylor, 1991; Devreker et al., 2008; Ueda et al., 2010). Species may migrate to surface water where they then either move upstream or downstream with the tide. On the other hand, if they move down to the low current layer at the bottom, net displacement is reduced. Such behaviour that interacts with the tidal current periodicity could explain retention or upstream penetration of zooplankton in the estuary, a phenomenon known as selective tidal transport (Hough and Naylor, 1991; Devreker et al., 2008; Schmitt et al., 2011).

The effectiveness of TVM is dependent on the animal's swimming ability as well as the local hydrodynamic conditions (Ueda et al., 2010; Kimmerer et al., 2014). Nevertheless, how the different species of copepods, with different swimming ability, disperses from or remain in the estuary (or coastal waters) is still poorly understood (Naylor, 2006). Some studies argue that the small estuarine copepods are unable to override a net seaward export due to their weak swimming ability (e.g. Kimmerer et al., 2002; Devreker et al., 2008; Schmitt et al., 2011), and therefore, their retention must result from TVM interacting with the local hydrodynamic processes, e.g. passive accumulation due to convergence of two different water masses (Devreker et al., 2008; Ueda et al., 2010; Kimmerer et al., 2014). In contrast, TVM has not been observed in neritic copepod species (Kimmerer and McKinnon, 1987; Shang et al., 2007). It may explain why neritic stenohaline zooplankton brought into estuaries by currents are unable to live successfully leading to a net degradation of their population size (Kimmerer and McKinnon, 1987; Heip et al., 1995).

While spatial and long-term (month, year) studies are the most common for estuarine zooplankton, short-term temporal studies (day, week) encompassing fine-scale samplings are less common. Fine-scale sampling (at hourly intervals or less) are however necessary to elucidate both DVM and TVM processes. Most studies on small-scale variability of copepods were conducted mainly in temperate estuaries (e.g. Devreker et al., 2010; Ueda et al., 2010; Goncalves et al., 2012) and only a few in tropical estuaries (e.g. Krumme and Liang, 2004; Magalhães et al., 2011). Such studies focused mainly on surface water and so-called truly estuarine copepods (e.g. *Eurytemora affinis*, *Acartia* spp., *Pseudodiaptomus* spp.), neglecting the euryhaline and marine euryhaline copepods. However, in the Matang estuary (Malaysia), Chew and Chong (2011) reported that euryhaline copepods made up at least 32% of the total zooplankton assemblage. Moreover, the estuarine zooplankton assemblage of Matang was primarily influenced by salinity and phytoplankton abundance, both dictated by the prevailing monsoon (Chew and Chong, 2011), and subjected to high risk of fish predation (Ooi and Chong, 2011; Chew et al., 2012).

The present study aims to better understand how estuarine, euryhaline and stenohaline copepods adapt to living in the highly variable environment of the estuary. Given the scenario of substantial riverine discharge, moderate tidal currents and intense zooplankton predation, it is hypothesized that copepod species differing in salinity tolerance adopt different strategies to maintain their position in the Matang estuary. The objective of this study is to test the hypothesis by analyzing the small-scale (two-hourly) temporal variability of copepod abundance by water depth, with respect to the tidal, diel light and lunar cycle during the dry and wet monsoon periods.

2. Methods

2.1. Study site

The Matang Mangrove Forest Reserve (MMFR) is located on the west coast of Peninsular Malaysia (4° 50'N, 100° 35'E) (Fig. 1). The

complex interconnected estuaries in the MMFR are fringed by largely *Rhizophora apiculata* Blum. The tidal regime of the estuaries is semidiurnal, with mean tidal heights of 2.1, 1.5, 0.9 and 0.3 m above Chart Datum at MHWS, MHWN, MLWN and MLWS, respectively (National Hydrographic Centre, Malaysia); hence, MMFR can be classified as a mesotidal delta (Hayes, 1975). Mean flow discharges recorded at the nearest hydrology station (approximately 33 km upstream) during the dry and the wet sampling periods were 18.7 m³ s⁻¹ and 26.7 m³ s⁻¹, respectively (Water Resources Management and Hydrology Division, Malaysia). In the Matang system, the range of maximum neap and spring tidal current speeds recorded at the mouth of the Jaha River were 25–30 cm s⁻¹ and 40–50 cm s⁻¹, respectively (Madin et al., 2010), while the maximum spring tidal current speed recorded at mid-stream of the Selinsing River was 56 cm s⁻¹ (H.R.Singh, MARA Technology University, pers.comm.). Water parameters are largely altered by the tides and climatic factors. Freshwater inflows and weak vertical mixing during neap tide form a temporary salt wedge which can extend 10 km upstream from the river mouth (Tanaka and Choo, 2000).

2.2. Field collection

A Eulerian survey was carried out at a fixed station (6.0 m – 7.3 m depth) located at the mouth of the Sangga Kecil River (Fig. 1). A 30 cm-mouth diameter Clarke-Bumpus sampler (KAHLSICO, USA) with 160-µm mesh net and opening-closing mechanism was used to collect zooplankton at two depth strata. Horizontal tows were made at surface (0.5 m from the surface) and bottom (0.5 m from the sediment bottom) water. Two-hourly samples were taken for 24 h, through two high tides and two low tides, 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) during the dry period of the year 2003. Another series of zooplankton samplings for the wet period in the same year was carried out 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). Each plankton tow was conducted for a duration of approximately 5 min to avoid excessive net clogging. Duplicate samples of zooplankton were collected at each depth stratum. Total filtration volume of each tow ranged from 23 to 111 m³. Towed samples were collected in separate bottles and preserved with 10% buffered formaldehyde before laboratory analysis.

At each sampling interval, water parameters were measured in-situ by a Hydrolab 4a multi-parameter sonde (HACH Hydromet, USA) at the surface and bottom water layer, while water samples for chlorophyll *a* (chl. *a*) analysis were collected from the surface layer.

2.3. Laboratory procedures

Individual zooplankton samples were gently sieved through stacked 1000-µm, 500-µm, 250-µm and 125-µm Endecott sieves. For enumeration, the samples were split between 1–5 times using a Folsom plankton splitter. Adult copepods were identified to species or the lowest possible taxon, while naupliar and copepodid stages were not included in the present study. All large copepods (>1 mm) were counted in a Petri dish. Small copepods (<1 mm) were subsampled using a 1-ml Stempel pipette before transferring into a 1-ml Sedgewick-Rafter cell for total counts. Copepod abundance was estimated as number of individuals per m³ (inds. m⁻³). Surface chl. *a* concentrations (µg L⁻¹) was measured using the fluorometric method (Parsons et al., 1984).

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