Available online at www.sciencedirect.com
ScienceDirect
Estuarine, Coastal and Shelf Science 76 (2008) 797–808
ESTUARINE COASTAL AND SHELF SCIENCE
www.elsevier.com/locate/ecss

Size-dependent distribution and feeding habits of *Terebralia palustris* in mangrove habitats of Gazi Bay, Kenya

Ellen Pape [a], Agnes Muthumbi [b], Chomba Peter Kamanu [c], Ann Vanreusel [a,*]

[a] *Biology Department, Marine Biology Section, State University of Ghent, Krijgslaan 281/S8, B-9000 Ghent, Belgium*
[b] *School of Biological Science, University of Nairobi, P.O. Box 30197-00100, Nairobi, Kenya*
[c] *Jomo Kenyetta University of Agriculture and Technology, P.O. Box 62000, Nairobi, Kenya*

Received 19 January 2007; accepted 14 August 2007
Available online 6 September 2007

Abstract

The gastropod *Terebralia palustris* often dominates the surface of muddy to sandy substrates of intertidal mudflats and mangrove forests, where they clearly destabilize the sediment. In the present study, it was investigated whether and to what extent the behaviour of juvenile and adult snails differs among habitats (mudflat vs. mangrove stand) in a *Sonneratia alba* mangal at Gazi Bay, Kenya. For this purpose we: (1) examined their distribution along three land–sea transects; and (2) applied stable isotope analysis to determine the feeding patterns of different-sized snails from the mangrove and mudflat habitats. Additionally, we investigated if these gastropods exert an impact on microphytobenthic (diatom) biomass, and whether this is size-dependent. The latter objective was met by either enclosing or excluding different-sized snails from experimental cages on the intertidal mudflat and the subsequent assessment of a change in pigment concentration of the sediment surface. In agreement with several previous studies conducted in other mangroves and geographical locations, a spatial segregation was demonstrated between juveniles (more common on the mudflat) and adults (more common in the mangrove forest). On the intertidal mudflat juveniles avoided sediment patches characterized by highly saline water in intertidal pools and a high mud content, while adults tended to dwell on substrates covered by a high amount of leaf litter. Stable carbon isotope analysis of the foot tissue of snails sampled from the *S. alba* stand and the mudflat indicated a transition in food source when a shell length of 51 mm is reached. Considering the $\delta^{13}C$ value of juveniles, it seems they might be selecting for microphytobenthos, which might explain their preference for the mudflat. The diet of size classes found in both habitats did not differ significantly, although juveniles inhabiting the mangrove forest were slightly more depleted in ^{13}C compared to those residing on the mudflat. Assuming juveniles feed on benthic microalgae and considering the lower microalgal biomass inside the mangrove forest, this may be a consequence of a higher contribution of other, more ^{13}C depleted organic carbon sources, like phytoplankton, to their diet. Experimental results indicate a negative, but insignificant, impact on benthic diatom biomass by juveniles (due to grazing) and adults (due to physical disturbance). This finding seems to be in agreement with the results of the stable carbon isotope analysis, strongly suggesting the selective feeding of juvenile *T. palustris* on benthic diatoms.

Keywords: Terebralia palustris; stable isotopes; mangroves; cages; microphytobenthos; sediment; meiobenthos; Kenya, Gazi Bay

1. Introduction

Mangroves create unique ecological environments that are characterized by a remarkable biodiversity. The muddy or sandy sediments of these forests are home to a wide variety of marine invertebrates. The important role of these animals in the food web, nutrient cycling and overall energy-flux of mangrove ecosystems has often been the subject of ecological research (for a review, see Kathiresan and Bingham, 2001). Most of the studies have only dealt with decapod crustaceans (Dittmann, 1993; France, 1998; Skov and Hartnoll, 2002), although they are not the sole representatives of mangrove macrofauna and they are greatly outnumbered by gastropods,

* Corresponding author.
E-mail address: ann.vanreusel@ugent.be (A. Vanreusel).

0272-7714/$ - see front matter © 2007 Elsevier Ltd. All rights reserved.
doi:10.1016/j.ecss.2007.08.007

especially by potamidids of the genus *Terebralia* (Kathiresan and Bingham, 2001). Recently, it has become apparent that *Terebralia palustris* (Potamididae: Gastropoda) is crucial in the nutrient cycling process in mangrove forests as this species is responsible for processing a significant amount of leaf litter (Slim et al., 1997; Fratini et al., 2004).

The snail *Terebralia palustris*, also known as mud creeper or mudwhelk, is the largest and most widely distributed member of the family of the Potamididae and should be regarded as one of the major constituents of the Indo-Pacific mangal invertebrate fauna, in terms of biomass and ecological impact (Fratini et al., 2004). *Terebralia palustris* is by far the largest prosobranch in mangrove habitats. In Arnhem Land, Australia, Houbrick (1991) observed *T. palustris* snails, measuring up to 190 mm. In Kenya the largest *T. palustris* shell measured is 130 mm (Fratini et al., 2004). These gastropods often are predominant on the surface of muddy substrates of mangrove forests (Nishihira, 1983). In Gazi Bay, Slim et al. (1997) noted an average density of 33 *T. palustris* m^{-2} in a *Ceriops tagal* vegetation zone.

Terebralia palustris is a truly amphibious species, active both at low and high tides (Fratini et al., 2000, 2001). However, this snail seems to avoid the driest landward and the most exposed seaward zone of the mangrove forest, by clustering on the typically fine substrata of the most shaded patches and in small tidal pools formed in between the aerial roots of mangrove trees (Houbrick, 1991; Slim et al., 1997).

Several authors (Wells, 1980; Houbrick, 1991; Slim et al., 1997) have noted a clear spatial segregation between juveniles and adults. Juvenile *Terebralia palustris* colonise the small creeks and large pools on the seaward front of the forests and are thought to migrate into the landward belts when reaching their adult stage. This migratory behaviour between open mudflats and mangrove forests seems to be related to a change in diet (Houbrick, 1991). However, Fratini et al. (2004) found no separation in habitat selection between juveniles and adults, as they were dwelling together in the mangrove stand and on the intertidal flats in Dabaso (*Rhizophora mucronata*) and Mida (*Avicennia marina*), Kenya.

It is widely recognized that juvenile and adult *Terebralia palustris* differ in their food preferences. Juveniles have been considered as either detrivores (Nishihira, 1983; Houbrick, 1991; Fratini et al., 2004) or deposit-feeders (Slim et al., 1997) while adults graze on plant materials such as leaf litter, mangrove propagules and fruits (Nishihira, 1983; Houbrick, 1991; Slim et al., 1997; Dahdouh-Guebas et al., 1998; Fratini et al., 2004). This has been confirmed by both stomach-content analysis (Fratini et al., 2004) and stable isotope analysis (Slim et al., 1997). The trophic dimorphism between juvenile and adult *T. palustris* has been associated with anatomical differences in the structure of their radula (Houbrick, 1991). The danger of being turned upside down or dragged into a burrow of sesarmid crabs might partly account for the fact that young *T. palustris* do not feed on leaves (Fratini et al., 2000). These crabs have been shown to heavily compete with *T. palustris* as they exhibit wide overlap in food items, zone of feeding and time of feeding (Fratini et al., 2000). This interspecific competition is assumed to be the main reason why adult snails are frequently observed to feed in clusters on a single fallen mangrove leaf, as it is believed that the crabs are only able to steal leaves from clusters that consist of less than eight individuals (Fratini et al., 2000).

Terebralia palustris is known to be a surface-dwelling organism and while grazing on the sediment, its heavy shell rearranges the mud surface by leaving an approximately 0.5 cm deep track (Carlén and Olafsson, 2002). Due to its high abundance and surface-dwelling behaviour, *T. palustris* is likely to have an impact on the biotic and abiotic properties of the sediment surface layer. Several authors (for a review, see Olafsson, 2003) have studied the interactions between macroepifauna and infaunal communities in marine soft-bottoms by means of cage exclusion experiments. Several studies (Nichols and Robertson, 1979; Branch and Branch, 1980; Schrijvers et al., 1995, 1997) have indicated a significant increase in microphytobenthic biomass in the absence of macroepifauna. Macrofauna may exert biological disturbance on infaunal communities by physical force, creation of microhabitats, predation or competition for food resources (Sherman and Coull, 1980; Palmer, 1988).

In the current study we investigated whether and to what extent the behaviour of juvenile and adult *Terebralia palustris* depends upon habitat. For this purpose, we compared a *Sonneratia alba* stand and an intertidal mudflat in terms of:

(1) The abundance of juvenile and adult gastropods, by examining their distribution along land–sea transects. Furthermore, snail abundance was studied in relation to relevant environmental conditions (humidity at low tide, leaf litter, etc.)
(2) The diet of juveniles and adults, by sampling several specimens representing different size classes from the mangrove forest and the open mudflat for carbon stable isotope analysis. This way the relative importance of size and habitat selection for the specific food uptake of *Terebralia palustris* was examined.

In addition, we conducted a combined in- and exclusion experiment on the intertidal mudflat to study the short-term (24 h) impact of juvenile and adult *Terebralia palustris* on pigment concentration of the sediment surface as a proxy for microphytobenthic (diatom) biomass.

2. Materials and methods

2.1. Site description

The present study was performed at Gazi Bay (39°30′ E, 4°22′ S), located about 50 km south from Mombasa, Kenya. The bay itself harbours large areas of seagrass beds, which are dominated by *Thalassodendron ciliatum* (Coppejans et al., 1992). The upper region of the bay receives freshwater from the Kidogoweni River, which cuts through the mangroves. Spring tidal range in Gazi Bay is reported to be 3.2 m (Kitheka, 1997). The distribution of *Terebralia palustris*