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Carbon and nitrogen balance of leaf-eating sesarmid crabs (*Neoepisesarma versicolor*) offered different food sources

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Abstract

Carbon and nitrogen budgets for the leaf-eating crab, *Neoepisesarma versicolor*, were established for individuals living on pure leaf diets. Crabs were fed fresh (green), senescent (yellow) and partly degraded (brown) leaves of the mangrove tree *Rhizophora apiculata*. Ingestion, egestion and metabolic loss of carbon and nitrogen were determined from laboratory experiments. In addition, bacterial abundance in various compartments of the crabs' digestive tract was enumerated after dissection of live individuals. Ingestion and egestion rates (in terms of dry weight) were highest, while the assimilation efficiency was poorest for crabs fed on brown leaves. The low assimilation efficiency was more than counteracted by the high ingestion rate providing more carbon for growth than for crabs fed green and yellow leaves. In any case, the results show that all types of leaves can provide adequate carbon while nitrogen was insufficient to support both maintenance (yellow leaves) and growth (green, yellow and brown leaves). Leaf-eating crabs must therefore obtain supplementary nitrogen by other means in order to meet their nitrogen requirement. Three hypotheses were evaluated: (1) crabs supplement their diet with bacteria and benthic microalgae by ingesting own faeces and/or selective grazing at the sediment surface; (2) assimilation of symbiotic nitrogen-fixing bacteria in the crabs' own intestinal system; and (3) nitrogen storage following occasional feeding on animal tissues (e.g. meiofauna and carcasses). It appears that hypothesis 1 is of limited importance for *N. versicolor* since faeces and sediment can only supply a minor fraction of the missing nitrogen due to physical constraints on the amount of material the crabs can consume. Hypothesis 2 can be ruled out because tests showed no nitrogen fixation activity in the intestinal system of *N. versicolor*. It is therefore likely that leaf-eating crabs provide most of their nitrogen requirement from intracellular deposits following occasionally ingestion of animal tissue (hypothesis 3).

Keywords: assimilation efficiency; carbon and nitrogen budgets; defaecation; ingestion; *Neoepisesarma versicolor*; sesarmid crab

1. Introduction

Leaf-eating sesarmid crabs play a significant role in the detritus food-chain and energy flow in most mangrove environments (Robertson, 1986; Poovachiranon and Tantichodok, 1991; Lee, 1998; Skov and Hartnoll, 2002). The crab *Sesarma messa* is known to process 30–70% of the total leaf production in Australian mangrove forests by eating both attached leaves and fallen leaf litter (Robertson et al., 1992). Similarly, populations of sesarmid crabs (e.g. *Neoepisesarma versicolor*) can handle 87% and potentially ingest 52% of the daily leaf litter fall in mangrove forests of Thailand (N. Thongtham, unpublished). By feeding on leaf litter and other debris that has fallen from trees, sesarmid crabs prevent tidal export of valuable nutrients from the mangrove environment (Lee, 1998). The crabs

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also initiate and enhance the breakdown of mangrove detritus and recycling of nutrients. After maceration and passage through crab guts the litter is incompletely digested and returns to the environment as faecal pellets, which contain readily available substrates for bacterial colonization and ultimately for other organisms of the detritus food-chain (Lee, 1997; Kristensen and Pilgaard, 2001).

Leaves of mangrove trees are characterized by a high concentration of polyphenolic compounds, such as tannins, which make them unpalatable to herbivores (Camilleri, 1992). The energy content, as well as availability of carbon and nutrients, vary depending on the tree species, and also differ between fresh, senescent and partly degraded litter. In general, leaves are low in nitrogen, which may be an important limiting factor for herbivores, whereas carbon is found in more available forms. In order to maintain growth, the C:N ratio of invertebrate food must not exceed 17 (Russel-Hunter, 1970), which is considerably lower than the C:N ratio of about 100 for mangrove leaf litter (Kristensen et al., 1995). Thus, excess carbon (about 75%) from the litter must be removed before it is an adequate nitrogen source for crabs. Nitrogen gained from the food is required for reproduction, growth and moulting (Linton and Greenaway, 2000) and when the nitrogen level in the food is below that required for maintenance, the survival of crabs is affected.

Although many studies have examined the role of leaf-eating and -handling by sesarmid crabs for the mangrove detritus food-chains (e.g. Robertson, 1986; Lee, 1997, 1998), only a few have examined how these crabs can survive, grow and reproduce on a nutrient-poor leaf diet (e.g. Micheli, 1993a; Kwok and Lee, 1995) and reproduce on a nutrient-poor leaf diet. Lee (1997) suggested that the sesarmid crab, *Sesarma messa*, is capable of utilizing carbon, but not nitrogen from *Rhizophora stylosa* leaf litter. Furthermore, Skov and Hartnoll (2002) speculated that leaf-eating crabs must obtain essential nutrients, like nitrogen, from other sources than the leaf litter.

This study attempts to determine carbon and nitrogen budgets of the sesarmid crab *Neoepisesarma versicolor* when fed fresh green, senescent yellow and partly degraded brown leaves of *Rhizophora apiculata*. By following the fate of leaf litter through the gut combined with measurements of element loss via metabolism, reliable carbon and nitrogen budgets are established for *N. versicolor* living solely on a leaf diet. Since all types of leaf litter appear to be inadequate nitrogen sources, the three following hypotheses to explain how sesarmid crabs may potentially meet their nitrogen requirement are evaluated and discussed: (1) supplementary diet consisting of bacteria and benthic microalgae; (2) bacterial nitrogen fixation in the crabs' gut; and (3) nitrogen storage following random and occasional ingestion of animal tissue (e.g. carcasses).

2. Materials and methods

2.1. Sampling and handling of crabs and leaf materials

Samples were collected in the Bangrong mangrove forest (8° 03′ N, 98° 25′ E) on the northeast coast of Phuket Island, Thailand. The forest is a tide-dominated fringe mangrove which stretches as a 1-km-wide lagoon about 2 km inland. The trees, *Rhizophora apiculata*, *Rhizophora mucronata* and *Ceriops tagal* dominate the vegetation. The benthic fauna consists mostly of fiddler crabs (family Ocypodidae) and sesarmid crabs (family Grapsidae). At least five species of the latter family are common with *Neoepisesarma versicolor* and *Chiromanthes* spp. occurring at densities of up to five individuals m^{-2} (N. Thongtham, unpublished). Gastropods, represented by the families Neritidae, Littorinidae and Potamididae, are distributed sparsely on the forest floor in the low intertidal zone and on mangrove roots (Kristensen et al., 2000; Holmer et al., 2001; Thongtham and Kristensen, 2003).

N. versicolor feeds primarily at night and spend most of the day inside or resting near the entrance of their burrows (Thongtham and Kristensen, 2003). The cool and moist burrows protect the crabs from overheating and desiccation by the sun. They mainly spend the active hours between dusk and dawn feeding on mangrove leaves and scraps of material from the sediment surface. Occasionally, they climb the lower branches of trees to feed on new shoots and leaves.

Specimens of *N. versicolor* were collected at night when they emerged from their burrows. Only intact crabs having a hard carapace (i.e. in the intermoult stage) and carrying no eggs were selected. The carapace width and weight of all individuals were measured after return to the laboratory. Twenty-four individuals of mixed sex with a carapace width of 3.2–3.7 cm (mean = 3.4 ± 0.35 cm) and weight of between 21 and 34 g (mean = 26.6 ± 0.74 g) were chosen for the experiments. The crabs were acclimated to laboratory conditions and allowed to empty their gut for 60 h before starting the experiments. The sex of the crabs was recorded, but there was no difference in feeding behavior and metabolism between sexes.

Three categories of *R. apiculata* leaves were used as a food source for the crabs: green (fresh), yellow (senescent), and brown (partly decomposed). Green and yellow leaves were picked from trees, while brown leaves were collected from the forest floor at Bangrong. After selecting leaves of each category with similar color and morphology, they were all divided into two halves along the midrib and labelled; one half was used for determination of dry/fresh-weight (D/F) correlation and the other half was used for the feeding experiment. Since mangrove leaves may lose 20–40% of their weight by leaching when placed in seawater (Benner et al., 1986;