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Do allochthonous inputs represent an important food resource for benthic macrofaunal communities in tropical estuarine mudflats?

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ABSTRACT

Tropical estuarine mudflats receive a variety of allochthonous organic material made up of riverine mangrove litter, as well as marine particulate organic matter (POM), and seagrass litter. Autochthonous microphytobenthos are also an abundant type of organic matter in these systems. Previous studies show that allochthonous mangrove detritus is the dominant energy source of the mudflat food web; however, recent studies suggest that its importance has been overestimated. To elucidate the food-web dynamics of tropical estuarine mudflats, we analyzed the stable carbon-nitrogen isotope ratios of primary producers (drift mangrove litter, drift seagrass litter, marine and riverine POM, and microphytobenthos), mudflat in situ organic matter, and benthic macroinvertebrates (as the primary consumers, they are an important biological link between organic matter and predators) in three estuarine mudflats in Trang Province, Thailand. Bayesian SIAR revealed that the mudflat sediments primarily originated from an allochthonous riverine source (i.e. imported mangroves), whereas mudflat in situ POM was mainly comprised of allochthonous marine POM. Isotope analysis indicated that most benthic invertebrates in mudflats depend on autochthonous benthic micro-algae and marine allochthonous seagrass litter (including epiphytes) for food, but this is not the case for allochthonous riverine mangroves. Our results suggest that the impact of allochthonous riverine inputs as a food resource is not notable in these particular estuarine mudflats. Further study is needed to explore the function of autochthonous and marine allochthonous resources in other tropical estuarine mudflats.

1. Introduction

Nutrients and organic materials flow across ecosystem boundaries (Polis and Hurd, 1996; Polis and Strong, 1996). Such allochthonous resources promote secondary productivity in ecosystems that have little or no primary productivity (Polis et al., 1997). In environments possessing an abundance of primary producers, imported materials can be directly consumed and incorporated into the food web by detritivores, or after bacterial trophic mediation (Cebrian and Lartigue, 2004; Findlay and Tenore, 1982). Thus, allochthonous input can be a major determinant of community structure in many ecosystems.

An estuary is a common ecotone that receives both riverine and marine allochthonous materials. Several studies of vegetated estuarine habitats (including mangrove, saltmarsh, and seagrass) have been conducted from a landscape perspective; these vegetated habitats receive allochthonous resources, by trapping imported materials in vegetative structures (Hogarth, 2007; Kathiresan and Bingham, 2001; Kon et al., 2012). Its status as an exporter of vegetative material to adjacent coastal habitats has also been reported (Bouillon et al., 2000; Costa et al., 2001; Lee, 1995). In contrast, few studies have investigated the ecological function of allochthonous resources in bare intertidal mudflats, despite their importance as a biological component of estuaries (Asmus and Asmus, 1990; Yokoyama et al., 2005; Yoshino et al., 2012).

In tropical regions, mudflats receive particularly large varieties of organic matter, derived from abundant allochthonous mangrove litter (Meziane et al., 2006), along with marine particulate organic matter (POM), and seagrass litter. In addition, autochthonous microphytobenthos are another abundant type of organic matter (Al-Zaidan et al., 2006). Thus, the basis of mudflat food webs has been explored, especially via comparisons between allochthonous and autochthonous resources (Asmus and Asmus, 1990; Yokoyama et al., 2005; Yoshino et al., 2012). Until recently, it was generally assumed that mangrove litter supported the food web via a detritus-based pathway (Camilleri, 1992), as it was assumed that mangrove litter contributed significantly to river-derived allochthonous food for mudflat consumers. However, recent studies using stable isotope analysis have revealed the importance of the trophic contribution of autochthonous resources, such as microphytobenthos, to the mudflat food web (Kang et al., 1999, 2003; Sauriau and Kang, 2000; Yoshino et al., 2012). Consequently, the relative importance of allochthonous (i.e. imported drift mangrove litter) and autochthonous (i.e. in situ microphytobenthos) resources as food web

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bases remains unclear, and several authors have suggested that their roles in tropical estuarine systems deserve further study (Bouillon et al., 2002; Micheli, 1993; Newell et al., 1995).

In these systems, benthic invertebrates (as primary consumers) are important trophic links between organic matter and predators (Heip et al., 1995). Accordingly, in order to investigate the food web base and structure, descriptions of invertebrate community structures must be clarified prior to continuing the exploration of nutrient sources. Here, we reveal the relative importance of allochthonous and autochthonous materials with regard to the provision of food to the benthic faunal community in tropical estuarine mudflats. This was done by (1) describing the environmental characteristics and faunal community structures of tropical estuarine mudflats, then (2) investigating the nutrient sources of benthic invertebrates via stable isotope analysis.

2. Materials and methods

2.1. Study site

The research was conducted in three estuarine mudflats in Trang Province, Thailand (7° 32′ N, 99° 21′ E) (Fig. 1), where the dry seasons are short (January–April) and the wet seasons are relatively long (May–December). Average precipitation in this area in 2010 was 60.3 mm/month in the dry season and 262.7 mm/month in the wet season. We selected three estuarine mudflats to act as field site replicates: Rajamangala (RJ), which is located at the mouth of an estuarine creek that is up to 10 km long and 400 m wide (Rajamangala river); Raytrang (RT), which is situated at the mouth of an estuarine creek which is 4.5 km long and 150 m wide (Raytrang river); and Changrang (CR), which is situated in a creek that is 3 km long and 100 m wide (Changrang river). All intertidal mudflats are subjected to semidiurnal tides with a tidal range of 0.5–3.5 m. The banks of each river are largely occupied by thick mangrove forests dominated by *Rhizophora apiculata* (Malpighiales: Rhizophoraceae), but the mudflats themselves are not forested. The mudflats used in this study were relatively intact, natural habitats.

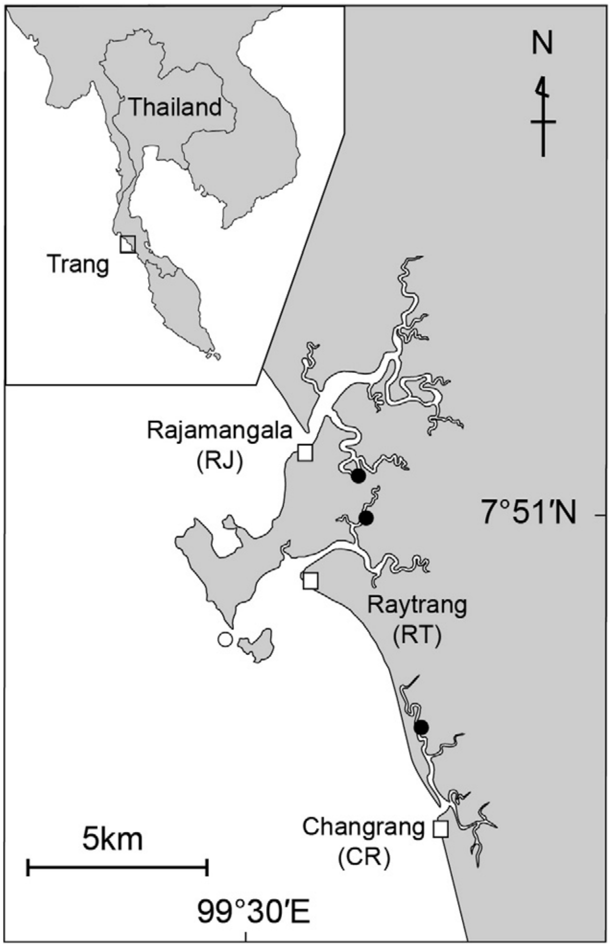

Fig. 1. Rajamangala (RJ) estuarine mudflat, Raytrang (RT) estuarine mudflat, and Changrang (CR) estuarine mudflat study sites in Trang Province, southern Thailand. □ indicates sampling stations in each estuarine mudflat. ● and ○ indicate stations where riverine and marine POM were collected, respectively.

2.2. Environment properties and faunal distribution

The environmental characteristics (i.e. water temperature and salinity, sediment grain size, and sedimentary organic matter) of each mudflat were surveyed 7–12 March (dry season), and 8–13 December (wet season) 2010. Water temperature and salinity were determined using a digital thermo-salino meter (ES-51, HORIBA Ltd, Kyoto, Japan). To quantify the sedimentary organic matter (SOM) content, a sample from the top 1–2 mm of sediment (ca. 30 g) was collected and sealed in a plastic bag. Four replicates were collected at each site. Dry weight of the soil was measured before and after combustion to a constant weight at 560 °C, and the fraction lost by combustion was used to estimate organic matter content by percentage. One sediment sample was taken from the substratum with a cylindrical corer (5 cm diameter, 20 cm high) to determine soil particle size. Median grain sizes were determined in the laboratory using the dry-sieving method (Bale and Kenny, 2005).

In all three mudflats, benthic macrofaunal samples were collected from five replicate quadrants (30 × 30 cm) randomly placed in the intertidal zone of each mudflat during low tide, and within the time frames detailed above. Macro-invertebrates were collected by excavating the soil to 20 cm below the surface, as described by Wada et al. (1987), who showed that benthic macro-invertebrates are widely distributed in the top 20 cm surface layer of soil. The sediment was sieved through a 1 mm mesh, and the residue was preserved in 10% neutral-buffered formalin fixative. The macro-organisms were sorted from the sediments, identified to species level, counted, and weighed in the laboratory. The species identified were then categorized by feeding group: as surface feeders (defined to be omnivores, surface grazers, deposit feeders that obtain their food from the sediment surface, as described by Kon et al., 2007), or suspension feeders.

2.3. Stable isotope analysis

To investigate the nutrient sources of invertebrates and the origins of the various organic matter types, we used carbon and nitrogen stable isotope analysis. Dominant species (species represented by more than three individuals per mudflat per sampling season, to maintain a minimum sample size for stable isotope analysis), suspended solids, and surface sediments were collected at each mudflat during the same date ranges described above. Epifauna were collected by hand, and infauna were collected by excavating the substrate sediment at low tide ($n = 3$–5 for each species). Suspended solids in the bottom water (600 ml) were sampled via filtration, using precombusted glass-fiber filters (Whatman GF/F, GE Healthcare, Little Chalfont, United Kingdom) ($n = 3$) to collect mudflat particulate organic matter (POM) in situ. Surface sediments were obtained by removing the top 1–2 mm of substrate at low tide ($n = 3$) for in situ sedimentary organic matter (SOM) analysis. In addition to benthic animals and in situ organic matter, we collected primary producers, to determine if they were food sources or the origin of organic detritus. All drift materials (i.e. mangrove and seagrass litter) were collected by hand ($n = 3$) at each mudflat. Although sufficient mangrove litter could be collected at all sites, the seagrass litter samples from Raytrang and Changrang were too small for stable isotope analysis. Therefore, we considered the seagrass litter samples from Rajamangla to be representative of all mudflats. Marine POM was collected offshore, and riverine POM was collected upstream