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The diets of *Littoraria ardouiniana* and *L. melanostoma* in Hong Kong mangroves

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Littoraria ardouiniana and *Littoraria melanostoma* are common snails in Hong Kong, living and feeding on mangrove trees. Gut content and stable isotopic analyses were conducted to investigate the littorinid's diets. Gut content analyses revealed these snails ingested bark, epidermal plant cells, fungi, and microalgae, but that broken plant cells were the most abundant food items in the stomach and faecal contents. The gut contents of the two littorinid species, either from the mangrove trees *Kandelia candel* or *Aegiceras corniculatum*, were similar and showed little temporal variation throughout the year. Dual stable isotopic analysis, which investigated the $\delta^{13}C$ and $\delta^{15}N$ values of the littorinids and their potential food items, indicated that these littorinids might feed on mixed diets composed of parts of the mangrove trees and other items available on the trees such as phylloplane fungi, microalgae and cyanobacteria. These epiphytic mangrove littorinids are generalist grazers which graze on the substratum non-selectively as they are constrained on their host trees, and their diets are, therefore, dependent on food availability on the trees themselves.

INTRODUCTION

Littorinids are predominantly herbivorous and feed on a variety of macroscopic and microscopic autotrophs (reviewed by Hawkins & Hartnoll, 1983; Norton et al., 1990). Since littorinids occur in a great variety of intertidal habitats such as rocky/boulder shores, mangroves and salt marshes, the food items they ingest are quite diverse. Many *Littorina* species are generalist herbivores, and are reported to feed mainly on algae (Hawkins & Hartnoll, 1983; Imrie et al., 1990; Voltolina & Sacchi, 1990). In salt marshes, however, the diet of *Littoraria irrorata* is composed of fungi and cordgrass, and may be enriched with diatoms or small invertebrates when the littorinids access the mud surfaces (Bärlocher & Newell, 1994). Mangrove littorinids of the genus *Littoraria* live and feed on the surfaces of the mangrove trees and can be considered as epiphytes (*sensu* Williams & Seed, 1992). *Littoraria* species are thought to be opportunistic feeders since they appear to browse the surface of the mangrove trees non-selectively (Jensen, 2000). Leaf epidermis, cork cells, fungi, algae and diatoms have been recorded in the guts of *Littoraria pallescens*, *Littoraria intermedia* and *Littoraria scabra* (Christensen, 1998; Jensen, 2000; Ohgaki, 1990). *Littoraria angulifera* forages on the prop roots of *Rhizophora* mangroves. The digestive tracts and faecal pellets of this species contain ground-up cork cells, trichosclereids, tracheids, calcium oxalate crystals, fungal hyphae, chlamydospores and undigested cyanobacteria (Kohlmeyer & Bebout, 1986), the relative proportions of these food items depending on the substrate last fed upon.

Gut content analysis is one of the most common methods used to study the diet of animals (e.g. Jones, 1968; Tsuda & Randall, 1971) and is a relatively straightforward, low-cost, and reliable method of investigating food ingested. It is, however, unselective and may often record material which is not assimilated (Michener & Schell, 1994). Some food items might lose their morphological characteristics more quickly than others after ingestion, thus affecting the relative accuracy of scoring (DeNiro & Epstein, 1978). To overcome this problem, stable isotope techniques have proved useful to investigate the significance of different potential food items in the assimilation of herbivores (Gearing, 1991; Rodelli et al., 1984). A combined tracer approach, such as using both $\delta^{13}C$ and $\delta^{15}N$, has been shown to be more effective than using just one isotope tracer, as the combined information of the stable carbon and nitrogen isotopic analyses can narrow down the list of potential food sources in a food web (Bunn & Boon, 1993; Michener & Schell, 1994). Investigation of the isotopic value of the potential food items can therefore provide an independent means of evaluating the effective diet of an animal and are a useful supplement to gut content analyses (Fry & Sherr, 1989).

In Hong Kong, *Littoraria ardouiniana* and *Littoraria melanostoma* are common on the leaves and stems of mangroves, such as *Kandelia candel* and *Aegiceras corniculatum* (Lee, 2001; Reid, 1986; Walthew, 1995). The aims of this study were to investigate what these littorinids ate and which food items they assimilated. To achieve this, the gut contents of these littorinids were studied using light microscopy, whilst the stable isotopic values of the two littorinid species and their potential food items were investigated to ascertain which food items were assimilated.

MATERIALS AND METHODS

Gut content analyses

Littoraria ardouiniana and *L. melanostoma* were collected from the mangrove at Sheung Pak Nai (22°27′N 113°58′E), New Territories, Hong Kong. The littorinids

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were collected when they were active, generally at night or during periods of rain. Monthly sampling was conducted in the fourth week of every month from May 1998 to May 1999. No *L. melanostoma* were collected from December 1998 to February 1999 or *L. ardouiniana* from November 1998 to February 1999 as no active littorinids could be found during the appropriate sampling period.

In general, approximately ten *L. ardouiniana* and ten *L. melanostoma* were haphazardly collected at each date, five from *Kandelia candel* and five from *Aegiceras corniculatum*. The littorinids were preserved at the site by injecting with 5% saline-buffered formalin, and then frozen and transferred to the laboratory. The stomach contents and faecal pellets were dissected and investigated using light microscopy. The stomach contents were homogenized, mounted on slides and observed under a light microscope (Olympus BX50) at ×100 magnification. Food items were identified and scored under 81 intersection points of a 100 square-ocular grid (Tsuda & Randall, 1971). Seven random views were observed for each snail. Food items were divided into six categories: bark; plant cells (e.g. epidermal layers of leaf and stem, vascular tissues, etc.); broken plant cells (plant cells without cell contents or organelles); fungi; others (identified but rarely occurring items such as cyanobacteria, diatoms, algae); and unidentified/digested material. The relative abundance of bark, plant cells, broken plant cells, fungi and the category 'others' among all identified food items was calculated as follows (Jones, 1968):

$$\text{Relative abundance (\%)} = \frac{\text{number of intersection points with items A}}{\text{intersections with all items}} \times 100 \quad (1)$$

Faecal pellets were examined in the same manner and also scored in terms of relative abundance.

To obtain balanced data, 54 littorinids were chosen randomly from each of the four categories (i.e. *L. ardouiniana* on *Kandelia candel*; *L. ardouiniana* on *Aegiceras corniculatum*; *L. melanostoma* on *K. candel* and *L. melanostoma* on *A. corniculatum*) from the monthly samples, half of which (27) were chosen to investigate variation in the relative abundance of broken plant cells, as this was the most abundant food item category (>73%) in the stomach contents, whilst the other half was chosen to investigate variation in the faecal contents. A three-factor analysis of variance (ANOVA) was conducted to investigate differences in abundance of broken plant cells between stomach and faecal contents in different littorinid species on different mangrove trees over the entire sampling period, with littorinid species (Snail), mangrove species (Tree) and gut content source (stomach or faeces; Gut) as fixed, orthogonal factors ($\Sigma N=2$ littorinid species×2 mangrove species×2 gut content sources×27 replicates=216). Due to inherent problems of non-independence between monthly sampling periods, no statistical analysis of temporal patterns was attempted.

Stable isotope analyses

Six *Littoraria ardouiniana* and six *L. melanostoma* (again three of both species from *Kandelia candel* and *Aegiceras corniculatum* respectively) were collected from Sheung Pak Nai on 29 September 1999. The littorinids were kept in the laboratory for 48 h without food to ensure that no stomach or faecal contents remained (DeNiro & Epstein, 1978; Gearing, 1991). The animals were then frozen, their shells removed and the flesh freeze-dried and ground to a powder using a pestle and mortar (Bunn & Boon, 1993).

Potential food sources of the littorinids, which included items commonly found in their gut contents, i.e. leaves, twigs and bark of *K. candel* and *A. corniculatum*, were collected from Sheung Pak Nai on the same day. As the littorinids only scraped the outermost layers of the trees (O.H.K.L., personal observation), the epidermal layers of these plant materials were peeled off and frozen.

All the items were freeze-dried and ground into powder (France, 1998). Three replicates of each specimen (*L. melanostoma* and *L. ardouiniana* on *K. candel* and *A. corniculatum*, the outermost layers of leaves, twigs and bark of *K. candel* and *A. corniculatum*, i.e. $\Sigma N=36$), were sent to the Stable Isotope Ratio Facility for Environmental Research (SIRFER, Department of Biology, University of Utah, USA) to perform carbon and nitrogen isotope analysis in continuous flow mode (Longeragan et al., 1997). Ratios of ^{13}C:^{12}C and ^{15}N:^{14}N were expressed as relative per mil (‰) difference between sample and standard, which were PeeDee limestone (PDB) and nitrogen gas in the atmosphere, respectively (Peterson & Fry, 1987):

$$\text{Ratio}(‰) = \delta X - [R_{\text{sample}}/R_{\text{standard}} - 1] \times 1000 \quad (2)$$

where X=^{13}C or ^{15}N; R = ^{13}C:^{12}C or ^{15}N:^{14}N.
The results were presented as a dual plot of carbon and nitrogen. One-factor ANOVAs were conducted to compare the $\delta^{13}C$ and $\delta^{15}N$ values of the different specimens (Longeragan et al., 1997).

RESULTS

Gut content analyses

Bark, plant cells (unbroken plant tissue such as the epidermis of leaves and vascular tissues), broken plant cells, fungi, microalgae, cyanobacteria, diatoms and some unidentified materials were found in the stomach and faecal contents of the littorinids. The unidentified or digested materials were always >50% of the stomach or faecal contents (Table 1). The relative abundance of identified food items found in the gut contents (both stomach and faecal contents from the entire sampling period) of the littorinids appeared to be different between the five categories, with broken plant cells being by far the most abundant food item (average ~76% of the identified items, Figure 1), whilst the relative abundance of bark (~11%), plant cells (~8%) and fungi (~5%) were similar.

The stomach contents of *Littoraria ardouiniana* and *L. melanostoma* were similar, the two littorinids occurring on *Kandelia candel* or *Aegiceras corniculatum* ingesting similar food items. In general, the stomach contents of the littorinids did not appear to vary greatly during the 13-month sampling period (Figure 1), although some food items did show slight temporal variation. The abundance of bark in the stomachs of *L. melanostoma* on *K. candel*, for example, appeared to be higher (19%) in May 1998 than in other

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Table 1. *Overall mean abundance (±SE%) of food items found in the stomach and faecal contents of* Littoraria ardouiniana *and* L. melanostoma *between May 1998 and May 1999.*

	Aegiceras corniculatum				*Kandelia candel*			
	L. ardouiniana		*L. melanostoma*		*L. ardouiniana*		*L. melanostoma*	
	Stomach (N=43)	Faecal (N=47)	Stomach (N=51)	Faecal (N=51)	Stomach (N=42)	Faecal (N=41)	Stomach (N=48)	Faecal (N=45)
Bark	2.4 ±0.6	4.7 ±1.0	0.7 ±0.3	2.0 ±1.0	1.6 ±0.5	2.9 ±0.9	1.1 ±0.5	1.8 ±0.6
Plant cells	3.5 ±1.8	2.0 ±0.7	4.1 ±1.8	1.6 ±0.8	2.4 ±1.3	1.9 ±0.6	4.9 ±1.5	2.4 ±0.7
Broken plant cells	22.8 ±3.9	16.3 ±2.6	23.2 ±3.4	19.2 ±3.9	24.0 ±3.7	18.3 ±3.0	34.0 ±4.1	28.1 ±4.2
Fungi	1.9 ±1.0	2.4 ±1.0	0.3 ±0.1	3.0 ±1.4	1.0 ±0.4	0.7 ±0.2	2.6 ±1.5	0.6 ±0.2
Others	0.1 ±0.1	0.1 ±0.0	0.1 ±0.1	0.0 ±0.0	0.5 ±0.2	0.1 ±0.1	0.2 ±0.1	0.1 ±0.1
Digested/Unidentified	69.1 ±4.2	72.0 ±3.6	71.8 ±3.8	73.5 ±4.1	70.5 ±4.1	76.1 ±3.2	57.2 ±4.6	66.9 ±4.6

months, resulting in a lower relative abundance of broken plant cells during this month (~44%; Figure 1). Broken plant cells were the most abundant food category in the stomachs of *L. melanostoma* on *A. corniculatum* (~80%) and *L. ardouiniana* on *K. candel* (>75%) during the entire sampling period (Figure 1) and for *L. melanostoma* on *K. candel* (~80%) and *L. ardouiniana* on *A. corniculatum* (>70%) with the exception of May 1998 and March 1999 (Figure 1).

The relative abundance of broken plant cells was not significantly different between gut and faecal contents and the two littorinid species, but was significantly

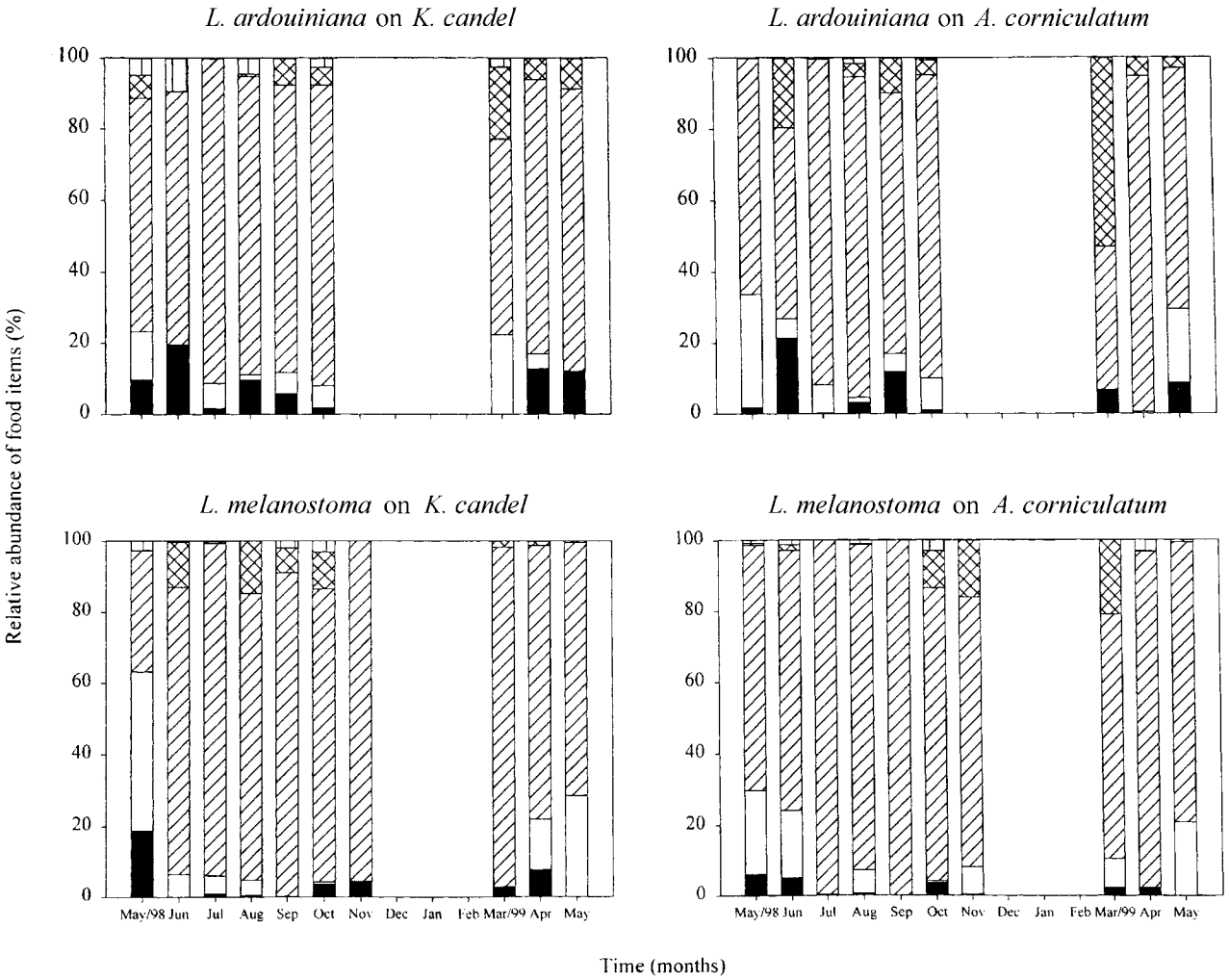

Figure 1. Mean, monthly relative abundance of food items in the stomach contents of *Littoraria ardouiniana* and *L. melanostoma* on *Kandelia candel* and *Aegiceras corniculatum*. Black bars, bark; white bars, plant cells; white bars with diagonal lines, broken plant cells; white bars with checked patterns, fungi; white bars with vertical lines, others. Data are missing from November to February for *L. ardouiniana* and from December to February for *L. melanostoma*.

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different between the two littorinid species on different mangrove species (three-factor ANOVA, Species×Tree; 1,208 df; $F=9.71$; $P=0.002$; all other factors or interactions were not significant). The stomach contents of *L. ardouiniana* on *K. candel* contained more broken plant cells than *L. melanostoma* (mean ±SE=71.9 ±4.1% and 53.9 ±5.9% respectively, Student–Newman–Keuls (SNK) tests following ANOVA), whilst more *L. melanostoma* on *A. corniculatum* contained broken plant cells (79.1 ±3.9%) than on *K. candel* (53.9 ±5.9%). The mean percentage of broken plant cells in the stomach ranged from 73% (*L. ardouiniana* on *A. corniculatum*) to 81% (*L. melanostoma* on *K. candel*), whilst the mean percentages of the other food categories were <11% (Table 2).

Stable isotope analyses

The δ^{13}C values of the littorinids ranged from −21.2 to −18.3 ‰, whilst those of the potential food items were −32.1 to −27.6 ‰ (Figure 2). The δ^{15}N values of the littorinids were 0.6–6.6 ‰ and those of the potential food items were −3.6–8.1 ‰. The δ^{13}C values of all specimens were significantly different (one-factor ANOVA, 9,20 df; $F=401.7$; $P<0.001$). The δ^{13}C values of the littorinids were significantly larger (less negative) than those of the mangrove plant tissues. The δ^{13}C values of *K. candel* were significantly larger than those of *A. corniculatum* (SNK tests). The similar δ^{13}C values of the littorinids indicated that the two species on either *K. candel* or *A. corniculatum* had similar isotopic values, and thus are likely to assimilate similar food. The δ^{15}N values of the specimens were also significantly different (one-factor ANOVA, 9,20 df; $F=29.8$; $P<0.001$). The SNK tests could only, however, reveal that the bark of *K. candel* had the smallest (the most negative) δ^{15}N value, whilst the δ^{15}N values of the other specimens were similar.

The dual plot of the stable isotope ratios of the littorinids and their potential food items showed that the carbon isotopic ratios of the two littorinid species could be distinguished from those of the mangrove trees, whilst the nitrogen isotopic ratios of the littorinids and most of their potential food items were more close together (Figure 2). The carbon ratios of the potential food items and the littorinids formed two distinct groups, indicating that the littorinids fed on a mixed diet composed of parts of the mangrove trees and other items, probably epiphytic microflora such as phylloplane fungi, algae or cyanobacteria.

Table 2. *Overall relative mean abundance (±SE%) of the identified food items from the stomachs of* Littoraria ardouiniana *(LA) and* L. melanostoma *(LM) found on* Aegiceras corniculatum *(AC) and* Kandelia candel *(KC) between May 1998 and May 1999.*

Littorinid	Bark	Plant cells	Broken plant cells	Fungi	Others
LM on KC	3.24 ±1.31	9.07 ±2.78	81.26 ±3.90	5.81 ±2.30	0.81 ±0.31
LM on AC	3.06 ±1.04	9.00 ±3.05	81.20 ±3.73	4.11 ±1.67	0.63 ±0.34
LA on KC	7.98 ±2.28	6.52 ±2.40	77.46 ±3.60	5.38 ±1.85	2.66 ±1.15
LA on AC	7.80 ±2.27	8.01 ±2.95	73.14 ±4.80	10.44 ±3.56	0.21 ±0.17

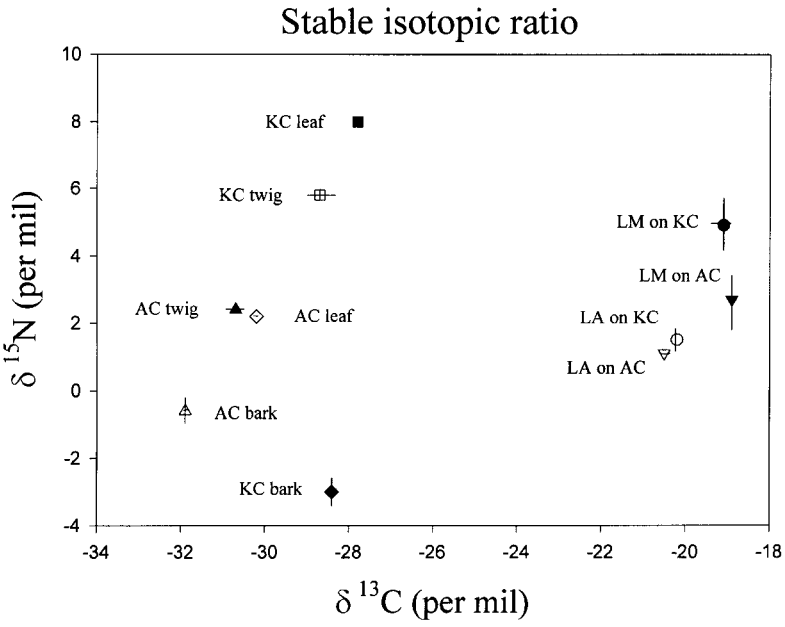

Figure 2. Dual plot of the mean isotopic values of δ^{13}C and δ^{15}N (N=3; ±SE) of *Littoraria ardouiniana* (LA) and *L. melanostoma* (LM) and their potential food items. KC, *Kandelia candel*; AC, *Aegiceras corniculatum*.

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DISCUSSION

Gut content analysis

As in other analyses of gut contents (e.g. Tsuda & Randall, 1971), high percentages of unidentified or digested material were found in the stomach contents and especially the faecal pellets of the littorinids, suggesting a high digestion rate in these littorinids. The identified food items from the stomach and faecal contents were mainly broken plant cells indicating that mangrove littorinids ingest a large amount of plant tissues during grazing. The relative abundance of other food items, such as fungi was, however, quite low, which probably reflects the low abundance of phylloplane fungi found on the mangroves (cover of phylloplane fungi was <10%; Lee, 2001). The abundance of other identified food items such as microalgae and cyanobacteria was even lower (<1%, O.H.K.L., unpublished data). *Littoraria ardouiniana* and *Littoraria melanostoma*, like many other littorinid species, appear to be generalist grazers, grazing on everything on the surfaces of the substrata on which they feed (Hawkins & Hartnoll, 1983). As mangrove leaves are the most abundant food items available in the mangrove forest, plant cells should, predictably, be the most abundant items found in the gut contents of the littorinids. When grazing on the mangrove itself, however, the littorinids only feed on the epidermal layers of their host plants and do not graze further into the inner layers, e.g. the mesophyll layers (SEM studies, Lee, 2001).

The diets of these two littorinid species are similar, regardless of the mangrove species on which they occur. The relative abundance of identified food items (e.g. broken plant cells) from the stomach contents and the faecal pellets was not different. This indicates that the littorinids could not digest and absorb all ingested materials, especially the plant cells, possibly due to the high lignin content of the plant tissue (Hagerman & Butter, 1991), although, overall >50%, of intersection points fell on digested or unidentified materials. The diets of the littorinids also showed little temporal variation. This may be because the littorinids mainly feed on the epidermal layers of the mangroves, the abundance of which did not change temporally, as mangroves are evergreen species. Since the major food source, i.e. the host, showed little seasonal variation and is temporally stable, the diets of these epiphytic littorinids also, showed little temporal change.

Stable isotope analysis

The mean δ^{13}C value of the mangrove leaves was −29‰, which was similar to previous records from mangroves (France, 1998; Loneragan et al., 1997; Peterson & Fry, 1987). It has been suggested that the mean δ^{13}C value of the potential food sources should be within the range >1 ‰–>2 ‰ of the mean consumer's value (Bunn & Boon, 1993; Peterson & Fry, 1987). A disparity should exist between δ^{13}C for animals and the food items on which they feed since there is a considerable selective assimilation of specific particles (France, 1998). Animals should, therefore, have δ^{13}C values within ±2 ‰ of their foods (Fry & Sherr, 1989). The isotopic carbon value (δ^{13}C) of *L. ardouiniana* and *L. melanostoma* was about −20 ‰ (but see Rodelli et al., 1984), and fell between those of the mangrove plant tissues (∼−29 ‰) and values for cultures of the phylloplane fungi, *Cladosporium oxysporum* and *Pestalotiopsis maculans*, in yeast extract media (∼ −12 ‰; Lee, 2001). This suggests that the littorinids fed on a mixed diet that is probably composed of mangrove plants and their associated phylloplane fungi as has been suggested for *Littoraria* species in Thailand (Christensen, 2001). The values for the cultured fungi should, however, be interpreted cautiously as they are likely to be influenced by the culture media used. It is likely that the mangrove littorinids also fed on other food items (e.g. mud or pedal mucus deposited on the mangrove surface, Lee & Davies, 2000), as the mean δ^{13}C values for primary and secondary consumers should be more negative than the potential food sources (Bunn & Boon, 1993). The isotopic values of both δ^{13}C and δ^{15}N of all the littorinids sampled, however, were similar, showing that *L. ardouiniana* and *L. melanostoma*, on either *Kandelia candel* or *Aegiceras corniculatum*, assimilated similar food items.

The isotopic carbon values separated the littorinids and the mangrove plant into two groups whilst, with the exception of the bark of *K. candel*, the nitrogen isotopic ratio could not distinguish between the specimens. The mean δ^{15}N value should fall within the range <1–5 ‰ of the consumer's value (Bunn & Boon, 1993; Peterson & Fry, 1987) which suggests the littorinids fed on all the food items tested. Another possible reason for the similar nitrogen isotopic ratio could be that this analysis was not sensitive enough to distinguish between organisms in the mangrove ecosystem which will have similar nutrient sources (Fry & Sherr, 1989). The δ^{15}N value of the bark of *K. candel* was significantly different from the other specimens and this suggests the littorinids do not digest and assimilate *K. candel* bark. There might also be a ^{15}N enrichment of consumers relative to their diet, of ∼ 3 ‰, because of the selective excretion of ^{14}N (Bunn & Boon, 1993; Peterson & Fry, 1987; Rodelli et al., 1984).

Diets of the littorinids

The diets of *Littoraria ardouiniana* and *L. melanostoma* were similar, and consisted of mangrove tree tissues (mostly leaf epidermal cells) and small amounts of phylloplane fungi and other items. These littorinids appeared to be generalist grazers, grazing on the surfaces of their hosts non-selectively. Herbivore food choice or preference is thought to be influenced by the morphology, composition and nutritional characteristics of the plant, as well as the nutritional requirement, digestive capability and the mode of feeding of the herbivore (Kennish & Williams, 1997; Wakefield & Murray, 1998). The availability of the food items, rather than the nutritional values (Lee, 2001) however, clearly affects the diets of these mangrove littorinids.

The percentage of phylloplane fungi found in the littorinid guts was much lower than that of the plant cells, but fungi may still play an important role in the diet of the littorinids. A relatively small ingestion of fungi contributes to a large percentage of the dietary requirements in some animals such as *Gammarus fossarum* (Amphipoda), *Asellus aquaticus* (Isopoda) and *Tipula abdominalis* (Diptera; Suberkropp, 1992). Fungi are known to increase the protein and lipid value of leaves (Bärlocher & Kendrick,

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1973; Bärlocher et al., 1989; Kaushik & Hynes, 1971) and to degrade the leaf polymers and phenolic compounds (Bärlocher & Newell, 1994; Bärlocher et al., 1989; Suberkropp, 1992) thus aiding assimilation. Fungi also provide essential nutrients such as vitamins, fungal polysaccharides and sugars to grazers (Bärlocher & Kendrick, 1973; Bärlocher et al., 1989; Jensen, 2000). The contents of fungal hyphae appear to be assimilated by mangrove littorinids very efficiently (Jensen, 2000) and thus, phylloplane fungi may play an important role in their diets.

Littoraria ardouiniana and *L. melanostoma* in Hong Kong mangroves are generalist grazers, feeding on the surfaces of the substrata, ingesting plant tissues and materials on the plant surfaces without obvious preferences for more nutritious but rare food items (phylloplane fungi, for example, have a higher nitrogen content than plant tissues; Lee, 2001). Mangroves provide a shelter that allow attachment and protection for *L. ardouiniana* and *L. melanostoma* from physical and biological stresses. The diet of these two species is constrained by food availability on their host. The two species are, however, able to coexist in the same habitat, probably as resources such as space and food are unlimited and the density of littorinid populations is low. As mangrove leaves are the most available food in the mangroves, these plant cells are the most abundant food items in the littorinid gut contents. Since these tissues are of relatively low nutritional value, especially in terms of nitrogen (Mattson, 1980; White, 1985; Lee, 2001), ingestion of phylloplane fungi or foraging on the lower levels of the mangrove trees might supplement the diet and provide essential nutrients to these grazers, therefore playing an important role in the overall feeding ecology of mangrove littorinids.

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