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红树林湿地相手蟹科动物摄食生态研究进展

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摘要: 相手蟹科物种是红树林湿地的主要底栖动物类群, 在生态系统中起着重要的作用。我国大陆地区目前已记录的相手蟹科物种数量为 12 种, 低于其它红树林地区(国内常用的采样方法会造成螃蟹物种数量和密度的低估), 其中褶痕相手蟹(*Sesarma plicata*)、无齿相手蟹(*S. deaani*)和双齿相手蟹(*S. bidens*)等是常见种。红树植物叶片是相手蟹科动物的主要食物来源, 相手蟹科动物通过地表摄食和洞穴贮存的形为消耗了大量的红树植物凋落叶, 使这些凋落叶的有机质和营养元素得以保留在生态系统内, 在凋落叶的周转和物质归还方面起到重要的作用。它们同时也摄食红树植物的繁殖体并且对不同物种的繁殖体具有摄食偏好, 这可能对一些红树物种的植被更新能力和红树植被群落结构产生影响。相手蟹科动物对不同物种和不同状态的红树叶片也存在摄食偏好, 通常对腐烂的叶片摄食偏好较强; 螃蟹的摄食偏好与叶片的营养成分、粗纤维和单宁含量以及 C/N 比等性质有关; 但在恶劣的野外环境下, 螃蟹则会表现出随机性摄食。目前关于相手蟹科动物生态学作用的认识仍不充分, 例如它们的种群大小和对凋落物的转化作用等, 有待于进一步研究。

关键词: 红树林; 相手蟹科; 螃蟹; 摄食生态; 凋落叶

Feeding ecology of sesarimid crabs in mangroves

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Abstract: Sesarimid crabs, common macro invertebrates in mangrove ecosystems, influence the structure and function of mangrove habitats through their burrowing activities and processing of leaf litter. A total of 12 sesarimid species have been recorded in mainland China, which may be an underestimate since more sesarimid species have been reported in Hong Kong and other tropical mangrove regions. (The reason for this underestimation could be due to the method commonly used to locate the crabs within mainland China. The most common method used is to place plot frame on the soil surface and simply dig to about 20–30 cm, and sift through the soil to locate crabs which could allow sesarimid crabs to escape deeper into the soil during the digging.) The most common sesarimid species in China are *Sesarma plicata*, *S. deaani* and *S. bidens*, while *Neosarmatium meinerti* is widely recorded in tropical areas of Australia and Kenya. Mangrove plant tissues, mainly leaves, are the main food source of sesarimid crabs, but crabs also feed on sediment detritus and faunal tissue to supplement the nutrient limited mangrove leaves. Some dietary specializations among different mangrove crabs have been recognized. Some crabs feed on only live leaves obtained by climbing into trees, while some species feed only on dead leaves on the mangrove floor. Crabs also have frequently been observed burying fallen mangrove leaves, to enhance leaf nutrition quality, prevent leaf litter from being removed by tidal flushing and avoid competition and predation when food or time available for collecting

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food is limited, and predator abundance is high. The feeding preference of sesarimid crabs for mangrove leaves with different conditions or from different mangrove species also has been reported from the laboratory and the field research. For example, sesarimid crabs in China prefer leaves of *Kandelia candel* over those of *Bruguiera gymnorrhiza* and *Aegiceras corniculatum*. Leaf characteristics such as C/N ratio, tannin, water and crude fiber contents determine the feeding preferences. Generally, sesarimid crabs prefer decomposed leaves, ascribed to the decreased tannin content and C/N ratio, and increases in water during leaf decomposition. It also has been suggested that crabs need to consume more decomposed leaves to obtain adequate C and N since they have lower C and N assimilation rates from those leaves. Feeding preferences have been more often demonstrated in laboratory studies while some field studies have revealed a lack of selective feeding of different mangrove species. This is probably due to the environmental stresses in field like predation, limited feeding time, and limited food availability. The ability of sesarimid crabs to remove leaf litter has been studied frequently in the past decades, and crabs have been shown to consume a large proportion of annual leaf fall production, far in excess of the local production in some mangrove forests. The ability of crabs to remove litter seems to be stronger in tropical areas than in subtropical or warm temperate areas. In subtropical areas like China, removal of leaf litter is affected by temperature and showed significant seasonal variation. Not only sesarimid crabs but some snails (e.g. *Terebralia palustris*) and ocypodoid/grapsid crabs (e.g. *Helograpsus haswellianus* and *Ucides cordatus*) also have been reported to consume mangrove leaves. Direct grazing of leaf litter by crabs accounts for a small proportion of leaf litter removed from mangrove floor in China, while the stocking of leaves in crab burrows for later consumption is the key way by which leaf litter is retained in the ecosystem, preventing tidal export. Through shredding and grazing of leaf litter, crabs also initiate and enhance the breakdown of mangrove detritus and recycling of nutrients. Sesarimid crabs also have been found to graze mangrove propagules and seeds, thus play a critical role in determining seedling recruitment and vegetation regeneration. It also has been suggested that the predation preference on some non-dominant mangrove species regulates their distribution with the vegetation community. The feeding ecology of sesarimid crabs and its involvement of in mangrove restoration, their retention of C and nutrients in mangrove soils and predation of seeds/propagule are worthy further studies.

Key Words: mangrove; sesarimidae; crab; feeding ecology; leaf litter

相手蟹科 (Sesarimidae) 动物是红树林大型底栖动物的常见类群^[1]。Robertson 发现红树林内相手蟹科物种通过转移贮存和摄食作用,可以消耗红树植物多达 28% 的凋落叶产量,证实了这一类群在红树林湿地凋落叶动态中扮演着重要的作用^[2]。在随后的时间内,红树林蟹类在红树林内食物链中的重要性引起了红树林研究人员的关注^[3-5]。通过摄食和消化作用,相手蟹科动物将红树凋落叶转化为碎屑,并以排泄物的形式排入红树林中^[6],这个过程加速了凋落叶的分解,促进了凋落叶中营养物质在生态系统的归还和循环过程^[7]。而它们的摄食行为在联系初级生产者和更高级消费者之间的关系、影响红树植物定植和生长,以及改变红树林沉积物环境方面也起着关键的作用^[1, 8-9]。因此,认识相手蟹科物种的摄食生态学特性,对了解其生态学作用,以及红树林湿地的生态学过程,例如凋落物归还、有机物和

营养物质的分配以及红树植被的更新等均具有重要意义。而相比红树林湿地生物多样性和凋落叶生产力等内容,对相手蟹科动物的摄食生态学的认识仍然有限,我国在这方面的研究也仅有零星的报道^[8-10]。本文从相手蟹科动物的摄食作用、摄食偏好和摄食习性等方面,综述了相手蟹科动物的摄食生态学特征,以期对红树林湿地生物多样性保护及生态学过程研究提供参考。

1 红树林湿地相手蟹科动物物种多样性

沙蟹科 (Ocyrodidae) 和方蟹总科 (Grapsoidae) 是红树林生态系统中最主要的两个类群^[11]。方蟹总科的相手蟹科旧属方蟹科 (Grapsidae),后从方蟹科独立出来,而物种也被重新分类^[12];该科包括拟相手蟹属 (*Perisesarma*)、近相手蟹属 (*Parasesarma*) 和小相手蟹属 (*Nanosesarma*) 等 30 个属^[13]。相手蟹

科的物种因其重要的生态学作用受到关注。在已报道的研究中, 马来西亚-新加坡和澳大利亚地区记录的相手蟹科物种较多, 分别为 44 和 37 种(表 1)。中国大陆地区有记载的物种数仅有 12 种, 约为香港地区的一半, 这可能与调查方法有关。大陆地区目前底栖动物群落(包括螃蟹)的调查主要采取挖掘法, 采样深度多为 20—30 cm; 在挖掘样方的过程中, 螃蟹可能会通过洞穴逃到采样深度以下的部分, 导致

其物种数和密度被低估。而在其它研究中则采取观察法、洞穴计数法或手捕法等对红树林螃蟹群落展开专门调查^[14-17]。不同地区红树林相手蟹科动物群落组成及其常见物种也不同。我国大陆地区红树林以褶痕相手蟹(*Sesarma plicata*)、无齿相手蟹(*S. deaani*)和双齿相手蟹(*S. bidens*)常见, 香港红树林以双齿相手蟹较为常见。

表 1 红树林湿地相手蟹科物种数量
Table 1 Diversity of sesarimid crabs in some mangroves

地区 Mangrove area	物种数 Species number	常见种 Common species	参考文献 Reference
北太平洋 North Pacific	11	—	[18]
马来西亚-新加坡 Malaysia-Singapore	44	<i>Sesarma versicolor</i> (<i>Epsisesarma versicolor</i>); <i>S. palawanensis</i> (<i>E. palawanse</i>); <i>S. singaporensis</i> (<i>E. singaporensis</i>); <i>S. kraussi</i> (<i>Sesarmoides kraussi</i>)	[19-22]
澳大利亚 Australian	37	<i>S. messa</i> (<i>Perisesarma messa</i>); <i>S. brevipes</i> (<i>Bresedium brevipes</i>); <i>Neosarmatium meinerti</i> ; <i>Perisesarma darwinensis</i> ; <i>P. semperi</i>	[23-24]
印度-马来西亚 Indo-Malaysia	25	—	[11, 21]
肯尼亚 Kenya	12	<i>N. meinerti</i>	[25-26]
中国香港 Hong Kong, China	26	<i>Perisesarma bidens</i>	[1, 27]
中国台湾 Taiwan, China	15	—	[28]
中国大陆地区 Mainland, China	12	<i>S. dehaani</i> (<i>Chiromantes deaani</i>); <i>S. bidens</i> (<i>P. bidens</i>); <i>S. plicata</i> (<i>Parasesarma plicatum</i>)	[29-42]

表中部分物种在原文中采用旧的命名方式, 本文根据新的分类体系附上这些物种的学名

2 相手蟹科动物对红树植物凋落物的摄食作用
凋落叶是红树林植物凋落物的主要组成部

分^[43] 相手蟹科物种已被证实在消耗红树植物凋落叶方面具有较强的能力(表 2)。

表 2 不同地区红树林相手蟹科螃蟹对凋落叶的去除比例

Table 2 Removal percentage of leaf litter by sesarimid crabs in mangroves

气候带 Climatic zone	地区 Location	红树物种 Mangrove species	消耗凋落叶生产量比例/% Removal percentage of litter production	参考文献 Reference
热带 Tropical	昆士兰, 澳大利亚	<i>Rhizophora stylosa</i>	28(全年)	[2]
	昆士兰, 澳大利亚	<i>Ceriops tagal</i> , <i>Bruguiera exaristata</i>	75(全年)	[44]
	苗柏河口, 马来西亚	<i>Bruguiera</i> spp, <i>Rhizophora</i> spp	42—54(全年)	[47]
	加济湾, 肯尼亚	<i>C. tagal</i>	18.6(全年)	[4]
	加济湾, 肯尼亚, 马鲁胡比, 坦桑尼亚	<i>Avicennia marina</i>	>100	[48]
亚热带 Subtropical	普吉, 泰国	<i>Rhizophora apiculata</i> , <i>C. tagal</i>	76(全年)	[49]
	九龙江口, 中国	<i>Kandelia candel</i>	33(全年)	[43]
	香港, 中国	<i>K. candel</i>	>57(夏季)	[50]

续表

气候带 Climatic zone	地区 Location	红树物种 Mangrove species	消耗凋落叶生产量比例/% Removal percentage of litter production	参考文献 Reference
	冲绳岛,日本	<i>Bruguiera gymnorrhiza</i> , <i>K. obovata</i>	<5(冬季) <37(夏季)	[46]
暖温带 Warm-Temperate	南澳大利亚 特兰斯凯,南非	<i>A. marina</i> <i>A. marina</i>	9.4(夏季) 43.58(全年)	[51] [52]

从这些研究结果发现,热带地区的红树林内,相手蟹科螃蟹对红树植物凋落叶的消耗比例较高,如澳大利亚的角果木(*Ceriops tagal*)和槽叶木榄(*Bruguiera exaristata*)林内,螃蟹对全年凋落叶的消耗比例分别为71%和79%^[44]。但是其它的一些热带地区中,底栖动物在凋落叶周转方面并未起到显著的作用,如墨西哥位于高潮带的红树林中,至少74%的凋落叶被潮水带出红树林系统^[45]。总体上看,亚热带和暖温带地区的凋落叶消耗比例低于热带地区。日本的研究人员发现,红树林内斑点拟相手蟹(*Parasesarma pictum*)在冬季对凋落叶的去除率小于凋落叶生产力的5%,而在夏季也不到37%^[46],低于前述的研究结果。我国九龙江口秋茄(*Kandelia candel*)红树林被相手蟹科动物消耗的凋落叶占全年凋落叶的比例为33%^[43],高于日本,但我国其它地区和红树物种的情况未见报道。

螃蟹对凋落叶的消耗能力依不同的红树植被或潮位而异^[44, 47]。除外,气候条件,如大气温度和降水,也是导致不同红树林生态系统内螃蟹对红树植物凋落叶消耗量差异的原因^[43]。低温会抑制螃蟹的胃部排泄功能和体内生物酶的分泌速度,限制螃蟹的活动,降低了螃蟹个体对食物的需求量和对凋落叶的摄食量^[53]。降水可以提高地面凋落叶的含水率,一定程度上改善了叶片的口感,促进螃蟹对凋落叶片的摄食率和消耗量。Slim等发现在湿润的环境下螃蟹对凋落叶的消耗率高于干燥环境下的消耗率^[4]。因此,在亚热带及暖温带地区,凋落叶的消耗则受气温和降水明显变化的影响,表现出明显的季节差异^[43]。而在热带地区,由于气温变化幅度较小,螃蟹对凋落叶的消耗则可能主要受干湿季降水量变化的影响,但这还需要进一步验证。

除相手蟹科物种外,红树林内沙蟹科、方蟹科和腹足类的一些物种在凋落叶的周转中也起到重要的作用^[4, 51, 54]。在肯尼亚加济湾红树林中,角果木红树

林内年产凋落叶的11%是被沼泽笋光螺(*Terebralia palustris*)摄食消耗的^[4]。在巴西北部红树林中,Nordhau发现红树林内螃蟹*Ucides cordatus*对凋落叶的去除率占到凋落叶生产力的81.3%^[54]。而在前述的部分估算凋落叶消耗率的研究中(表2),非相手蟹科物种的摄食作用可能被忽略。红树林内螺类对凋落叶的消耗低于螃蟹的作用,这与两类底栖动物的摄食行为有关,螺类主要在地表啃食叶片,而螃蟹除了地表啃食外,还可以将凋落叶拖至洞穴内贮存和啃食。

微生物分解在红树林凋落物的分解过程中的作用是明显的,但是大量的研究表明,相手蟹科动物的摄食在凋落物分解过程中的作用却要强于微生物。在澳大利亚东北部红树林,螃蟹*Sesarma messa*的摄食作用加速了红树叶片的分解失重^[2]。Rebertson和Daniel发现相手蟹科动物对凋落物的消耗速率是微生物分解速率的75倍^[44]。通过比较红树凋落叶初级生产力和地面凋落叶现存量,Twilley等推断潮汐和螃蟹对凋落叶周转速率为微生物对凋落叶分解速率的10—20倍^[55],同样的作用在其它研究中也已被证实^[47, 52]。通常被螃蟹消化后的凋落物被分解为小于200 μm的颗粒,可以增加凋落物碎屑的比表面积,促进微生物在碎屑中的繁殖^[6],进一步加速了凋落叶的分解。

螃蟹对红树植物繁殖体(凋落物的组成之一)的摄食作用也受到关注^[56]。尽管螃蟹对繁殖体的摄食作用存在时空上的差异,但是这种摄食作用确实对红树林植被的更新起到了一定的作用^[57],在众多因素中,螃蟹对非优势物种繁殖体的摄食偏好被认为是影响红树种类分布的主要因素之一^[58-60]。肯尼亚红树林中,相手蟹科动物在24 h内就摄食掉85%的红树繁殖体^[61],对植被更新和恢复造成了不利的影响。Bosire等认为红树林内的螃蟹对繁殖体的摄食作用在繁殖体凋落后的短时间内较强烈,螃蟹对

不同种类红树繁殖体的摄食偏好可能是促进优势种繁衍更新的主要原因,并且螃蟹对繁殖体的摄食在影响繁殖体生长和植被更新方面起到重要的作用^[62]。但也有研究结果表明,螃蟹对繁殖体的摄食作用与红树物种的多样性之间没有直接关系^[57, 63-64],其它非生物因子,如潮汐作用、土壤盐度和植被郁蔽度等,则可能都是影响红树植被更新的重要因素^[60, 65-66]。

3 相手蟹科动物的摄食习性

红树植物叶片是红树林内的螃蟹,特别是相手蟹科动物的主要食物来源。植物组织成份在一些红树林内螃蟹的胃部成份中所占比较达 61%—90%^[5, 67-68]。肯尼亚红树林中共有 5 种螃蟹主要是以植物叶片为食,其中相手蟹科的 *Sesarma ortmanni* 和 *Selatium elongatum* 为严格草食性物种^[25]。但红树林内的螃蟹也通过摄食一些动物组织以补充食物来源^[25, 61, 67, 69],这可能由于红树叶片中 C/N 较高的原因。通常认为食物中 C/N 小于或者等于 17 有利于无脊椎动物的生长^[70],而从各项研究结果来看,红树植物叶片中 C/N 显然高于这个数值,有些红树物种叶片的 C/N 甚至达到 100^[3, 7, 71-73]。

除对红树凋落叶的摄食外,研究人员在螃蟹的摄食习性方面也进行了一定的研究。在非洲东部红树林中,不同种类螃蟹的摄食习性也存在差异^[74]。红树林内的螃蟹可以爬到树上摄食新鲜叶片^[75-77]。肯尼亚红树林中 *Sesarma leptosoma* 在每天固定时刻爬到红树植物上摄食新鲜叶片,在摄食时间以外,*S. leptosoma* 通常在红树植物的根系中活动,很少爬行到红树林开阔的地面上^[75],它们主要根据光照判断其开始摄食的时间^[76]。肯尼亚红树林中的另一物种 *S. elongatum* 则喜欢在高潮的时候爬到红树植物上略高于海水表面的位置,摄食漂浮于海水表面的红树叶片和藻类^[77]。

从文献报道来看,摄食地面凋落叶是相手蟹科物种摄食的主要方式^[25, 61, 78]。Bosire 等认为红树林内叶片初级生产力不超过 10% 的部分是被动物在树上啃食去除的^[62]。Johnstone 发现红树植物上 20% 的叶片是在凋落之前被摄食^[79],但在该研究中,摄食红树叶片的主体包括螃蟹和昆虫,而该研究未排除昆虫对叶片的作用。

在摄食过程中,大个体的螃蟹对其活动范围内出现的个体大小相似的同性个体具有强烈的排斥性^[77],说明红树林内的不同摄食主体在生境上存在一定的重叠和竞争关系。同样的竞争关系也存在螃蟹和沼泽笋光螺之间,为了获取足够的食物来源,螃蟹甚至会将红树叶片上摄食中的螺个体推开,抢夺叶片^[74],沼泽笋光螺则通过群体摄食某一红树叶片来增强在红树林内摄食叶片中的竞争性,限制螃蟹抢夺被它们摄食中的红树叶片^[80]。

除在地面摄食凋落叶外,螃蟹也将红树叶片拖至洞穴内,撕碎后摄食或者贮存^[2, 17, 43]。我国九龙江口秋茄林内的凋落叶仅有 12% 是被螃蟹在地表啃食掉的,多数则是被贮存在洞穴内^[43]。Giddins 等认为螃蟹会将叶片贮存数个星期后再摄食,在贮存过程中,红树叶片中的单宁类物质通过淋溶作用减少,而叶片氮含量在微生物的作用下提高,叶片的营养得到改善^[67]。但其它研究发现被贮存在洞穴内的叶片在两个星期内就被螃蟹摄食^[4],而在这段时间内,叶片的氮含量、C/N 未发生明显的变化^[3, 5, 77]。这些结果推翻 Giddins 等的假设,说明改善红树叶片营养状态并不是螃蟹贮存叶片的主要原因。这种贮存叶片的行为使螃蟹可以在较短时间内尽量多保留红树叶片,防止叶片被潮水冲走引起的食物缺失^[2],降低螃蟹摄食过程中被其它动物捕食的风险,也可以使螃蟹在周围环境不利的条件下,如高潮时、高温或者干旱的条件下,保证其进食行为不受影响^[47, 81]。因此,在多捕食者、潮汐作用明显或者凋落叶数量有限的红树林中,螃蟹对贮存凋落叶于洞穴内的现象可能更明显^[47]。

4 相手蟹科动物的摄食偏好

红树林螃蟹对不同的叶片类型具有一定的摄食偏好。大红树(*Rhizophora mangle*)的叶片是加勒比海和东太平洋红树林内的相手蟹科 *Aratus pisonii* 喜好摄食的红树叶片^[68, 82-83]。巴西北部红树林中螃蟹 *Uca cordatus* 在室内和野外条件下对大红树叶片的摄食偏好也强于其它红树叶片^[5]。在其它一些研究中,螃蟹对白骨壤属(*Avicennia*)红树植物叶片具有较强的摄食偏好^[47, 84-85]。这些不同类型的叶片性状上存在差异,如叶片的大小、状态、韧性、营养成份含量以及一些化学成份等,会影响叶片的口感^[86],而

叶片中的 C/N 和单宁物质被认为是影响螃蟹对红树叶片摄食偏好的主要因素^[5 68, 70 87-89]。

Micheli 研究澳大利亚北部红树林内的螃蟹 *Sesarma messa* 和 *S. smithii* 对 4 种红树红海榄 (*Rhizophora stylosa*)、白骨壤 (*Avicennia marina*)、槽叶木榄和角果木叶片的摄食偏好, 在实验室条件下, *S. messa* 对这 4 种红树的凋落叶未表现出明显的摄食偏好, 而 *S. smithii* 对红海榄叶片有较强的摄食偏好; 在野外红树林中, 螃蟹对角果木叶片的消耗率却明显高于对其它 3 种红树叶片^[3]。红树叶片中单宁含量、含水率、有机质含量、C/N 和叶片韧性均不是影响该研究中螃蟹摄食偏好的因素。螃蟹对白骨壤属红树植物叶片具有较强的摄食偏好可能与这些叶片中单宁含量和 C/N 较低有关^[47 84-85]。褶皱相手蟹在室内条件下对秋茄叶片的摄食偏好强于桐花树 (*Aegiceras comiculatum*) 和木榄 (*Bruguiera gymnorrhiza*), 叶片中 C/N、含水率和粗纤维是决定螃蟹对不同叶片类型摄食速率的关键因子^[43]。李旭林等也发现, 褶皱相手蟹和无齿相手蟹对秋茄叶片的摄食偏好也强于桐花树^[10]。

螃蟹可能会对林内优势红树物种的叶片存在较强的摄食偏好。在马来西亚的木榄红树林中, 螃蟹对木榄叶片的去除率明显高于对其它几种红树植物叶片的去除率^[47]。同样, 福建九龙江口螃蟹在室内条件下对优势物种秋茄的叶片有较强的摄食偏好, 但在野外红树林中螃蟹对 3 种红树 (秋茄、木榄和桐花树) 叶片不存在摄食偏好^[17]。这说明在一些恶劣的环境下 (短暂的摄食时间、捕食者的压力以及缺少凋落物等), 红树林内螃蟹更多地采取随机性摄食, 其摄食行为更多地受到凋落叶可获取性的限制, 而不表现出明显的摄食偏好。

在红树叶片腐烂过程中, 由于微生物的作用, 叶片的氮含量增加, C/N 相应降低, 可以提供更好的营养比; 叶片中的部分单宁溶解到海水中^[87 90-91], 会增加红树叶片的可口度^[67 88]。从已报道的研究结果看, 螃蟹对红树腐烂叶片的摄食率明显高于对新鲜和凋落叶片的摄食率^[3, 17 67 89], 说明红树腐烂叶片具有较强的摄食偏好。但研究人员同时也发现某些物种 (*Neosarmatium versicolor*) 对腐烂叶片中 C 和 N 元素的吸收率较低^[89], 这可能是螃蟹对腐烂叶片的摄食率较高的原因之一, 因为螃蟹在摄食腐烂叶片时

需要足够大的摄食量来保证从食物中摄取生长所需的营养元素。其它一些研究也证明螃蟹对一些 C/N 比较高的叶片有较强的摄食率^[5 68]。

也有研究证明红树叶片中单宁含量未对相手蟹科物种对不同红树种类叶片的摄食偏好产生影响。在 Micheli 的研究中, 几种红树叶片的单宁含量为 6.76%—17.34%, 其含量与螃蟹对不同红树种类叶片的摄食偏好无关^[3]。其它红树林蟹类 *U. cordatus* 和 *A. pisonii* 对大红树叶片的摄食偏好强于对萌芽白骨壤 (*Avicennia germinans*) 叶片的摄食偏好, 尽管萌芽白骨壤叶片的单宁含量低于前者^[5 83]。除红树林外, 研究人员也发现单宁并未影响到片脚类动物和海胆对海草的摄食^[92-94]。这可能是因为在进化过程中, 这些草食性的底栖动物形成了一些专门的适应机制用于抵御单宁对它们消化系统所产生的不利影响。

5 研究展望

红树林湿地凋落叶动态过程, 包括凋落叶的初级生产、分解、输出和动物啃食, 这些决定着红树植物与次级生产的联系以及与近海生态系统碳素和营养元素的生物地球化学循环之间联系。螃蟹通过对凋落物的贮存、摄食和转化作用, 可以减少凋落叶的流失, 促进被保留在生态系统内凋落叶的分解, 以及碳和营养元素的归还和积累, 并改变土壤中微生物群落及其活性。但现在国内外对这一类群在红树林生态系统中作用的认识仍有待于进一步深入, 特别是我国关于相手蟹科物种的摄食生态学研究近几年才见诸报道。

尽管相手蟹科动物在红树林生态系统凋落物周转等方面所起的积极作用已经被证实, 但其真实贡献还有待于进一步探讨, 这是因为前人的一些研究中, 螃蟹对凋落叶的消耗率是基于螃蟹个体对叶片的摄食率和螃蟹的密度进行计算。这种在室内条件下获得的螃蟹的摄食率可能与实际情况有所偏差, 并且关于螃蟹密度的准确定量上仍受到质疑 (采取洞穴数量或者观察法等半定量的方法)。而基于野外测定获取的消耗率通常也缺少长期观测 (如周年) 数据。因此, 采取可靠有效的调查和研究方法来估算相手蟹科动物群落大小及其对凋落叶 (物) 消耗率是今后研究中需要增强的内容。我国的红树林自然

分布地包括热带和亚热带区域, 植被类型多样; 但受调查方法的限制, 目前所记载的相手蟹科物种数量仍较少, 它们的种群大小也不清楚。因此, 需增强对相手蟹科动物多样性的研究, 这有助于进一步了解红树林湿地中诸多生态学过程。国内红树林中已报道的草食性动物仅有相手蟹科的物种^[10, 17], 但由于红树林底栖动物群落的地区差异较大, 一些腹足类动物或其它螃蟹物种也可能摄食红树凋落叶, 而目前我国还未见此类报道, 因此其它大型底栖动物对凋落叶的摄食行为也需要进一步观察。

此外, 被相手蟹科动物摄食转化后的有机物(以碎屑或者粪便形式进入到生态系统)在红树林湿地中的去向及所起到的作用仍不清晰。尽管有研究已经证实螃蟹粪便可进一步被其它底栖动物利用^[7], 并且是有机质和营养元素在红树林土壤中累积的介质^[95], 但多数研究仍停留在螃蟹对叶片的摄食率上, 这样尚不能完整地认识螃蟹摄食作用的生态学作用。结合螃蟹摄食过程中对叶片中营养物的同化异化作用, 研究其摄食行为对红树林土壤环境和其它底栖动物的影响, 也是探讨凋落叶和螃蟹在生态系统中作用时的重要内容。

红树植物凋落叶的营养组成和单宁含量等性质因物种而异, 导致相手蟹科动物对红树凋落叶的选择性摄食(摄食偏好)。因此, 不同红树林地中, 螃蟹对凋落叶的消耗量也不同, 凋落叶在红树林生态系统内的保留量也不同, 而这关系到红树林凋落叶中碳/营养元素的归还和积累, 以及红树林湿地的碳埋藏过程。不同的红树植被下, 螃蟹群落的结构也有所不同^[96]。如何将红树林大型底栖动物对凋落物的摄食作用及其生态作用与红树林生态恢复结合, 在实现红树植被覆盖的同时提高底栖动物多样性及其生态功能, 是今后红树林生态恢复的一个值得关注的內容。由于红树植物种类以及底栖动物区系上的差异, 国外的研究结果对我国红树林生态恢复的指导意义有限。因此, 研究我国红树林湿地包括相手蟹科动物在内的主要大型底栖动物种类对红树叶片的摄食作用, 在我国红树林恢复措施的重要方面即红树植物的种类选择上, 预测红树林生态恢复中底栖动物亚系统的生态修复效果具有指导意义。在红树林生态恢复过程中, 底栖动物对红树植物繁殖体的摄食作用也需要考虑, 因为这关系到红

树林植被的自我维系和更新能力, 甚至红树林恢复的成败。

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