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Effect of mangrove litter species and availability on survival, moulting, and reproduction of the mangrove crab *Sesarma messa*

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Abstract: The performance of adult individuals of the herbivorous mangrove crab *Sesarma messa* (a common brachyuran crustacean found in mangrove forests of northeastern Australia), fed different amounts and different species of mangrove leaves was investigated with long-term rearing experiments carried out in mesocosms. Survival, at the end of a 10-week period, was not significantly different for crabs fed *Ceriops tagal* leaves ad libitum, fed limited amounts of *C. tagal* leaves, or provided with no leaves. Crabs moulted more frequently when supplied with excess or limited amounts of leaves than in the starved treatment. More ovigerous individuals were also observed in the treatment that received leaves ad libitum than in other two treatments. In a second experiment, crabs were fed *C. tagal*, *Rhizophora stylosa*, or *Bruguiera exaristata* leaves ad libitum for 9 weeks. As in the first experiment, survival was not significantly different among the treatments, while crabs moulted more frequently when fed *R. stylosa* leaves than the other two species of leaves. Only two crabs were bearing eggs, at the end of the experiment, so that a comparison of the reproductive performance among different treatments could not be made. Despite the low nutritional quality of mangrove leaf litter, its species and availability proved to have significant effects on both growth and reproduction of *S. messa*, suggesting a direct link between the forest primary production and secondary production of sesarmid crabs in the mangrove forests of northeastern Australia.

Key words: Feeding ecology; Mangrove; Northeastern Australia; Rearing experiment; Sesarmid crab; *Sesarma messa*

Introduction

Mangrove forests of South-East Asia and Australia are sites of significant primary production (Christensen, 1978; Bunt et al., 1979, 1984). Contrary to most wetland ecosystems investigated, where primary production enters the food web mostly as detritus (Smalley, 1960; Heald, 1971; Odum & Heald, 1975; Pfeiffer & Wiegert, 1981; Twilley, 1985; Twilley et al., 1986), a large proportion (30–80%) of the annual production of mangrove forests of the Western Pacific is directly consumed by macroinvertebrates, particularly by sesarmid crabs (Robertson, 1986; Robertson & Daniel, 1989).

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Recent research investigating trophic links among faunal components of mangrove systems of tropical Australia further showed that eggs and larvae of mangrove crabs are a major prey item for juvenile fish in coastal waters (Robertson et al., 1988), possibly explaining why densities of juvenile fish have been found to be 4 to 10 times greater in mangrove creeks than in nearby seagrass and sandflat habitats (Robertson & Duke, 1987). Mangrove crabs may thus consitute an important link between the primary production of mangrove forests and the secondary production of several fish and crustacean species that utilize estuaries as nursery grounds. Investigating what factors regulate the productivity of mangrove crab populations might help making predictions about the patterns of abundance and distribution of commercially important fish and crustaceans.

Mangrove leaves just fallen from trees are poor in nitrogen and rich in tannins (Giddins et al., 1986; Neilson et al. 1986; Robertson, 1988). Tannins are polyphenolic compounds which bind to digestive enzymes, decreasing the animal absorption efficiency, and have been shown to deter herbivory by various grazers (Swain, 1979; Hay & Fenical, 1992, and references therein). Mangrove litter can thus be considered a low quality food for the macroinvertebrates of mangrove ecosystems. Giddins et al. (1986) suggested that sesarmid crabs let litter decompose inside their burrows for several weeks before eating it. During this time tannins are lost from the leaves through leaching, while the nitrogen content increases through bacterial activity, resulting in a higher quality food. At least two sesarmid species (*Sesarma messa* and *Sesarma smithii*), found in great abundances in the mangrove forests of North Eastern Australia, however, are reported to commonly feed on fresh mangrove litter (Robertson, 1986; Micheli, 1993), raising the question of how such crab species meet their nitrogen requirements and how the crabs deal with the high tannin concentrations of mangrove leaves (Giddins et al., 1986; Robertson, 1986). In particular, it is not known whether sesarmids are able to survive, grow and reproduce when feeding exclusively on mangrove leaves or if they need to have access to alternative, more nutritious food items, in addition to mangrove litter.

The quantity and quality of the mangrove litter available to sesarmid crabs also vary seasonally and spatially. Primary production of mangrove forests, in fact, significantly differs among different sites, and also exhibits seasonal fluctuations. The dry season (coinciding with the Winter months, in tropical Australia) generally is the time of minimum productivity, and the wet season (i.e. the Summer months) is that of maximum productivity (Williams et al., 1981; Boto et al., 1984; Twilley et al., 1986). The sesarmid crab *S. messa*, therefore, is faced with the lowest annual primary production during its breeding season, which coincides with the end of the dry season (F. Micheli, unpubl. data).

Crabs are also likely to feed on leaves of different mangrove species, since *S. messa* is found in mangrove forests of different species composition (Jones, 1984; Micheli, 1992). Leaves of different mangrove species have significantly different nitrogen and tannin concentrations (Robertson, 1988), thus they have variable nutritional quality.

Crabs' survivorship and reproductive output might differ depending on what mangrove species dominates their feeding site.

In order to investigate the link between the quality and availability of mangrove litter and the secondary production of sesarmid crabs in mangrove forests, *S. messa* individuals were reared on different diets for over 2 months. During this time, survival, moulting frequency and reproducive output of the crabs were monitored. In a first experiment, crabs were provided with one of three possible levels of availability of *Ceriops tagal* fresh litter: ad libitum amounts of litter, limited amounts of litter, and no litter. In a second experiment, crabs were fed ad libitum with fresh litter of one of three mangrove species commonly found in the study area: *C. tagal*, *Rhizophora stylosa*, and *Bruguiera exaristata*.

Materials and Methods

EFFECT OF LITTER QUANTITY

Adult individuals of *Sesarma* (*Perisesarma*) *messa* Campbell 1967 (carapace length > 15 mm, based on secondary sexual characters, namely abdomen width and cheliped size; Hartnoll, 1982) were kept from July to October in nine plastic aquaria (60 cm long, 40 cm wide and 50 cm deep) filled about 2/3 of their volume with sediment taken from the same site where the test animals were captured, a mid intertidal *C. tagal* stand, located at Cape Ferguson (19° 17′ S: 147° 03′ E) near Townsville, North Queensland. Sediments were sieved through a 2-mm sieve, and all the macroinvertebrates retained by the sieve were removed.

Aquaria were maintained in an outside shadehouse, at ambient temperature and natural photoperiod. Each aquarium was connected to a plastic drum containing sea-water (salinity $\approx 30‰$) by an inlet and an outlet hose; drums were equipped with self-timing pumps, so that a simulated tide took place for one hour every day, covering the mud surface with about 10 cm of water.

Three treatments, with three replicates of each, were established in the aquaria: (1) no litter was added to the aquaria; (2) limited litter: ~ 6 g (wet weight) of senescent (i.e. yellow leaves, easily abscissed from trees, Giddins et al., 1986) *C. tagal* leaves were added to each container once a week. Previous trials showed that this quantity was completely consumed by the crabs half way through the week; (3) excess litter: 25–30 g (wet weight) of *C. tagal* senescent leaves were added weekly to each container. Such quantity was never completely consumed, by the end of the week, throughout the duration of the experiment. Leaf remains were removed from each aquarium, at the end of each week, before addition of fresh litter.

Crabs were captured with pit traps, built with sections of PVC pipe and deployed in the field using an auger. Three males and three females (their weights ranging from 2.8 to 11.1 g, average = 5.976, SE = 0.316 g, $n = 54$) were randomly assigned to each

of nine aquaria after having been measured across the carapace, weighed to the nearest 0.001 g, and individually marked by glueing a numbered plastic tag to the gastric region of the carapace. Although a relatively wide size range of crabs was used, there was no significant difference in the average weight of the animals assigned to different containers (ANOVA: $F = 0.15$, df 8 and 45, NS).

Only animals having a hard carapace (i.e. in the intermolt stage), no eggs and no wounds or mutilations were used for the experiment. A density of six animals/aquarium (i.e. per 0.24 m^2) was chosen because there were 5.8 ± 0.9 crab holes/0.24 m^2 (based on counts of crab burrows within five 2 m^2-quadrats deployed haphazardly on the forest floor) at the field site where experimental animals were collected. It is likely, however, that there is not a one-to-one relationship between burrow and crab densities because burrows often had more than one entrance (pers. obs.), and that the experimental densities might have been greater than the natural densities of *S. messa* in the field.

The containers were checked every 2–3 days for ovigerous and moulting individuals, for a total of 10 weeks. Dead animals were removed and immediately substituted with others of the same sex and size, in order to keep the density of crabs in each container constant. Survival, growth and reproduction data relative to the replacement animals were not included in the analysis.

At the end of the experiment the animals were weighed to determine any change in weight that may have occurred during the experiment. Crabs, however, exhibited a high incidence of mutilation (all animals were missing at least one limb at the end of the experiment), probably due to a high degree of aggressivness caused by overcrowding of the containers. This artifact most likely biased the data, so that the change in the crab weight, over the 10-week duration of the experiment, was not used as a measure of the crab performance. Ovigerous females were separated at the end of the incubating period (when egg colour changes from red-orange to dark brown) and put in plastic jars containing seawater, until hatching occurred. Three subsamples of 200 larvae were counted and put on paper filters. Such subsamples, as well as the remaining larvae, were oven-dried (65 °C, 3 days) and weighed. From the weight of the subsamples, the total number of larvae was calculated for each brood.

Crabs were frequently seen, both in the course of the present experiments and in the field feeding on the sediment surface (Giddins et al., 1986; Robertson, 1986; Micheli, 1993), probably picking up microbial organisms living on the mud surface. In order to compare the availability of this alternative food source in the three treatments, bacterial counts were performed at the end of the experiment. Three samples (3.14 ml of volume each) of sediment were taken from each container with a plastic syringe with the lower end removed. At the same time when sediment samples were taken from the aquaria, three sediment samples were also taken in the field (in the forest where sediments for the aquaria had been taken, see above) in order to compare bacterial densities in the experimental aquaria with those naturally occurring in the field. Sediment samples were preserved in 10% formalin solution (prepared with 0.2 μm filtered

seawater), stored at 4 °C and used for bacterial density determination, following the epifluorescence staining technique described in Hobbie et al. (1977).

EFFECT OF LEAF SPECIES

A second rearing experiment was carried out for 9 weeks in November–January '89, in order to assess the effect of different leaf species on the performance of *S. messa*. Senescent mangrove leaves were added weekly ad libitum (see above, treatment no. 3) to each of the nine containers (see above), after having removed the leaf remains from the previous week. Crabs were given leaves of one of the three mangrove species most commonly found at Cape Ferguson: *C. tagal* (treatment no. 1), *R. stylosa* (treatment no. 2), and *B. exaristata* (treatment no. 3). As in the previous experiment, three replicate aquaria were assigned to each treatment.

Because of the high incidence of mutilation observed in the previous experiment (see previous section), a lower density was adopted, and four animals (two males and two females), were placed in each aquarium. The number of live, moulting, and ovigerous individuals was recorded weekly, for a total of 9 weeks. As in the previous experiment, dead crabs were replaced right away.

ABSORPTION EFFICIENCY

In order to determine the extent to which *S. messa* can utilize mangrove litter, absorption efficiency (AE) or organic matter in senescent mangrove leaves was calculated using the equation proposed by Conover (1966):

$$\mathrm{AE} = (F - E)/(1 - E) * F$$

where F is the ash-free dry weight/total dry weight ratio in the food and E is the same quantity for the faeces.

Ten individuals of *S. messa* were allowed to feed on mangrove leaves in separate plastic bowls containing 0.5 cm of seawater, in the laboratory. Room temperature was 21 ± 0.5 °C, and crabs were exposed to a natural photoperiod. Crabs were kept in the containers for one week, then four senescent mangrove leaves, one of each of the four species most commonly found in the study area (*C. tagal*, *R. stylosa*, *B. exaristata* and *Avicennia marina*) were added to each container. Laboratory and field leaf choice experiments had previously shown that *S. messa* consumed leaves of the four most common mangrove species found in the study area at similar rates (Micheli, 1993). Crabs are therefore likely to feed on mixtures of leaves of different species, as dictated by the local tree species composition. Each leaf was cut through the mid rib, so that half could be given to the crab, while half was put in a separate bowl, as a control for the leaf weight loss not due to crab grazing. Leaves were weighted to the nearest 0.001 g at the beginning of the experiment, and wet weights were converted to dry weights using a dry weight-wet weight relationship previously determined for each leaf species (Micheli, 1992).

After 24 h, leaf remains and control leaves were collected, oven dried (at 65 °C, for 5 days), and reweighed. Leaves were then ashed (500 °C, for 24 h), in order to determine ash-free dry weights. The total amount of organic matter ingested by each crab was calculated by adding up the crab ingestion rates for each leaf species.

After leaf remains had been removed, crabs were kept in their containers for a further 24 h. Crabs were then removed and all faecal material was captured on GFC filters. The filters were oven-dried at 65 °C until constant weight was reached. Faecal material was then weighed to the nearest 0.001 g, ashed (muffle furnace, 500 °C, 24 h) and reweighed.

STATISTICAL ANALYSES

The final proportions of individuals that were still alive, had moulted or produced eggs at the end of each of the two experiments were compared among treatments with one-way ANOVAs. Percentages were arcsin-transformed, prior to ANOVA. ANOVA was also performed on the bacterial density data. Average bacterial densities from each aquaria (determined for three replicate cores per container) were used in the analysis. Means were compared, after analyses of variance, with the Student-Neuman-Keuls (SNK) procedure (Underwood, 1981).

RESULTS

EFFECT OF LITTER QUANTITY

There were no significant differences in survival of *S. messa* fed different amounts of *C. tagal* leaves for 10 weeks (ANOVA: $F = 0.63$, df 2 & 6, NS). Growth and reproduction, on the contrary, were significantly affected by food ration (ANOVA: $F = 106.95$, df 2 and 6, $p < 0.001$, for % moulting; $F = 20.05$, df 2 and 6, $p < 0.01$, for % ovigerous) (Fig. 1). Significantly more crabs had moulted, by the end of the experiment, in treatments no. 2 and 3, i.e. when mangrove leaves had been administered weekly to the crabs, than in treatment no. 1, where crabs had been allowed to feed on the sediment surface only (SNK, at $\alpha = 0.05$) (Fig. 1). Significantly more ovigerous females were also observed in treatment no. 3, where crabs were allowed to feed on mangrove leaves ad libitum than in treatments no. 1 and 2, where no and limited mangrove litter, respectively, were provided (SNK, at $\alpha = 0.05$) (Fig. 1).

Crabs which were fed ad libitum also started moulting and carrying eggs earlier than those which were fed limited amounts of leaves (Fig. 2). No crabs moulted or reproduced for the entire duration of the experiment in treatment no. 1, i.e. when no litter was provided (Figs. 1 and 2).

Fecundity seemed to be greater for crabs fed litter ad libitum than for those on a limited diet (crabs from treatment no. 3 produced, on average, more larvae, Table I), although this result could not be statistically tested because only two individuals layed eggs in treatment no. 2.

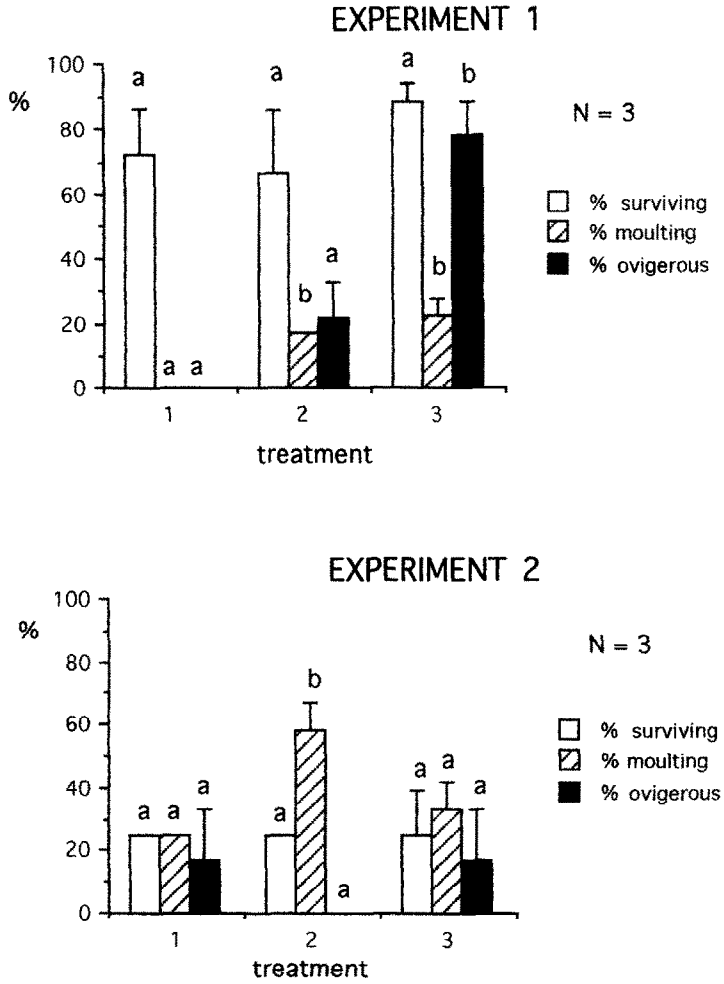

Fig. 1. Final percentages of crabs surviving, undergoing moult, and carrying eggs in the experiments investigating the effect of litter quantity (experiment 1: treatment no. 1 = no litter; treatment no. 2 = limited litter; treatment no. 3 = excess litter), and of leaf species (experiment 2: treatment no. 1 = *C. tagal*; treatment no. 2 = *R. stylosa*; treatment no. 3 = *B. exaristata*) on the crab performance. For each variable showed (i.e. % surviving, % moulting, and % ovigerous), bars (± 1 SE) marked with the same letter were not significantly different at $\alpha = 0.05$ (SNK).

Bacterial densities were significantly different among the three treatments (ANOVA: $F = 51.38$, df 2 and 6, $p < 0.001$). However, the assumption of heteroschedasticity was not met, even after square root transformation of the data (Cochran's $C = 0.94$, df = 3, $k = 3$). The variance of the data obtained for the treatment where crabs were fed ad libitum was, in fact, much greater than in the other treatments (excess leaf treatment: var. = 242.11; limited leaf treatment: var. = 3.96; no leaf treatment: var. = 3.29). Bacterial densities in the aquaria where leaves were provided ad libitum were, on av-

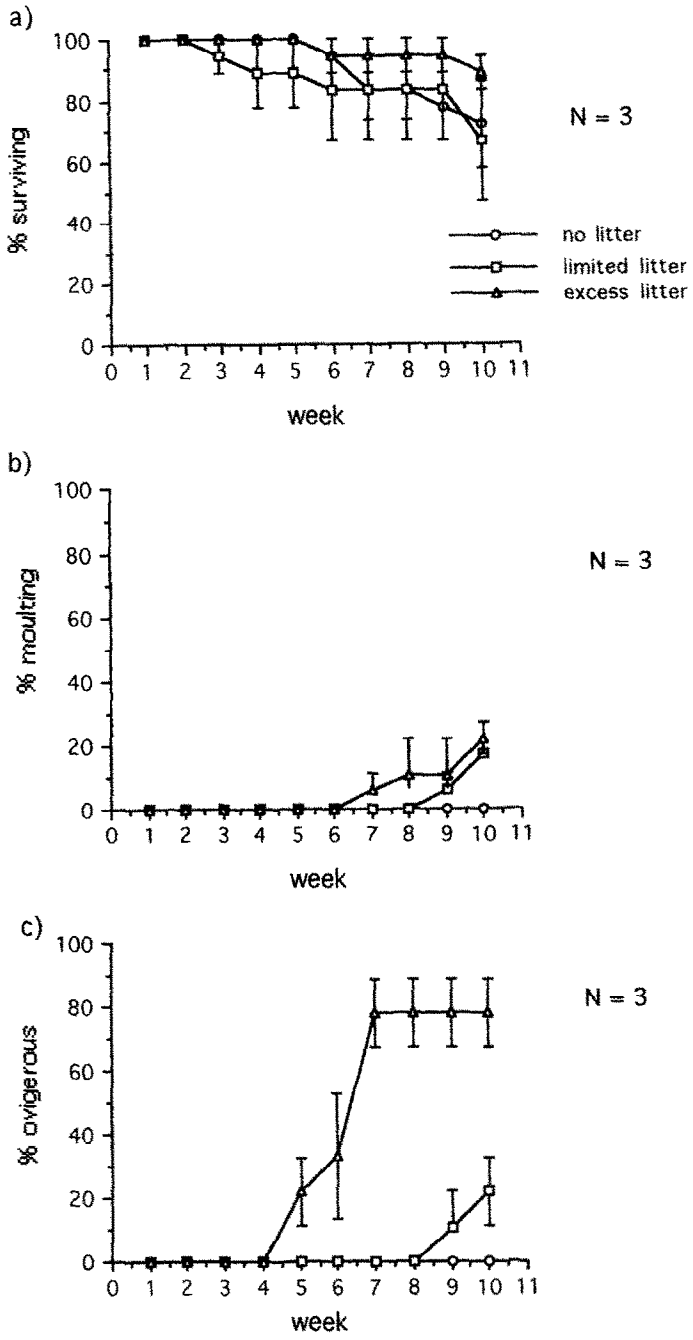

Fig. 2. Cumulative percentages of crabs surviving (a), undergoing moult (b), and carrying eggs (c), in the experiment performed to investigate the effect of mangrove litter quantity on the performance of *S. messa*. Mean percentages ± 1 SE.

TABLE I

Reproductive output of *S. messa* females after 10 weeks from (1) no leaf litter, (2) limited amounts of *C. tagal* litter, and (3) excess amounts of *C. tagal* litter treatments. Nine females were assigned to each treatment at the beginning of the experiment. Means ($\pm$ / - 1 SE) are given. Dry weights of larvae are given as g dry weight of larvae/g wet weight of crab. Numbers of larvae released are given as no. of larvae/g wet weight of crab. No ovigerous females were observed in treatment no. 1.

	Treatment		
	No litter	Limited litter	Excess litter
Mean dry weight of larvae	-	0.078 (0.019) $n = 2$	0.080 (0.012) $n = 7$
Mean no. of larvae released	-	143.9 (8.41) $n = 2$	191.1 (21.85) $n = 7$

erage, greater than in both other treatments (excess leaf treatment: average = 99.42 bacteria/3.14 ml of sediment, SE = 8.98, $n = 3$; limited leaf treatment: average = 48.73, SE = 1.15, $n = 3$; no leaf treatment: average = 40.18, SE = 1.05, $n = 3$). Bacterial densities determined for the sediment cores taken in the field fell within the range of those observed in the experimental aquaria (average = 60.0, SE = 11.97, $n = 3$).

EFFECT OF LEAF SPECIES

There was no significant difference in survival of crabs fed *R. stylosa*, *B. exaristata* or *C. tagal* leaves for 9 weeks (ANOVA: $F = 0.369$, df 2 and 6, NS). The final percentage of survivors was considerably lower than that obtained in the other rearing experiment (Fig. 1), due to a surprisingly high mortality occurred during the last week of the experiment (Fig. 3).

Moulting frequency significantly differed among the treatements (ANOVA: $F = 6.5$, df 2 and 6, $p < 0.05$). A greater proportion of crabs moulted when fed *R. stylosa* leaves than either *C. tagal* or *B. exaristata* leaves (SNK, at $\alpha = 0.05$) (Fig. 1). Only two of the total number of females became ovigerous during the course of the experiment, probably because November–January is at the end of the breeding period for *S. messa* (F. Micheli, unpubl. data).

Moulting crabs were found first in the aquaria assigned to treatment no. 2 (i.e. where *R. stylosa* leaves were provided), then in the aquaria which received *B. exaristata* leaves (treatment no. 3), while moulting occurred only during the last week of the experiment for crabs fed *C. tagal* leaves (treatment no. 1) (Fig. 3).

ABSORPTION EFFICIENCY

Absorption efficiencies of *S. messa* fed a mixture of four species of senescent mangrove leaves (i.e. *C. tagal*, *R. stylosa*, *B. exaristata*, and *A. marina*) ranged from 7.49 to 79.88% ($n = 10$), with an average of 37.29% and a standard error of 7.96%. Since the

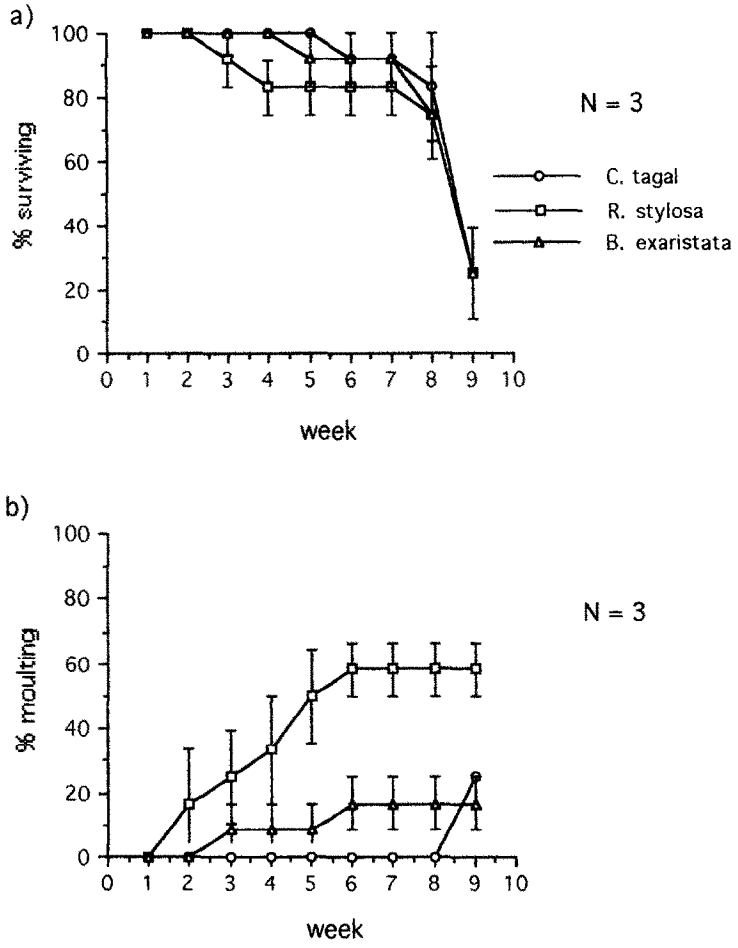

Fig. 3. Cumulative percentages of crabs surviving (a), and undergoing moult (b), in the experiment performed to investigate the effect of mangrove leaf species on the performance of *S. messa*. Mean percentages ± 1 SE.

four leaf species were offered to the crabs contemporaneously, it was not possible to determine whether *S. messa* exhibited differential absorption efficiencies of the different leaf species. Crabs, as already found in a previous experiment (Micheli, 1993), consumed leaves of all four mangrove species offered in similar proportions.

Discussion

These experiments showed that both growth and reproduction of *S. messa* are influenced by the quantity and the species of mangrove leaves available to the crabs.

Similar survivorship, on the contrary, was observed for crabs fed different diets. Growth and reproduction, as already observed (Rushton & Hassall, 1983), proved to be more sensitive to changes in food quantity and quality than survival is.

Of particular interest was the result of a significantly greater proportion of females carrying eggs in the treatment where mangrove litter was provided ad libitum. This result indicates that there might be a direct relationship between litter production of mangrove forests and the production of crab larvae, i.e. the principal food source for a variety of juvenile fish and crustacean species that use mangrove creeks as nursery sites (Robertson et al., 1988). Even though the majority of fish and crustacean species that inhabit mangrove creeks do not feed directly on mangrove detritus, highly productive forests might be expected to support greater secondary production in nearby waters by supporting high levels of productivity of sesarmid crabs.

Spawning in *S. messa*, occurs towards the end of the dry season (ovigerous females were observed mostly in September–October; Micheli, unpubl. data), which coincides with the time of minimum litterfall for most mangrove species in North queensland (Williams et al., 1981; Boto et al., 1984). The greatest numbers of moulting individuals, in contrast, were found during the wet season, when litterfall is at its maximum. Reproduction of *S. messa* in the field seems therefore more likely to be affected by litter limitation than growth.

The hypothesis that the availability of mangrove leaves might be limiting the crab production of larvae was not tested in the field. The scarce amounts of litter observed on the forest floor (Robertson, 1986; Robertson & Daniel, 1989; pers. obs.), and the high rates of consumption of tethered mangrove leaves observed in a previous field study ($\approx 50\%$ of the initial weight of mangrove litter deployed in three different forests had been consumed after 24 h, while over 90% had been consumed after 8 days; Micheli, 1993), however, seem to support the hypothesis that litter availability to the crabs is limited during the dry season.

In spite of the high concentration of polyphenolics characteristic of mangrove leaves (Giddins et al., 1986; Neilson et al., 1986; Robertson, 1988), *S. messa* is able to assimilate leaf material and utilize it for growth and reproduction. *S. messa* absorption efficiency of senescent mangrove leaves compared well with the absorption efficiencies reported for other crustaceans feeding on different plant or algal materials (*S. messa*: 37.3%, senescent mangrove leaves, present study; *S. smithii*: 35%, senescent mangrove leaves, Giddins et al., 1986; the amphipod *Allorchestes compressa*: 50% *Ekclonia radiata* talli, Robertson & Lucas, 1983; the mysid shrimp *Mysis stenolepis*: 30–50%, cellulose, Foulds & Mann, 1978; the isopods *Armadillium vulgare*: 55%, thistle leaves, Hubbell et al., 1965; and *Asellus aquaticus*: 30%, decaying alder leaves, Prus, 1971).

Conover's (1966) method for measuring absorption efficiency is based on the assumption that the ash fraction is unchanged by the digestive process. Such method has the advantage of not needing a measure of the animal defaecation rate and gives results which compare well with those obtained with direct gravimetric determination (Conover, 1966), and nitrogen uptake measurments (Corner et al., 1967). Further, the

absorption efficiency value here determined for *S. messa* (37.3%) is strikingly close to the value that Giddins et al. (1986) measured in a congeneric sesarmid species, *S. smithii*, using a different technique (35%). An alteration of the ash fraction of the gut contents, however, is known to occur in some crustaceans (Prus, 1971; Page, 1983), molluscs (Grahame, 1973) and fishes (Lambert, 1984). The assumption of this method, therefore, is not met in all cases, and this result should be interpreted with caution.

Rhizophora stylosa leaves gave a better rearing performance than *C. tagal* or *B. exaristata* leaves. More crabs, in fact, moulted when feeding exclusively on the former leaf species than on either of the other leaf species offered. *R. stylosa* had both the greatest nitrogen and tannin contents, among the three species considered (Robertson, 1988; Micheli, 1993). The performance of the crabs might have been expected to be positively correlated with the nitrogen concentration of the food offered. The fact that the food which was the richest in tannins proved to be the highest quality one for the crabs, on the contrary, was an unexpected result. This result seems to contradict the hypothesis that tannins deter herbivory by mangrove crabs (Giddins et al., 1986).

S. messa did not select any of four mangrove leaf species (*R. stylosa*, *C. tagal*, *B. exarista*, and *Avicennia marina*), in the course of laboratory leaf choice experiments (Micheli, 1993). A congeneric sesarmid species (*S. smithii*), however, did prefer *R. stylosa* leaves over all others (Micheli, 1993), in agreement with the present result of *R. stylosa* leaves being a better quality food, for sesarmid crabs, than the other species. A greater secondary production of crab populations might be expected in *Rhizophora* forests than in *Ceriops* and *Bruguiera* stands.

The presence of an alternative food source in the aquaria i.e. microbial organisms living in the mud surface layers, might confound the interpretation of the results of these experiments. In the first rearing experiment, bacterial densities in the surface sediments were greater, although very variable, in the aquaria where mangrove litter was added ad libitum than in the other treatments. Bacterial production might have been indirectly enhanced, in the ad libitum treatment, by the grazing activity of crabs. The crab consumption of leaves, and the consequent expulsion of the undigested fraction with faeces, considerably reduces leaf fragment size with respect to the litter shedding from the trees and decomposing on the forest floor. Plant material which has been mechanically and chemically modified in the crab digestive system may be rapidly colonised by bacteria. Crab faeces therefore may offer an ideal substratum for bacterial growth (Robertson & Daniel, 1989). The principal food sources of sesarmid crabs, i.e. mangrove litter and sediment microbes, might be tightly linked by the crab feeding cycle itself. Grazing on mangrove litter by sesarmid crabs could be one of the factors responsible for the high bacterial productivity measured in mangrove sediments (Alongi, 1988). Alternatively, bacterial densities might have been greater where leaves were provided ad libitum than in the other treatments because of a less intense consumption of microbes by the crabs in the presence of an unlimited alternative food source. Crabs might prefer to feed on mangrove leaves and might switch to feeding on sediment microbes only when no leaves are available. This explanation, however, seems contradicted by the observation that

crabs, in the field, spend most of their time foraging on the sediment surface, even in the presence of mangrove leaves (Micheli, 1993).

Crabs assigned to the ad libitum treatment, might have exhibited enhanced growth and reproduction because of the greater availability of microbes rather than of mangrove leaves. A more rigorous test of the hypothesis that the growth and reproduction of *S. messa* are directly and positively correlated to the amount of mangrove leaves invested should have involved the use of sterilised sediments, in the aquaria. There was, however, little variability in the proportions of ovigerous crabs observed in different aquaria of the ad libitum treatment (Fig. 1) in spite of the large between-aquaria variability of bacterial densities within this treatment (see Results). Unlimited litter availability seemed to have had variable effects on bacterial production, but consistently positive effects on the crab reproductive performance, suggesting a direct relationship between litter quantity and reproductive output.

In conclusion, these experiments suggest that crab secondary production in mangrove forests is directly linked to the forest primary production and possibly also to the forest tree species composition. Spatial and temporal variation in the forest productivity and composition might thus affect crab population structure and larval output in subtidal areas, unless compensating factors, not identified with these laboratory experiments, intervene in the natural scenario.

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