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Utilization of floating mangrove leaves as a transport mechanism of estuarine organisms, with emphasis on decapod Crustacea

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ABSTRACT: Floating mangrove leaves with associated organisms were sampled approximately every 2 h over 4 consecutive tidal cycles from 1 to 3 December 1987 in the estuary of Punta Morales, Gulf of Nicoya, Costa Rica. Crabs were the predominant animals collected (77.8 %), followed by shrimps, fishes and other crustaceans. The 4 most abundant decapod crustacean taxa found attached to the leaves were *Uca, Callinectes, Penaeus* and *Macrobrachium*. Megalopal and juvenile stages of decapods, clingfish *Tomicodon* sp., as well as amphipods and isopods, were attached to the drifting leaves. Organisms were significantly more numerous during flood than ebb: mean total number of individuals per leaf was one order of magnitude greater during incoming than during outgoing tide (2.3 versus 0.1). This transport mechanism may minimize both the risk of predation and the energy required to immigrate into the preferred habitat. This strategy may be important for recruitment of crabs and shrimps in mangrove ecosystems.

INTRODUCTION

Larval transport of many estuarine species between estuaries and adjacent coastal waters of temperate zones has been well documented (McConaugha et al. 1983, Johnson et al. 1984, Johnson 1985, Epifanio et al. 1984, Epifanio 1988, McConaugha 1988). Many species exhibit behavioral patterns that facilitate retention of larval stages within estuaries, while others are advected from the estuary, with subsequent reinvasion of megalopal and juvenile stages. Behavior of larvae favoring retention involves changes in vertical position throughout larval development (Bousfield 1955) or vertical migration in response to tidal changes (Carriker 1951, 1967, Cronin & Forward 1979, Boicourt 1982, Epifanio et al. 1984, Sulkin 1984). On the other hand, there is ample evidence that hatching rhythms in species of decapod crustaceans accelerate transport out of the estuary. Fiddler crabs (*Uca* sp.) release their larvae during nocturnal spring tides facilitating transport into deeper channels where environmental conditions are less severe (Christy 1982, Morgan 1987). Also, semilunar hatching on spring tides disperses larvae quickly from tidal creeks and upper estuaries where predation could be considerable (Christy 1982).

Despite the extensive literature on patterns of recruitment and dispersal in estuarine organisms, little is known about the role of floating material as a transport mechanism for larval and juvenile stages reinvading estuarine areas. Several studies have documented the occurrence of large numbers of decapod crustaceans in drifting clumps of algae (Hooks et al. 1976, Kingsford & Choat 1985, Virnstein & Howard 1987) and the possible importance of floating algae in offering protection against predation (Gore et al. 1981). In addition, different developmental stages of crabs have been observed to cling to a variety of flotsam (Williams 1980, Zeldis & Jillet 1982, Shanks 1983, 1985). Although leaf-carrying behavior of the crab *Neodorippe (Neodorippe) callida* has been reported from the mangrove swamps in Singapore (Ng & Tan 1986), no published information is available concerning the role of drifting leaves as a transport mechanism of estuarine organisms.

The purpose of the present study was to evaluate the importance of floating mangrove leaves as a transport

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mechanism of larval and juvenile stages of decapod crustaceans and the possible implication of this strategy for recruitment of estuarine organisms.

MATERIALS AND METHODS

Study area. The Gulf of Nicoya is an embayment located at ca 10° N, 85° W on the Pacific coast of Costa Rica. Seasonal variation in the chemical and physical characteristics of the Gulf is controlled by a rainy season extending from May through November, and a dry season from December through April (Epifanio et al. 1983, Voorhis et al. 1983). The upper Gulf, north of San Lucas, is surrounded primarily by mangrove swamps along the eastern shore, and rocky beaches along the western shore (Voorhis et al. 1983). Mean tidal range is 2.3 m.

The study site (Fig. 1), Punta Morales, is a small secondary estuary located on the eastern shore of the mid upper Gulf. It is bordered by extensive mangrove swamps and is characterized by a main channel (average depth 5 m at high tide) with input of water from the Morales river and numerous smaller creeks.

Sampling. Floating mangrove leaves were collected approximately every 2 h during 4 consecutive tidal cycles from 1 to 3 December 1987. Leaves were sampled from a small boat directly from the surface (less than 15 cm) by hand-dipping a 25 µm plankton net with a mouth opening of 25 cm. Duration of sampling ranged from 5 to 15 min, depending on the abundance of floating leaves. An average of 57 leaves were collected during flood and 150 during ebb. Immediately after collection, leaves were transferred into a 10 l bucket, rinsed individually and counted. Associated organisms were sorted, preserved in 4 % buffered formalin and transferred into 70 % ethanol upon return to the laboratory. All animals were counted and identified to the lowest taxa possible using a dissecting microscope. Available keys were used to aid identification (Sandifer 1973, Williams 1974, Arango unpubl.). Size of decapod crustacean juveniles was determined using an ocular micrometer; shrimps were measured from rostrum to end of telson, crabs from tip to tip of lateral spines on carapace.

Statistical procedures. Samples taken between high slack water and low tide were grouped under 'ebb' and samples after low slack water until high tide were grouped under 'flood'. All statistical analyses of data are based on the sum of 3 samples taken during each phase of the tidal cycle (ebb and flood) for each of the 4 consecutive tidal cycles. Each sample value is the mean number of organisms per leaf. A Wilcoxon-test for 2 matched samples (Winkler & Hays 1975) was used to determine the significance of differences in abundance of organisms during ebb and flood.

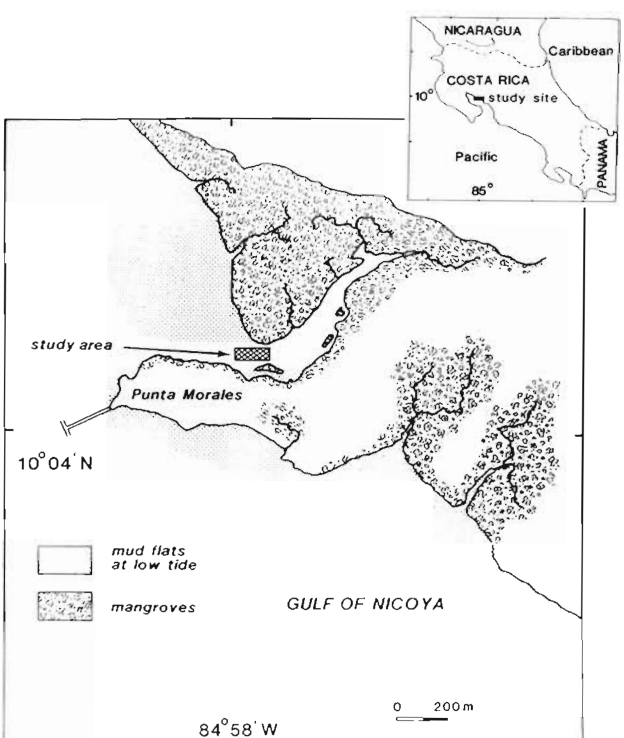

Fig. 1 Location of study site

RESULTS

A total of 2182 floating mangrove leaves and 2103 associated individuals were collected during the 4 tidal cycles. Ten different decapod crustacean families were identified (Table 1). Fig. 2 shows the percentage of the different groups of organisms associated with leaves. Crabs constituted the majority of the species followed by shrimps, fishes and others (amphipods 93.3 % and isopods 6.7 %).

Within the Natantia, species of the genus *Penaeus* and *Macrobrachium* were predominant, comprising 81.6 % of the collected shrimps; the majority of the specimens were juveniles (Table 1). As adults of *M. panamense* occur around the study area (Wehrtmann pers. obs.), the collected juveniles may belong to this species. However, early juveniles of *Macrobrachium* are very difficult to identify to species (Holthuis pers. comm.). In brachyuran crabs, *Uca* sp. megalopae were by far the most abundant taxon, constituting 93.5 % of the total number of crabs, followed by *Callinectes* sp. juveniles with 3.0 %. The 2 predominant genera of fish were *Tomicodon* sp. and *Pomadasys* sp., representing 69.2 % of the fish sampled.

Although zoeal stages of decapod crustaceans and fish (with the exception of *Tomicodon* sp.) were col-

Table 1. Numbers, percentages, and developmental stages of decapod crustaceans associated with floating mangrove leaves in the estuary of Punta Morales, Gulf of Nicoya, Costa Rica

Taxa	n	Stage	%
Shrimps			
Penaeidae			
Penaeus californiensis	9	Juvenile	4.7
Penaeus occidentalis	5	Juvenile	2.6
Penaeus stylirostris	23	Juvenile	12.0
Penaeus vannamei	52	Juvenile	27.2
Penaeus sp.	3	Mysis	1.6
Atyidae			
Atya sp.	1	Juvenile	0.5
Palaemonidae			
Macrobrachium sp.	64	Juvenile	33.5
Palaemonetes schmitti	6	Zoea I	3.2
	2	Zoea II	1.1
Alpheidae			
Unidentified Alpheidae	7	Zoea I	3.7
	1	Zoea II	0.5
	1	Zoea III	0.5
	3	Juvenile	1.6
Processidae			
Ambidexter panamense	1	Zoea I	0.5
	1	Zoea VIII	0.5
Unidentified	12	–	6.3
TOTAL	191		100
Crabs			
Ocypodidae			
Uca sp.	1530	Megalopa	93.5
Grapsidae			
Unidentified Grapsidae	42	Megalopa	2.5
Grapsus sp.	8	Juvenile	0.5
Portunidae			
Callinectes sp.	49	Juvenile	3.0
Xanthidae			
Unidentified Xanthidae	1	Juvenile	0.1
Pinnotheridae			
Pinnixia sp.	2	Zoea IV	0.1
Pinnotheres sp.	1	Juvenile	0.1
	1	Megalopa	0.1
Unidentified	1	Megalopa	0.1
TOTAL	1635		100

lected together with the leaves from the surface layer, they were not found attached to them.

Decapod crustacean juveniles of different size ranges within each group were obtained. *Penaeus californiensis, P. occidentalis* and *Macrobrachium* sp. (total length 7.2 to 12.2 mm, mean 8.7 ± 1.4 mm) as well as *Callinectes* sp. (carapace width 2.0 to 36.0 mm, mean 7.6 ± 5.2 mm) varied considerably in size, indicating that different age groups use drifting leaves for transport. In contrast, *P. vannamei* and *P. stylirostris* showed little variation in size (Table 2).

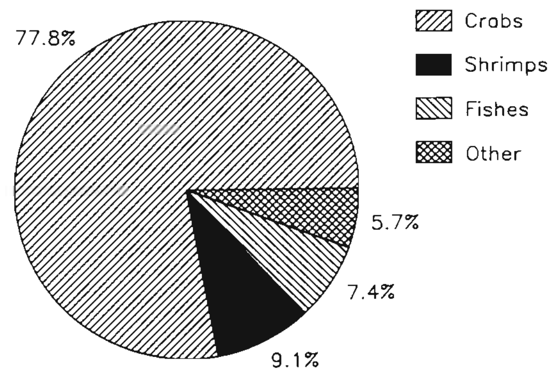

Fig. 2. Percentage of different groups of organisms associated with floating mangrove leaves in the estuary of Punta Morales, Gulf of Nicoya, Costa Rica

Overall, the overwhelming majority of the collected organisms were encountered on the flood (92.9 % vs 7.1 % on the ebb). The mean number of organisms per leaf during the 4 tidal cycles is shown in Fig. 3. Peaks of abundance were always obtained during incoming tides, with an average maximum peak of 8.5 organisms per leaf during the fourth tidal cycle. Mean number of organisms per leaf during floods and ebbs were significantly different ($p < 0.05$) and one order of magnitude greater during incoming tides than during ebb (2.3 versus 0.1).

Fig. 4 represents the percent abundance of the main groups during the 4 tidal cycles. In general, all animals occurred predominantly during flood with the exception of *Uca* sp. and fishes during the first tidal cycle sampled. In all cases, there was a significant difference ($p < 0.05$) in percent abundance between ebb and flood. Percent abundance of the 3 most common decapod crustaceans attached to the floating leaves is shown in Fig. 5. Juveniles of *Penaeus* and *Macrobrachium* occurred predominantly during flood. As in shrimp taxa, brachyuran crabs of the genus *Uca* were mainly obtained during incoming tides. Although juveniles of *Callinectes* were obtained in small numbers (49 individuals), the species was mainly present during flood.

Table 2. *Penaeus* spp. Size distribution (mm $\bar{x}$ ± SD) of juveniles attached to floating mangrove leaves

Species	TL ($\bar{x}$)	SD	Min.	Max.
P. vannamei	10.6	0.6	9.1	11.7
P. stylirostris	8.7	0.4	8.1	9.4
P. californiensis	12.0	3.5	9.6	19.0
P. occidentalis	12.9	3.8	9.0	17.5
Total	10.5	1.9		

DISCUSSION

Different behavioral strategies for larval dispersal and recruitment of estuarine populations are well studied; however, the use of floating leaves as a transport mechanism for larval and juvenile stages has not previously been described. Preliminary results of this study clearly show that drifting mangrove leaves are utilized by different groups of organisms entering the estuary of Punta Morales. In addition, Wehrtmann (pers. obs.) found megalopae and juvenile decapod crustaceans attached to floating leaves in coastal waters of the National Park Manuel Antonio (9° 15′ N, 84° 25′ W), located ca 120 km southeast of the Gulf of Nicoya. This observation suggests that the described transport mechanism is not restricted to the estuary of Punta Morales but may also occur in other coastal areas surrounded by mangroves.

The occurrence of *Penaeus* and *Macrobrachium* on floating leaves in the study area indicates a zone of overlap in the distribution of juvenile stages of these 2 genera. This is in agreement with results reported by Gamba & Rodriguez (1987) from a tropical lagoon in Venezuela. The predominance of *Penaeus* juveniles during flood can be interpreted as a transport into the nursery area, while juvenile *Macrobrachium* may utilize drifting mangrove leaves as a transport mechanism to reinvade the upper riverine regions where parent populations are located.

Numerous studies (Christy 1978, Bergin 1981, Christy & Stancyk 1982, Morgan 1987) have demonstrated that some species of *Uca* occur and spawn in the upper and mid reaches of estuaries. Zoeal stages are exported to the lower estuary, returning to the parent population as megalopae or juveniles. Our results show a similar pattern of recruitment with reinvasion of *Uca* megalopae into the estuary with incoming tides. The present findings, however, indicate that megalopae reenter the estuary not only by vertical migration related to the tides (Epifanio et al. 1988) but also by taking advantage of drifting leaves during floods (Fig. 5). In the present study, both *Uca* sp. megalopae and *Callinectes* juveniles appear to employ this additional recruitment strategy. Additionally, the occurrence of larger *Callinectes* juveniles (e.g. 36.0 mm) in our samples may be explained as a utilization of floating leaves as a feeding substrate.

Previous studies found high densities of small fish in association with drift algae (Kingsford & Choat 1985, 1986). Our collection contained several fish taxa; however, only the gobiesocid clingfish *Tomicodon* sp., the most abundant species collected during the study period, was found attached to the floating leaves. The Gobiesocidae are characterized by a sucking disc, which allows the fish to adhere to different types of substrates (Nelson 1984). This may explain the presence of this organism found attached to floating leaves. Further information concerning fish associated with mangrove flotsam in the estuary of Punta Morales will be provided by Szelistowski (unpubl).

Although no data on the importance of drifting leaves for dispersal and recruitment of estuarine populations are available, several studies have been conducted on the relationship of drifting algae and macrocrustaceans (Hooks et al. 1976, Gore et al.

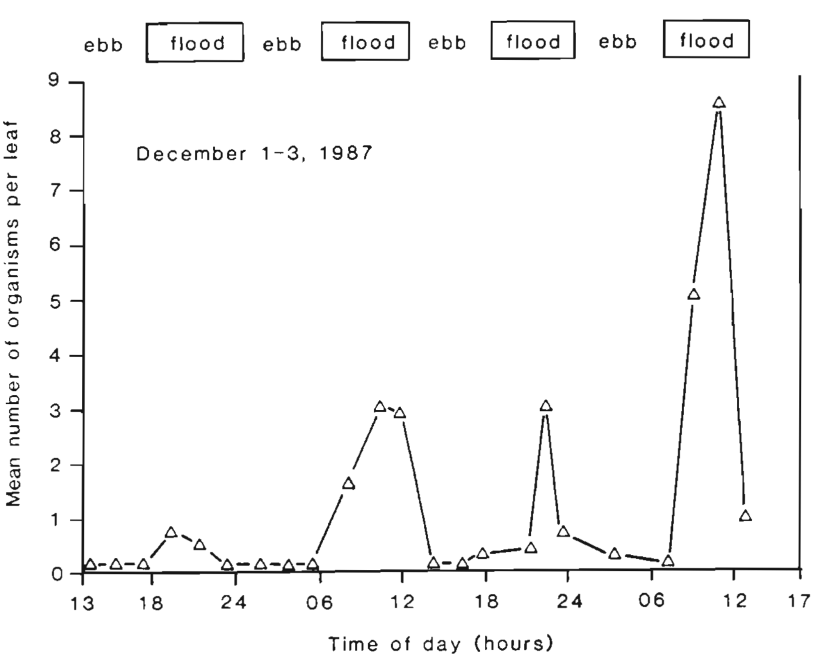

Fig. 3. Total mean number of organisms associated with floating mangrove leaves collected

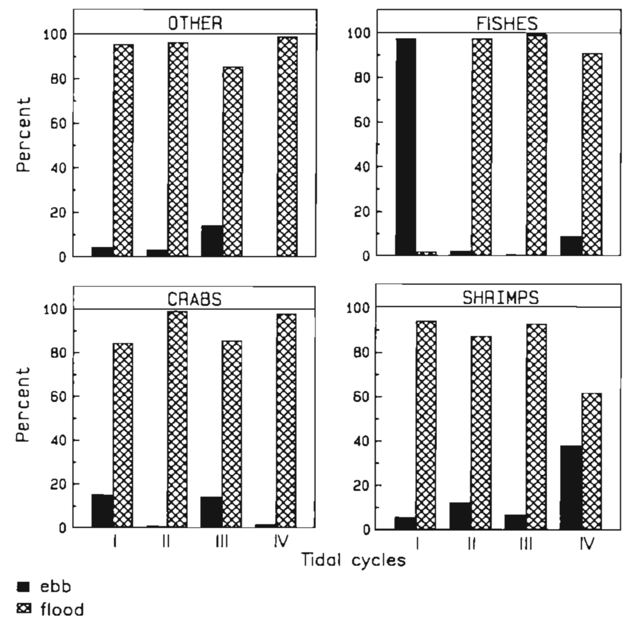

Fig. 4. Percent abundance of the groups of organisms associated with floating mangrove leaves during 4 tidal cycles (1 to 3 December 1987)

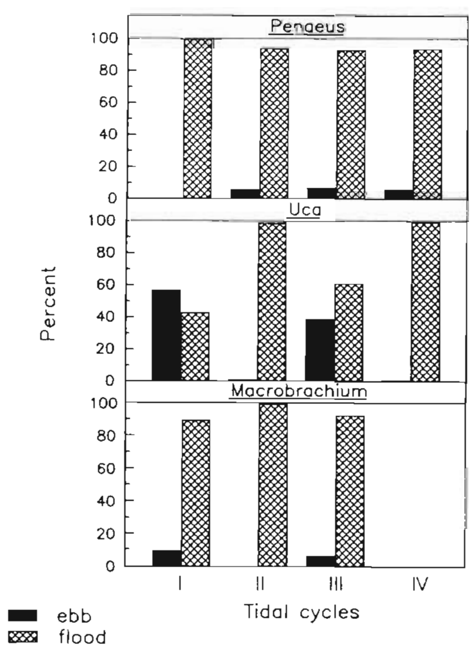

Fig. 5. Percent abundance of the 3 most common decapod crustacean taxa attached to floating mangrove leaves

1981, Virnstein & Howard 1987), showing a large number of organisms associated with clumps of drifting algae from estuarine waters. Caridean shrimps formed a major part of the macrocrustacean fauna. Furthermore, juvenile and prejuvenile shrimps were the most abundant invertebrates around drift algae collected at the northeastern coast of North Island, New Zealand (Kingsford & Choat 1985). In accordance with the above-mentioned studies, our data document that decapod crustaceans are not only associated with drift algae, but also with floating mangrove leaves.

Mangrove forests are open systems in which tidal flushing adds or removes litter (Woodroffe et al. 1988). Remarkable concentrations of floating debris, especially of mangrove leaves, were found at several tidal fronts observed at low tide in the mouth of the Punta Morales estuary during the sampling period. This zone of concentrated material may improve the possibility of larval and juvenile stages encountering and attaching to leaves. Laboratory studies (Shanks 1985) as well as field studies (Phillips 1972, Williams 1980, Zeldis & Jillett 1982) documented that larval and juvenile stages of different decapod crustaceans show a tendency to cling to objects in the water. Furthermore, colonization experiments demonstrated that fish and invertebrates were quickly attracted to soaked algae left to drift (Kingsford & Choat 1985).

The significantly smaller number of organisms obtained during outgoing tides might indicate that the animals detach from the leaves further up the estuary. However, the location where detachment occurred as well as the cues responsible for such behavior are unknown. A possible explanation may be that these organisms can sense enhanced turbulence associated with tidal changes, thus providing a cue for detachment.

In general, our findings fit well with results reported for decapod crustaceans concerning life history and behavioral strategies of dispersal and recruitment. Transport by floating leaves appears to be important for recruitment of crabs and shrimps in mangrove ecosystems. It is likely that species attached to leaves take advantage of reduced predation pressure by organisms inhabiting the water column. In addition, this strategy might be advantageous in minimizing energy utilization during reinvasion into the estuary. According to Rulifson (1983), juvenile penaeid shrimp must actively spend energy to remain in the water column during tidal transport. This is probably also true for juveniles of other decapod crustaceans. Thus, organisms using floating leaves to immigrate into the estuary would not have to spend energy to remain on the surface during flood.

We suggest that the described mechanism is important for transport and recruitment of larvae and juveniles in tropical and sub-tropical estuaries dominated by mangroves. In addition, the observed behavior might minimize both the risk of predation and the energy required for the immigration into the preferred habitat during this critical life history stage, resulting in higher survival rates.

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