

FOOD PATHWAYS ASSOCIATED WITH PENAEID SHRIMPS IN A MANGROVE-FRINGED ESTUARY

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ABSTRACT

High abundance and production of juvenile *Penaeus* spp. in tropical estuaries has been attributed to high concentrations of mangrove-derived detritus in the nursery habitats. Examination of the diets of *Penaeus notialis*, *P. subtilis*, and *P. brasiliensis* in the mangrove-fringed Laguna Joyuda, Puerto Rico showed that even the smallest juveniles are predators consuming capitellid polychaetes (20–38% of diets) and amphipods (20–76%). Less than 25% of the diets was detritus. Ontogenetic variation in diets was greater than interspecific variation, and there was no evidence for dietary separation among the sympatric species. Seasonal shifts in foods reflected abundance patterns of macrobenthic prey species. Despite the consumption of prey organisms generally classified as detritivorous, stable carbon isotope ratios in the penaeids (–18.1 to –15.0‰), their food items (–18.8 to –17.7‰), and primary producers indicated that shrimps and the majority of sediment dwellers in Laguna Joyuda obtain most of their carbon from benthic algae (–14.4‰) and not from mangrove detritus (–25.0 to –22.9‰).

The juveniles of penaeid shrimps are abundant in many tropical and subtropical estuaries of the world, particularly where wetland habitats such as marsh grasses or mangroves are prominent coastal features (Edwards 1978; Staples 1980; Stoner 1988). The relationship between wetlands and commercial shrimp has been attributed to at least two factors: high food abundance and shelter from predators, the relative importance of which is still debated (Boesch and Turner 1984). Early wetland studies (Odum and Heald 1972, 1975) suggested that a large variety of fishes and invertebrates including *Penaeus* spp. were directly dependent upon detritus from the vascular wetland plants. More specific studies of penaeid diets have since revealed that the shrimps are omnivorous or carnivorous in many shallow-water habitats (Moriarty 1976, 1977; Chong and Sasekumar 1981; Moriarty and Barclay 1981) and that some species may have a direct influence on the abundance of small macrofauna (Leber 1983, 1985).

The most important commercial shrimp species in the Caribbean Sea and along the north coast of South America are *Penaeus notialis*, *P. subtilis*, *P. brasiliensis*, and *P. schmitti*, all of which have nurseries in coastal wetland habitats (Stoner 1988).

Although the biology of tropical Atlantic penaeids has been studied in a few localities (Neiva 1969; Nikolic and Ruiz 1969; Lindner 1971; Garcia 1974; Garcia et al. 1985), we have found no information on their diets.

Examinations of shrimp diets reported here were conducted in a small coastal lagoon in Puerto Rico where *Penaeus* populations are large and where four species coexist (Stoner 1988). In this report, diets of the three most abundant *Penaeus* species are described with particular reference to ontogenetic variation, similarities among the species, the significance of detritus, and seasonality in diets as related to the abundance of foods in the field.

Because foods are retained and assimilated differentially in the gut, examination of gut contents does not necessarily give a true indication of the relative importance of foods. For example, detritus has been reported as a significant component of the gut contents of *Penaeus* spp. (Odum and Heald 1972), but detritus is known to be indigestible compared with soft-bodied prey organisms such as polychaetes. Furthermore, in the case of predators, the primary source of carbon is not revealed through gut analysis. For these reasons, stable carbon isotope ratios were measured for *Penaeus* spp. and most other organisms common in the lagoon.

METHODS AND MATERIALS

Shrimps were collected in Laguna Joyuda on the west coast of Puerto Rico (lat. 18°07'N, long.

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67°11'W). The study site and shrimp and fish populations in the lagoon have been described by Stoner (1986, 1988). Briefly, Laguna Joyuda is a polyhaline basin with a total surface area of 1.21 km² and an average depth of approximately 1.5 m. One narrow channel 0.5 km long represents the only connection to the Puerto Rico shelf. Lagoon sediments are mostly fine mud and sand with very high organic content derived from red, white, and black mangroves which surround approximately 75% of the shoreline. Over the last 20 years the lagoon has had a salinity range of 4 to 44‰, depending upon precipitation and degree of channel closure (A. W. Stoner, unpubl. data).

Four penaeids utilize the lagoon as a nursery area. *Penaeus notialis* and *P. subtilis* are approximately equal in abundance and together comprise over 92% of the total penaeid assemblage (Stoner 1988). *Penaeus brasiliensis* made up 7.0% of the total collection in 1984 to 1985, and *P. schmitti* was relatively uncommon, making up <0.3% of the total (Table 1). For this study, we examined the diets of the three most abundant shrimp species.

Penaeids were collected with a 5 m otter trawl with 2.5 cm wings and body, and 5 mm cod end liner. All collections were made between nautical twilight and midnight at three sites: a northern muddy bottom arm of the lagoon (station 5), a sandy mud site in the central basin (station 3), and a sandy mud site near the channel (station 1). Collections were made monthly, during the last quarter of the moon, from July 1985 to June 1986.

Shrimps were divided into size classes on the basis of carapace length (CL) for gut content analyses. Penaeid shrimps between 3 and 6 mm CL could not be identified to species and were simply identified as *Penaeus* juveniles (all were of the grooved variety and, therefore, did not include *P. schmitti*). Shrimps larger than 6 mm CL could be identified and were examined by individual species in 4 mm size classes, up to 26 mm CL in the case of *P. subtilis*. To yield sufficient numbers of individuals in

all size classes for each monthly collection, members of individual species were pooled from all sampling areas. In the case of *P. brasiliensis*, collections from 2-mo intervals were pooled to analyze seasonal variation in the diets of this less abundant species. Food items taken from the proventriculus of up to 25 shrimp were pooled for each sampling date and size class, and preserved with 70% isopropanol and a dilute solution of rose bengal stain.

We used the gravimetric sieve fractionation procedure developed by Carr and Adams (1972) to analyze gut contents of the shrimp. This procedure has been widely used for juvenile fishes (Sheridan 1979; Stoner 1980; Livingston 1984) and a variety of decapod crustaceans, including *Penaeus* spp. (Laughlin 1982; Leber 1983). Gut contents were washed through a series of six sieves of decreasing mesh size (2.0–0.075 mm mesh) and each sieve fraction was examined with a dissecting microscope. Because all of the items in a particular sieve fraction were of approximately equal size, the relative proportion of the gut contents made up of each food type was measured directly by counting. After examination, each sieve fraction was dried overnight at 80°C and the total contribution of each food type to total dry weight was calculated.

With few exceptions, each food particle was placed in a mutually exclusive category (Table 2). In most cases, food items or fragments could be identified to major taxonomic group such as Amphipod or Polychaete. The classification "Animal Remains" was applied where fragments were unidentifiable to taxon, but where the tissue was stained by rose bengal. The major food categories were used for statistical interpretation of diets; however, whenever an animal or plant could be identified to a lower taxonomic level, this information was recorded.

Similarities between and among the diets of various shrimp species and size classes were measured with Czekanowski's coefficient (Bray and Curtis 1957; Field and McFarlane 1968). Dendo-

TABLE 1.—Composition of the penaeid shrimp assemblage at three stations in Laguna Joyuda, Puerto Rico, during the 12-mo study period. Values are total numbers collected in 72 trawl samples and percentages of totals at the individual sites (parentheses).

Species	Station		
	1	2	3
<i>Penaeus notialis</i>	282 (49.1)	271 (53.6)	229 (48.6)
<i>P. subtilis</i>	236 (41.1)	185 (36.5)	217 (46.1)
<i>P. brasiliensis</i>	54 (9.4)	50 (9.9)	22 (4.7)
<i>P. schmitti</i>	2 (0.4)	0 (0)	3 (0.6)
Totals	574	506	471

TABLE 2.—List of the general food categories encountered in the foreguts of *Penaeus* species and the codes employed in histograms for shrimp diets.

AM Amphipod	OS Ostracod
CC Calanoid copepod	PM Plant material (green)
CY Cyclopoid copepod	PO Polychaete
CZ Crab zoea	RU <i>Ruppia maritima</i>
DE Detritus	SA Sand
FO Foraminifera	TA Tanaidacean
FR Fish remains	TH <i>Thalassia testudinum</i>
HC Harpacticoid copepod	
GA Gastropod	MS Miscellaneous—used in histograms for all food items making up <4% of the total dry weight.
IE Invertebrate egg	
NE Nematode	

grams were then constructed by complete linkage classification.

Plant and animal materials were collected from the lagoon for stable carbon isotope analyses on several occasions between 1981 and 1984. These were taken to give an indication of the range of $\delta^{13}\text{C}$ values between organisms associated with mangroves, plankton, and benthos and to test the efficiency of using the technique to identify food pathways. Materials were collected with trawl, sieve, plankton net, and by hand. All materials were fresh and not exposed to chemical preservatives. In the field, samples were placed in plastic bags on ice as temporary storage. Within 24 hours, these samples were flushed free of salt using deionized water, dissected to acquire tissue uncontaminated by gut contents and outside shells, treated for 5 to 10 minutes with 5% phosphoric acid to remove carbonates, double rinsed in deionized water, and oven-dried at 70°C until brittle. Dried samples were ground to a fine powder with a mortar and pestle, packaged in plastic bags, labeled, and stored for later mass spectrometer analyses. The homogenized samples were combusted at 550°C for 24 hours in the presence of CuO in evacuated sealed pyrex tubes using techniques modified from Stofer (1980). CO_2 gas was analyzed from the combusted samples on a Finnigan - MAT 251³ isotope ratio mass spectrometer. $\delta^{13}\text{C}$ was calculated according to Craig (1957) and methods and definitions generally followed those reviewed by Fry and Sherr (1984). For small animals and all plants, the entire organism (with guts removed where possible) was used in analyses. For large animals, muscle tissue was removed from the body and used separately for analyses. In most cases, organisms were pooled to acquire mean $\delta^{13}\text{C}$ values for n individuals. Unlike more complex marine systems (Fry et al. 1982), our $\delta^{13}\text{C}$ were well separated between groups of species and distinctions were relatively clear-cut. Since diversity was also relatively low in the lagoon, $\delta^{13}\text{C}$ signatures in food pathways based on the dominant primary producers were easily detected. Some organisms with known restricted diets, that were closely associated with particular plants in the system, were selected as controls to follow trophic fractionation of $\delta^{13}\text{C}$. These included *Uca vocator* from the intertidal forest floor (a mangrove detritus feeder), *Haminoea antillarum* from the middle of the lagoon (an algae grazer), and *Balanus eburneus* and *Isognomon alatus* (filter feeders). Based on

results of Fry et al. (1984), we assumed that ^{13}C enriched the isotope ratio by about 1‰ from one trophic level to the next.

RESULTS

The Shrimp Community

The shrimp community composition during the study period was similar at the three sampling sites, except that *Penaeus schmitti* were not collected at station 3 (Table 1). *Penaeus notialis* dominated the shrimp assemblage in the lagoon (50.4%), followed by *P. subtilis* (41.1%), and *P. brasiliensis* (8.1%). Only five individuals of *P. schmitti* (0.3%) were collected in 12 months of sampling. Catch per unit effort over time was highly variable for each of the three primary species, with no distinct seasonality (Fig. 1). *Penaeus subtilis*, however, showed a general increase in abundance over the sampling period. *Penaeus brasiliensis* populations remained relatively low and stable throughout the year examined. Population and community structure of the penaeids in Laguna Joyuda has been examined in detail elsewhere (Stoner 1988) and the important point to be made here is that the three most abundant *Penaeus* spp. in Laguna Joyuda are sympatric in both time and space.

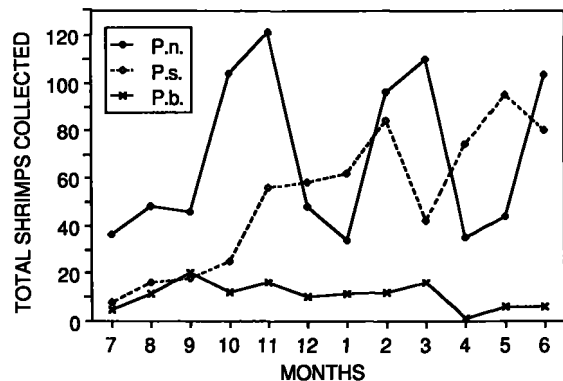


FIGURE 1.—Abundance of the three dominant *Penaeus* species in Laguna Joyuda, Puerto Rico, during the study period. The unit of effort for each sampling date is 18 trawl samples, pooled over all three stations. P.n. = *Penaeus notialis*; P.s. = *P. subtilis*; P.b. = *P. brasiliensis*.

Shrimp Diets

Over 1,300 *Penaeus* guts were examined for the present study. The proventriculi of most individuals contained freshly consumed food items; 89% of all

³Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

P. notialis, 87% of all *P. subtilis*, and 78% of all *P. brasiliensis* contained food. At least 50% of all animals in any one size class contained food on a given sampling date, but no seasonal or ontogenetic pattern in empty guts was evident.

The primary dietary components of all three penaeids were amphipods, polychaetes, harpacticoid copepods, and detritus (Fig. 2). For all species increase in shrimp size was correlated with decrease in the relative importance of harpacticoid copepods in the guts. Other small taxa such as nematodes and foraminifera also decreased with shrimp size. Detrital components of the diets remained relatively constant at approximately 20 to 25% of the gut contents. Abundance of polychaetes and amphipods changed relatively little with size in *P. notialis* and *P. subtilis*, except that amphipods increased in importance with size in *P. subtilis* and large quantities

of amphipods were taken by the largest size class. Cluster analyses for the diets of individual species revealed little ontogenetic variation for these two species, except with the distinct separation of the largest *P. subtilis* (Fig. 2). For both *P. notialis* and *P. subtilis*, all size classes between 7 and 22 mm CL were clustered within similarity indices of 0.78. Although only three size classes were represented for *P. brasiliensis*, ontogenetic variation in *P. brasiliensis* was greater than in the other two species (Fig. 2). Polychaete consumption decreased from 47% of the diet in the 7 to 10 mm class to 22% in the 15 to 18 mm class, while amphipod consumption increased from 0 to 61%. Detritus consumption also decreased with size in *P. brasiliensis*, contributing to the low similarity indices among the size classes.

Four major clusters of shrimp feeding types were

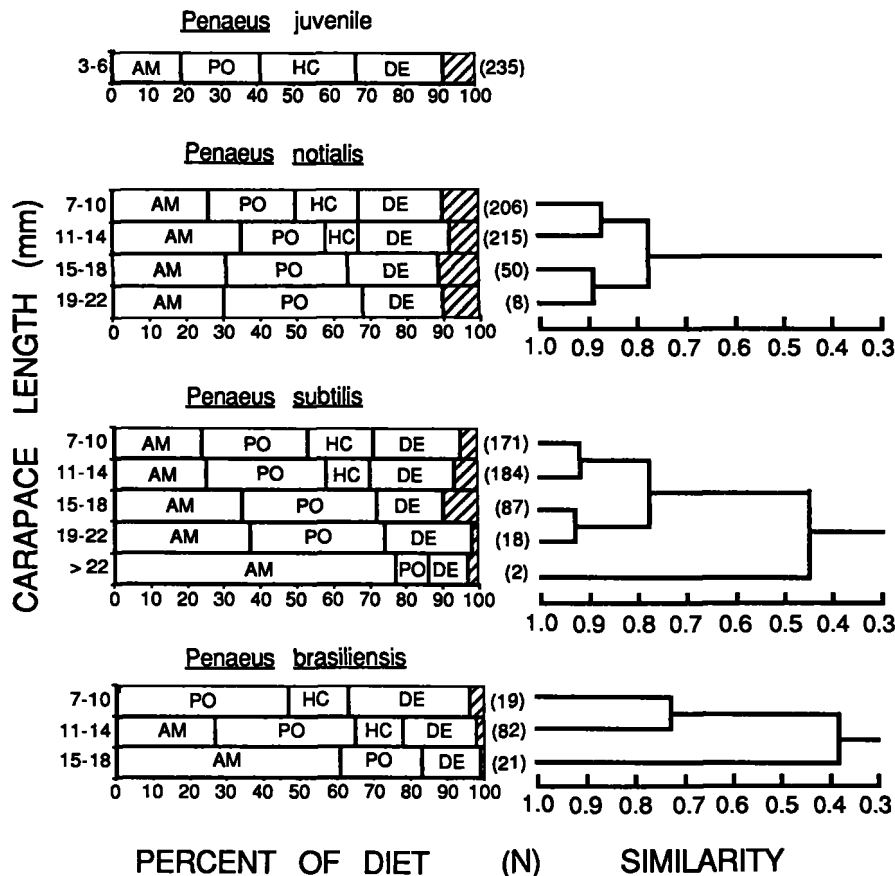


FIGURE 2.—Diets of the three dominant *Penaeus* species in Laguna Joyuda, Puerto Rico, shown as a function of shrimp size. Food categories are identified in Table 2. The similarity index used in the cluster diagrams is Czekanowski's coefficient.

revealed when the full matrix of similarity indices, including all species and size classes, was incorporated into a cluster analysis (Fig. 3). The greater ontogenetic variation in diets of *P. brasiliensis* resulted in the three size classes for the species falling into three distinct clusters, while all four size classes of *P. notialis* were included under two clusters. The largest *P. subtilis* were clustered with the largest *P. brasiliensis*. Except for *P. brasiliensis*, all shrimps between 7 and 14 mm CL were found in one trophic group and all between 15 and 22 mm CL were found in a second group.

Species or generic level identification of prey organisms indicated no species-specific differences among the diets of the three shrimp species. For all three species, all amphipods identifiable to species were *Grandidierella bonnieroides* and all identifiable polychaetes were nereids (probably *Nereis occidentalis* and *Stenionereis martini*). In *P. subtilis* and *P. brasiliensis*, all harpacticoid copepods were *Euterpina* spp. In *P. notialis*, 86% were *Euterpina* spp. and 14% were *Microsetella* sp. The calanoid copepods were a mixture of *Acartia tonsa* and *Pseudodiaptomus* spp.

Animals classified in groups 2 and 3 of the multi-species cluster (Fig. 3) contained sufficient numbers of individuals to make seasonal analyses of diets (Figs. 4, 5). Although harpacticoid copepods were taken in lower amounts by group 3 shrimps, by and large both groups showed similar seasonal trends in diet. Amphipods were taken in large numbers from July to October 1985 and from March through June 1986. Polychaetes and harpacticoid copepods were consumed most abundantly in November through March. Consumption of detritus was relatively constant in both groups, with slightly higher detrital intakes in group 2 individuals during November and December 1984.

Carbon Isotopes

The $\delta^{13}\text{C}$ values for three different samples of tissues from *Penaeus* spp. ranged from -15.0 to -18.1‰ (Table 3). These values were much higher than the plankton fraction $<35\ \mu$ (comprised primarily of dinoflagellates; -26.8 to -27.2‰) or the primary copepod species in the lagoon, *Acartia tonsa* (-24.0 to -25.9‰). The $\delta^{13}\text{C}$ values for the shrimps are also much higher than the values for either mangrove leaves (green or dead), or detritus particles from the sediment, mostly of mangrove origin. The only primary producers with $\delta^{13}\text{C}$ values within the range of *Penaeus* spp. were the seagrass *Thalassia testudinum* (-16.1‰) and the

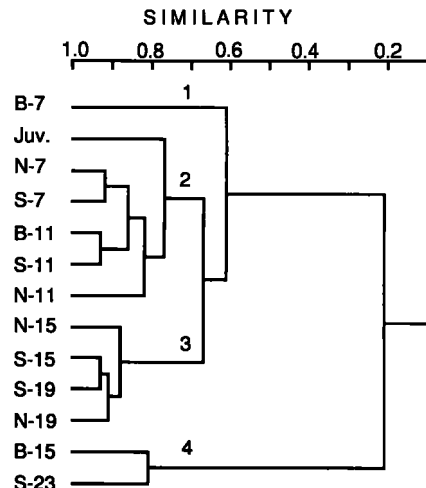


FIGURE 3.—Cluster diagram for the diets of shrimps incorporating all species and size classes. The cluster strategy is the same as that in Figure 2. Food categories are identified in Table 2.

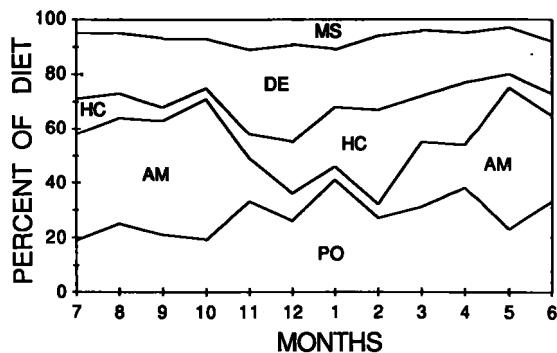


FIGURE 4.—Diets of shrimp trophic group 2 by sampling date.

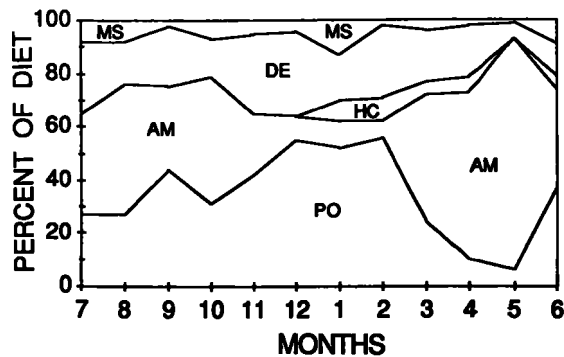


FIGURE 5.—Diets of shrimp trophic group 3 by sampling date.

algal mat comprised primarily of the filamentous blue-green alga *Spirulina* sp. Because there are only small patches of *T. testudinum* in Laguna Joyuda and the blue-green algae dominated the lagoon floor, the data suggest that the main source of carbon for penaeid shrimps in Laguna Joyuda is benthic blue-green algae. Blue-green algae also appear to be the primary source of carbon for other decapod crustaceans in the lagoon including *Callinectes* spp. and hermit crabs (Paguridae) (Table 3).

The carbon isotope data, suggesting algal sources of carbon for *Penaeus* spp., are consistent with the results of dietary analyses. The primary prey of penaeids were the amphipod *Grandidierella bonnieroides* and capitellid polychaetes. The $\delta^{13}\text{C}$ value for *G. bonnieroides* was within the range for *Penaeus* spp., -17.7‰ . Similarly, when the bodies of capitellids were analyzed after removal of the guts, the $\delta^{13}\text{C}$ value of -18.8‰ also agrees with

shrimps after adjusting for trophic fractionation of 1‰ less (Fry et al. 1984). Other organisms with $\delta^{13}\text{C}$ values similar to that of blue-green algae were the bubble snail *Haminoea antillarum* and the bivalve *Macoma brevifrons*. The carbon isotope ratios of these benthic feeders were more negative than *Spirulina* (-14.1‰), implying modification of $\delta^{13}\text{C}$ values from other sources; however, the major input appears to be from blue-green alga.

By contrast, organisms associated with the mangrove forest, *Uca vocator* (-23.0‰) and *Aratus pisonii* (-23.3‰), closely resembled carbon isotope ratios of detritus (-22.9 to -25.0‰). Moreover, the $<35\ \mu$ plankton fraction (-26.8 to -27.0‰) and associated grazers, *Acartia* (-24.0 to -25.9‰), *Balanus* (-24.0‰), and *Isognomon* (-24.4‰), were not separable from the mangrove group. These data indicate that mangrove carbon is likely being incorporated into plankton-based food

TABLE 3.—Carbon isotope ratios in organisms associated with the penaeid shrimp food web in Laguna Joyuda, Puerto Rico.

Organisms	Tissue or composition	Number of pooled indiv.	Date of collection	$\delta^{13}\text{C}$
Plankton				
<35 μ fraction		—	9/29/83	-26.8 to -27.2
<i>Acartia tonsa</i>	whole bodies	500	1/21/81	-25.9
<i>Acartia tonsa</i>	whole bodies	500	9/8/83	-25.2
<i>Acartia tonsa</i>	whole bodies	500	9/27/83	-24.0
Macroalgae				
<i>Spirulina</i> sp.	entire filaments	—	2/14/83	-14.2
<i>Caulerpa sertularoides</i>	entire alga	—	9/29/83	-20.2
Seagrass				
<i>Thalassia testudinum</i>	green leaves	—	9/29/83	-16.1
Mangroves				
<i>Avicennia germinans</i>	roots	—	2/14/84	-24.0
<i>Rhizophora mangle</i>	green leaves	—	9/24/81	-29.2
<i>Rhizophora mangle</i>	dead leaves	—	2/14/84	-27.3
Detritus				
Particulates from the sediment		—	9/24/81	-22.9 to -25.0
Polychaetes				
Capitellidae	body without gut	13	9/24/81	-18.8
Capitellidae	whole bodies	10	2/14/81	-23.1
Capitellidae	whole bodies	10	9/30/81	-22.0
Capitellidae	whole bodies	10	2/14/84	-22.9
Nereidae	whole bodies	2	2/14/84	-21.6
Mollusca				
<i>Haminoea antillarum</i>	whole bodies	1	9/24/81	-15.8
<i>Isognomon alatus</i>	whole bodies	6	9/24/81	-24.4
<i>Macoma brevifrons</i>	whole bodies	6	9/24/81	-18.8
Crustacea				
<i>Aratus pisonii</i>	leg muscle	10	9/30/81	-23.3
<i>Balanus eburneus</i>	whole bodies	20	9/24/81	-24.0
<i>Callinectes danae</i>	claw muscle	2	2/14/84	-15.4
<i>Callinectes sapidus</i>	claw muscle	1	2/14/84	-16.4
<i>Grandidierella bonnieroides</i>	whole bodies	52	2/14/84	-17.7
<i>Pagurus</i> sp.	leg muscle	3	2/14/84	-16.2
<i>Penaeus notialis</i>	tail muscle	12	9/31/81	-18.1
<i>Penaeus notialis</i>	tail muscle	10	2/14/84	-15.4
<i>Penaeus subtilis</i>	tail muscle	10	2/14/84	-15.0
<i>Petrolisthes</i> sp.	whole bodies	12	9/24/81	-23.5
<i>Uca vocator</i>	leg muscle	10	9/30/81	-23.0

chains in the lagoon. This can be supported using *Acartia* as a link, since the copepod is known to feed on detritus particles and because the growth of *Acartia* is improved with detritus is included in the diet (Roman 1984). Suspended detritus particles from mangroves were a component of our <35 μ plankton fraction, suggesting availability to planktonic consumers.

DISCUSSION

Early studies of penaeid diets led to the general conclusion that the shrimps were largely detritivorous with incidental amounts of animal or plant material in the guts (Williams 1955; Darnell 1958; Odum and Heald 1972). Dall (1968) concluded that several Australian penaeids were not predators, but consumers of small-sized and disabled animals. Although penaeid shrimps are known to sort sediments for organic particles with their delicate pereopods (Dall 1968; Lindner and Cook 1970) it is now apparent that penaeid shrimps are capable of taking prey organisms such as large polychaetes, as well as the more difficult prey such as gastropods and bivalves, caridean shrimps, crabs, echinoderms, and even fishes (Moriarty 1977; Marte 1980; Leber 1983). Lindner and Cook (1970) reported that *Penaeus setiferus* is cannibalistic at times. The relatively constant low amount of detrital particles in the guts of shrimp from Laguna Joyuda suggests that the less readily digestible detritus is taken incidentally with animal prey or as a response to low prey abundance. In addition, Gleason and Zimmerman (1984) showed that nematodes, oligochaetes, polychaetes, and copepods were stripped from detritus by *P. aztecus* during feeding. Reports of shrimp filled with unrecognizable debris assumed to be detritus may be a consequence of actual detritus consumption or incomplete development of methods sufficient to make animal remains identifiable.

Despite considerable attention given to feeding in the commercially significant penaeids, relatively few investigators have examined ontogenetic variation in diets. In this study, even within juvenile size classes, there were clear patterns of dietary change with shrimp size. All three of the subject species abandoned smaller prey organisms such as foraminifera, nematodes, and harpacticoid copepods in favor of amphipods, polychaetes, and shrimp as the predators became larger. Similar findings were reported by Leber (1983) for *P. duorarum*. These ontogenetic shifts in prey are undoubtedly related to increasing size of the chelae and mouth parts and must be considered in any ecological interpretation of trophic

position; Moriarty (1977) suggested that the great opportunism of penaeid shrimps precluded their being placed in one trophic group throughout their life cycle.

On the other hand, with the exception of accelerated ontogenetic shifts in the diets of *P. brasiliensis*, interspecific variation in feeding in Laguna Joyuda were relatively minor. Despite high abundance and great temporal and spatial overlap in the *Penaeus* spp. of the lagoon (Stoner 1988), coupled with very low biomass values for macrofauna (<2 g dry wt/m²), there is no evidence for resource partitioning among the grooved shrimps.

Seasonal diets in *Penaeus* spp. were coincident with seasonal trends in the abundance of major prey organisms. In the lagoon, the one important amphipod species, *Grandidierella bonnieroides*, demonstrated maxima between July and September and again from May to June; this corresponded with maximum amphipod consumption between July and October and March through June in the same year as benthic studies. Polychaete consumption was highest between November and March (particularly in the group 3 shrimps), corresponding with the October to April peak in capitellid abundance in the lagoon. Consequently, the oscillation in polychaete and amphipod feeding appears to be related to the availability of foods.

The hypothesis that mangrove estuaries are fueled primarily by carbon from mangrove detritus has become established from the pioneering work on mangrove-associated food webs conducted in the North River estuary of south Florida (Odum and Heald 1972, 1975). Mangrove litter inputs to Laguna Joyuda are high (Levine 1981), the sediments are rich in organic content, and detritus comprised a portion of the gut contents of juvenile shrimp. It is unlikely, however, that a large amount of carbon derived from detritus or detritus-associated microbes contributes in a large way to the tissues of the shrimp in the lagoon. In fact, the only organisms which had carbon isotope ratios similar to that of detritus were those normally found in direct association with the trees such as fiddler and mangrove crabs. The $\delta^{13}\text{C}$ values for shrimp in Laguna Joyuda were, in fact, very similar to values for penaeids from the open waters of the Gulf of Mexico (Fry and Parker 1979).

Benthic algal primary production in Laguna Joyuda is probably highly significant because carbon isotope ratios in the algae and shrimp were similar. Gleason (1986) also found that juvenile *P. aztecus* penaeids in a Galveston Bay salt marsh derived their carbon from blue-green algae, green

algae, and epiphytes of salt marsh grasses, not from *Spartina detritus*. Algal foods also proved to be the primary source of carbon for penaeids in Georgia marshes (Hughes and Sherr 1983) and in *P. duorarum* inhabiting seagrass beds in the Gulf of Mexico (Leber 1983) where food webs have long been considered detritus based. The significance of algal production in mangrove areas has been pointed out by Rodelli et al. (1984). They concluded that both mangrove and algal carbon were utilized by most of animals in a Malaysian swamp, but virtually no animals collected at distances >2 km from the swamp contained mangrove-derived carbon. To this date, there is little evidence to suggest that natant species such as fishes and decapod Crustacea can use detritus as a primary food source even if microbially enriched (Boesch and Turner 1984).

Localities where mangroves grow often support a variety of other primary producers, and variation in the relative significance of detrital and algal carbon sources may be associated with tidal amplitude and flushing. Laguna Joyuda, with microtidal influences, appears to be fueled by algal carbon whereas shrimp-producing mangrove areas in Ecuador have meso- and macrotidal regimes and no apparent algal growth (Zimmerman, pers. observ.). That mangroves provide critical substratum and protective cover for a large number of organisms is undisputed; however, the assumed significance of mangrove-derived detritus should be examined further.

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