

JEMBE 01627

## Carnivory vs. herbivory in juvenile *Penaeus setiferus* (Linnaeus) and *Penaeus aztecus* (Ives)

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(Received 13 August 1990; revision received 4 October 1990; accepted 27 March 1991)

**Abstract:** Postlarval *Penaeus setiferus* (Linnaeus), the white shrimp, and *Penaeus aztecus* (Ives), the brown shrimp, were reared for 24 days on vegetal, animal, and combination diets. Incremental weight change was used to compare shrimp growth rates among dietary treatments. Both species grew most quickly when fed a combination diet. Shrimp fed an animal diet also grew, but those fed vegetal diets either did not survive or grew very little. There were significant differences between the relative responses of the two species. Brown shrimp fed an animal diet of *Artemia* grew significantly more than did the white shrimp. Furthermore, the diatom *Skeletonema* was capable of producing growth in white shrimp that was similar to that produced by an *Artemia* diet until Day 20, but shrimp fed this vegetal diet did not survive until Day 24. There was no difference in the growth between white and brown shrimp fed a combination diet. The differences between the two species in their ability to utilize plant and animal material can be related to the resources available at their times of immigration.

**Key words:** Carnivory; Herbivory; Marsh; Penaeid

### INTRODUCTION

It is known that creeks adjacent to marshes are nursery habitat for many estuarine species (Weinstein, 1979; Currin et al., 1984; Kuipers & Dapper, 1984; Rozas et al., 1988), and it is thought that marshes at least indirectly contribute to the secondary productivity of estuaries (Odum, 1980; Boesch & Turner, 1984). But until recently, the importance of marsh surfaces as nursery habitat was not realized. Evidence for the occurrence of transient juveniles on marsh surfaces was demonstrated by Zimmerman & Minello (1984a), in the northern Gulf of Mexico, and by Rozas & Odum (1987) and Hettler (1989) on the southern Atlantic coast. The extent of marsh utilization depends on the available feeding opportunities, protective advantages, control by tidal flooding and marsh geomorphology (Zimmerman & Minello, 1984b; McIvor & Odum, 1988).

Juvenile penaeid shrimp are common transient members of Gulf of Mexico and southeastern US Atlantic salt marsh communities. Their life cycles involve eggs that hatch offshore into larvae that pass through several planktonic stages. Upon reaching the postlarval form, the shrimp migrate into estuaries, possibly through the timed use

of landward moving water masses. Once in estuarine areas, penaeids become benthic and live out most of their juvenile existence. As they approach maturity, subadult shrimp return to the offshore areas (Perez Farfante, 1969; Copeland & Bechtel, 1974; Weinstein, 1979; Williams, 1984). During their estuarine residence, plants on marsh surfaces give young penaeid shrimp a place to hide (Minello & Zimmerman, 1983) which increases their survival (Minello et al., 1989). The advantages of marsh habitats as feeding grounds to shrimp are not as evident because we know very little about their natural dietary habits.

While the two predominant species of penaeids in the western Gulf follow the same general life cycle, the timing of their immigration into estuaries differs. *Penaeus aztecus* (Ives), the brown shrimp, first enter the marsh as postlarvae from late March to early April, while *Penaeus setiferus* (Linnaeus), the white shrimp, do not appear until late May or June (Pearson, 1939; Williams, 1955; Baxter & Renfro, 1967; Perez Farfante, 1969; Copeland & Bechtel, 1974; Williams, 1984). The marsh differs during these periods in several respects. Benthic infauna and epifauna are at their highest seasonal abundances during the spring. Coull (1985), over an 11-year period in South Carolina, showed meiofaunal abundances in marsh areas with muddy substrata to be greatest in late winter to early spring. These numbers declined dramatically after the arrival of seasonal predators (Coull & Palmer, 1984). Similar trends are reported in the western Gulf of Mexico. In Corpus Christi and Galveston Bays, for example, abundances of small benthic invertebrates peak in the winter and spring, and then decline through the summer and fall months (Flint & Kalke, 1985; Zimmerman et al., 1990). By comparison, edaphic algae in a Mississippi salt marsh have the highest levels of production during the spring and summer, becoming low during the fall and winter (Sullivan & Moncreiff, 1987). A similar pattern has been observed for algae growing beneath short *S. alterniflora* in Delaware (Gallagher, 1971). In Georgia salt marshes, Pomeroy (1959) showed that the effects of tides and seasons result in a near constant rate of algal production throughout the year. Thus, algae are likely to be increased in availability during the summer, or at a minimum, may remain at a constant level year around. In addition, the physical environment of the marsh seems less favorable in the summer as it is a warmer place, with higher salinities and lower water levels.

Penaeid shrimp feeding habits are difficult to determine partly because identification of gut content material is hampered by the digestive process. Shrimp use their mouthparts and a gastric mill to shred and grind food and the contents of their guts most often contain unidentifiable, partially digested material with a few isolated hard parts. As a result, shrimp have been described as opportunistic omnivores, believed to consume any available plant and animal resources, including organic detritus (Williams, 1955; Young, 1959; Darnell, 1961). Unfortunately, this reveals very little about feeding preferences and dietary differences among species.

Penaeids feed by browsing along bottom surfaces. The foods available to them in salt marshes are mainly microalgae, infauna and epifauna, and vascular plant detritus. Microalgae, including diatoms, grow epiphytically on *Spartina* surfaces, edaphically on

the sediment surface, or are settled from the water column. Animal material includes infaunal polychaetes and oligochaetes, and epibenthic polychaetes, harpacticoid copepods and pericarideans (Rader, 1984; Fleeger, 1985). Among the latter, tanaidaceans and amphipods are abundantly found in salt marshes (Thomas, 1976; Heard, 1982; Rader, 1984). Plant detritus, taken to mean decomposing plant remains together with the associated microbial community, is available from *Spartina* fragments (De la Cruz, 1965).

Plant material has been documented in the diet of many penaeids, including grooved and nongrooved species (Brisson & Pace, 1978; George, 1978; Chong & Sasekumar, 1981; Hughes & Sherr, 1983; Gleason, 1984; Kitting et al., 1984; Gleason & Wellington, 1988). Evidence comes both from the observation of plant matter in the gut and from experimental feeding studies. Diatoms have been often reported as dietary items (Jones, 1973; George, 1978; Chong & Sasekumar, 1981; Gleason & Zimmerman, 1984; Gleason & Wellington, 1988), as well as other small benthic and epiphytic algae (Condrey et al., 1972; Kitting et al., 1984). It has been suggested that brown shrimp eat phytoplankton (Hughes & Sherr, 1983; Gleason & Wellington, 1988), but penaeid shrimp are not known to be filter feeders. They may, though, be consuming species such as *Skeletonema* which settle from the water column onto the bottom. Isotopic analysis has shown that edaphic and planktonic algae in some salt marshes, particularly in microtidal areas, may be of more direct trophic importance than vascular plant carbon (Sullivan & Moncreiff, 1990). However, herbivory may not play a major role in the growth of the brown shrimp. When small *P. aztecus* were fed plant material, including epiphytes and diatoms, by Gleason & Zimmerman (1984), they grew at rates suggesting mere maintenance.

Brown shrimp and white shrimp are both known to consume animal material while feeding in salt marshes. Through immunological assay of proteins in gut contents, Hunter & Feller (1987) showed that many common marsh organisms may be eaten by either species. Additional evidence from Zimmerman (unpubl. data) reveals quantitative differences in feeding on infauna between the two species. When shrimp were given access to cores of marsh sediment, brown shrimp removed significantly more annelid worms and pericarid crustaceans than did white shrimp. This suggests that while both species have a carnivorous element to their diet, fauna may be more important to brown shrimp. The question remains, however, do the congeneric white shrimp and brown shrimp utilize food resources differently? Investigations cited above and differences in stable carbon isotope signatures (Zimmerman, unpubl. data) suggest that they do.

We have conducted experiments to determine the relative importance of animal and plant foods in diets of juveniles of two co-occurring shrimp species. *P. setiferus* and *P. aztecus* were compared for differences in growth using diets of microalgae, plant detritus, animal material, and combinations of materials.

## METHODS

Experimental diets of plant and animal material were provided separately and in combinations to postlarval shrimp to assess the effect of diet on shrimp growth. The methods followed Gleason & Zimmerman (1984) in order to assure comparability with that investigation. Dietary treatments consisted of the diatoms *Skeletonema costatum* and *Chaetoceros* sp., detritus from *Spartina alterniflora*, epiphytic algae from *Spartina* stems, *Artemia* nauplii, and combinations of *Artemia* and *Skeletonema*, and *Artemia* and epiphytes. The diatoms and *Artemia* were cultured in the laboratory. Epiphytes and detritus were collected from a nearby *Spartina* marsh on Galveston Island. The plant foods were cultured and/or collected and handled according to Gleason & Zimmerman (1984). Epiphytes, consisting mainly of blue-green algae (*Microcoleus*, *Oscillatoria*, and *Chroococcus*) and pinnate diatoms (*Nitzschia* and *Navicula*), were scraped from *Spartina* stems using a scalpel. The epiphytes resembled the blue-green algal mat complex associated with low energy zone tidal flats (Pulich & Rabalais, 1986). Detritus was obtained by sieving organic material from the upper 5 cm of marsh sediment with a 250- $\mu$ m sieve. Visible annelids and pericarids were picked from the epiphytes and detritus and most meiofauna were removed by rinsing the materials in filtered seawater. The component of meiofauna which remained, mostly nematodes, was incorporated into the diet. Fresh vegetal material was introduced into the treatments every other day. *Artemia* nauplii were hatched from eggs (Metaframe, San Francisco Bay Brand) in five polyethylene containers each with 10 l aerated seawater. Nauplii were provided to individual shrimp at the rate  $\approx 700 \cdot \text{day}^{-1}$ . All potential food items were provided ad libitum. White shrimp were fed all of the dietary treatments and brown shrimp were fed only the animal diet (*Artemia*) and a combination diet (*Artemia* + *Skeletonema*). Gleason & Zimmerman (1984) reported previously on the effects of plant diets (*Skeletonema costatum*, *Isochrysis* sp., *Spartina* detritus and epiphytes) on the growth of brown shrimp. Unfed treatments were used as controls in both the current and the previous investigation.

Postlarvae of brown shrimp and white shrimp were obtained from June to September 1985 from beach areas in front of Galveston Island. They were captured along the shore by hand towing a 1-m beam trawl (Renfro, 1963). At the laboratory, each was placed in 150 ml seawater in individual 250-ml glass beakers without food. After 24 h starvation, feeding experiments were initiated. Each experimental group (treatment) consisted of 25 shrimp in individual beakers without a substratum. The experimental apparatus, a large shallow bath 245-cm long  $\times$  53-cm wide  $\times$  8-cm high, accommodated up to 125 beakers (four dietary treatments and a control). Cu tubing in the bottom of the apparatus served as a heat exchanger between the freshwater bath and a Masterline 2095 heating/cooling circulator which maintained seawater temperature in the beakers at  $25 \pm 1^\circ\text{C}$ . Daylight 40-W fluorescent lights, situated 70 cm above the beakers, were used to maintain a 12-h light-dark cycle. Every other day 2/3 of the seawater in each beaker was exchanged. Seawater was obtained from the front beach of Galveston Island

and was vacuum filtered through Whatman GF/D filter paper and stored in darkness prior to use in the experiments. Salinity ranged from 19 to 22‰ between experiments but did not vary within experiments. Temperature and dissolved  $\text{O}_2$  were monitored in 10 randomly selected beakers twice daily (0800 and 1600) and in all beakers every other day (0800). Dissolved  $\text{O}_2$  ranged between 2 and 8 ppm, within the range of naturally occurring levels in the salt marsh. Three sets of feeding experiments were conducted consecutively using differing combinations of brown and white shrimps and foods as they were available. Each experiment lasted for 24 days [vs. 16 days in the previous investigation by Gleason & Zimmerman (1984)]. At 4-day intervals shrimp were individually weighed to the nearest 0.2 mg on a microbalance, and measured to the nearest 0.1 mm from tip of rostrum to tip of telson (total length, TL) using a dissecting microscope. Initial postlarval sizes were 8–12 mm. Postlarvae usually metamorphosed into benthic juveniles within the first 24 h. 4-day interval weight changes were used to indicate effect on growth of dietary treatments within and between species.

Differences between treatments and species were analysed using ANOVA performed on data corrected for heteroscedasticity by log-transformation. A two-way ANOVA (diet  $\times$  day) was used to analyse differences between plant, animal, and combination dietary treatments over time (each 4-day interval for 24 days) in each species. For white shrimp, all dietary combinations were used. For brown shrimp, only the animal diet, the combination diet, and control were used. The effect of plant diets on brown shrimp growth was taken from results of Gleason & Zimmerman (1984). In the current investigation, a three-way ANOVA (species  $\times$  diet  $\times$  day) was used to analyse differences between shrimp species given the same treatments (i.e., *Artemia*, *Artemia* + *Skeletonema*, and control). All ANOVA took into account unbalanced sample sizes resulting from mortality, through the use of the SAS general linear model procedure. Tukey's studentized range test was used in conjunction with the two-way ANOVA to examine the relationship between diets. Tukey's test was designed for pairwise comparisons and takes into account unequal cell sizes (SAS Institute, 1982). To analyse interaction in the three-way ANOVA, contrasts were constructed to compare diets between species.

## RESULTS

ANOVA of log-transformed weight interval changes in white shrimp and brown shrimp showed highly significant interactions between the day of weighing and the diet involved (Table I). The responses of both species to the diets seemed to change over time.

For *P. setiferus*, the combination diets (*Skeletonema* + *Artemia* and epiphytes + *Artemia*) when compared did not produce significantly different amounts of growth. *Skeletonema* + *Artemia* diets differed from each other and all other diets. The response to *Chaetoceros* was not different from that to epiphytes, while the epiphyte-induced

TABLE I

ANOVA for *P. setiferus* and *P. aztecus* with dependent variable as transformed interval change in weight.

Source	df	F	P
<i>P. setiferus</i>			
Diet	7	120.00	0.0001
Day	5	155.30	0.0001
Day * diet	26	23.60	0.0001
<i>P. aztecus</i>			
Diet	2	54.35	0.0001
Day	5	95.54	0.0001
Day * diet	7	11.15	0.0001

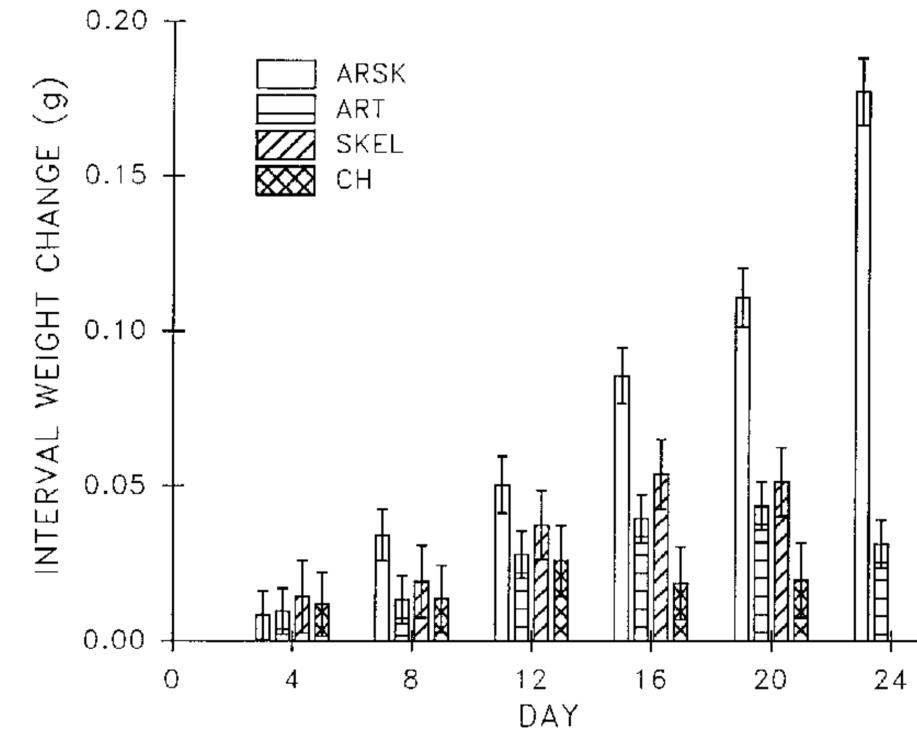
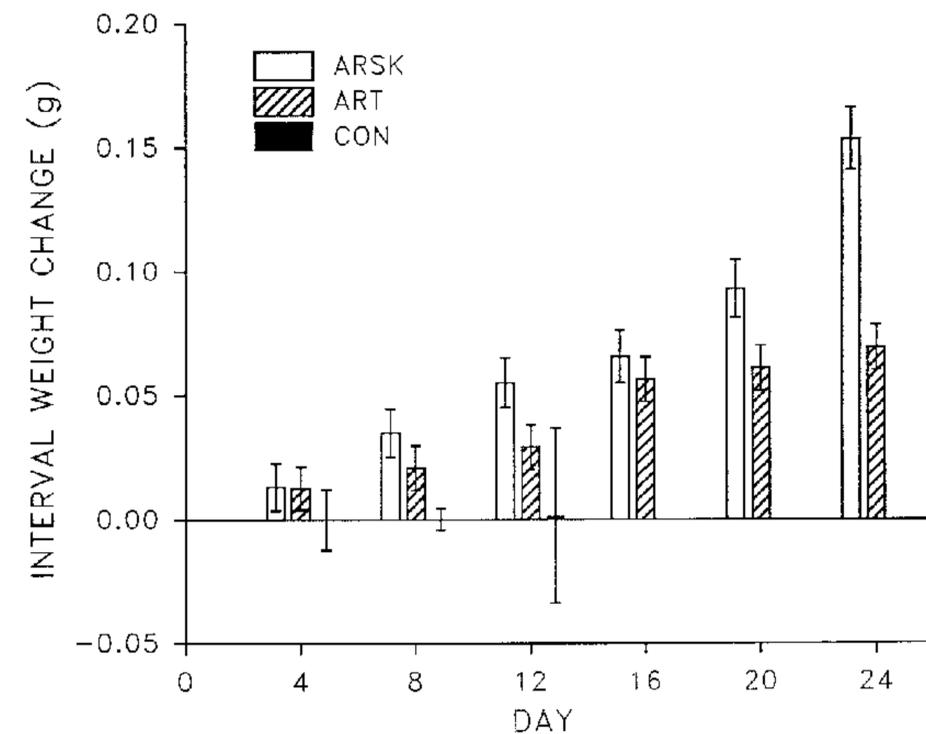
growth was not different from the control or detrital treatment (Table II). Growth of white shrimp fed a combination diet far outdistanced those fed other diets (Fig. 1). Individual *Artemia* + *Skeletonema* diets produced similar levels of growth, but the diatom-based diet was unable to sustain life until Day 24. Other vegetal diets produced little or no growth. Animals fed detritus all died before Day 12. The starved control group died before Day 16. These groups were not included on Fig. 1, so that the other treatments could be more easily seen. The combination diet of epiphytes + *Artemia* was also not plotted in Fig. 1, as it was not significantly different at any time from the *Skeletonema* + *Artemia* diet. A visual comparison of all eight treatments is available in Table II.

TABLE II

Comparisons of log-transformed mean interval weight changes corresponding to diets fed to *P. setiferus* using Tukey's studentized range test. Bars indicate diets that are not significantly different at  $\alpha = 0.05$ .

Artemia + Skeletonema	
Epiphytes + Artemia	
Skeletonema	
Artemia	
Chaetoceros	
Epiphytes	
Control	
Detritus	

Using Tukey's studentized range test on the *P. aztecus* data, all three treatments were found to differ significantly from each other at the  $\alpha = 0.05$  level. Once again, a combination diet produced the most growth (Fig. 2). The brown shrimp control group, as with the white shrimp, all died before Day 16. Combination and *Artemia* diets in the current study produced orders of magnitude more growth than did vegetal diets fed to brown shrimp by Gleason & Zimmerman (1984). Moreover, brown shrimp did not

Fig. 1. A comparison of interval weight change over time of *P. setiferus* when fed four different diets: arsk, *Artemia* + *Skeletonema*; art, *Artemia*; skel, *Skeletonema*; ch, *Chaetoceros*. Bars,  $\pm 2$  SE.Fig. 2. A comparison of mean interval weight change over time for *P. aztecus* fed following diets: arsk, *Artemia* + *Skeletonema*; art, *Artemia*; con, control. Bars,  $\pm 2$  SE.

show similarity in growth between the *Artemia* + *Skeletonema* diets as did white shrimp (Fig. 3).

An ANOVA combining data of both species (Table III) revealed no significant difference in growth rates between the species over time (species \* day), but all other interactions were significant. The species responded to the diets in differing manners (species \* diet) and the growth produced by the diets changed over time (day \* diet). Finally, the three-way interaction (species \* day \* diet) showed that the two species responded differently to the same diets over time. Graphic analysis of the three-way

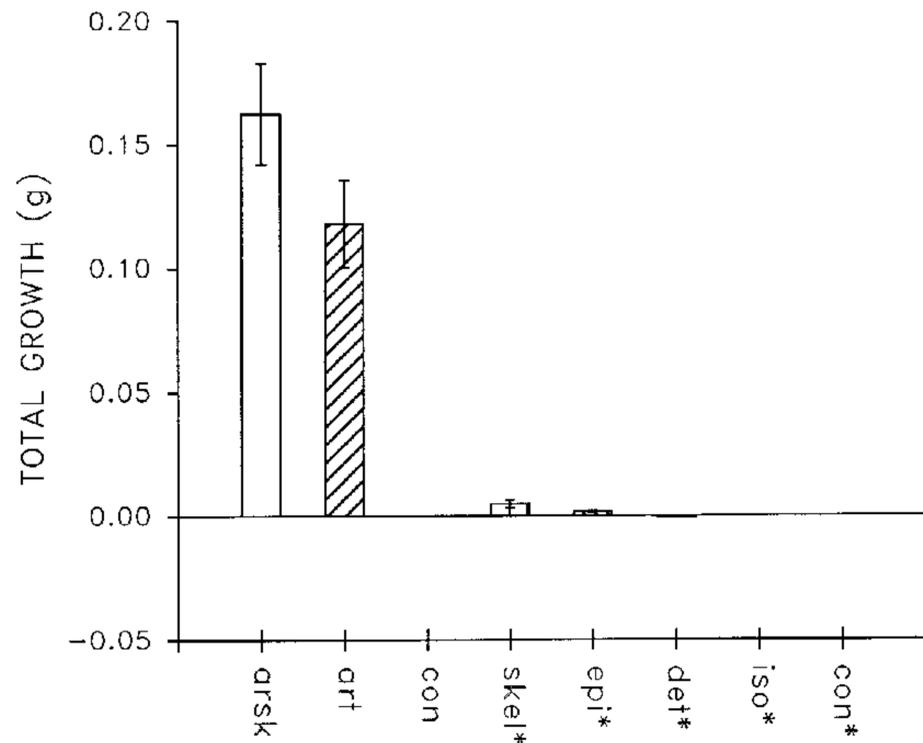


Fig. 3. Total weight gained by Day 16 for *P. aztecus*. An asterisk denotes data from Gleason & Zimmerman (1984). arsk, *Artemia* + *Skeletonema*; art, *Artemia*; con, control; skel, *Skeletonema*; epi, epiphytes; det, detritus; iso, *Isochrysis*. Bars,  $\pm 2$  SE.

TABLE III

ANOVA of data representing both *P. setiferus* and *P. aztecus* with transformed interval change in weight as dependent variable.

Source	df	F	P
Species	1	0.32	0.5730
Diet	2	190.80	0.0001
Day	5	185.10	0.0001
Species * diet	2	16.00	0.0001
Species * day	5	0.40	0.8502
Day * diet	7	40.77	0.0001
Species * day * diet	7	4.71	0.0001

interaction (Fig. 4) showed that early in the experiment, all the diets produced similar growth in brown shrimp. As time passed, the combination diet produced significantly more growth than the other treatments. After Day 12, the growth produced by the *Artemia* diet seemed to reach a plateau. White shrimp followed much the same pattern,

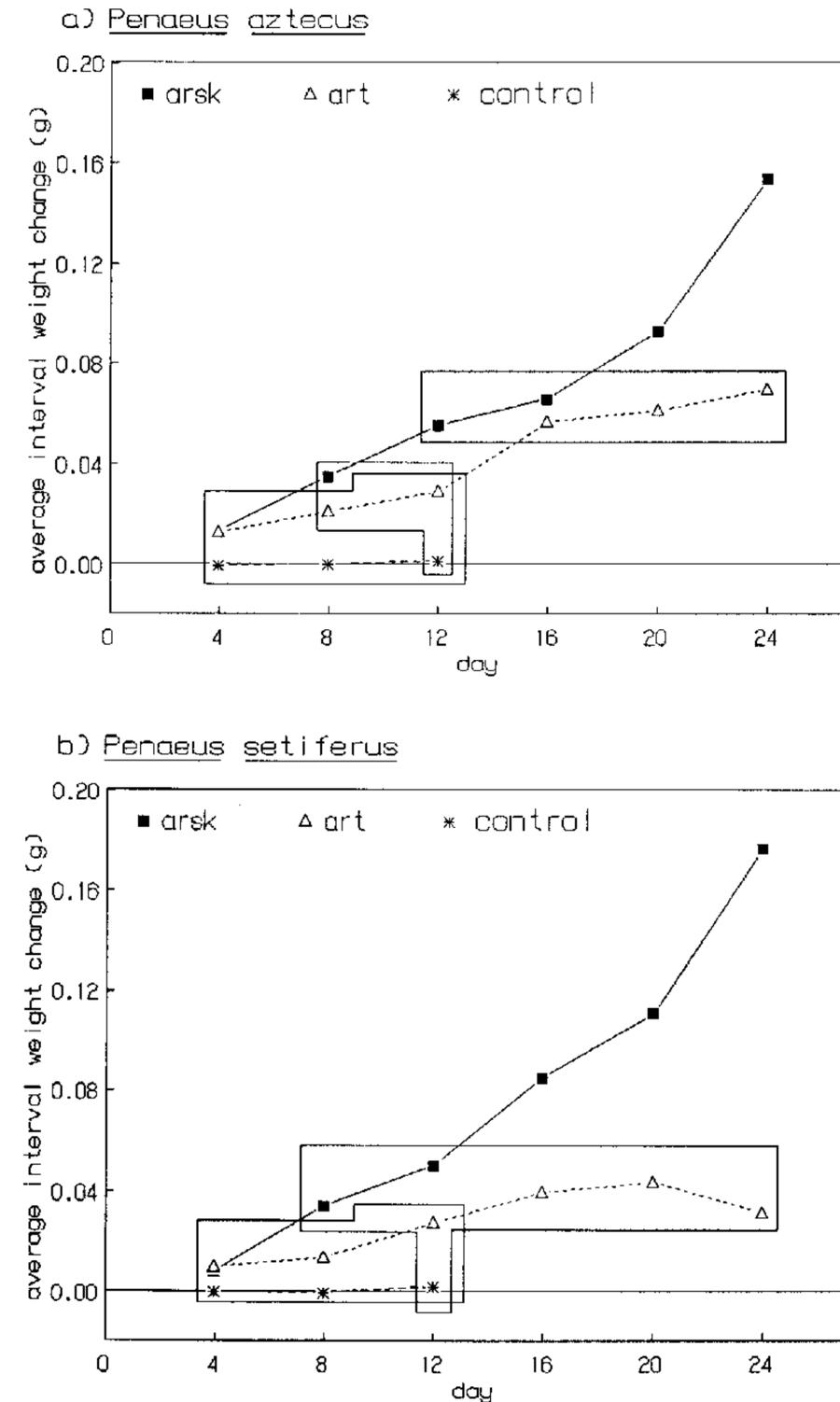


Fig. 4. Average interval weight change over time for *P. aztecus* (a) and *P. setiferus* (b) in following treatments: arsk, *Artemia* + *Skeletonema*; art, *Artemia*; and control. Boxes indicate means which are not significantly different according to their 95% CI.

but growth from the *Artemia* and combination diets became significantly different earlier. As in brown shrimp, growth of white shrimp fed the *Artemia* diet plateaued after Day 12, but the level was lower than in the brown shrimp. Contrasts showed no significant difference between the two species overall, probably reflecting the strong similarity in the species over time. Similarly, there was no difference in the way they responded to the combination diet (Table IV). But, a highly significant difference was found when the responses to the animal diet (*Artemia*) were compared. White shrimp grew slower than the brown shrimp when both were fed *Artemia*. Both brown and white shrimp grew the most rapidly when fed a combination diet (Fig. 5). All control animals died before Day 16. Controls were not plotted in Fig. 5 so that other comparisons could be distinguished more easily.

TABLE IV

Contrasts constructed from log-transformed mean interval weight changes resulting from diets fed *P. setiferus* and *P. aztecus*. Arsk, *Artemia* + *Skeletonema*; art, *Artemia*; con, control; pa, *P. aztecus*; ps, *P. setiferus*. Contrasts marked by an NS do not show significant differences at  $\alpha = 0.05$  level.

Contrast	F	P
pa vs. ps	0.77	0.3808 NS
ps arsk vs. pa arsk	1.79	0.1814 NS
ps art vs. pa art	14.21	0.0002
ps con vs. pa con	0.00	0.9878 NS

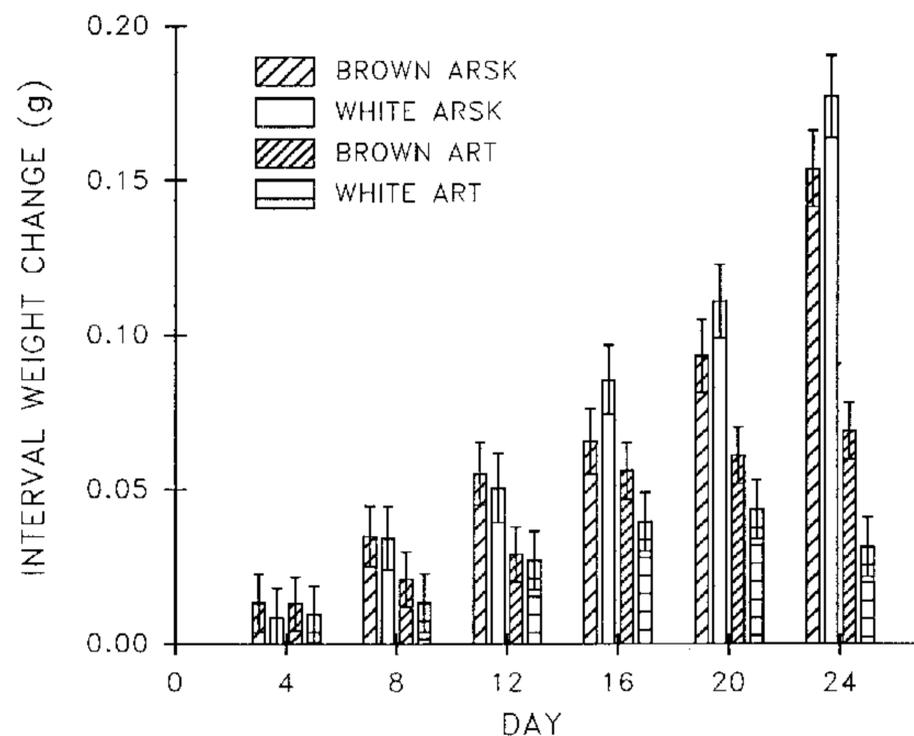


Fig. 5. Interval weight change over time of *P. aztecus* and *P. setiferus* which have been fed *Artemia* and *Skeletonema* (arsk) or *Artemia* alone (art). Bars,  $\pm 2$  SE.

## DISCUSSION

Juvenile *P. setiferus* and *P. aztecus* use Texas salt marshes as nurseries and apparently utilize marsh food resources differently. The extent to which such dietary differences reflect resource partitioning has only recently been suggested (Zimmerman et al., 1984).

In general, brown and white shrimps grew the most when fed a mixed animal and plant diet. Animal material (*Artemia*) alone produced moderate growth, while vegetal material alone produced the least growth. The two shrimp species differed, however, in the level of their response to dietary composition. Brown shrimp had greater differences in growth between *Skeletonema* + *Artemia* treatments than did the white shrimp. Brown shrimp given vegetal diets alone by Gleason & Zimmerman (1984), including *Skeletonema*, produced little or no growth as compared to our animal (*Artemia*) and combination diets. Similar results for the brown shrimp were reported by Zein-Eldin (1963), using another system. Animals fed live brine shrimp or ground fish grew larger and had better survival rates than those given blue-green algae or *Ectocarpus*, a brown alga. The significance of the differences cannot be determined, though, as statistical tests were not performed. Although white shrimp had low growth rates on vegetal diets in the present study, they were higher than those of brown shrimp. However, brown shrimp always produced more growth on a mixed animal/plant diet than a strictly animal diet. In white shrimp, growth produced by animal and vegetal (*Skeletonema*) diets was not significantly different up to Day 20; yet, the vegetal diet was not capable of sustaining life after Day 24. This suggests that white shrimp effectively utilize plants, such as diatoms, although it cannot be their sole source of nutrition. In addition, significant differences in growth between the combination and the animal diets were seen earlier in the white shrimp than in the brown shrimp. By Day 16, white shrimp growth resulting from the *Artemia* + *Skeletonema* treatment was already above that of the *Artemia* fed animals, however, with brown shrimp, this divergence occurred at Day 20. This difference might be attributed to a relative lesser ability of the white shrimp to utilize animal material in their diet as compared to the brown shrimp.

If one species had an intrinsically greater overall growth rate, one would expect the weight gains to be consistently higher. These results were not observed in our experiments, indicating no innate differences in growth rates. However, field data indicate higher growth rates in *P. setiferus*. Rates of  $> 2 \text{ mm} \cdot \text{day}^{-1}$  for small juvenile *P. setiferus* (Johnson & Fielding, 1956; Wheeler, 1968) are nearly twice those of *P. aztecus* (Knudsen et al., 1977), differences we ascribe to environmental conditions. The influence of plant material appears to be of greater significance to growth of white shrimp than that of brown shrimp. White shrimp grow at an equal level with that of brown shrimp when fed a combination diet, while growing slower than the brown shrimp when fed an animal diet. These results can be related to the conditions in the marsh at the time of immigration of each species. *P. aztecus* enters the marsh during the spring when abundances of benthic animals are at their highest. *P. setiferus* begins marsh residence during the summer when the levels of benthic animals have been reduced by

the feeding of earlier immigrants. For growth, white shrimp need animal matter in their diets, but they also may utilize epiphytic and epibenthic algae, such as diatoms. During the summer, primary production of algae in the salt marsh is at its highest, making it a readily available and reliable food source.

In Texas during the spring, brown shrimp tend to be found in significantly higher densities on the marsh surface versus nearby in unvegetated areas (Zimmerman & Minello, 1984a). This distribution pattern corresponds to high abundances of faunal foods on the marsh surface (Zimmerman et al., 1990) and to seasonally high water levels in the spring (Hicks et al., 1983). By contrast, densities of white shrimp in the summer are often similar in open water and marsh habitats. Edaphic algae, however, as noted before, are abundantly available as summer food, both on the marsh surface and in nearby shallow creeks. The habitat utilization patterns of the two species may also indicate differences in feeding.

Almost since the beginning of research into the feeding of *P. setiferus* and *P. aztecus*, detritus has been regarded as a potentially important food for the shrimp. This has been implied through the identification of material as detritus in shrimp guts (Flint, 1956; Darnell, 1961, 1964; Jones, 1973). In our study, when *P. setiferus* were fed detritus, they died at an earlier date than the starved animals. This suggests that detritus might be disregarded as a source of nutrition for shrimp. In attempting to utilize the material, the animals apparently expended more energy than they received. Moriarty & Barclay (1981) reported low bacterial abundance and high protein levels in the guts of three Australian penaeid species, indicating that detritus may be of limited importance to other species as well.

Conversely, potentially detritivorous shrimp may need an abrasive material such as sand to assist in the digestion of the detritus. It has been suggested that penaeids use sand and other coarse material in their gastric mill much as a bird uses gritty material in its crop (Suthers, 1984). This might be indicated by the mere presence of indigestible matter in the gut. Juvenile *P. setiferus* consume indigestible grit and never completely empty their gastric mill during a daily cycle (McTigue & Feller, 1989). When penaeids feed, they use their maxillipeds to turn and sort material before it enters the mouth (Alexander & Hindley, 1985). The presence of sand and shell fragments in the digestive system of a selective feeder would seem to be more or less intentional. Another possibility is that what has been routinely identified as detritus (usually attributed to plant material) in the gut of brown and white shrimps is in fact mixed plant and animal matter that, through digestion, is unidentifiable by the investigator. The penaeid gastric mill grinds and recirculates material until it is small enough to pass beyond a large medial tooth (Young, 1959). Under this treatment, food is often reduced to an unrecognizable state.

The role of plants in the penaeid diet has received much attention. While it seems that brown and white shrimps can make use of a variety of plant sources, some plants, particularly diatoms, yield better growth than others. Even among diatoms, some, such as *Skeletonema*, are better when compared to others, such as *Chaetoceros*. This suggests

that the value of algae in marshes to shrimp may greatly depend upon the composition and relative abundances among algal species. Thus, while plants are supplemental to animal material in diets, they may partly control shrimp growth rates in nature. As a habitat quality issue, this deserves further research.

*P. aztecus* and *P. setiferus* spend their juvenile stages in the same area, but their timing of peak abundances differ. This difference can be related to life history strategies that include feeding habits. The optimal diet for either species contains animal and plant material, but our experiments show that plants are of greater importance to the white shrimp. We propose that *P. setiferus* is a generalist which makes use of the high algal productivity during summer months to compensate for decreased prey abundances. By contrast, *P. aztecus* is more specialized, depends heavily upon animal material in its diet, and relies upon early season exploitation to achieve optimal growth. It is tempting to speculate that these strategies have evolved in response to interspecific competition, but the evidence is circumstantial.

*P. aztecus* and *P. setiferus* belong to two different subgroups within the penaeids, the grooved and non-grooved shrimp. It is possible that differences in the two species may in part be related to early dietary divergence in the evolution of the two groups. While there is no evidence to fully support or refute this idea, this would seem to be an interesting area of research.

In conclusion, white and brown shrimps are both omnivores, yet they show feeding differences based upon the degree of carnivory and herbivory. These differences may reflect resource partitioning and life history strategies tied to temporal availability of food. Brown shrimp gain specialized advantage through carnivory during the spring months when white shrimp are not present. White shrimp gain advantage through herbivory during summer months by feeding in places and on resources unimportant to brown shrimp. Our results also suggest that plant detritus may be of very limited growth value to shrimp, although this finding is inconclusive. The relationship between abrasive material in the gut and the ability to digest detritus needs to be pursued.

#### ACKNOWLEDGEMENTS

We thank E. Klima and the staff of the National Marine Fisheries Service Laboratory at Galveston for supporting this project. A. Brown and D. Cristossomo contributed greatly during the early stages of this work and J. Matis provided valuable statistical advice. Helpful reviews of the manuscript were provided by D. Aldrich, K. Neal Baxter, J. Thomas-Martinez, T. Minello, and Z. Zein-Eldin.

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