COMPARISON OF THE ASSIMILATION OF DIFFERENT DIETS BY *PENAEUS SETIFERUS* AND *P. AZTECUS*

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ABSTRACT

Juvenile penaeid shrimp showed high and comparable assimilation efficiencies (80-85%) on a variety of plant and animal diets. In general assimilation efficiencies for proteins and lipids were consistently high; for carbohydrates, low. Organic assimilation per gram organic weight of white shrimp, *Penaeus setiferus*, proceeded at 3.7 mg hr^{-1} on an axenic diatom and 8.4 mg hr^{-1} on an artificial diet. The assimilation efficiency was lower for shrimp feeding on the algal mat coating *Spartina alterniflora* than on two components of the mat. Feeding mechanisms and probable natural diets are discussed as a basis for further study.

In tidal estuaries where consumers are heavily dependent on an input of autochthonous and allochthonous detritus, the trophic structure is obscured by the seemingly omnivorous habit of many of the residents. Historically, the feeding habits of these omnivores have been investigated by examination of gut contents, correlation of numbers of omnivores with type of benthic community, and comparison of the types of foods available in different areas with the species composition of consumers (Darnell, 1964; Corner and Cowey, 1968; Edmondson and Winberg, 1971). While these investigations have been valuable and are the bases of our present understanding of estuarine communities, it should be noted that a large percentage of the foregut contents of many estuarine species is unidentifiable (Darnell, 1964).

In Louisiana estuaries shrimp is seasonally one of the dominant organisms and commercially the most important one. Although speculation about the diet of juvenile shrimp in inland waters has been widespread, the datum base in the literature for these speculations is not convincing. Studies of shrimp gut contents (Flint, 1956; Darnell, 1964) seem to indicate that the organism ingests the dominant materials in the sediments. In Lake Ponchartrain, for instance, Darnell (1961) found that 58% of the stomach contents of adult white shrimp was unidentifiable detritus. Little is known, however, about the ability of shrimp to digest different food sources. Nose (1964), working with *Penaeus japonicus*, reported a higher assimilation efficiency of animal than of plant proteins. Fujii et al. (1963) and Dall (1965) have studied the activity of digestive enzymes of several species of shrimp.

This study concerns the assimilation by the white shrimp, *Penaeus setiferus*, and the brown shrimp, *P. aztecus*, of the organic components of four different defined diets and a natural substrate. Except for the rates reported, the assimilation parameters were measured by a modification of the ratio method of Conover (1966a). Therefore, quantitative recovery of food or feces was not required.

METHODS AND MATERIALS

CALCULATION OF ASSIMILATION PARAMETERS OF ORGANIC MATERIAL

Direct calculation of net assimilation is difficult in aquatic environments because of the need to measure quantitatively both ingestion

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and egestion of food by the organisms under study. Recently, this problem was circumvented by Conover (1966a). He developed a method for determining the net assimilation efficiency of organic matter (U')[3] without quantitative recovery of either the uneaten food or the feces, based upon the assumption that the assimilation process affects only the organic portion of the food. This is a critical assumption since the ash in the food is treated as an inert label to measure the quantity of food ingested. If this assumption is made, the general definition of assimilation efficiency,

$$U' = \frac{(I - N)}{I} \times 100 \qquad (1)$$

where I is the organic weight ingested, and N is the organic weight egested, reduces to Conover's equation,

$$U' = \frac{(F' - E')}{(1 - E')\,(F')} \times 100. \qquad (2)$$

$F' = I/F$ = ratio of organic weight to dry weight of food ingested, and $E' = N/E$ = ratio of organic weight to dry weight of material egested. Symbols are defined in Table 1. Conover (1966a) and Corner, Cowey, and Marshall (1967) found close agreement between assimilation efficiencies calculated by the ratio method and direct quantitative recovery of food and feces. In both cases the comparison was made with zooplankton feeding on phytoplankton.

Assimilation, however, is a complex function controlled by (1) the net assimilation efficiency (U'), or digestibility; (2) the concentration of ash; and (3) the rate of ingestion. For our work, we found it helpful to modify Equation 2 to consider (a) the combined effect of digestibility and organic concentration upon the amount of food assimilated and (b) the net assimilation rate. A further modification was required to consider the assimilation of specific organic moieties. The reasoning and equations are presented briefly below. A more detailed derivation can be found in Condrey (1971).

[3] Conover uses the term "assimilation efficiency." Strictly this should be "net assimilation efficiency" since it measures the difference between assimilated organics and previously assimilated organics which are lost in the feces (peritrophic membrane, digestive secretions). The two terms are used interchangeably in this paper.

TABLE 1.—List of symbols.

Symbol	Explanation
A	Net organic weight assimilated.
A_X	Net amount of an organic moiety assimilated.[1]
E	Dry weight of feces.
E'	Ratio of organic weight to dry weight of feces. (N/E).
e'_X	Ratio of organic moiety to dry weight of feces.
F	Dry weight of food.
F'	Ratio of organic weight to dry weight of food. (I/F).
f'_X	Ratio of organic moiety to dry weight of food.
I	Organic weight ingested.
I_X	Quantity of an organic moiety ingested.
N	Organic weight egested.
N_X	Quantity of an organic moiety egested.
R	Ratio of organic weight to oxidizable carbon.
r_i	Ratio of an organic moiety to total organic weight of food. (I_X/I).
r_n	Ratio of an organic moiety to total organic weight of feces. (N_X/N).
U'	Percent assimilation efficiency of total organic weight $(A/I)(100)$.
U'_X	Percent net assimilation efficiency of an organic moiety. $(A_X/I_X)(100)$.

[1] When denoting a specific organic moiety the subscript X is replaced by P for protein, L for lipid, CH_2O for carbohydrates, C for oxidizable carbon.

FEEDING EFFICIENCY

A comparison of the amount of organic matter assimilated per unit of diet ingested is:

$$A/F = (F')\,(U'/100). \qquad (3)$$

This is a valuable type of representation for simultaneous comparison of the relative organic weight assimilated on different diets, as is demonstrated in Figure 1. The ratio is termed "feeding efficiency" for lack of a better term. Note that whereas U' is a ratio of organic weight assimilated to organic weight ingested, the feeding efficiency considers the effect of differing organic concentrations in the diet. As will be shown, this may be of considerable importance when comparing net assimilation of diets sim-

ilar in organic content but differing in ash concentration.

NET ASSIMILATION RATE

Where either the ingestion or egestion rate is determined, Equation 2 can be readily adapted to yield the net assimilation rate. For the latter case, the organic weight egested (N) is defined as the product of the ratio of organic matter to dry weight egested (E') and dry weight egested (E). Net assimilation, in terms of egested material, is

$$A = \frac{(E)\,(E')\,(U')}{(100 - U')} \qquad (4)$$

where $(100 - U')$ is the percentage of ingested organic food that is egested. When E is reported in terms of dry weight of feces deposited per unit time, Equation 4 yields the rate at which net assimilation of organic matter proceeds.

ASSIMILATION PARAMETERS FOR SPECIFIC ORGANIC MOIETIES

NET ASSIMILATION AND FEEDING EFFICIENCIES OF AN ORGANIC MOIETY

The determination of the net assimilation efficiency of an organic moiety (U'_x) independent of U' is not possible by direct substitution in Conover's equation (Equation 2). This becomes clear if one considers the equation for net assimilation efficiency of a specific organic moiety.

$$U'_x = \frac{I_x - N_x}{I_x} \times 100 \qquad (5)$$

where I_x is the amount of the moiety ingested and N_x the amount of the moiety egested. Conover was able to derive Equation 2 from Equation 1 by setting I equal to total particulate matter egested minus its ash. Clearly this relationship does not hold for I_x and N_x in Equation 5.

Let r_i and r_n be ratios of the weight of the organic moiety of interest to the total organic weight of the food and feces respectively. Then

$$I_x = r_i I = r_i(FF'), \qquad (6)$$

and

$$N_x = r_n N = r_n(FF')\,(1 - U'/100). \qquad (7)$$

Substituting in Equation 5:

$$U'_x = \frac{r_i - r_n\ (1 - U'/100)}{r_i} \times 100. \qquad (8)$$

From Equations 6 and 7 the feeding efficiency of an organic moiety is:

$$A_x/F = F'\,[r_i - r_n\ (1 - U'/100)]. \qquad (9)$$

NET ASSIMILATION RATE OF AN ORGANIC MOIETY

The amount of a particular organic moiety egested can be defined as

$$N_x = (E)\,(E')\,(r_n). \qquad (10)$$

Similarly,

$$I_x = \frac{(E)\ (E')\ (r_n)}{(1 - U'/100)}. \qquad (11)$$

When E is defined as the amount of feces deposited per unit time, Equations 10 and 11 become rate equations for determining the amount of a moiety ingested and egested per unit time. The assimilation rate of the moiety is the difference between the values of I_x and N_x.

EXPERIMENTAL TECHNIQUES

FEEDING

Juvenile shrimp, *Penaeus setiferus* and *P. aztecus*, 24 to 83 mm long, were collected from Barataria Bay, La., and maintained in aerated aquaria containing acid-washed quartz sand, filled with membrane-filtered bay water at 20°-23°C.

Test foods were given to shrimp which had been starved for 12 hr, in groups of 10 to 14, unless otherwise noted. Animals were allowed to feed ad lib. for 12 to 36 hr. Fecal material

was collected soon after voided with a fine-tipped eye dropper. It was placed in a Syracuse dish in saline solution (0.6% $CaCl_2$, 2.5% NaCl) and, under a dissecting microscope, cleaned of all adhering extraneous material such as sand grains. Torn or broken strands were rejected. To remove adherent salts, the fecal material was then washed with 3% ammonium formate on preignited, washed, and tared glass fiber filters and dried at 65°C to constant weight. Reproducibility of blank filters washed with two 1-ml aliquots of 3% ammonium formate varied from 0.01 to —0.05 mg. No correction was made for the sporadic weight loss of the blanks. Dried samples were frozen until analyzed. Sufficient fecal material was obtained for 2-8 replications of each analysis. Analyses of the fecal pellets produced on the detritus diet used 0.2 to 1 mg samples. The high variability of results with these samples was greatly reduced by increasing sample size. Therefore, subsequent analyses of fecal material employed 1 to 10 mg feces per replication. Errors in samples less than 1 mg in weight were presumed to be caused by inhomogeneity of fecal material and magnification of the absolute errors involved in weighing and chemical analyses. Replications for each analysis were chosen from fecal samples collected at different feeding intervals. There was no indication of a change in the assimilation efficiency of a given diet with time.

To avoid undue handling, shrimp were sized and identified to species only after feeding. Therefore, feeding occurred with mixed sizes and species. Three diets—diatom, Chow, and algal mat—were fed to white shrimp only, and two diets—detritus and AF-1—were fed to white and brown shrimp. In tests in which individual shrimp were fed differences were not found in assimilation efficiency due to size (see for instance Table 7) or species. Therefore, the results reported here are assumed to apply equally to both species within the size range used.

FEEDS

The digestibility of four defined diets, two artificial and two natural, was investigated. In addition, in a fifth test, shrimp were allowed to graze on the algal community coating the base of culms of the oyster grass, *Spartina alterniflora*, and the assimilation of this food source was measured.

The four defined diets were: (1) an axenic culture of the periphyton diatom, *Cylindrotheca fusiformes*; (2) a heavily bacterized culture of the same diatom (termed hereafter "detritus"); (3) AF-1,[4] an artificial food consisting of rice bran (52.0%), shrimp meal (30.5%), fish meal (8.0%), fish solubles (2.0%), mineral mix (2.0%), soy protein (3.0%), and Calgon (0.2%); and (4) Trout Chow,[5] consisting primarily of fish meal, fish solubles, soybean meal, ground wheat, and ground yellow corn, with a guaranteed minimum analysis of 40% crude protein, 2.5% crude fat, and 5.5% crude fiber.

The method used rests on the assumption that the food is representative of the ingested material, that is, that selection does not occur. In order to minimize the possibility that the shrimp could select by sorting of particles, and to prevent dispersion and suspension of the defined diets during feeding, all these diets were bound by mixing with a 2% algin solution (Meyers, Butler, and Hastings, 1972). The mixture was extruded through a syringe of 1-mm pore diameter into a 0.6 to 1.2% $CaCl_2$ solution. The calcium ion sequestered the algin, producing either strands or small spheres of bound food which were readily accepted by the shrimp. Details of this method are discussed at length in the aforementioned article.

CHEMICAL ANALYSES

After drying, samples of food and feces were digested along with the glass fiber filters on which they were isolated. Filter blanks carried through the same analytic procedures indicated no detectable contamination from this source.

[4] Prepared by Dr. Samuel P. Meyers and D. Butler, Department of Food Science, Louisiana State University, Baton Rouge, La.

[5] Ralston Purina Company, St. Louis, Mo. Reference to trade names in the publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

Oxidizable carbon analyses were by the wet dichromate procedure of Johnson (1949) as reviewed by Strickland and Parsons (1968). Glucose was used as a standard. The limitations of this method are discussed by Johnson (1949). Total nitrogen was determined by a micro-Kjeldahl technique with ninhydrin color development; lipids in terms of fatty acids by saponification followed by complexing with pinacyanol; and carbohydrates in terms of glucose using the anthrone reaction. Methods are those described by Strickland and Parsons (1968). Protein was estimated by multiplying the nitrogen values by 6.25.

Ash-free dry weights were determined from samples heated to dryness after addition of 1 ml of nitric acid and then ignited at 500°C (2 hr). For the defined diets (i.e., diatom, detritus, AF-1, and Trout Chow), F' values were obtained from samples treated in this manner. Because of small sample size, accurate determinations of ash-free dry weight could not be made for fecal material. Therefore E' was calculated from oxidizable carbon in the feces, assuming that the ratio of total organic weight to oxidizable carbon (R) determined for the food was true also for the feces. Markedly different diets yielded a ratio of oxidizable carbon to organic weight of 1.92 to 2.33 (Table 2). This gives an estimate of the likely error involved in the assumption. Insufficient material was obtained from the algal mat for ash-free dry weight determination of F', and this value was estimated by multiplying the oxidizable carbon concentration by 2.

Analyses of variance were performed on the raw data and are shown as standard errors of the mean in the appropriate tables.

RESULTS

The effect of using 10 to 14 shrimp as a group in each test was to average individual variation. As shown in Table 3 variation in fecal analyses among subsamples within the tests was extremely low, the coefficient of variation usually less than 5%. Individual variability is shown in the results of the feeding study on a natural algal mat (Table 8). In this test, the substrate presented to the shrimp was not homogeneous. The coefficient of variation of U' for individual shrimp fed on diets ranging from 20 to 31% oxidizable carbon was 16%.

Comparison of total organic concentration to the sum of protein, lipids, and carbohydrate re-

TABLE 2.—Chemical analyses of defined diets.

Diet	Total organic wt	Oxidizable carbon	Organic wt	Nitrogen	Nitrogen	Lipids	Lipids	Carbohydrates	Carbohydrates
	Dry wt	Dry wt	Oxidizable carbon	Dry wt	Organic wt	Dry wt	Organic wt	Dry wt	Organic wt
	F'	f'_C	R	f'_N	r_i	f'_L	r_i	f'_{CH_2O}	r_i
	%	%		%	%	%	%	%	%
Diatom	85 ± .01[1]	43 ± 1.2	1.98	7.6 ± .04	8.9	19 ± 1.4	22	5.7 ± 0.4	6.7
Detritus	80 ± .06	42 ± 1.1	1.92	5.1 ± .46	6.4	20 ± 4.8	25	11 ± 0.4	14
AF-1	82 ± .00	35 ± 1.3	2.33	5.4 ± .00	6.6	7.4 ± 1.3	9.1	20 ± 0.3	24
Chow	89 ± .00	46 ± 2.1	1.93	7.2 ± .06	8.1	4.6 ± 0.1	5.1	25 ± 0.0	28

[1] Figures are mean values from 2-8 determinations ± standard error.

TABLE 3.—Chemical analysis of feces produced by shrimp fed on defined diets.

Diet	Oxidizable carbon	Nitrogen	Nitrogen	Lipids	Lipids	Carbohydrates	Carbohydrates
	Dry wt	Dry wt	Organic wt	Dry wt	Organic wt	Dry wt	Organics
	e'_C	e'_N	r_n	e'_L	r_n	e'_{CH_2O}	r_n
	%	%	%	%	%	%	%
Diatom	22 ± 1.1	2.4 ± .00	5.6	0.69 ± 0.1	1.7	9.1 ± 1.3	21
Detritus	20 ± 6.2	4.1 ± .10	10.7	8.1 ± 0.9	23	13 ± 1.5	35
AF-1	29 ± 1.3	3.4 ± .02	5.1	3.3 ± 0.3	5.0	18 ± 2.4	27
Chow	32 ± 0.8	3.4 ± .02	5.5	3.5 ± 0.1	5.7	21 ± 2.2	34

vealed that in the foods 75 to 85% of organic weight was accounted for. These results were consistent, indicating the presence of organic components which are not detected by any of the three methods. Recovery of organic fractions from fecal material was, with the exception of the detritus diet, lower than with foods, ranging from 60 to 74% of organic weight of the feces. The implication is that the unaccounted organic components of the food are also poorly assimilated by shrimp and accumulate in the feces. We have not been able to identify the chemical nature of these components.

DEFINED DIETS

Net Assimilation Efficiency of Total Organic Weight and of Organic Moieties

Tables 2 and 3 show results of chemical analyses of the defined diets and of the feces of shrimp fed on these diets. Data are presented not as amounts, but as percentages for incorporation into the ratio equations.

Assimilation efficiencies calculated from these data (Table 4) revealed that the organic matter of three of the diets was assimilated with a high degree of efficiency. These diets were the diatom, 87%; the detritus, 85%; and the Chow, 80%. The similarity in overall digestibility suggests an adaptive trituration and enzymatic apparatus operating as efficiently against diatom frustules as against bacterial cell walls. The ability to assimilate effectively varied diets of animal, vascular plant, and algal origin denotes the true omnivorous habit of the shrimp.

TABLE 4.—Net assimilation efficiencies of total organic matter, protein, lipids, and carbohydrates for shrimp fed on defined diets.

Diet[1]	Total organic wt U'	Proteins U'_P	Lipids U'_L	Carbohydrates U'_{CH_2O}
	%	%	%	%
Diatom	87	92	99	59
Detritus	85	75	86	63
AF-1	55	65	75	49
Chow	80	86	78	76

[1] Diatom and Chow diets were fed to white shrimp, and detritus and AF-1 diets were fed to white and brown shrimp.

Although the two artificial diets were comparable in chemical analyses, the overall digestibility of AF-1 (55%) was low compared with the Chow. According to Brazka (in Edmondson and Winberg, 1971), this indicates either a "specific barrier" in digestion of the diet or superfluous feeding. Of the components of AF-1, the shrimp meal, because of its high chitin content, may be the cause of the inefficiency of assimilation.

In general, lipids and proteins were digested with a higher efficiency than total organic assimilation while carbohydrate assimilation lagged. The main exception to these generalizations was the detritus protein, which was assimilated with an efficiency of 75% compared to 85% for U'. Bacterial cell walls reportedly account for from 10 to 40% of the dry weight of the cells and are composed of as much as 75% protein (Pelczar and Reid, 1965). The lower digestibility of detritus protein may be due to an enzymatic inability to attack the compacted cell wall protein. However, the results for this diet are not clear since the assimilation efficiencies for the specific organic moieties are all equal to or lower than U'. This implies either that (1) the correction factors and standards employed were not representative of the organic moieties present in the samples or that (2) an unmeasured fraction of the total organic weight was assimilated with a higher efficiency than the total organic matter. These difficulties are inherent in any general analysis of this type and indicate the necessity for care in interpretation of results.

For protein digestibility our results are considerably higher than those of Nose (1964), who used a chromium oxide tracer to study assimilation of protein by *Penaeus japonicus*. On a diatom diet he found a U'_p of 62.5%; on *Ulva*, a green alga, a maximum of 30%. The experiments are difficult to compare with ours because Nose also found a direct proportionality between nitrogen content of the diet and U'_p. Assimilation efficiency of protein increased with diet nitrogen. His diatom and *Ulva* diets were 1.36 and 1.64% nitrogen, respectively, compared to our analyses of 7.6% in *Cylindrotheca fusiformis*. At the diet nitrogen concentration we measured one would expect, using the proportional-

ity Nose demonstrated, a U'_p of about 80% compared to our observed value of 92%. Thus his low values for protein assimilation on plant diets may have been a function of the low nitrogen analysis of the food rather than an inherent inability of shrimp to digest plant proteins efficiently.

Feeding Efficiency

Feeding efficiency (grams assimilated per gram dry weight of particulate material ingested) is presented in Figure 1 and Table 5. As is demonstrated by the figure, the magnitude of the assimilation efficiency of an organic moiety itself may be misleading, as its nutritive value depends not only on digestibility but also on its concentration in the food. For instance, in the diatom diet the lipids were assimilated with an efficiency of 99%, but the feeding efficiency was only 19% (when expressed as milligrams per milligram of food × 100). Furthermore, although in this diet the lipid fraction was the most readily assimilated, twice as much protein as lipid was assimilated per unit dry weight ingested. Also although the digestibility of AF-1 carbohydrates was the lowest of the four diets (U'_{CH_2O} = 49%), feeding efficiency for carbohydrates was higher than from either the detritus or the diatom because of the high carbohydrate concentration in AF-1. For the defined diets feeding efficiency parallels U' because of their high and comparable ash-free dry weights.

TABLE 5.—Feeding efficiency—the assimilation of total organic weight, protein, lipid, and carbohydrate per milligram dry weight of diet ingested.

Diet	Total organic wt A	Proteins A_P	Lipids A_L	Carbohydrates A_{CH_2O}
	μg	μg	μg	μg
Diatom	740	440	190	34
Detritus	680	240	170	70
AF-1	450	210	56	97
Chow	710	390	35	190

Minimum Rates of Net Assimilation

In tests with *C. fusiformis* and Trout Chow diets, fecal pellets were recovered quantitatively over 36- and 12-hr feeding periods, respectively. Because a small but undetermined amount of fecal material was lost, the fecal release rates reported for these diets are minimal. As is shown in Table 6, defecation of shrimp when fed

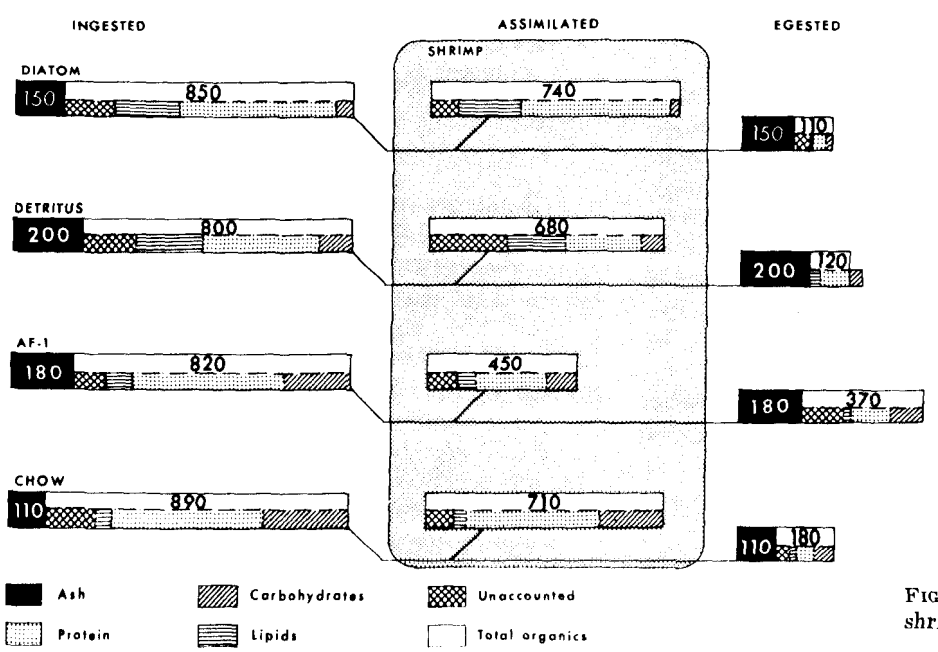

FIGURE 1.—Organic budget of shrimp fed on defined diets.

TABLE 6.—Minimum fecal release rates[1] of *Penaeus setiferus* fed on *Cylindrotheca fusiformis* and Chow.

Diet	Fecal release rate	Dry wt shrimp	Percent organic wt shrimp	Fecal release rate
	mg/hr	*g*	*%*	*mg/g organic shrimp/hr*
Diatom	5.79	5.09	83	1.3
Chow	9.06	3.15	83	3.4

[1] Calculations give minimum fecal release rates because some small loss of feces may have occurred.

on *C. fusiformis* proceeded at a minimal rate of 1.3 mg dry weight per gram organic weight of *P. setiferus* per hour. With the Chow, the release rate was more rapid, 3.4 mg hr^{-1}.

The minimal fecal release rates were employed to determine the rates at which total organic assimilation and assimilation of organic moieties occurred. These values (Table 7) reflect all three assimilation parameters, that is, digestibility, concentration in the food, and ingestion rate. The similarity in digestibility and total organic and protein composition of the two diets (see Figure 1) was obscured by the higher ingestion rate on the Chow. When viewed in time, net assimilation of organic material proceeded more than twice as fast on the Chow as on the diatom.

The protein assimilation rate followed a pattern similar to the rate of assimilation of total organic material; however, because of the high Chow carbohydrate analysis, sugars were assimilated more than 13 times as fast from the Chow than from the diatom. Conversely, even though ingestion of the diatom diet was relatively slow, its high concentration of easily digested lipids resulted in a faster assimilation of lipids than from the Chow.

We have reported assimilation rates in terms of the organic content of the feeding penaeids so that these rates are indicative of rates of replenishment. Johannes and Satomi (1967) reported the rate of net assimilation of *Nitzschia closterium* by *Palaemonetes pugio*, the grass shrimp, as 1.3 mg organic carbon per gram dry weight *P. pugio* per hour. This is somewhat lower than the rate we measured for *Penaeus setiferus* on *C. fusiformis* (2.1 mg oxidizable carbon per gram dry weight per hour). Johannes and Satomi employed quantitative recovery of food and feces rather than the ratio method.

TABLE 7.—Minimum rates of ingestion, net assimilation, and egestion of total organic weight, protein, lipid, and carbohydrate per gram organic weight *Penaeus setiferus*.

Diet	Organic moiety	Ingested *I*	Assimilated (net) *A*	Egested *N*
		mg hr^{-1}	*mg hr^{-1}*	*mg hr^{-1}*
Diatom	Total organic wt	4.3	3.7	0.6
	Protein	2.4	2.2	0.2
	Lipid	0.92	0.91	0.01
	Carbohydrate	0.29	0.17	0.12
Chow	Total organic wt	10.5	8.4	2.1
	Protein	5.3	4.6	0.7
	Lipid	0.53	0.41	0.12
	Carbohydrate	2.9	2.2	0.7

The rate of organic assimilation is not necessarily proportional to the rate of incorporation into body tissue. However, for an omnivore feeding on a richly diverse flora and fauna, mutual compensation should prevent the nutritional imbalance of any specific food from exerting a profound effect (Provasoli, Shiraishi, and Lance, 1959). The data make clear the distinction between digestibility (U') and assimilation rate. The latter is a function of both U' and ingestion rate. A rapid ingestion rate can compensate for low digestibility. For example, Meyers[6] has preliminary growth experiments which suggest that the growth rate on AF-1 is high although U' on this diet is low (Table 4).

ALGAL MAT

In order to estimate the ability of the shrimp to graze a naturally occurring food material, white shrimp were allowed to feed individually on the algal mat coating *Spartina alterniflora* culms. This mat consisted mostly of diatoms and filamentous green algae growing on and among the red algae *Polysiphonia* and *Bostrichia*. Such communities are found on the bottommost foot of the streamside *Spartina* in many shallow brackish water bays along the southeastern Louisiana coast.

[6] Personal communication, Dr. Samuel P. Meyers, Louisiana State University, Baton Rouge, La.

Penaeids were able to remove sections of the algal mat from the surface of *S. alterniflora* with either the mandibles, or the mandibles and the first and second walking legs. These sections were then rotated in the mandibular area by the maxillipeds. Rejection of uningested particles occurred in the mandibular region. At no time was regurgitation of particles entering the proventriculus observed.

Despite rejection of portions of the mat, the concentration of oxidizable carbon in the algal mat presented to each shrimp was employed as an approximation of oxidizable carbon ingested. Thus, in this test we were unable to account for selection. Table 8 shows the concentration of oxidizable carbon occurring in the mat and feces.

TABLE 8.—Net assimilation efficiencies of individual *Penaeus setiferus* fed on algal mat.

Shrimp length	Algal mat oxidizable carbon	Feces oxidizable carbon	AE^1
	Dry wt[2]	Dry wt	
mm	%	%	%
24	24	8.0	80
30	25	9.4	77
32	22	11	64
35	20	11	56
36	22	12	62
37	26	8.6	81
40	22	14	52
42	29	16	66
44	31	13	76
Mean			68
Standard deviation	3.6	2.6	10.7

[1] A ratio of organic weight to oxidizable carbon of 2 was chosen to convert oxidizable carbon to total organic weight.
[2] Individual values recorded have a coefficient of variation of 10%.

Assimilation efficiency ranged from 52 to 81%, with a mean of 68%. The feeding efficiency (Figure 2) was 33%. Thus, digestibility of the algal mat appears to be lower than that of two of its constituents, i.e., *C. fusiformis* and detritus. The lower (68%) AE for the algal mat compared to the defined diets may be explained by the following considerations. First, the green and red algae present in the mat have cellulose cell walls which are probably not digestible, or may be more resilient to trituration, by the shrimp. Second, the ash content of the mat was about 50%, and Conover (1966b) has reported an inverse relationship between ash content and digestibility of various algal diets ingested by *Calanus hyperboreus*. A third possibility concerns the rejection of portions of the mat as a means of selection. The occurrence in the rejected material and in the feces of the same algal species indicated that rejection was not a method of selection for specific organisms. However, the rotation of the detached mat in the mandibular area close to the excurrent respiratory stream appeared to result in removal of adherent silt. If this observation is valid, the organic fraction in the algal mat as it occurs on *Spartina* would be lower than that of the ingested material, and efficiencies of net assimilation and feeding would have been underestimated in this study.

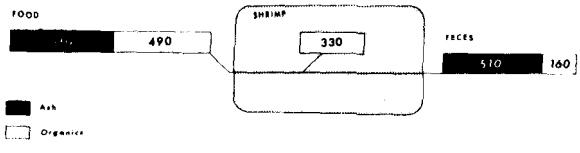

FIGURE 2.—Organic budget of shrimp fed on algal mat.

CONCLUSIONS

The results of this study and others begin to form a picture of the feeding process in shrimp, which is still far from complete, but does explain some of the observed phenomena. We describe this process for a shrimp feeding on an algal-microbial community such as that described above, not as a definitive statement but as a hypothesis for further testing.

A portion of the mat is torn off by the first and second walking legs and passed to the maxillipeds. Rotation of the mat in the proximity of the excurrent respiratory stream results in washing most of the silt away from the periphery of the mat. Once cleaned, the peripheral area is torn off by the mandibles and ingested. Thus selection for organic material occurs. Continued rotation of the mat entangles the inner algal filaments and silt into a ball. This knotting of the filaments impedes further silt removal. At this point, the uningested portion is rejected.

Ingested material enters the proventriculus where it is ground between the teeth of the gastric mill and forced through the filter press into the digestive gland (Dall, 1967). Passage of the ingested material through the proventriculus is governed in part by the time required for this trituration. As the digestive gland fills, ingestion slows. Thus the ingestion rate is governed by the filling of the digestive gland which is in turn regulated by the time required to render the food small enough to enter this organ. In this respect the shrimp is viewed as a conservative grazer, ingesting no more than it can effectively assimilate at one time (see Corner and Cowey, 1968, on the question of superfluous feeding.)

The assimilation of an organic moiety is a function of (1) the activity and concentration of the digestive enzymes of the shrimp and (2) the form of the moiety in a specific diet. Differences in rates of assimilation of different organic moieties indicate that lipases and proteinases are more active in the shrimp's digestive processes than are carbohydrases. The form of the moiety determines its susceptibility to catalytic attack. For instance, the diatom lipids were assimilated almost entirely (99%); whereas assimilation efficiency of the detritus lipids, which occurred at about the same concentration in the diet, was 86%. We suggest that lipids in the diatom occur primarily as oil droplets in the cell and are easily leached and attacked by lipolytic enzymes. Incorporation of the lipids into structural materials such as cell membranes in bacteria could make them less accessible by enzymes and reduce assimilation efficiency. For structural components of a diet, then, assimilation efficiency would be related to the degree of maceration or trituration of the food.

Material not entering the digestive gland passes from the proventriculus to the intestine to be voided at the anus. The physical requirement in the shrimp for material to occupy the space in the proventriculus above the filter press probably places a mechanical limit upon its assimilation efficiency.

The results suggest three generalizations concerning the type of diet shrimp may be expected to feed on in the natural environment. (1) Juvenile shrimp exhibit a high and comparable assimilation efficiency on a variety of plant and animal materials. (2) Proteins and lipids are, in general, assimilated more efficiently than carbohydrates. (3) Rates of assimilation on different material vary, and this variability is considered to be related to how rapidly the diet can be ground and filtered for assimilation. These generalizations show the shrimp to be a true omnivore in the sense that it is able to assimilate a wide variety of foods. The most digestible food is high in protein and lipids, low in carbohydrates.

Since the animal occurs seasonally in high concentrations in the marsh, its natural diet must be present in large volumes and must be rapidly replenished. Data from our laboratory[7] indicate that the benthic meiofaunal biomass in the Louisiana saline bays is insufficient to comprise a major volume of the shrimp's diet. On the other hand, the rates of production of detritus from the marsh grass *Spartina*, and of the periphyton and benthic communities, have been found to be high (Kirby, 1971; Stowe et al., 1971; Pomeroy, 1959). Thus, of the naturally occurring foods, the benthic algal communities and the detrital microbial communities on dead *Spartina*, because of their rapid turnover rates, appear to be the most likely sources.

ADDENDUM

An excellent article by Forster and Gabbott (1971) was published during final revision of this publication. They investigated the nitrogen and carbohydrate assimilation of certain commercial foodstuffs by *Palaemon serratus* and *Pandalus platyceros*. Nitrogen assimilation of the different diets varied from 80 to 95% whereas the assimilation of simple carbohydrates varied from 66 to 102%. Thus the nitrogen assimilation efficiencies reported in our paper agree with their findings while our carbohydrate assimilation efficiencies are lower.

[7] H. J. Bennett, Louisiana State University, Baton Rouge, La. (Unpublished.)

The primary question raised by Forster and Gabbott for our results is the reliability of Conover's ratio method. They were unable to account for 29 to 40% of the ash, and were not certain whether this was assimilated or lost to solution. With the ratio method assimilation of ash leads to underestimation of assimilation efficiency. For such a case the corrected assimilation efficiency (U'_{correct}) is given by the equation:

$$U'_{\text{correct}} = U'/100 + (A_u/A_f) [E'(1 - F')/F'(1 - E')] \times 100$$

where A_u/A_f is the fraction of ash assimilated. Similarly for U'_x the corrected value is found by the same equation except that the second term is also multiplied by r_n/r_i. From these equations it can be seen that the error incurred by failure to correct for assimilation of ash varies inversely with the ash content of the food and directly with the organic content of the feces. Thus errors are magnified when U' is low. If we assume that the upper limit of ash assimilation reported by Forster and Gabbott applied to our studies, the error in our U' values would be less than 10% for all diets except AF-1, which would have been in error by 35%. Similarly, high U'_x values would have small errors, low values relatively large errors.

We consider it likely that the high apparent ash assimilation of Forster and Gabbott are related to the organism used and the experimental conditions. They point out that loss of ash may have occurred through regurgitation and excretion. These parameters would be important when shrimp are fed for a short period (15 min) and feces collected subsequently over a long period (20 hr). On the other hand in our tests we observed no regurgitation, the shrimp fed continuously, and feces were collected about every 2 hr. These conditions should minimize ash loss.

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