

GULF OF MEXICO SHRIMP PRODUCTION: A FOOD WEB HYPOTHESIS¹

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ABSTRACT

The desire to better understand the dynamics of commercial shrimp populations which support an important regional fishery on the south Texas outer continental shelf stimulated us to investigate an extensive data base for links in the various ecosystem components that related to these dynamics. A correlational model was developed that suggested relationships between pelagic and benthic components of the south Texas marine ecosystem. Utilizing tracers, such as nickel concentrations in biota, sediment, and water, we identified pathways of natural transfer between zooplankton, the benthos, and coastal shrimp populations. These results stimulated us to develop a theoretical food web for the shrimp populations, focusing on transfer of carbon. The results of this exercise indicated that the majority of primary production (approximately 80%) is diverted to the benthos. Furthermore, it appeared that the secondary production of benthic infauna was not sufficient to alone support the coastal shrimp populations. We concluded that at least part of their nutrition was derived from the detritus pool which was maintained by the excessive amount of primary production diverted to the benthos. The evidence presented here suggests that the marine ecosystem in the coastal waters of south Texas functions differently than other ecosystems studied in recent years and pinpoints the need for a better understanding of the basis upon which our marine living resources are supported, in order to predict not only fishery yields but also effects of environmental disturbance.

The commercial shrimp fishery in the U.S. waters of the Gulf of Mexico is one of the most productive fisheries the United States pursues. This fishery provides better than 20% of the gross dollar value for the total U.S. harvest (U.S. National Marine Fisheries Service 1976) and represents the largest fishery in terms of weight harvested and effort expended along the gulf coast. For example, from a coastal area of Texas covering 10,000 km², an average of 5.7×10^6 kg/yr of brown shrimp, *Penaeus aztecus*, was landed in 1975-76, which represented an annual value of \$18 million. A decline in this fishery could cause economic loss, at least on a regional scale.

Research emphasis on the populations of penaeid shrimp that support the commercial fishery in the northwestern Gulf of Mexico has been directed towards laboratory behavioral studies, migratory habits, and the development of models relating harvest to environmental factors and management strategies. Although the data derived from these studies contribute to our understanding of the natural fluctuations that occur in the fishery, they do not provide adequate information about where the penaeid populations fit

into the trophic structure of the marine ecosystem and how these populations function. Due to this lack of knowledge, environmental managers would not be able to predict with confidence how a major perturbation in the Gulf of Mexico would affect the shrimp populations.

For years information has been accumulating on primary production, zooplankton biomass, and the distribution of benthic fauna in important marine fishery areas. Attempts to quantify links between these components have been provided by Steele (1974) for the North Sea ecosystem and by Mills and Fournier (1979) for the Scotian shelf. Arntz (1980) more recently attempted to relate benthic production with that of commercially important demersal fishes in the Baltic Sea. With the completion of a 3-yr multidisciplinary environmental study of the south Texas continental shelf (Flint and Rabalais 1981), one more fishing area has been characterized.

The Texas shelf ecosystem is a dynamic system driven by a complex aggregation of meteorologic and oceanographic events. Superimposed upon these phenomena are influences from local rivers and estuaries as well as from distant points such as the Mississippi River and the deep oceanic waters of the gulf basin (Flint and Rabalais 1981). The shallower waters of the Texas shelf are biologically a critical part of this ecosystem because of

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METHODS

their larger standing crops of phytoplankton, zooplankton, and benthos (Flint and Rabalais 1981) which are capable of supporting the large shrimp fishery yield in these waters.

Based upon a desire to better understand the characteristics of an important resource of the Texas continental shelf, we used the south Texas environmental study data as well as information from the published literature to develop a model of the trophic relationships supporting the brown shrimp fishery. This analysis provided insight into the general structure of marine ecosystems which support fisheries. It also provided the necessary data to judge whether the generalization of Dickie (1972) and Mills (1975)—that despite geographic differences most coastal ecosystems with productive fisheries have similarly constructed food webs—is well founded or not.

A multidisciplinary research program (1975-77) was conducted on the south Texas outer continental shelf (STOCS) at 25 stations (Figure 1). The study included water mass characterization, pelagic primary and secondary production as described by floral and faunal biomass, and benthic productivity as described by macroinvertebrate infaunal and epifaunal densities as well as demersal fish densities and biomass. The study, summarized by Flint and Rabalais (1981), provided a data base depicting the general characteristics of a marine subtidal area with important natural resources.

The focus of the results presented in this paper is on data collected from a "Reference Station" (Figure 1) which we consider representative of Statis-

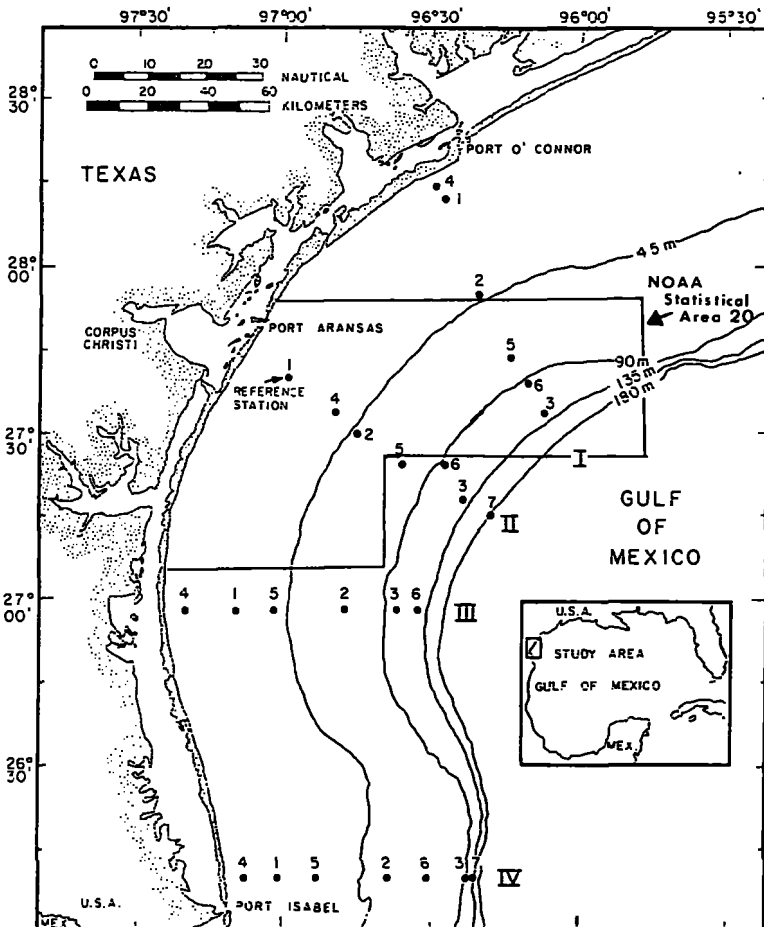


FIGURE 1.—Map of the south Texas continental shelf with location of sampling sites for 1975-77 environmental study. NOAA shrimp catch Statistical Area 20 is superimposed along with the Reference Station representing the source of data used in the text.

tical Area 20, the shrimp landing reporting region (U.S. National Marine Fisheries Service 1978) most closely associated with the STOCS study area. As mentioned previously, the shallower waters of the south Texas shelf are more productive, and the maximum yield of the brown shrimp fishery is within the depth range of this station (Grant and Griffin 1979). This site was characterized by one of the largest data bases of all 25 stations. Water column variables were sampled monthly during 9 mo in 1976 and 1977, and benthic variables were sampled monthly during 9 mo in 1976 and seasonally (winter, spring, and fall) in 1977. Details of sampling procedures are available in Flint and Rabalais.³

The STOCS data base contained adequate data on various biotic and abiotic components to allow for an integrated investigation of ecosystem relationships, with the shrimp populations as the ultimate focus of this exercise. Our approach was twofold. In the first step, we evaluated all variables in relation to one another using a correlation matrix. These comparisons included components within the pelagic environment, within the benthic environment, and between the two environments. Variables considered were similar to those listed in table 3 of Flint and Rabalais (1981). We looked for relative changes in population densities and biomass of biota that might be expected to be associated, such as phytoplankton and zooplankton or brown shrimp and benthic macroinfauna. Also, tracers, such as hydrocarbons and trace metals, identified relationships between components of the ecosystem based on organism body burdens and concentrations of the tracers in water samples and sediments.

Bivariate Pearson correlation coefficients were

used (Sokal and Rohlf 1969). All correlation coefficients, either positive or negative, were evaluated for their biological meaning. Those suspected of ecosystem relationships were put in a two-by-two correlation matrix, within which the number of significant correlations ($P < 0.01$) had to be more than 5% of the total for us to conclude that they were not chance produced (Bernstein et al. 1978).

The goal of this first step was to develop a correlational model of relationships in the data that suggested patterns in trophic coupling between shrimp populations and other biotic components. The patterns derived in step one prompted us to develop biomass estimates for the related components. The goal of the second step was to develop a theoretical model of energy flow in a trophic web which included penaeid shrimp as our central focus. Data from the STOCS Reference Station were used to estimate floral and faunal biomass as follows.

Chlorophyll *a* was measured according to standard techniques (Strickland and Parsons 1968). Biomass of zooplankton was determined from oblique (surface to near bottom to surface) tow samples taken with a 1 m net of 223 μm mesh. Neuston biomass was determined from samples collected in a 505 μm mesh neuston net towed in surface waters for 15 min. Zooplankton and neuston data were originally reported as ash-free dry weights but were converted to wet weights using a conversion factor of 0.15 for crustaceans (Lie 1968). Microplankton samples were collected in a 50 l Niskin bottle at the surface and at one-half the depth of the photic zone. Wet weight biomass was estimated by measuring volume displacement and assuming that a cell density of 1 μ^3 equalled 10^{-6} μg wet weight.

Benthic macroinfauna (>0.5 mm) samples were taken with a 0.1 m Smith-McIntyre grab. Estimates of benthic infaunal biomass (Table 1) in the south Texas shelf area ranged between 0.5 g/m^2

³Flint, R. W., and N. N. Rabalais (editors). 1980. Environmental studies, south Texas outer continental shelf, 1975-1977. Vol. III. Final report to the Bureau of Land Management, Department of the Interior, Wash., D.C. Contract AA551-CT8-51, 648 p.

TABLE 1.—Comparison of abundance and biomass of macrobenthos from the northwestern Atlantic Ocean and northwestern Gulf of Mexico.

Atlantic Ocean ¹			Gulf of Mexico				
Depth	Density (no./m ²)	Wet weight (g/m ²)	Depth	Density ¹ (no./m ²)	Wet weight ¹ (g/m ²)	Density ² (no./m ²)	Wet weight ³ (g/m ²)
30	26,060	7.69	12			1,536	0.63
40	7,390	2.44	16	1,373	0.74		
			30	14,623	4.09	675	0.28
Average	16,725	5.07		7,998	2.42	1,106	0.46

¹Measures from Rowe et al. (1974).

²Measures from the South Texas Outer Continental Shelf Study, 1975-77.

³Wet weight calculated from densities of organisms using the density to wet weight ratio of the respective values from Rowe et al. (1974).

(STOCS study) and 2.4 g/m^2 (Rowe et al. 1974). Since the data from Rowe et al. (1974) were based on a single sampling effort and the measures from the south Texas study were based on 12 separate sampling periods, we biased our infaunal biomass estimates towards the STOCS data and derived a biomass figure from a regression between total density and total biomass of infaunal samples (Table 1). Epifaunal invertebrates and demersal fish were sampled in 15-min bottom tows with a 10.7 m Texas box otter trawl with a 25 mm stretched mesh cod end. Wet weights were determined directly from the trawl samples.

Because biomass measurements were made on the penaeid shrimp during only one season in the whole STOCS study, we felt the data were not sufficient to completely characterize the biomass levels for the shrimp. Thus, shrimp biomass data were taken from Gulf Coast Annual Shrimp Landing Reports (U.S. National Marine Fisheries Service 1976, 1978). The shrimp fishery yields, however, did not represent the total production of shrimp in the coastal gulf waters. Therefore, for our model we estimated the biomass of shrimp populations that was not reflected by the catch statistics. A survival curve for the shrimp population was calculated (Figure 2), based upon a total population egg production rate of 10^{11} [based on a mean of 800,000 eggs/adult female $>140 \text{ mm}$ total length and a 1:1 sex ratio (Pérez Farfante 1969)] with a survival rate for the hatch of 1%. This

resulted in a recruitment rate of 10^5 juveniles to the population (Figure 2). The three additional data points on the curve were determined by splitting the shrimp biomass from the catch statistics (shaded area) into three size classes and calculating the number of shrimp of mean size within each of these classes. The curve was then extrapolated from recruitment through each of these data points with the mean size at emigration from the bays indicated (Figure 2).

The results of this two-step exercise provided information to estimate production and develop an energy flow model for the components of the south Texas shelf food web according to the ideas of Steele (1974) and Mills and Fournier (1979). Primary production estimates on an annual basis were calculated from chlorophyll *a* measurements according to the methods of Ryther and Yentsch (1957). A turnover ratio of 7 was used to convert macrozooplankton standing stocks to annual production (Steele 1974). Certain factors, such as tows failing to reach the bottom and net clogging causing $<100\%$ efficiency, contribute known biases to zooplankton sampling methods (Hopkins 1963; Wiebe and Holland 1968; Fasham 1978). Because of this and the fact that the water column was usually homogeneous in the shallow waters at the Reference Station (Flint and Rabalais 1981), we doubled the zooplankton production estimates. A turnover ratio of 10 was used for the microzooplankton standing stocks because we assumed a

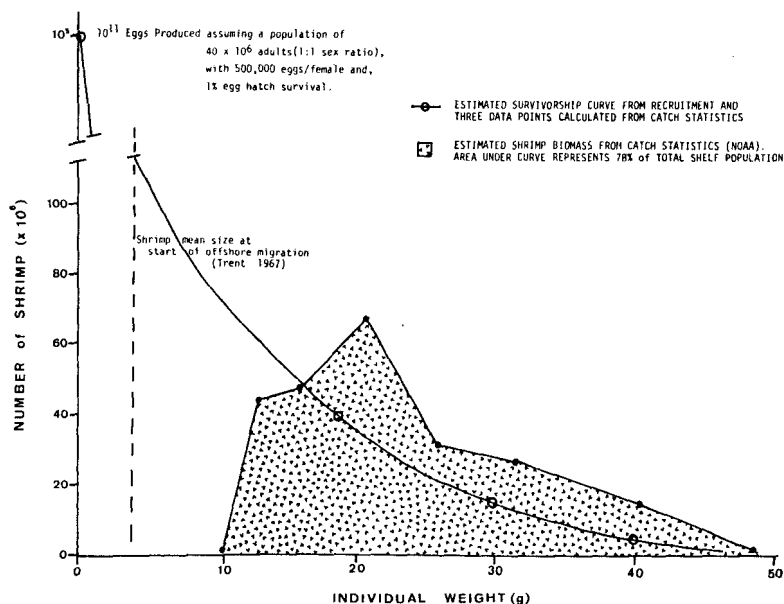


FIGURE 2.—Plot of the reported shrimp (*Penaeus aztecus*) fishery yield according to size class (shaded area) along with an estimated survivorship curve (solid line) for the south Texas continental shelf from NOAA Statistical Area 20 (see Figure 1).

larger ratio for the smaller sized microplankton as found by Droop and Scott (1978) and Mills and Fournier (1979). Benthos standing stocks were converted to annual production using a turnover ratio of 4.5 (Nichols 1977; Arntz 1980). A conversion for heads-on weight (1.61) and a turnover ratio of 0.8 (E. Klima⁴) were used to determine annual production from estimated shrimp standing stocks. A 6% conversion between wet weight and carbon content of metazoans (G. T. Rowe⁵) was used to determine carbon equivalents of annual production estimates.

RESULTS

Correlational Model

Significant correlation coefficients identified in the bivariate correlation analysis along with rela-

tionships in the data that suggested patterns in trophic coupling were used to develop the model illustrated in Figure 3. There was a relationship between the water column fauna, in this case zooplankton, and the sediment detritus pool as evidenced by the correlations between zooplankton nickel body burdens and sediment nickel concentrations as well as several zooplankton hydrocarbon body burden variables and hydrocarbons observed in the sediment (Figure 3). The analysis further indicated that primary producer biomass, represented by bottom water chlorophyll *a* concentrations, was related to density changes in benthic macroinfauna, potentially through the detritus pool (Figure 3). Relationships also existed between sediment hydrocarbon concentrations and bacterial density, indicating another potential link through the detritus pool.

Within the benthos, meiofaunal and macroinfaunal densities were correlated to bacterial densities, and macroinfaunal densities were correlated with meiofaunal densities (Figure 3). The constant ratio of benthic faunal densities to bacteria and not organic carbon (Figure 3) suggested

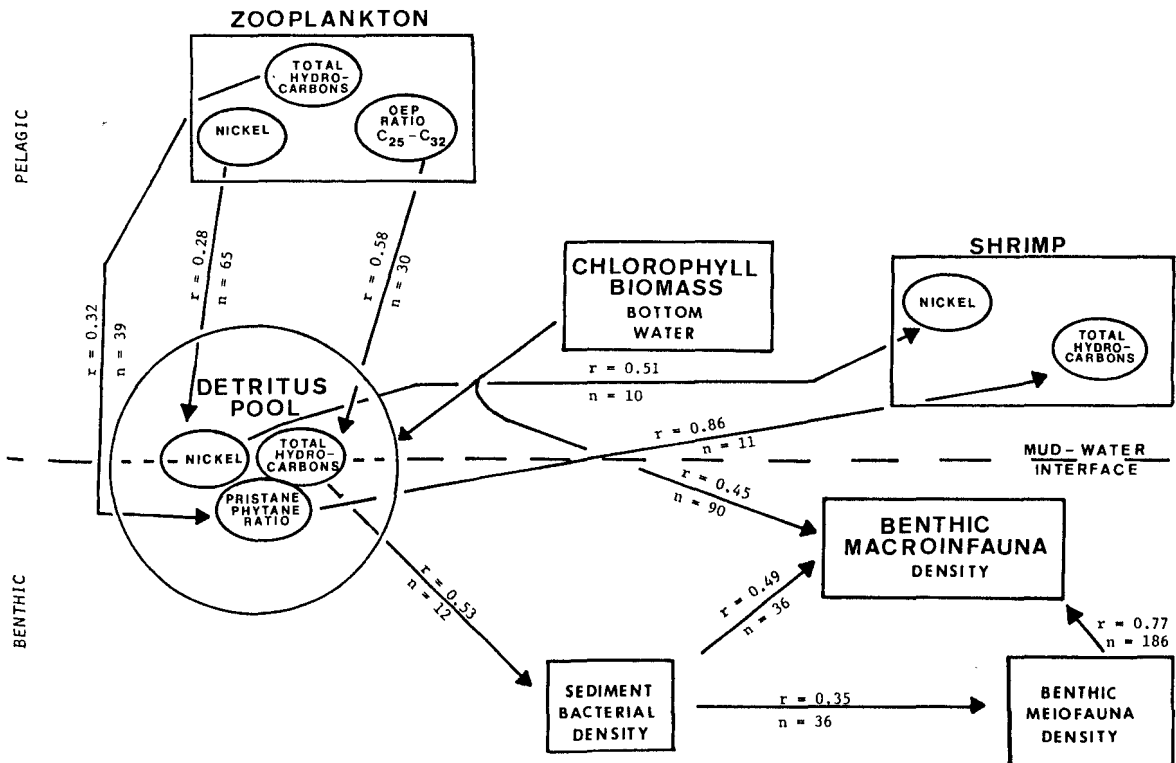


FIGURE 3.—Schematic representation of significant ($P < 0.01$) correlation coefficients (r) found between south Texas continental shelf environmental variables measured for 1976-77. Sample size (n) is also shown for each correlation.

bacteria as a food source. The meiofauna-macrofauna correlation completed the trophic web between the sediment inhabitants.

Finally, densities of shrimp on the Texas shelf were tied to the sediment detritus pool by correlations between shrimp body burdens of nickel and total hydrocarbons and sediment nickel concentrations and a sediment hydrocarbon variable (Figure 3). The correlations between zooplankton nickel body burdens, nickel concentrations in the sediment, and shrimp nickel body burdens (Figure

3) allowed us to propose a trophic coupling hypothesis for the shelf shrimp populations that included both pelagic and benthic components.

Trophic Web

Primary production for Texas inner shelf waters, determined from the Reference Station chlorophyll *a* measurements, was bimodal annually with peaks usually occurring in spring and fall (Figure 4). Since the spring peak in biomass for 1977 was not measured and presumably missed by the timing of our sampling, the estimate of $103 \text{ g C/m}^2 \text{ per yr}$ representing the amount of carbon fixed in the primary level of the trophic web (Figure 5) was probably low.

Macrozooplankton biomass on the Texas shelf averaged $3.57 \text{ g/m}^2 \text{ wet weight}$ (Table 2). From this amount, annual production of macrozooplankton was estimated to be $24.98 \text{ g/m}^2 \text{ per yr}$. In conversion for sampling bias, the production estimate was doubled to $49.96 \text{ g/m}^2 \text{ per yr}$. The carbon equivalent of zooplankton production was estimated to be $3 \text{ g C/m}^2 \text{ per yr}$. Similarly converted biomass data from the neuston component of the planktonic community added $0.2 \text{ g C/m}^2 \text{ per yr}$ (Table 2) to the macrozooplankton portion of the trophic web (Figure 5). Standing stock of microzooplankton was $0.47 \text{ g/m}^2 \text{ wet weight}$ which converted to an annual production of 0.9 g C/m^2

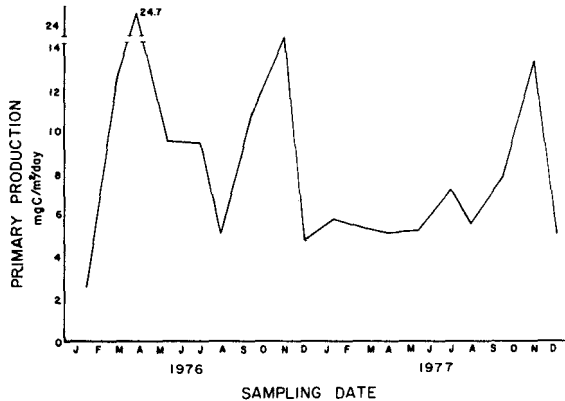


FIGURE 4.—The 2-yr cycle of primary production (carbon fixation) for Texas coastal waters between 1976 and 1977. Primary production calculated according to methods of Ryther and Yentsch (1957) using chlorophyll *a* measurements.

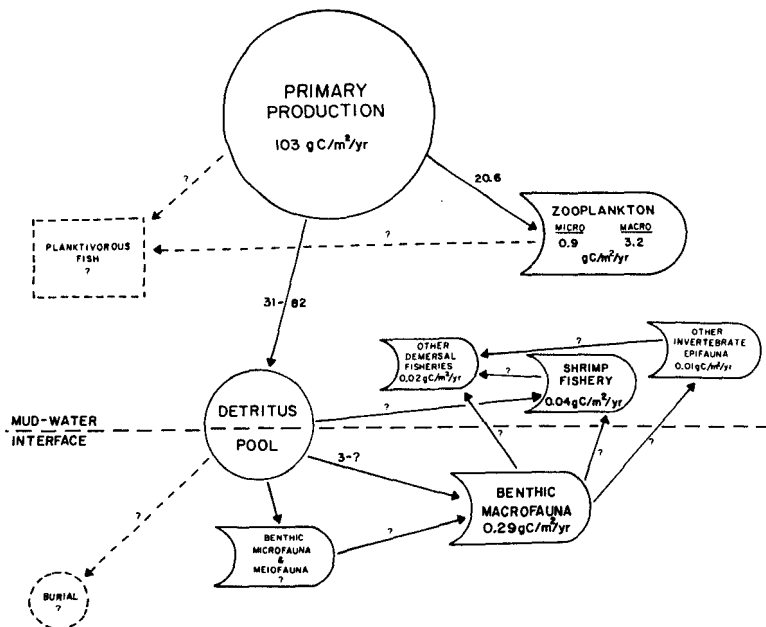


FIGURE 5.—Theoretical model of an annual production and energy flow food web for the south Texas continental shelf. All material flows represent gram C/square meter per year.

TABLE 2.—Procedures for calculating the amount of annual production for zooplankton components.

Macroplankton: Zooplankton biomass (wet weight)	3.57 g/m ²	assume → TR = 17	24.98 g/m ² per yr	sampling → bias conversion	49.96 g/m ² per yr	assume carbon → equivalent = 6% wet weight ² assume carbon	3.0 g C/m ² per yr
Neuston biomass (wet weight)	0.16 g/m ²	assume → TR = 17	1.13 g/m ² per yr	sampling → bias conversion	3.40 g/m ² per yr	assume carbon → equivalent = 6% wet weight ²	0.2 g C/m ² per yr
Microplankton: biomass (wet weight)	0.47 g/m ²	assume → TR = 310	4.65 g/m ² per yr	sampling → bias conversion	13.96 g/m ² per yr	assume carbon → equivalent = 6% wet weight ²	0.9 g C/m ² per yr
Total							4.1 g C/m ² per yr

¹Turnover ratio (TR) for zooplankton from Steele (1974).

²Assume carbon equivalent equal to 6% wet weight for metazoans (G. T. Rowe pers. commun).

³Assume higher turnover ratio for microplankton than TR = 7 from Steele (1974).

per yr (Table 2). The estimated total production for the zooplankton components of the food web on the inner Texas shelf was 4.1 g C/m² per yr (Table 2, Figure 5).

If we assume a minimum transfer efficiency of 20% between primary producers and zooplankton as suggested by Steele (1974), which is more conservative than the 27-32% suggested by Mills and Fournier (1979), then 20.6 g C/m² per yr (Figure 5) would be required to support these fauna and 82 g C/m² per yr of primary production would remain. With the exception of a small proportion of this 82 g C/m² per yr, which may support pelagic planktivorous fish, we believe that the majority of the primary production is directed elsewhere.

We derived a biomass figure for the benthic macroinfauna of 1.1 g/m² which we then converted to an annual production of 0.29 g C/m² per yr (Figure 5). From shrimp catch statistics, we estimated shrimp production at 0.03 g C/m² per yr. Based on the hypothesized survival curve (Figure 2), the estimate of shrimp production from catch statistics was found to represent 78% of the actual shelf population production as indicated by the shaded area under the curve. Therefore, with the additional 22% of unharvested shrimp biomass, the annual shrimp production was 0.04 g C/m² per yr (Figure 5). Additional data from the STOCS study indicated that demersal fish and invertebrate epifauna composed 0.02 and 0.01 g C/m² per yr production, respectively (Figure 5). The combination of these amounts with the shrimp production estimates accounted for 0.07 g C/m² per yr produced by fauna living in the bottom waters. Comparing this trophic level with the infaunal production (0.29 g C/m² per yr) and assuming a 10% transfer efficiency, benthic infaunal production appears to be an insufficient food source to solely support the demersal component of the inner shelf food web.

DISCUSSION

Research emphasis on the populations of shrimp that are fished in the gulf has been directed towards migratory habits (e.g., Inglis 1960; Klima 1964; Kutkuhn 1966; Trent 1967), dockside catch statistics (e.g., Gunter 1962; Caillouet and Patella 1978; U.S. National Marine Fisheries Service 1978), the development of models relating fishery harvest to environmental factors such as freshwater inflow (e.g., Hildebrand and Gunter 1952; Martin et al. 1980), and natural history (e.g., Heegard 1953; Iversen and Idyll 1960; St. Amant et al. 1966). Other studies have focused on behavior under laboratory conditions (e.g., Aldrich et al. 1968; Lakshmi et al. 1976). More recently, simulation of the shrimp fishery emphasizing different management strategies has been attempted by Grant and Griffin (1979). These studies, however, fail to pinpoint which factors maintain the shrimp production which supports a thriving fishery. Sources and pathways of nutrition and ramifications of interruption of this flow still remain to be determined.

Other recent studies on important fishery areas (Steele 1974; Mills and Fournier 1979; Arntz 1980) point out the need to understand the general structure of marine ecosystems and the trophic webs which support species important to fisheries. Our study consolidates information on primary production, secondary production, and abundance of benthic animals into a theoretical model of the northwestern gulf shrimp fishery food web.

The Texas shelf supports large phytoplankton biomasses with high annual production, especially in inner shelf waters where plankton are most abundant (Figure 6). Spring blooms in phytoplankton biomass are correlated with riverine inputs and nutrient maxima (Flint and Rabalais 1981). The patterns of inner shelf phyto-

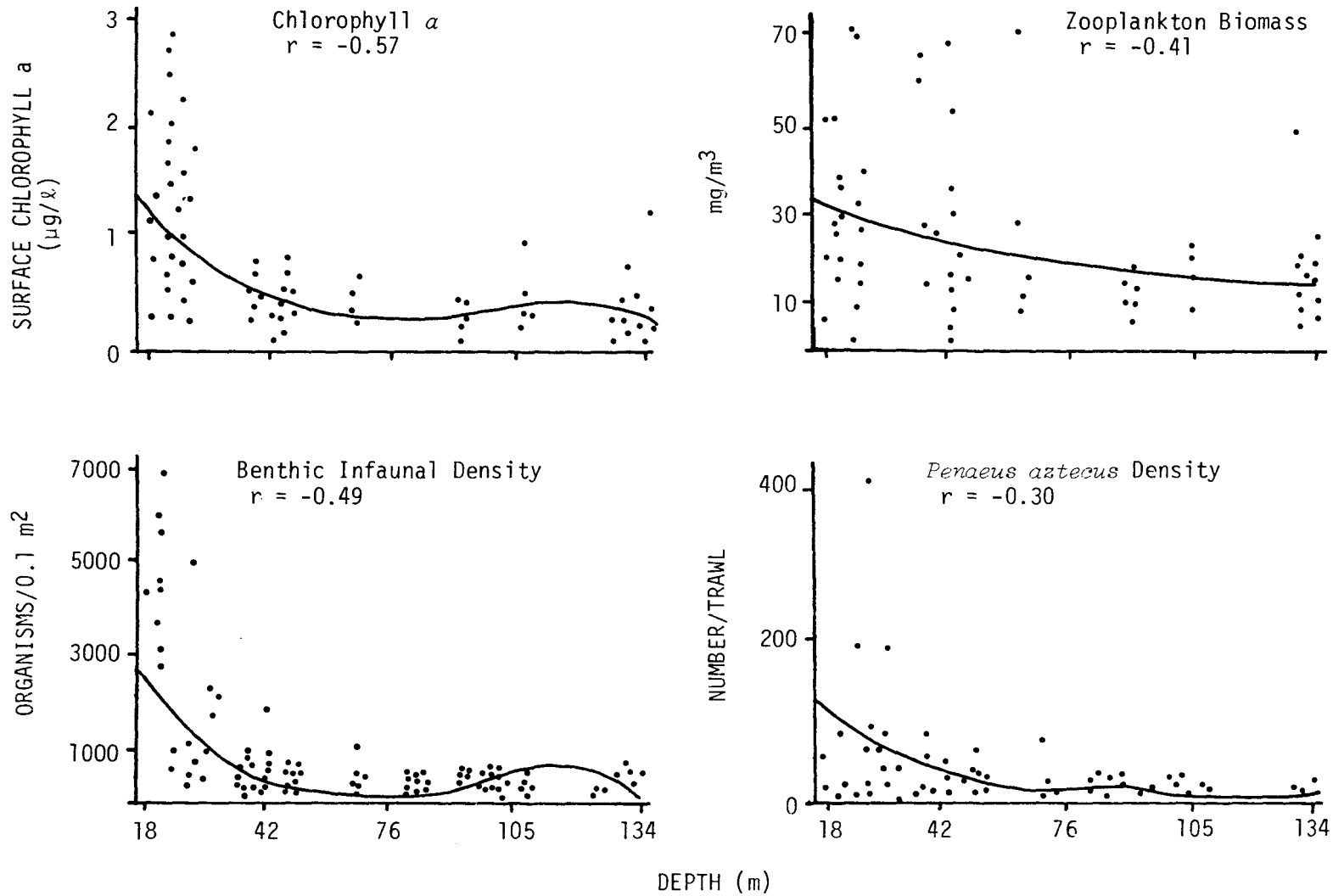


FIGURE 6.—Chlorophyll a, zooplankton biomass, benthic infaunal density, and shrimp (*Penaeus aztecus*) density for the south Texas continental shelf study 1976-77. Best fit fourth order polynomial regression lines are presented along with the significant ($P < 0.05$) correlation coefficients (r) (from Flint and Rabalais 1981).

plankton productivity are paralleled by zooplankton biomass (Figure 6) with peaks in shallow waters and decreases in an offshore direction. Likewise, both infaunal and epifaunal (represented by *P. aztecus*) benthic organisms are more numerous along the inner shelf (Figure 6) where general productivity is greatest in response to larger food supplies, greater habitat heterogeneity, and nutrients. These productive shallow waters are critical to the shrimp fishery populations. Greatest shrimp harvests for this part of the Gulf of Mexico are recorded for these shallow waters (Grant and Griffin 1979).

Although our estimate of primary production ($103 \text{ g C/m}^2 \text{ per yr}$) may be low because one spring bloom (1977) was missed by sampling frequency, this value is similar to values reported for other fish-producing areas. Mills and Fournier (1979) reported 102 and $128 \text{ g C/m}^2 \text{ per yr}$ for the Scotian shelf and slope, respectively, and Steele (1974) reported $90 \text{ g C/m}^2 \text{ per yr}$ for the North Sea ecosys-

tem. With the exception of a small portion which may support pelagic planktivorous fish, we believe that the majority of the northwestern gulf primary production is directed to the bottom. The amount of pelagic fish production supported by primary production on the Texas inner shelf is unknown; however, the amount of zooplankton biomass measured is not sufficient to support large populations of pelagic planktivorous fish. As indicated by the lack of a commercial fishery, the planktivorous fish that primary production could support represent small standing stocks in this area of the Gulf of Mexico. Thus, almost 80% of the total primary production biomass remains and presumably much of this reaches the bottom in coastal waters.

Further evidence for this conclusion is shown by the phytoplankton biomass distributions in the water column (Figure 7). The bottom waters support equal or greater biomass of primary producers than the surface or middepth waters as

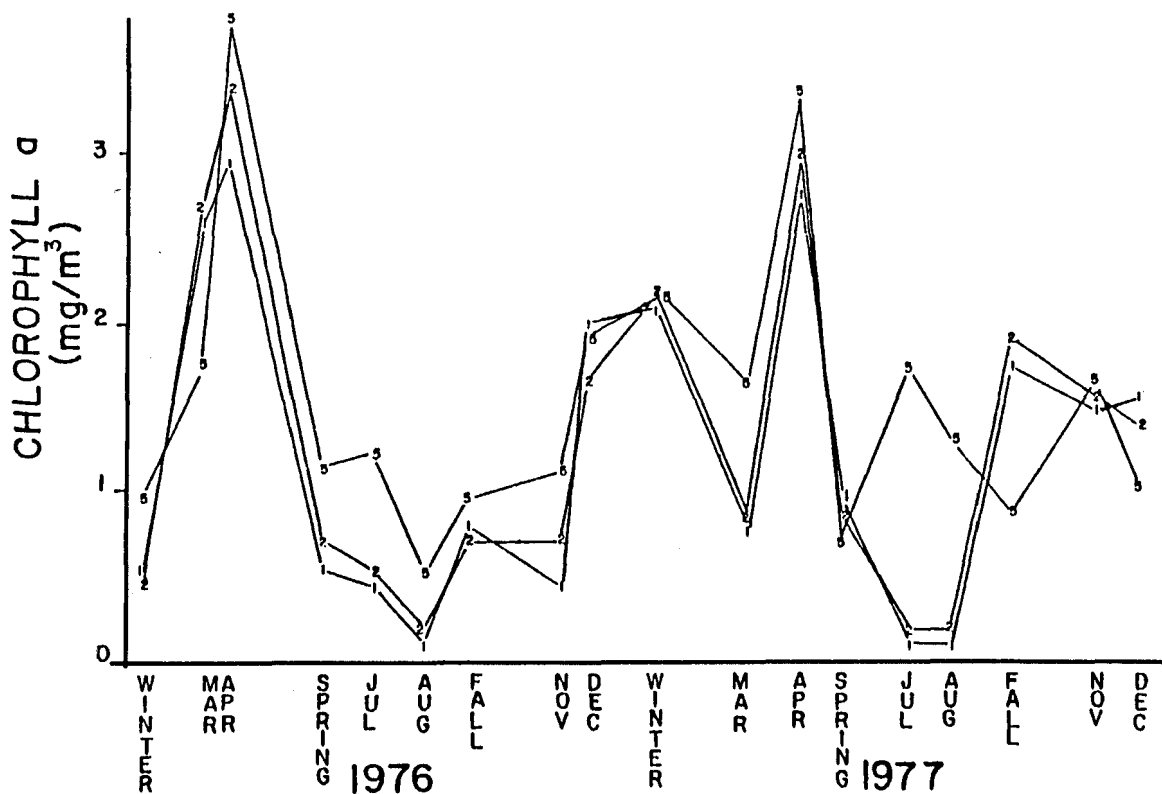


FIGURE 7.—Plot of surface (1), one-half the depth of the photic zone (2), and bottom (5) water chlorophyll *a* concentrations for the south Texas continental shelf environmental study between 1976 and 1977 at the Reference Station in Figure 1 (from Kamykowski, D.L., and S. Milton. 1980. Phytoplankton and productivity. In R. W. Flint and N. N. Rabalais (editors), Environmental studies, south Texas outer continental shelf, 1975-1977, Vol. III, p. 231-284. Final report to the Bureau of Land Management, Wash., D.C. Contract AA551-CT8-51).

shown by the chlorophyll *a* concentrations in the water column (Figure 7). These increases with depth indicate that much of what is produced in the pelagic zone reaches the bottom and accumulates.

The lack of stratification of the water column on the inner shelf during most of the year makes this conclusion reasonable. The water column is almost always well mixed in shallower waters <30 m depth (Flint and Rabalais 1981, figure 4), allowing for a direct transport of photic zone primary production to the bottom. This characteristic is also ideal for processes related to benthic-pelagic coupling, which we suspect are important in this coastal ecosystem.

Because mixing in the shallow shelf waters results in a relatively homogeneous water column, it is reasonable to propose a trophic coupling hypothesis for shrimp which includes both pelagic and benthic components. The relationships based on nickel tracers (zooplankton→sediment→shrimp) support this scheme. Also, zooplankton fecal pellets are a major input to the marine detritus pool (Cushing 1966; Steele 1974). Under the hydrographic conditions present, the discrimination between pelagic and benthic parts of the ecosystem is decreased and the potential for trophic coupling between the sea floor and overlying waters becomes more meaningful.

A key question about shrimp production concerns the component(s) of the benthic community from which shrimp derive their nutrition. Several studies have attempted to determine the role of benthic infauna as a food source for commercially important demersal species. Boesch (in press) found alterations in macrobenthic communities that resulted in reductions in populations which were dominant food items for demersal fishes and invertebrates. However, the contribution of energy flow to higher trophic levels from these populations and whether the larger fish and invertebrates were severely affected were unknown. Additional observations such as those of McIntyre et al. (1970) on molluscan siphon cropping by a commercially important fish species, and Arntz (1980) on changes in benthic infaunal biomass directly associated with demersal fish predation, implicate the benthos as important food items for species of commercial value.

Based upon our theoretical model of production estimates and energy flow for the south Texas coastal environment, benthic infaunal production

appears to be an insufficient food source to solely support the demersal component of the inner shelf food web. If we assume a minimum 10% transfer efficiency for the infaunal biomass produced, which is 0.29 g C/m^2 per yr, this trophic level could not support the 0.07 g C/m^2 per yr of total production by fish, shrimp, and other invertebrates, nor the 0.04 g C/m^2 per yr annual production of *P. aztecus*. Our calculations do not include meiofauna production. Even if this component were known, there probably would still not be enough carbon production by fauna in the benthos to directly support all higher trophic levels in the bottom waters. In addition, the correlation analysis did not identify any significant correlations between shrimp densities and densities of fauna inhabiting the sediment.

The correlations between shrimp body burdens and tracers in the sediment, however, provide evidence for another means of shrimp gaining nutrition, the detritus pool. These correlations support conclusions from other studies (Cook and Lindner 1970; Caillouet et al. 1976) that shrimp rely upon food provided by the marine detritus pool for at least some of their nutrition. Condry et al. (1972) observed that brown shrimp ate dead diatoms and algal mat material in an estuarine habitat. Moriarty (1977) recorded microbial feeding by shrimp from detritus substrates, and Foulds and Mann (1978) found evidence that crustaceans are able to digest cellulose. The dependence of these populations on the detritus pool is a reasonable conclusion.

Another potential contribution to the detritus pool comes from the discards—small shrimp, fish, and other invertebrates—from the methods of harvest employed by the shrimp fishery. According to Bryan and Cody,⁶ approximately 116 million kg of catch-associated organisms are discarded annually on the shelf off south Texas. Most of this material eventually reaches the bottom and becomes an additional source of food for scavengers, such as shrimp, to supplement the food sources from the benthic habitat.

The theoretical food web we propose for the penaeid shrimp fishery of the shallow nearshore waters of the south Texas continental shelf is in contrast to the food web described by Steele (1974) for the North Sea ecosystem and its related

⁶Bryan, C. E., and T. J. Cody. 1975. Discarding of shrimp and associated organisms on the Texas brown shrimp (*Penaeus aztecus*) grounds. Final Rep. to Texas Parks and Wildlife Department PL88-309, Project 2-276R, 38 p.

fisheries. Whereas we propose a detrital-based food web dependent on about 80% of the primary producer biomass being directed to the bottom, Steele (1974) indicated that only 30% of the primary production reached the benthos in the North Sea. On the other hand, Mills and Fournier (1979) observed that the majority of primary production was diverted to the bottom on the Scotian shelf. This primary production, however, was not adequate to satisfy the requirements of the benthic or pelagic food chains. The importance of herbivorous zooplankton and secondary consumers, such as ctenophores and chaetognaths, was emphasized by Mills and Fournier as elements potentially characterizing the structure of energy transfer in the Scotian shelf ecosystem. From the evidence available, the inner shelf ecosystem of the northwestern Gulf of Mexico, with its food webs leading to commercially important penaeid shrimp, appears different in structure from other areas with major commercial fisheries. The concept that food webs leading to these fishery populations are similarly constructed is not supported by our study, which only further points out what Mills and Fournier (1979) emphasized—detailed regional studies are needed before predictive models can be developed for these fisheries.

Our theoretical model of the trophic structure supporting the penaeid populations in the northwestern Gulf of Mexico is an approach to the detailed regional studies that are necessary. Much still needs to be done to define the pathways of nutrition and the implications of these pathways being interrupted by major environmental disturbances. Research on shrimp migratory patterns, behavior, response to environmental factors, and fishery statistics alone will not provide adequate information about the functioning of an ecosystem with respect to the trophic structure supporting a commercial fishery. Our study pinpoints some of the potential pathways of energy flow. The need for research to define the functioning of the ecosystem of which penaeid shrimps are a part cannot be overemphasized.

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