SEASONALITY AND COMMUNITY STRUCTURE OF THE BACKSWAMP INVERTEBRATES IN A LOUISIANA CYPRESS-TUPELO WETLAND

Fred H. Sklar

Coastal Ecology Institute
Center for Wetland Resources
Louisiana State University
Baton Rouge, LA 70803

Abstract. Core and floating "scoop" samples were taken monthly for two years in a Louisiana hardwood swamp for the characterization and identification of the benthic habitats far removed from waterways and bayous. Most backswamp macroinvertebrates have physiological and behavorial adaptations to withstand both desiccation and anoxia. The most ubiquitous taxa included amphipods, oligochaetes, diptera larvae, isopods, and fingernail clams. The biomass and density of backswamp benthic communities were some of the highest recorded for any "unpolluted" freshwater or estuarine soft-bottom habitat. The average number of invertebrates living in the sediments (5,690/m^2) was significantly less than the numbers living in the floating mats of Lemna spp. (10,508/m^2). The biomass distribution was just the opposite. There was a significantly greater invertebrate biomass in the sediments (8.4 g AFDW/m^2) than in the floating vegetation (4.2 g AFDW/m^2). Diversity (H) was relatively low, averaging only 1.8 in the floating vegetation and 1.4 in the sediments. Seasonal changes in density, biomass, and diversity were bimodal with peaks occuring during spring and fall, and were a function of the seasonality of wetland flooding and temperature.

INTRODUCTION

Little is known of the benthic community structure, function, and temporal dynamics in bottomland hardwood swamps of the South. Although 78% of the 1,555,700 ha of fresh water wetlands in the continental United States are located in Mississippi and Louisiana (Odum et al., 1979) almost all of the invertebrate studies have been in northern and/or salt water wetlands (Crow and Macdonald, 1979). The fresh water swamps of Louisiana are very productive ecosystems. Annual primary production can vary between 903 g/m^2 and 1,936 g/m^2 depending upon the hydrologic regime (Sklar and Conner, 1983). It is realistic to assume that swamp invertebrate communities, like coastal benthic communities, have an impact upon nutrient and production rates by acting as a food source for higher trophic levels (Wolff 1977, Arntz 1980) and as nutrient regenerators (Rowe and Smith 1977, Zeitzschel 1980). Sklar et al. (1982), using a dynamic simulation model of carbon flows in an impounded cypress-tupelo wetland, found that swamp invertebrate respiration accounted for 15% of the total community respiration. The purpose of this study was to investigate the seasonality and community structure of the invertebrate populations from the Lac des Allemands cypress-tupelo backswamps of Louisiana. Backswamps refer to those areas far removed from natural and man-made waterways. They are difficult-to-reach shallow-water habitats that few people venture to sample.

Macroinvertebrate communities vary substantially with different habitats. Krecker and Lancaster (1933) working in marshes surrounding the Great Lakes observed nine times the number of invertebrates among emergent vegetation than among submerged vegetation. Many researchers have noted the uniquely suited assemblages of fauna associated with aquatic vegetation (Scotland, 1934, 1940; Krecker, 1939; O'Hara, 1967; Krull, 1970; Hansen et al., 1971; Tilton and Schwegler, 1979). Most backswamp areas of Louisiana have rather extensive mats of floating vegetation, usually dominated by Lemna sp. (duckweeds). The importance of this habitat as both refuge and food source for backswamp invertebrates is unkown. McKim (1962) found that vegetated areas of fresh water wetlands generally had greater densities of invertebrates than coastal areas without vegetation. The only studies of swamp invertebrates in Louisiana (Bryan et al. 1976, Beck 1977, and Ziser 1978) have shown that macroinvertebrates prefer mixed vegetation habitats of high detritus concentrations (i.e. backswamp areas) over rivers, lakes, canals and bayous. Unfortunately, none of these studies took sediment core samples and Ziser did not take any sediment or water column samples. These studies did seem to indicate however, that backswamp habitats and their associated fauna were the basis for highly productive and diverse consumer populations (i.e. fish, birds, and reptiles) .

This research was designed to have general ecological significance and specific wetland management value, by addressing the following goals and objectives: 1) identify the taxa, assemblages, and community structure of the aquatic macroinvertebrates living in the backswamp areas of Cypress-Tupelo wetlands, 2) assess the significance of floating vegetation as a niche for backswamp invertebrates and 3) examine the factors associated with the regulation of benthic community structure

DESCRIPTION OF AREA

The Des Allemands swamp system is located in the headwaters of the Barataria Basin Hyrologic Unit, an interdistributary basin bordered by the Mississippi River, Bayou Lafourche and the Gulf of Mexico (Fig. 1). The swamp is separated from the lower basin by a highway embankment (U.S. 90) and the only significant downstream outlet is the bayou draining Lac des Allemands. There is little direct tidal effect within the upper basin, but prolonged southeasterly winds can raise water levels in the swamp (Byrne et al., 1976). The area selected for study in the Des Allemands swamp forest (Fig. 1) is a natural baldcypress-water tupelo forest subject to flooding to depths of over 60 cm for most of the year. This site is relatively undisturbed and water flows freely through the area during periods of inundation. The typical hydrologic cycle can be broken down into a wet season (winter-spring) and a dry season (summer-fall). In general, these swamps become completely dry for one month (August). However, it doesn't take much rainfall or much interference (from spoil banks and canals) of the normal laminar sheet flow to prevent these systems from ever drying out (Sklar and Day 1984).

Within the Des Allemands swamp, two types of plant communities exist --bottomland hardwood and baldcypress-water tupelo. Bottomland hardwood forests are found in swamplands of brief occasional flooding. They are composed of oak (Quercus spp.), willow (Salix nigra), elm (Ulmus americana), maple (Acer drummondii), boxelder (Acer negundo), cottonwood (Populus spp.) and a variety of other woody species. Baldcypress-water tupelo forests, found in poor drainage areas, where frequent long inundations are common, are dominated by baldcypress (Taxodium distichum), water tupelo (Nyssa aquatica), maple (Acer drummondii) and ash (Fraxinus spp.). Within the baldcypress-water tupelo forests there is often a floating mat of duckweed (Lemna minor, Spirodela polyrrhiza, Wolffia and Wolffiella), Riccia, Pistia, and the common frog's bit (Limnobium spongia). A complete listing of the species is given in Conner et al. (1981).

A recent study of the soil structure (Paille, 1980) found the study area composed of Barbary clay soils. Although little is known of the spatial and temporal soil structure within a swamp site, the homogeneous and relatively uniform distribution of bottomland vegetation in each location (Conner et al., 1981) implies a lack of any large scale patchiness in soil structure.

The uptake and release of nutrients across the mud-water interface is regulated to a large degree by the development and extent of an aerobic surface layer (Mortimer 1941, Pomeroy et el, 1965; Patrick and Khalid 1974). Therefore, by consuming oxygen a benthic community indirectly effects this nutrient cycle. The biological oxygen demand of the organisms in the sediment lowers the amount of dissolved oxygen thereby helping to increase redox-mediated phosphate release (Kemp and Day 1981). Because the concentration of oxygen at the interface is also a function of turbulence and water flow (Howeler and Bouldin 1971) the aerobic zone tends to be reduced during periods of low water flux and high water levels. McNamara (1978) found very high oxygen consumption during the summer months when high temperatures, low water movement and high BOD resulted in the development of anoxic conditions. Backswamp oxygen levels are, on the average, very low (2 mg/l) (MacNamara 1978; Kemp 1978), therefore, high respiration rates, as measured by MacNamara (1978) (i.e. 7-10 mg O_2/l/day) can have a significant impact on the development of reducing conditions which, in turn, can stress or alter the oxygen dependent invertebrate community.

METHODS

SAMPLING TECHNIQUES

Sediment core samples and floating vegetation samples were taken monthly, from Febuary 1977 until January 1979. A 20 cm-diameter stovepipe corer (314 sq. cm) was used for sampling the

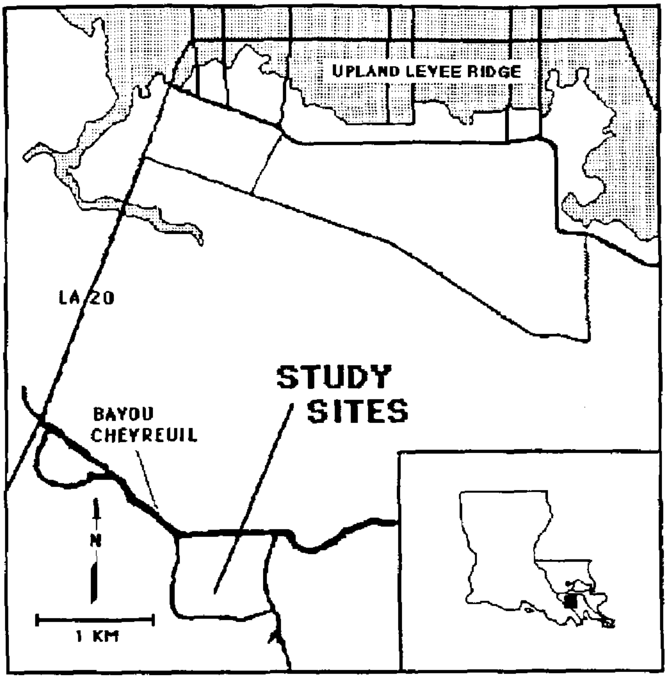

Figure 1. The Des Allemands cypress-tupelo wetland is located in the upper Barataria Basin, Louisiana. Samples were collected within an area most likely to have a "natural" hydrologic regime (Sklar and Day 1984).

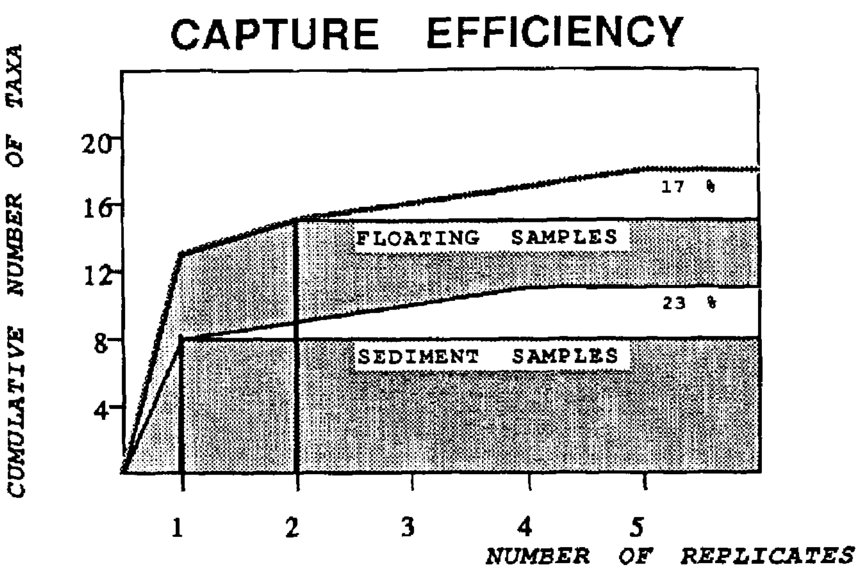

Figure 2. The relationship between the number of replicates and the number of taxa gives the capture efficiency for each sampler.

community of animals associated with the bottom sediment. Estimates of standing stock obtained with a stovepipe corer are as good as or better than those obtained with an Ekman grab (Flannagan 1970; Kajak 1971; Brinkhurst 1974) and require less sorting effort because of the lower volume of sediment (Paterson and Fernando 1971). The stovepipe corer was manually forced into the sediment about 60 cm, until the hard clay substrate which underlies the soft upper 'ooze', was reached. The entire water column (except for the floating vegetation which was gently pushed aside before the corer was used) and sediment to a depth of 30-40 cm were removed with a long-handled ladle and poured into large, heavy duty plastic bags. The plastic bags were brought to a field lab where each sample was mixed well and washed through a square 500 µm sieve divided into four 30 cm x 30 cm quadrants. During low water periods, when samples were mostly sediment, tap water was added until a well mixed slurry was produced. The contents from two randomly chosen quadrants were preserved in a 10% formalin solution with rose bengal added to facilitate sorting (Mason and Yevich 1967).

The floating vegetation produced a mat that was easily sampled from underneath with a 12 cm-diameter "scoop" (114 sq. cm). The scoop was a long-handled (i.e. 2 meters), wide mesh, strainer filled with four layers of laboratory grade cheesecloth. The scoop was put into the water column through a prepared clearing in the duckweed mat and slowly moved to a sampling site and then slowly lifted up. Everything except the free-floating microflora was retained by the cheesecloth and preserved in a 10% formalin-rose bengal solution.

All samples were washed onto 500 µm sieves before sorting and preserved in 80% ethanol after sorting, except for soft bodied animals which were kept in 10% formalin. Animals were counted, weighed and identified to species level whenever possible. Problems identifing diptera larvae and oligochaetes were particularly acute. In most cases only the genus or family could be reliably identified. An average ash free dry weight (AFDW) for each species was calculated from a minimum of 3 replicates (rare species) or from a maximum of 15 replicates (abundant species). Animals were placed on preweighed miniature aluminum foil weighing pans and dried for 24 hours at 90°C (Cummins and Wuycheck 1971). Pans were placed in a desiccator and allowed to cool to room temperature before being weighed on a Cahn Automatic Microbalance. Samples were then combusted for 3 hours at 500°C and reweighed. Empty pans were also weighed, dried and muffled, so that corrections for oxidation of the aluminum could be made. Weights were corrected for formalin and ethanol preservation according to the findings of Howmiller (1972).

DATA ANALYSIS

Density differences between replicates were used to estimate the accuracy of the sampling techniques. A normal distribution of replicate values was assumed and confidence intervals were calculated according to the benthic survey formula of Elliot (1971):

$$n = s^2 / E^2 \cdot x^2 \qquad (1)$$

where n represents the number of samples; s, the variance; E, the percent error; and x, the mean of the samples.

The stovepipe corer, and the FV scoop sampler were very accurate estimators of actual population densities (Sklar 1983). The percent error for two FV samples and one sediment sample was 9.0% (i.e. 91% confidence interval) and 17% (i.e. 83% confidence interval), respectively. This means that the biotic environment was relatively homogeneous and that the mean of two FV samples had a .91 probability of reflecting the true population density while the density in one sediment core had a .83 probability of reflecting the true benthic density.

The efficiency of capturing all the species with one stovepipe core sample and two FV scoop samples was based on a graphical representation (Fig. 2) of the number of species collected from sediment replicates and floating vegetation replicates (Sklar 1983) as suggested by Pielou (1969). The number of species expected from an average replicate was compared with the number expected from as many replicates needed to collect all species. Capture efficiency for one sediment sample and two FV samples was 77% and 83%, respectively, assuming that when the lines in Fig. 2 reach a plateau 100% of the species are being sampled.

A variety of community structure indicies were calculated from monthly species density data from the control site, the crawfish farm site, and the open area of the impounded site. The first of these is the widely used information-based Shannon diversity index:

$$H = -\Sigma_i\, p_i \log p_i \qquad (2)$$

where pi is the proportion of individuals in the i-th species. This function increases as a function of both the number of species and the equitability of species abundance, thus it is desirable to consider indices that treat these two aspects separately. Towards this end, "species richness" as suggested by Margalef (1969) was used:

$$D = (S-1) / \text{Log } N \qquad (3)$$

where S is the number of species and N is the number of individuals, and "evenness" as suggested by Pielou (1966) was used as a measure of equitability:

$$J = H / \text{Log } S \qquad (4)$$

where Log S is the maximum possible diversity (Gatlin, 1972).

Multivariate ordination and classification techniques were preformed with the ORDANA program (Bloom et al. 1977). Data was first standardized on a square meter basis, then both species and attributes (i.e. samples) were simultaneously standardized according to total abundances, a technique known as double standardization (Boesch, 1977). The Canberra Metric coefficient in its dissimilarity form was the resemblence measure used:

$$D = 1/m\, \Sigma(|x_{ij}-x_{ik}| / (x_{ij}+x_{ik})) \qquad (5)$$

where xij is the value of the i-th species in the j-th collection and m is the total number of species in both collections. The Canberra Metric was used because it removes the bias created when samples contain large numbers of one or two species (Boesch, 1977; Clifford and Stephenson, 1975), unfortunately it also tends to underestimate similarity (Bloom, 1981). To compensate, a group average clustering strategy was used and a effort was made to interpret the resulting dendograms conservatively. That is to say, the subjectivity of group selection was recognized and countered by not grouping units below approx. 50% similarity and by avoiding spuriously isolated attributes. When the number of clustering attributes was small, as when clustering monthly similarities (i.e. 12 attributes), an agglomerative hierarchical clustering was used with a cluster intensity coefficient (B) of -.25 as suggested by Boesch (1977).

RESULTS

DENSITY AND BIOMASS

Sixty six species of macroinvertebrates, within 18 orders, were identified from the Lac des Allemands Swamp (see Sklar 1983 for a complete species list). There were 17 taxa of aquatic invertebrates that averaged over 100 individuals per sq. meter. Amphipods, diptera larvae, isopods, and aquatic oligochaetes were very abundant, averaging over 1000 individuals per sq. meter (Table 1). Fourty four percent of the species sampled averaged less then 10 individuals per m^2. Total average density for both habitats combined was 16,198/m^2/month with a standard error of 3400. The average density of macroinvertebrates was significantly ($P<.01$) greater in the floating vegetation than in the sediments. Floating invertebrate populations averaged 10,500 individuals/m^2/month and had a maximum of 41,282. The benthic population averaged 5,690/m^2/month and had a maximum of 12,739.

The abundance and biomass data for each invertebrate species were ranked, and the top ten organisms are listed in Table 1. These data indicated that the ranking of the top ten taxa in terms of density, was not the same as the ranking in terms of biomass. Five taxa (Nais spp., Aulophorus vagus, Hyalella azteca, Chironomidae spp., and Asellus obtusus) dominated in terms of abundance. Four taxa (Sphaerium partumeium, Asellus obtusus, Lumbricidae, and Nais spp.) dominated in terms of biomass. Predators, such as Procambarus clarkii, Dytiscus sp., Belostoma bakeri, Erythemis spp., Neoplea striola, and Enallagma spp. were a dominant component of community structure in terms of biomass but not in terms of density. The top ten organisms accounted for only 75% of the average total biomass and 78% of the total average density.

Table 1. The ten most dominant swamp invertebrates by density and biomass.

RANK	TAXA	MEAN DENSITY No./sq m
1	Nais spp.	2399
2	Aulophorus vagus	2369
3	Hyalella azteca	2168
4	Chironomidae	1781
5	Asellus obtusus	1144
6	Tanypodinae	817
7	Sphaerium partumeium	630
8	Promentus sp.	498
9	Neocataclysta sp.	389
10	Ceratopogonidae	371
	Total	12,566
	Cumulative Percent of Total	78%

RANK	TAXA	MEAN BIOMASS mg AFDW/sq m
1	Sphaerium partumeium	2216
2	Asellus obtusus	1945
3	Lumbricidae	1889
4	Nais spp.	1175
5	Hyalella azteca	542
6	Dytiscus sp.	459
7	Procambarus clarkii	407
8	Chironomidae	392
9	Paleomentes palodusus	295
10	Belostoma bakeri	281
	Total	9,601
	Cumulative Percent of Total	75%

Although most of the macroinvertebrate population was found living within the duckweed mats, most of the biomass was found in the sediments (Fig. 3). The average monthly macroinvertebrate total biomass was 12.6 g AFDW/m^2 and ranged from a low of 3.3 g AFDW/m^2 in Sept. '78 to a high of 22.9 g AFDW/m^2 in April '77. In the floating vegetation the biomass ranged from 0.5 to 15.7 g AFDW/m^2. In the sediment it ranged from 1.5 to 22.5 g AFDW/m^2. The average biomass of swamp invertebrates was 8.4 g AFDW/m^2 and 4.2 g AFDW/m^2 in the sediments and floating vegetation, respectively. On the average, 67% of the biomass of aquatic swamp invertebrates was found in the top 20 centimeters of mud. Biomass differences between habitat types were significantly different at the .05 probability level.

Community Ordination

A more detailed analysis of the structural differences between swamp habitats, derived from the frequency and abundance of all species (not just the top ten), was based on numerical classification

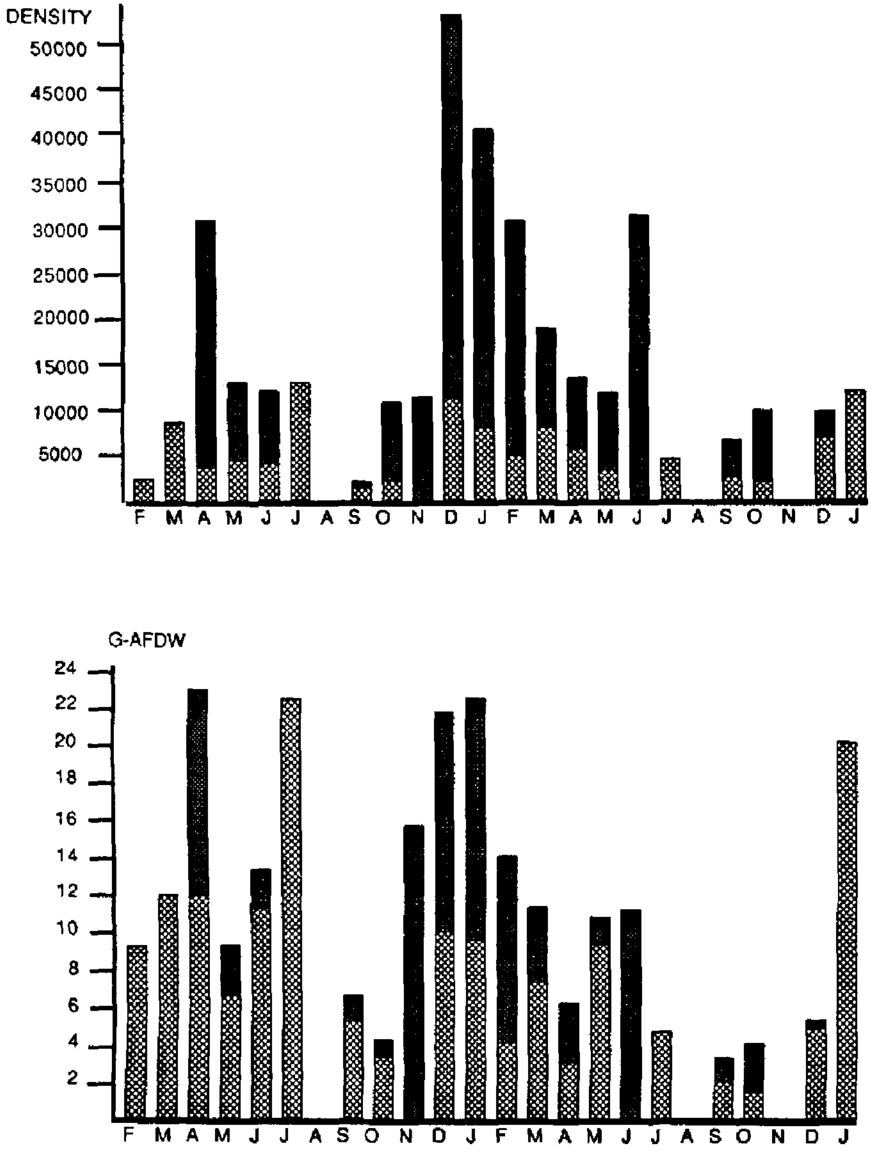

Figure 3. Mean monthly density per square meter (Top) and biomass, gm ash-free dry wt. per square meter (Bottom) of backswamp invertebrate communities living in the sediment (light hatch marks) and in the floating Lemna mats (dark hatch marks). Sediment core samples were not taken in November of 1977 and in June of 1978.

techniques. These techniques, which have become widely accepted, especially in benthic ecology, were used to cluster (i.e. group) species with similar temporal attributes within a particular swamp habitat. A dendogram, used to illustrate these clusters, was produced for each habitat (Fig. 4). Comparing these dendograms produced three general observations: 1) swamp communities were divided into a minimum of three large clusters ('dominant', 'rare', and 'absent'), 2) the most ubiquitous floating cluster (i.e. group E) and the most ubiquitous benthic cluster (i.e. groups D & E) were alike in that they have two taxa in common (#25 and #10, Hyalella azteca, and chironomid larvae, respectively) however, they were also very different because five species were clearly habitat specific, and 3) the structure of the invertebrate community (i.e. the species composing the clusters and the level of similarity between species and clusters) was quite different for each swamp habitat.

Temporal Distribution

The physical variables in Des Allemands exhibited a seasonality typically found in temperate zone ecosystems ; winter water temperatures were, on the average, 15°C lower than summer temperatures (12.7°C and 27.4°C, respectively), daily surplus precipitation was greatest during winter (i.e. 10.9 cm), and retention of winter water surplus coupled with low evapotranspiration rates resulted in maximum water depth during spring (i.e. 60 cm). The seasonality of invertebrate biomass and density however,was not what one would expect for a North American habitat. Populations tended to decrease during low water and high temperature periods (i.e. late summer), and increase during the high litterfall and low temperature periods (i.e. fall and winter); a trend opposite from that found in most temperate aquatic systems where lowest diversity and density usually occurs during winter.

The seasonal distribution of macroinvertebrates from the swamp habitats was bimodal (Fig. 5). There was an early summer peak and an autumn peak. The autumn peak decreased as a result of cold weather however, a mild winter can prevent a winter die-back. For example, high biomass occurred during the winter of '77-'78 (Fig. 3B) due to the fact that the floating vegetation never froze. Under average conditions, as temperatures increase in the spring, populations of swamp invertebrates increase. Populations decrease again in late summer in response to the development of anoxic conditions or late summer dry down. Summer dry-down is a result of high evapotranspiration rates and low runoff. Anoxic conditions are the result of a high water table coupled with high temperatures.

Using ordination techniques to classify swamp invertebrate populations according to their temporal similarities resulted in an average swamp seasonality of three seasons (Fig. 6). Populations fell into a winter grouping (cluster 1), a spring grouping (cluster 2), and a summer-fall grouping (cluster 3). The summer-fall grouping was the most interesting because it represented a community of few organisms capable of tolerating both anoxic conditions and very dry conditions. These were the same organisms that clustered into the dominant groupings in Figure 4.

Diversity, Richness and Evenness

It is customary, although not necessarily informative (Hurlbert, 1971), when doing an analysis of community structure to include calculations of diversity (H), richness (D), and evenness (J). Values for H, D, and J , average diversity and richness was significantly (P<.05) greater in the floating vegetation (1.8) than in the sediment (1.4). Evenness did not vary significantly among habitats indicating that richness was the primary component behind differences in diversity. The maximum values of diversity (2.3) and richness (2.6) were recorded in the floating vegetation. The average seasonality for each of these indices of community structure in both the floating vegetation and sediments are shown in Figure 7. In the spring, as temperatures increased and duckweeds grew, the diversity (Fig. 7A), the species richness (Fig. 7B), and the evenness (Fig. 7C) in the floating vegetation increased to maximum values. Benthic communities reached maximum values in February but decreased in spring, as diversity and richness increased in the floating vegetation. As a result of dry conditions and/or the development of anoxic sediments the summer was a period of minimum H, D, and J for both floating and benthic habitats. In the fall-early winter, as water levels rose and water quality improved, a second increase in the indices was observed in the sediment and floating vegetation. The trends illustrated in Figure 7 indicate, 1) a bimodal variation in H, D, and J in the FV, 2) a tendency for H, D, and J to flucuate more in the sediments than in the FV and 3) a close correlation between species richness and diversity.

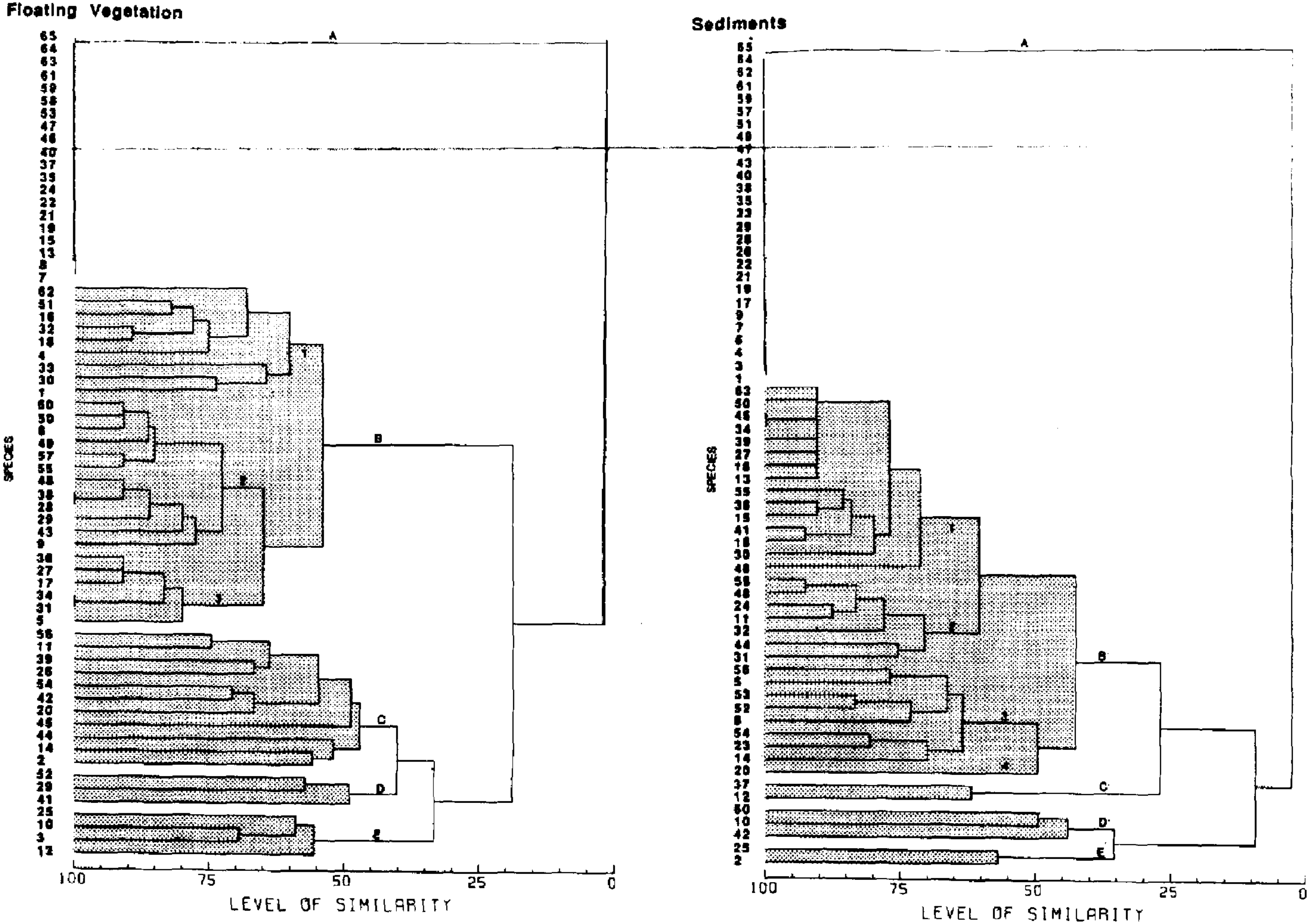

Figure 4. Caberra Metris similarity ordination technique was used to cluster invertebrate abundance and temporal distribution in the floating vegetation (Left) and sediment (Right). A = extremely rare or absent. B = rare. C = cool-water species. D and E = dominant communities. The highly ubiquitous group was E in the floating community and D in the sediment.

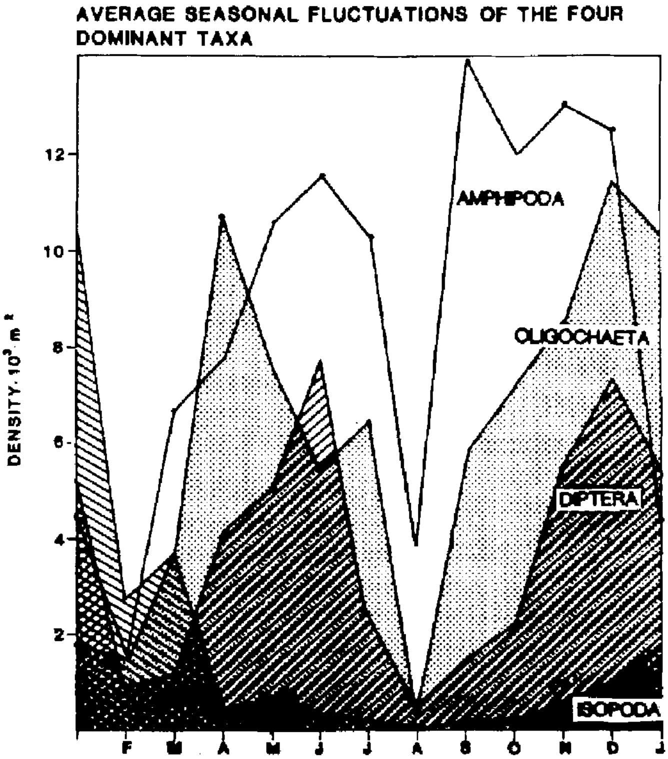

Figure 5. Average seasonal fluctuations in density $\cdot 10^3 m^{-2}$ of the four dominant backswamp macroinvertebrate taxa. All habitats and sampling sites combined.

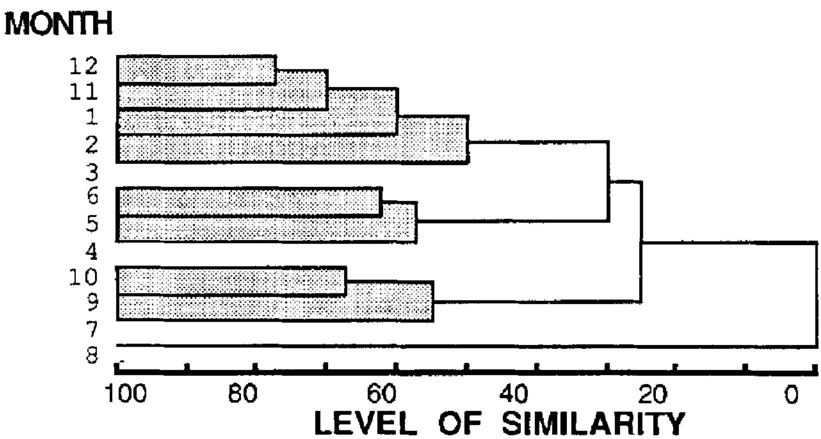

Figure 6. Dendrogram of monthly similarity of community structure. 1= Jan., 2=Feb., etc. The Canberra Metric Index was used with double standardization and a Beta of -0.25.

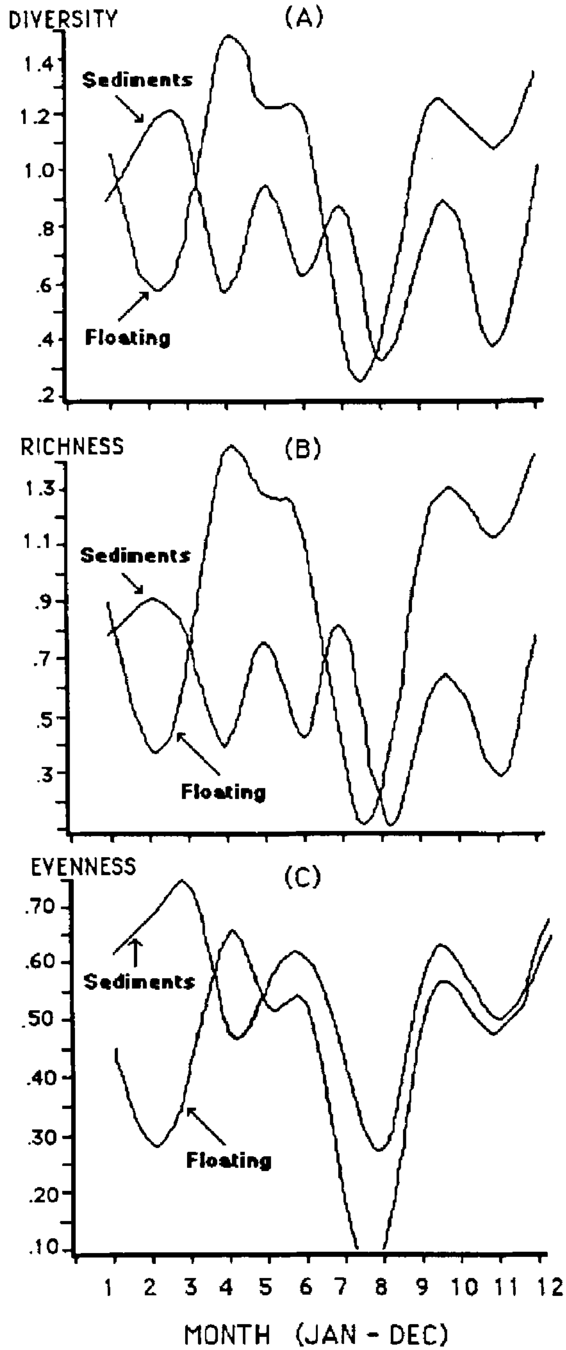

Figure 7. Average monthly variation in diversity (A), richness (B), and evenness (C) in the floating vegetation and sediments.

DISCUSSION

The aquatic macroinvertebrate community in cypress-tupelo swamps can be characterized by populations capable of withstanding periodic dry-downs and a low oxygen environment. Their long-term survival is a function of their flexibility in responding to rather dramatic short-term environmental changes. The summer dry-down periods, for example, is a month-long physiological stress for every aquatic organisms. The aquatic invertebrate populations survive as a result of their ability to tolerate desiccation, migrate, or metamorphose into a terrestrial form. Many swamp invertebrates deposit the next generation as eggs in the sediment shortly before the swamps dry out and actually require a dry period for the eggs to hatch (e.g. Odonata). Gastropods, crustaceans, and bivalves, on the other hand, must dig down to the water table and estivate untill water levels increase again in the fall. The interesting aspect of these swamp invertebrates is their ability also to survive anoxic conditions when the swamps do not dry out (Sklar 1983).

The most ubiquitous backswamp invertebrates were those organisms most tolerant of both wet and dry years. Aulophorus vagus, for example, constructs a case made of duckweed and has accessory appendages to aid in the absorption of oxygen (Pennak 1978). Similarly, dipterans are successful apparently because their blood has a high oxygen absorption efficiency and they have the ability to migrate vertically. Vertical migration also accounts for the abundance of Hyalella azteca. Usually found on sediments these amphipods maintained very dense floating populations in the Des Allemands swamp. Hyalella has often been cited as the dominant macroinvertebrate of submerged vegetation and of shallow water bodies (Rosine 1955, O'Hara 1967, Krull 1970, Hansen et al. 1971). Hansen et al. (1971) tagged water hyacinth with P-32 and found Hyalella azteca to be the major consumer of the floating vegetation and the dominant prey for some 70% of the aquatic predators. In Iowa marshes studied by Voights (1976), amphipods were the most abundant invertebrates and reached peaks of 1400 individuals/m^2 . In the Des Allemands swamp of Louisiana amphipods reached densities of 10,500/m^2.

Other dominant swamp invertebrates included the isopod, Asellus obtusus and the fingernail clam, Sphaerium partumeium. Neither was usually found in the floating Lemna mats and as a result they were not considered as typical swamp organisms by Ziser (1975) who only examined the Lemna community. Bryan et al. (1976) however, found both these species in abundance throughout the swamps of the Atchafalaya Basin, Louisiana.

Benthic population densities can range from a low of 66/m^2 in the deep water abyssal plains of the Gulf of Mexico (Rowe et al. 1975) to highs of over 23,000 in shallow estuarine lakes (Sikora and Sikora 1982). With an average density of 16,198/m^2 and an average biomass of 12 g ash-free dry wt./m^2, the biomass and density of the macroinvertebrates from the Des Allemands swamp is one of the highest recorded for any soft-bottom aquatic ecosystem in the world (Table 2). Biomass levels similar to those found in Des Allemands were observed in Long Island Sound (Sanders 1956), off Sapelo Island (Smith 1973), in Galveston Bay (Gilmore and Trent 1974), and in other estuarine-influenced habitats. In general, biomass levels in freshwater systems are an order of magnitude less than what was observed in Des Allemands.

The reason for such high biomass levels is not clear. However, it is possible to ascribe this high secondary production to two unique backswamp attributes. First, as in an estuary, the regularly pulsing hydrologic regime (i.e. tides for an estuary; wet and dry seasons for a swamp) acts as an energy subsidy rather then a stress (Conner and Day 1976). The occurrence of an annual dry-down tends to moderate the stress of low oxygen conditions by oxygenating sediments. In many European fish-ponds, drying and refilling stimulates benthic growth and diversity, largely because of the decomposition of accumulated organic matter (LeCren and Lowe-McConnell 1980). The pulsing nature of swamp hydrology would also be responsible for maintaining a community away from some equilibrium "climax" situation and thus, fostering rapidly growing r-selected organisms (Margalef 1968). The second attribute of swamps is their high rate of primary production. Annual net production rates for the trees can reach 2000 g/m^2 (Sklar and Conner 1983) and the floating vegetation was estimated to contribute an additional 900 g/m^2/yr (Sklar 1983). For freshwater wetland systems the primary food base appears to be rather robust.

The seasonality of the backswamp fauna was a function of the hydrologic regime. During late summer the benthic densities were so low that the attributes of community structure clustered

Table 2. Comparative summary of soft-bottom macroinvertebrate research.

Study Site	N/sq m	Biomass/sq m	Source
MARINE			
Gulf of Mexico-Shelf	4058	1.3 gWW	Rowe et al. 1975
Slope	556	0.4 gWW	"
Abyssal plain	66	.05 gWW	"
Atlantic - Shelf	10507	4.5 gWW	"
Slope	3325	5.9 gWW	"
Abyssal plain	175	0.2 gWW	"
Baltic	3547	10.5 gAFDW	Ankar & Elmgren 1976
Baltic	50-5000	200-2.5 gWW	Andersin et al. 1977
Georgia coast	744-14213	20-7.3 gAFDW	Smith 1973
English Channel	4685	-	Eagle & Hardiman 1977
ESTUARINE			
Beaufort, N.C.-mud	107	38 gWW	Williams & Thomas 1967
Zostera bed	672	294 gWW	
Zostera bed, N.C.	-	6.5 gAFDW	Thayer et al. 1975
Spartina marsh, La.	-	15-45 gWW	Day et al. 1973
Tampa Bay, Fl.	18550	27.5 gDW	Conner & Simon 1979
Long Island Sound	16466	54.6 gDW	Sanders 1956
Galveston Bay, Tx.	3726	82.8 gWW	Gilmore & Trent 1974
Juncas marsh, Fl.	475	123 gWW	Subrahmanyan et al 1976
Hampton Roads, Va.	2571	-	Boesch 1973
Buzzards Bay, Mass.	8985	12.2 gDW	Sanders 1960
Chesapeake Bay, Va.	4460	-	Virnstein 1977
Mudflats, Malaysia	304	356 gWW	Broom 1982
Atchafalaya Bay, La.	924	-	Bryan et al. 1976
Lake Ponchartrain, La.	23485	8.5 gAFDW	Sikora & Sikora 1982
FRESH			
Lake Michigan-with veg.	3411	-	McKim 1962
without veg.	42	-	"
N.C. swamp-wet season	27871	3.2 gDW	Wharton et al. 1981
Mink Creek, Idaho	6707	10.8 gAFDW	Minshall 1981
Cibolo Creek, Tx.	5199	-	Davis 1982
Eutrophic lakes, Iowa	3819	1.3 gDW	Tebo 1955
Bernaldo Bayou, Tx.	673	0.3 gDW	McCullough et al. 1982
Lemna mats, N.Y.			
per 100 gWW of plant	152	2.1 gWW	Krull 1970
Reservoir, Okl.	879	0.2 gAFDW	Wilham & Dorris 1972
Arkansas-stream	15726	-	Warren et al. 1964
Stream with dry-down	5748	-	"
Hydrilla beds, Fl.	1717	-	Scott & Osborne 1981
Cypress swamp, La.			
per 100 gWW Veg.	1821	-	Ziser 1978
Hyacinth mats, Fl.	16484	-	O'Hara 1968
Atchafalaya Basin, La.	2885	-	Beck 1977
Des Allemands, La.			
Control site	16198	12.6 gAFDW	This Study
per 100 gDW Veg.	11363	4.5 gAFDW	"

separately from those found the rest of the year (Fig. 6). The changes in abundance (Fig. 5) and diversity (Fig. 7) were generally bimodal and controlled by seasonal changes in hydrology and temperature. Merritt and Lawson (1979) found the seasonal trends of floodplain macroinvertebrate abundance in Michigan were also bimodal and hydrologicaly influenced. The same bimodal pattern was observed by Ziser (1978). He found a low of 500 individuals/100 gWW Lemna in winter and a second low of 50/100 gWW Lemna in late summer. Ziser's swamp site however, did not dry out. As a result, the summer depletion occured as a result of the development of strongly reducing conditions rather than the stress from a dry-down event.

Louisiana swamps do not always freeze during the winter season thus, backswamp invertebrate communities do not always have a bimodal seasonality. During the winter of '77-'78 the density of invertebrates actually increased to a high of over 50,000/m^2 (Fig. 3). High density or biomass of invertebrates during winter in the floodplains of the southeast U.S. may not be very unusual. A thick mat of floating vegetation or a high water level or both can insulate benthic organsims from short cold spells. Wharton et al. (1977) found large numbers of aquatic insects, isopods, and clams during the winter in a North Carolina Swamp.

The temporal distribution of swamp invertebrates appears also to be related to the seasonality of organic inputs. Spring peaks and fall peaks of backswamp invertebrate populations coincide with high rates of photosynthesis and litterfall, respectively. There was, in particular, a strong relationship between the accumulation of floating vegetation and the adundance of invertebrates. The total density, biomass, and diversity of invertebrates living in the Des Allemands swamp were significantly correlated ($P<.01$) with floating vegetation and had coefficients of determination of .79, .60, and .67, respectively. The close association between floating vegetation and invertebrates (Fig. 8) illustrates the importance of the floating vegetation as a habitat, refuge, and possible food source for backswamp fauna.

It is difficult to say which taxa are endemic to cypress-tupelo wetlands. Of the ten taxa listed as endemic to the Atchafalaya swamp by Bryan et al. (1976) only two, the caterpillar, Neocataclysta, and the alder fly, Chauliodes were observed in Des Allemands. The Atchafalaya swamp was dominated by the bivalve, Sphaerium; the fly, Chaoborus, and tubificid worms. By contrast, Des Allemands was dominated by the amphipod, Hyalella, chironomid flies, and naidid worms. Georgia floodplain pools are often dominanted by stoneflies (Parsons and Wharton, 1978) however, none were observed in Des Allemands. The reason for these differences brings us back to the topic of floating vegetation.

When the taxonomic composition in Des Allemands is compared with that from other habitats with floating vegetation, few differences can be found. Scotland (1940) was the first person to examine the animals of the Lemna association. Most of the species that she identified for a duckweed covered lake in Ithaca were the same as those from Des Allemands. In a more quantitative study, Krull(1970) identified nine major invertebrates of the Lemna association, six of which were found in Des Allemands in large numbers. As an aside, he also found that the biomass of invertebrates associated with Lemna was greater than any other aquatic plant, thereby making it the most nutritional substance for waterfowl. Of the 85 species of invertebrates collected by Ziser (1978) in a Lemna dominated floodplain lake, 37 were the same as in Des Allemands. Similarily, O'Hara (1967) identified 55 species associated with water hyacinth (Eichhornia crassipes) in Lake Okeechobee, of which 50% were the same as that in Des Allemands. The similarity between Des Allemands and lake systems, along with the lack of similarity between Des Allemands and the Atchafalaya system suggests that when river influences are eliminated, a river swamp becomes more like a "pond" system. Successional pattern in backswamp invertebrates is apparently dependent upon the degree of water fluctuation and throughputs.

The Des Allemands swamp supports an abundant invertebrate population and if indeed, they are an important link in the food chain (Hansen et al. 1971, Whitlatch 1981), then it would follow that they contribute significantly to the carbon and nutrient dynamics of the entire system. The functional significance of backswamp invertebrates however, is not known. Experimental work on this subject has been lacking. My own work in an impounded swamp has lead to the development of a dynamic simulation model for carbon (Sklar et al. 1982). The model indicated that of the 1269 g/m2/yr entering the swamp as primary organic matter (i.e. leaf litter and Lemna) only 187 g/m2/yr is exported. Are the invertebrate populations significant processors of this organic matter? No one knows.

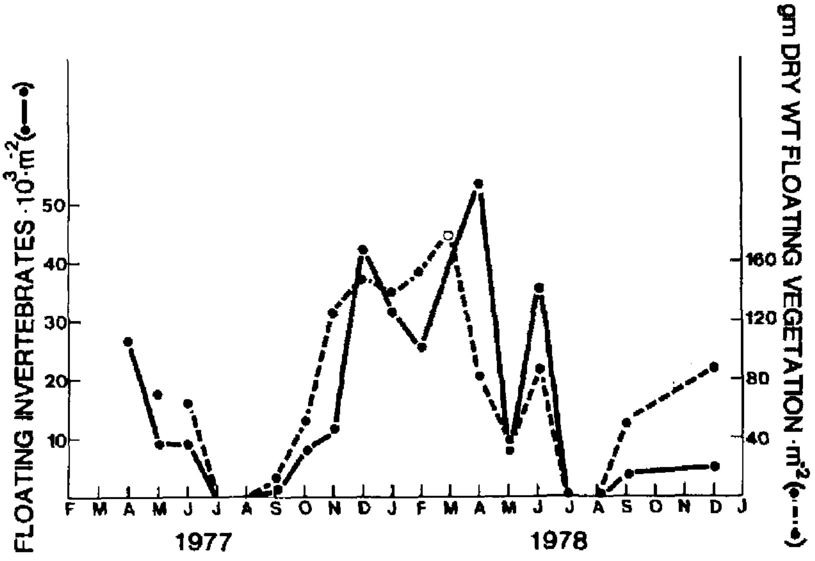

Figure 8. Mean monthly invertebrate density tracks the seasonal changes in dry weight of the floating vegetation over the course of two years.

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