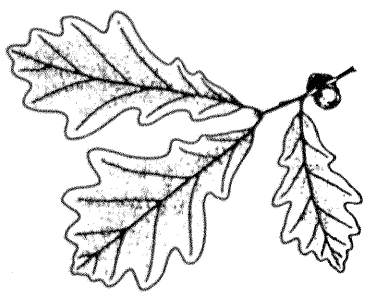
WETLAND INVERTEBRATE DISTRIBUTION IN BOTTOMLAND HARDWOODS AS INFLUENCED BY FOREST TYPE AND FLOODING REGIME[1]

Donald L. Batema, Gray S. Henderson and Leigh H. Fredrickson[2]



ABSTRACT.--Wetland invertebrates in bottomland hardwoods were studied to examine the linkage among forest type, flooding regime and invertebrate populations. Sixteen plots were established, representing two forest types (1) pin oak-sweetgum (Quercus palustris Muenchh.-Liquidamber styraciflua L.) and (2) overcup oak-red maple (Q. lyrata Walt.-Acer rubrum L.) and two flooding regimes (1) natural flooding and (2) greentree reservoirs (impounded bottomland forests managed for waterfowl). Invertebrates responded rapidly to flooding and within four weeks peak numbers occurred on pin oak sites (6275 individuals/m^2). Chironomid larvae, isopods (Ascellus sp), fingernail clams (Pisidium sp), amphipods (Crangonyx sp) and oligochaetes were the dominant taxa identified. For both flooding regimes, pin oak sites had greater invertebrate densities in fall (Oct-Nov) than overcup oak sites, but in spring (Mar-May), overcup oak sites had greater densities. Functional feeding groups of invertebrates were dominated by shredders and collectors.

INTRODUCTION

Study of wetland invertebrates in bottomland hardwood forests has been neglected, neither being in the discipline of aquatic nor terrestrial biology. The dynamics of invertebrate populations in forested wetlands are related to a fluctuating water regime (Wharton et. al. 1976, Parsons and Wharton 1978, Moore 1970). Invertebrate populations in these dynamic environments respond quickly to water and nutrient inputs (Parsons and Wharton 1978). Winter floods contribute nutrients and energy to the floodplain primarily in the form of leaves, and in turn, these inputs support rapid increases in the abundance of invertebrates.

Bottomland hardwoods in the Mississippi Alluvial Valley have a definite pattern of vegetation distribution as a result of the interaction of subtle changes in topography and the varying frequency, duration and depth of flooding (Bedinger 1978, Fredrickson 1978). In the northern portion of the valley, forest types change from the lowest sites dominated by bald cypress (Taxodium distichum (L.) Rich.) and water tupelo (Nyssa aquatica L.), to the highest sites characterized by a mixed oak-hickory forest (Fredrickson 1978). The annual and long term fluctuations in precipitation and flooding which determine vegetation patterns also influence animal adaptive strategies within certain forest types (Fredrickson 1978, Wharton et. al. 1981, White 1985). However, the influence of forest type on invertebrate distribution and abundance is still not well understood.

Throughout the Mississippi Alluvial Valley, bottomland areas have been impounded to provide nurseries for crayfish (Sklar and Conner 1981) or reservoirs for migrant and wintering waterfowl (Rudolph and Hunter 1964). Creation of crayfish farms and greentree reservoirs alters the natural flooding of bottomland forests. Instead of a dynamic water regime, these managed impoundments are flooded and drained at set times and specific water levels maintained. The effect of impounded

[1]A paper presented at the Fifth Central Hardwood Conference held at the University of Illinois, Urbana Illinois on April 15-17, 1985.

[2]Donald L. Batema, Graduate Research Assistant; Gray S. Henderson, Professor and Leigh H. Fredrickson Professor; School of Forestry, Fisheries and Wildlife; University of Missouri, Columbia, Missouri 65211

water on invertebrate communities in crayfish farms results in lower species diversity and biomass (Sklar and Conner 1981). Significant quantities of invertebrates are present in a greentree reservoir in southern Illinois to provide an adequate food resource for migrating waterfowl (Hubert and Krull 1973). In contrast, invertebrate production on one managed and two naturally flooded sites in Missouri was relatively low (White 1985). It is unclear to what extent invertebrate community structure changes with alteration of natural flooding regimes.

To better understand the response of invertebrates to a dynamic hydroperiod, a wetland invertebrate study was conducted during the 1983-1984 dormant season in a bottomland hardwood forest within the Mingo basin in southeast Missouri. The objective was to document the influence of forest type and flooding regime on wetland invertebrate community structure in bottomland hardwood ecosystems.

MATERIALS AND METHODS

Study Area And Experimental Design

The study area was located on the Mingo National Wildlife Refuge and the adjacent Duck Creek Wildlife Management Area in Stoddard, Bollinger and Wayne counties in southeast Missouri. The area is a relict valley of the Mississippi river and represents the largest remaining tract (22,000 hectares) of bottomland hardwood forest in Missouri (Korte and Fredrickson 1977). The climate is characterized as continental, humid, warm temperate (Krusekopf 1966). The average annual rainfall is 111.8 cm (U.S. Weather Bureau 1940-1969). Soils are of the Calhoun series, Typic Glossaqualfs, fine-silty, mixed, thermic.

Two tree zones within a continuum of bottomland forest types were selected for study: (1) a low zone, flooded throughout the dormant season, is dominated by overcup oak (Quercus lyrata Walt.), red maple (Acer rubrum L.), cottonwood (Populus spp.), elm (Ulmus spp.) and ash (Fraxinus spp.), and is referred to as the overcup oak-red maple forest type (OCRM); (2) a zone with a slightly higher elevation, shorter flooding duration and lower water depths is characterized by pin oak (Q. palustris Muenchh.), sweetgum (Liquidamber styraciflua L.), willow oak (Q. phellos), elm, and ash, and is referred to as a pin oak-sweetgum site (POSG). These forest types are classified as Palustrine, forested wetland, broad-leaved deciduous, seasonally flooded wetlands (Cowardin et. al. 1979).

In addition to selecting two forest types, two different flooding regimes were compared: (1) natural flooding (Mingo National Wildlife Refuge) and (2) managed greentree reservoirs (Duck Creek Wildlife Management Area). Greentree reservoir flooding differs from natural flooding in the timing, depth and duration of flooding. An impoundment provided water for the greentree reservoir (Pool 3) at Duck Creek around mid-October and constant water levels were maintained until the pool was drained in January. Within each forest type and flooding regime, four replicated plots were established, for a total of sixteen study plots. Each plot was approximately 0.25 hectares.

Field And Laboratory Methods

Invertebrate samples were collected using 18x18 x10 cm boxes constructed from 0.65 cm hardware cloth. A sample of the O1 litter layer was placed into each box. Prior to flooding, twelve hundred invertebrate boxes were placed on the sixteen plots. Seventy-five boxes per plot were arranged in a 5 row by 5 column grid with three boxes per grid point. Each grid point was marked with a surveyors flag. A randomly selected sample of five boxes per plot was retrieved monthly from the onset of flooding to complete drydown (October to May). Boxes were lifted from the water in a three sided (23x23x20 cm) hardware cloth box lined with 0.4 mm bugnet to retain invertebrates. At the time of collection, water temperature and water depth were recorded.

Invertebrates were sorted from the leaf litter using a sequence of washing, sieving and floatation. Each sample was placed on a 0.65 cm sieve and litter not passing through the sieve was washed and sorted for invertebrates. The portion passing through was collected and water poured through a 0.5 mm sieve to retain invertebrates. This procedure was repeated until the detritus was free of sediment. Invertebrates that did not float during washing were picked from the remaining detritus. Organisms retained by the 0.5 mm sieve and those hand picked were stored in 70 percent ethanol.

Invertebrates were identified to family or genus and counted. Taxonomic identification followed Borror et. al.(1981), Edmundson (1959), Merritt and Cummins (1978) and Pennak (1978), with the following exceptions: isopods (Williams 1972), amphipods (Holsinger 1976) and fingernail clams (Burch 1975). Data analyses were conducted using a SAS package (SAS Institute, Inc., North Carolina).

RESULTS

Water levels on POSG sites in both the greentree reservoir and naturally flooded areas are consistently lower than on OCRM sites (fig. 1). Water entered the greentree area in mid-October by gravity flow from an impoundment and water levels were maintained between 20 and 40 cm except for a flooding event in December. This flooding event also inundated the naturally flooded sites (fig. 1). Water levels declined on the greentree sites after the December maximum, due mainly to drainage of the pool to water control levels. On naturally flooded sites, inundation persisted after the period when greentree sites were drained. Maximum water depth was reached on the naturally flooded area in March, probably in association with high rainfall (fig. 1).

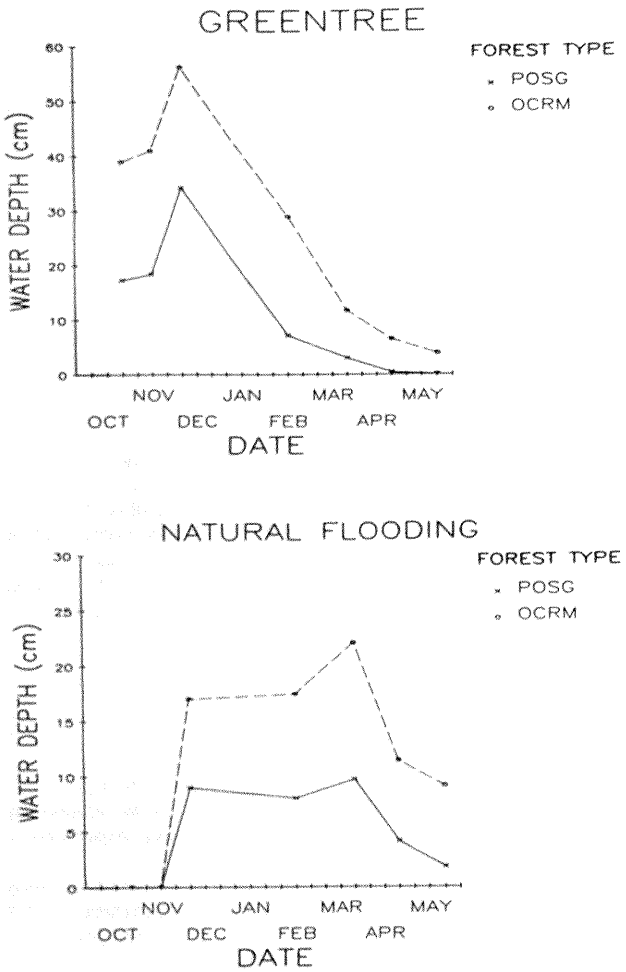


FIGURE 1.--Water depths on greentree reservoir and naturally flooded bottomland hardwood sites, 1983-1984.

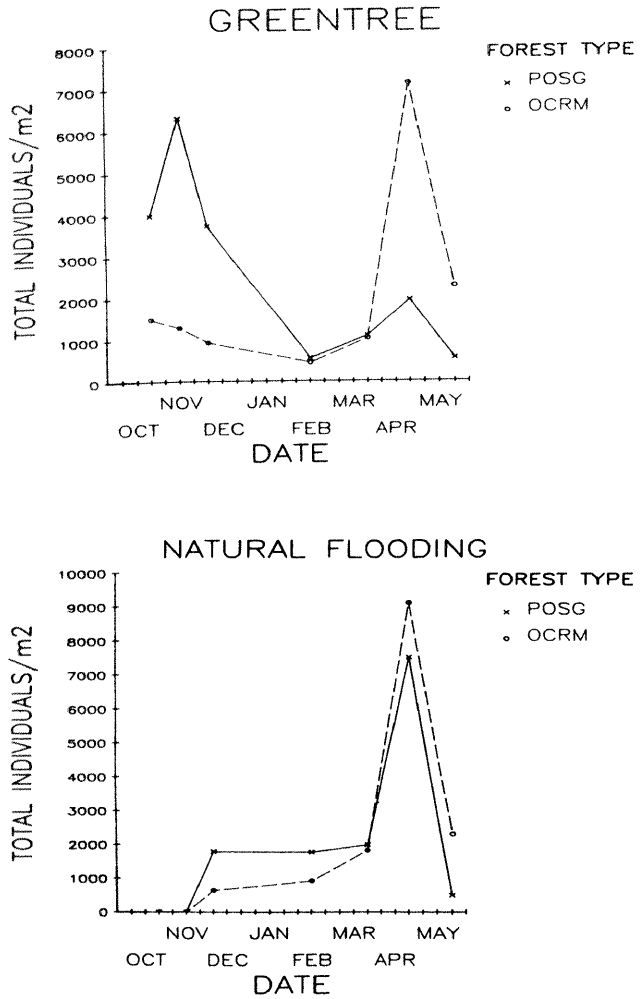


FIGURE 2.--Total densities of wetland invertebrates on greentree reservoir and naturally flooded bottomland hardwood sites.

Wetland invertebrates were present on all plots within two weeks after inundation (fig. 2). Not only did invertebrate populations respond quickly to flooding, but high densities were recorded. Within four weeks of flooding, POSG sites in the greentree reservoir had peak numbers of invertebrates (6400 individuals/m^2) that were dominated by chironomids and isopods (fig. 2). A second peak, in April, is the result of a hatch of isopods, and to a lesser extent, chironomid larvae. Mean invertebrate densities on POSG sites were as much as four times those of OCRM sites during fall and winter. In spring, however, this relationship was reversed and OCRM sites had up to four times the invertebrate density than did POSG sites (fig. 2).

On naturally flooded sites invertebrate densities reach a maximum at the same time in April for both forest types (fig. 2). As in the greentree reservoir POSG sites had greater invertebrate densities in fall and winter, whereas OCRM sites had greater invertebrate densities in spring. Further, maximum invertebrate densities in naturally flooded areas were greater than corresponding densities in the managed area (OCRM sites: 9000 individuals/m^2 and 7000 individuals/m^2, respectively). Possibly the higher water levels on OCRM sites and naturally flooded areas influence these density responses (fig. 1). April water depths on the greentree area ranged from about 1 to 7 cm, whereas naturally flooded sites ranged from 4 to 12 cm.

The assemblage of invertebrates in these bottomland forests were characterized by relatively few taxa. These taxa were: chironomid larvae, isopods (Ascellus sp.), amphipods (Crangonyx sp.), fingernail clams (Pisidium sp.) and oligochaete worms. Between 84 and 97 percent of all organisms on a plot were represented by a combination of these five taxa (table 1). The mean densities of the dominant invertebrate taxa were similar among flooding regime in winter, but in spring invertebrate densities were greater in the naturally flooded forest than in the greentree reservoir (table 1).

The relative composition of bottomland hardwood invertebrates differed between forest type and flooding regime (table 2). POSG sites tend to have

large numbers of chironomids, lesser numbers of isopods and oligochaetes and relatively few fingernail clams and amphipods. On OCRM sites the amphipods and fingernail clams were more prominant, and isopods and chironomids had similar densities (table 2). Each taxa tends to have greater densities on naturally flooded POSG and OCRM sites than on corresponding sites on the greentree reservoir.

TABLE 1.--Dominant taxa as percent of all organisms found per treatment (combination of forest type and flooding regime) and, in parentheses, the total densities as individuals/m^2.

FOREST TYPE	FLOODING REGIME	FALL	WINTER	SPRING
POSG	GT	93.1(5045)	96.7(2100)	89.7(1002)
OCRM	GT	84.2(1304)	95.6(582)	96.1(3332)
POSG	NF	-[1]	94.0(1678)	90.8(3175)
OCRM	NF	-	89.1(706)	97.6(7502)

[1]all plots dry

TABLE 2.--Mean densities (individuals/m^2) of the five dominant taxa from the different forest types and flooding regimes through the seasons.

TAXA	FOREST TYPE	FLOODING REGIME	FALL	WINTER	SPRING
CHIRONOMID	POSG	GT	3815	1433	110
	OCRM	GT	448	180	375
	POSG	NF	-[a]	1028	665
	OCRM	NF	-	183	1134
ISOPOD	POSG	GT	860	556	781
	OCRM	GT	386	280	2429
	POSG	NF	-	550	2282
	OCRM	NF	-	413	2701
AMPHIPOD	POSG	GT	62	8	4
	OCRM	GT	234	58	99
	POSG	NF	-	40	99
	OCRM	NF	-	65	372
FINGERNAIL CLAM	POSG	GT	22	3	13
	OCRM	GT	208	97	341
	POSG	NF	-	4	16
	OCRM	NF	-	3	50
OLIGOCHAETES	POSG	GT	286	90	94
	OCRM	GT	28	39	88
	POSG	NF	-	56	113
	OCRM	NF	-	42	70

[a]all plots dry

A detrital based invertebrate community is represented in a simplified view of the trophic relationships of bottomland hardwood invertebrates (fig. 3). In this scheme, shredders are the first to act on leaf material (coarse particulate organic matter or CPOM), breaking it into smaller pieces. The fragments and feces produced (fine particulate organic matter or FPOM) are gathered or filtered by collectors. Grazers are organisms that scrape algae, fungi and bacteria from the surface of the litter. Predators find the majority of their prey from the shredder and collector groups.

The relative proportion of organisms in different trophic groups shows that in each season and for both forest type and flooding regime, the shredders and collectors were dominant trophic groups in flooded bottomland hardwoods (fig. 4). Isopods and amphipods were the main shredders, but other shredders include lepidopteran larvae (fall), dryopid beetle larvae (fall) and crane fly larvae (spring). Collectors were dominated by chironomids, oligochaetes and fingernail clams, but crayfish and moth fly larvae were also important. Naturally flooded sites had a more equal distribution of functional feeding groups in winter than did greentree reservoir sites (fig. 4).

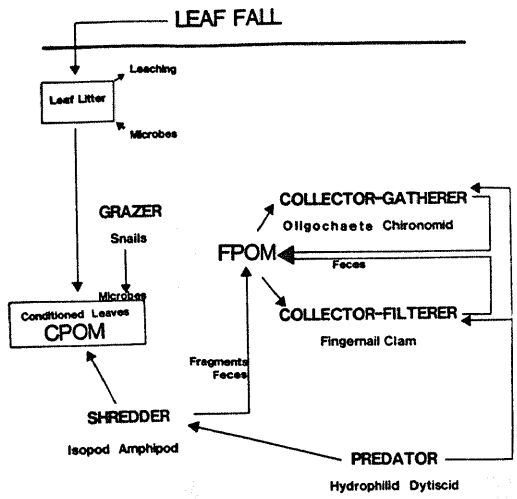


FIGURE 3.--A simplified representation of the trophic structure in bottomland hardwood ecosystems.

Grazers were more prominent on OCRM sites than on POSG sites, primarily because of greater densities of gastropods, such as planorbid and physid snails, on OCRM sites. Except in winter, the predator component on all sites within a season are similar (fig. 4). Dytiscid and hydrophilid beetle larvae were important predators on all sites in spring. Other common predators include; water mites and dipteran larvae (marsh fly, horse fly, phantom midge and biting midge). Because invertebrate communities in bottomlands are dominated by detritivores (shredders and collectors), grazers and predators are not numerically major components. However, these organisms can play important roles at least on a seasonal or site basis (fig. 4).

Terrestrial and semi-aquatic invertebrates were more prominent on POSG sites than on OCRM sites (fig. 4). POSG sites had lower water levels and shorter flood duration than OCRM sites (fig. 1), and probably this can account for a larger terrestrial component on POSG sites. Spiders, collembollans and rove beetles were invertebrates in this group with rather high mobility. These organisms were capable of colonizing litter surfaces after flood waters receded or escaped their advance. Other common invertebrates less tolerant of and often caught by flooding events include: ants, lepidopterans, centipedes and millipedes.

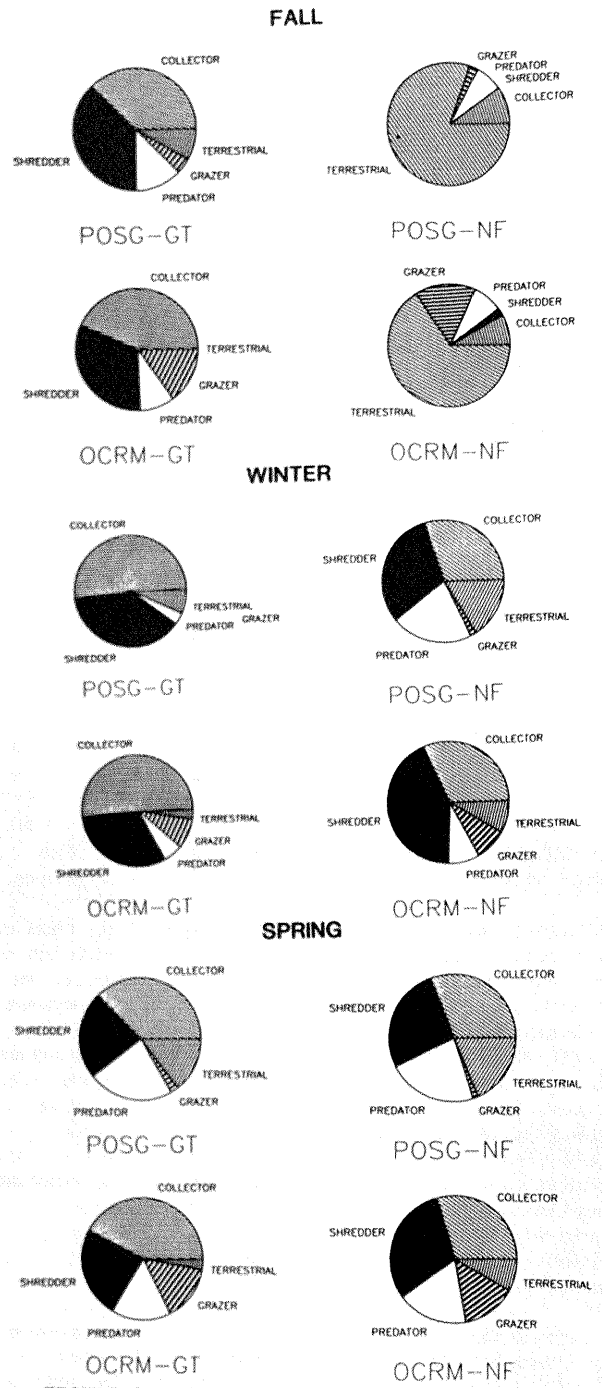


FIGURE 4.--Relative proportion of invertebrate functional feeding groups (GT= Greentree reservoir, NF= Natural flooding. No water on NF plots in fall).

DISCUSSION

Invertebrates responded within two weeks to flooding in bottomland hardwood forests (fig. 2). The rapid appearance of invertebrates has been noted in other wetland invertebrate studies in naturally flooded forests (Parsons and Wharton 1978, White 1985, Zizer 1978). Fingernail clams and snails were collected within five days after flooding in a greentree reservoir in southern Illinois (Hubert and Krull 1973), and after three weeks fingernail clams, isopods, amphipods and snails were abundant. The greatest number of individuals occurred at six weeks post flooding (Hubert and Krull 1973). POSG sites in the greentree reservoir in this study had peak numbers of invertebrates four weeks after flooding (fig. 2).

Invertebrate populations in bottomland hardwoods are 'pulsed' as a result of water and nutrient inputs (Parsons and Wharton 1978). A pulse or peak in the invertebrate population on POSG sites coincides with flooding in the greentree reservoir (fig. 2). A second peak occurs in the greentree and naturally flooded areas in spring (fig. 2). These peaks are probably related to water and nutrient inputs because other studies on Missouri bottomlands have demonstrated similar peaks in water column nutrients, zooplankton and larval fishes (Wylie 1985, Stewart 1983).

Peaks in invertebrate numbers come at a time when invertebrates can be exploited by higher trophic groups. Waterfowl are a major vertebrate group that ultilize invertebrates as a food source (Krapu 1974, Swanson et. al. 1974). Invertebrates are important protein sources for ducks during periods such as egg laying, early duckling development and molting (Drobney and Fredrickson 1979, Krapu 1974). Therefore, invertebrates are actively sought to satisfy dietary needs. Female wood ducks (Aix sponsa) in bottomland hardwoods switched to an invertebrate diet during the egg laying period in spring (Drobney and Fredrickson 1979). Wood ducks are well adapted to feed at the waters edge with a pecking type of foraging that is effective for aquatic as well as semi-aquatic and terrestrial invertebrates (Fredrickson and Heitmeyer 1985). Mallards (Anas platyrhychos) use bottomland forests extensively in fall and winter and ultilize invertebrates during molt and the predeparture phase (Heitmeyer 1985). In contrast to wood ducks, mallards feed more by subsurface dabbling on aquatic forms associated with the forest litter (Fredrickson and Heitmeyer 1985). Nevertheless, during major floods, when the semi-aquatic forms are available, mallards can readily exploit these resources as well.

In a review of the fauna of bottomland hardwood forests (Wharton et. al. 1981) the most common invertebrates noted were: fingernail clams, oligochaetes, snails, freshwater shrimp, isopods and amphipods. In managed greentree reservoirs the most common invertebrates include: isopods and amphipods in winter; pulmonate snails, fingernail clams and isopods in spring; and amphipods, isopods, snails and fingernail clams in fall (Hubert and Krull 1973). Invertebrate distribution found in this study resembles that of other studies of bottomland hardwood sites (tables 1, 2).

The most common invertebrate fauna on POSG and OCRM sites were those taxa associated with leaf litter that is seasonally flooded with water of

varying depth. This invertebrate community differs from that of other wetland habitats in bottomland hardwoods (emergent marshes and drainage ditches). For example, mayflies, dragonflies and corixids are rare or absent in the bottomland pools of this study. However, invertebrates associated with Mississippi River floodplain marshes are dominated by aquatic insects and snails (Reid 1985). Likewise, fauna in the drainage ditches associated with bottomland forests had much greater insect diversity than in the floodplain pools (Hubert and Krull 1973). These types of communities differ from the detrital based communities found in the forested bottomland areas.

Wetland invertebrates found in the seasonally flooded bottomland sites are unique in another sense as well. They are adapted to the dynamic nature of the hydroperiod. The temporary presence of water along with the fluctuating water regime requires that the invertebrates possess the following characteristics: (1) the ability to withstand dry periods (2) rapid development times (3) the ability to produce numerous offspring (4) have univoltine life cycles and (5) high mobility (Wiggins et. al. 1980).

Invertebrates common to Missouri bottomland hardwoods exhibit several of these traits. Fingernail clams, isopods and beetles are adaptable to dry periods. Viable fingernail clams were collected from the O2 litter layer in August, the driest month in the annual cycle. Isopods mature rapidly after flooding commences and females are already gravid by December or January (White 1985). Young hatch in the early spring and growth of immatures allows adequate development so they can aestivate upon drydown. Because of rapid development time, high fecundity and a life cycle that can be completed in one wet season, isopods represent an invertebrate adapted to seasonal water regimes that typlify bottomland hardwoods.

The use of functional feeding groups in invertebrate studies has been stressed to evaluate community structure and decomposition and energy flow in aquatic systems (Cummins 1973). Bottomland hardwood invertebrate communities of this study were dominated by shredders and collectors (figs. 3,4). Shredders, including isopods and amphipods, commonly feed on CPOM. Typically shredders have low assimilation rates (high consumption rates), which suggest their importance in the production of FPOM used by collectors (fig. 3). Collectors have a wide range of morphological-behavioral adaptations for aquiring FPOM, but generally belong to one of two groups (Anderson and Sedall 1979): (1) collector-filterers (fingernail clam, figure 3) feed on FPOM in suspension and (2) collector-gatherers (chironomid and oligochaetes, figure 3) feed on FPOM deposited on the bottom.

The five dominant invertebrate taxa (table 2) found in Missouri bottomland sites had representatives in each of these major functional feeding groups. An important role of these organisms is particle size reduction and eventual mineralization of leaf material. The grazers and and predators (figs. 3,4) are not directly involved in detrital processing but influence the process by removing senescing microbial colonies and thus enhancing microbial growth (grazers) (Fenchel and Harrison 1976), and by cropping the detritivores (predators).

CONCLUSIONS

Bottomland hardwood invertebrate communities were dominated by a few taxa: isopods, amphipods, fingernail clams, chironomids and oligochaetes. These representative invertebrates are uniquely adapted to the seasonal water regime typical of forested wetland types. Forest type influenced both invertebrate abundance and community structure. POSG sites had more individuals/m^2 during fall and winter months, but in spring OCRM sites had greater invertebrate densities. Chironomids and isopods are dominant on POSG sites, while OCRM sites are dominanted by chironomids, isopods and to a lesser extent by amphipods and fingernail clams. Bottomland hardwood invertebrate communities are characterized by detritivores. Shredders and collectors, which are numerically important, probably serve an important community function by mineralizing organic matter.

LITERATURE CITED

ANDERSON, N.H. and J.R. SEDALL. 1979. Detritus processing by macroinvertebrates in stream ecosystems. Ann. Rev. Entomol. 24:351-377.

BEDINGER, M.S. 1978. Relation between forest species and flooding. In: Wetland functions and values; the state of our understanding. P.E. Greason, J.R. Clark and J.E. Clark, eds., Amer. Water Resour. Assoc., Minneapolis, Minn.

BORROR, D.J., D.M. DELONG and C.A. TRIPLEHORN. 1981. An introduction to the study of insects. Fifth edition. Holt, Rinehart and Winston. 812 pp.

BURCH, J.B. 1975. Freshwater Sphaeriacean clams (Mollusca: Pelecypoda) of North America. Second printing. EPA Identification Manual No. 3, Cincinnati, Ohio. 95 pp.

CUMMINS, K.W. 1973. Trophic relations of aquatic insects. Ann. Rev. Entomol. 18:183-206.

COWARDIN, L.M., V. CARTER, F.C. GOLET and E.T. LAROE. 1979. Classification of wetlands and deepwater habitats of the United States. Office of Biological Services, Fish and Wildl. Service, U.S. Dept. Inter., Washington, D.C. FWS/OBS-79/81

DROBNEY, R.D. and L.H. FREDRICKSON. 1979. Food selection by wood ducks in relation to breeding status. J. Wildl. Mgmt. 43:355-363.

EDMUNDSON, W.T. (ed.) 1959. Freshwater biology. Second edition. John Wiley and Sons, Inc. New York. 1248 pp.

FENCHEL, T. and P. HARRISON. 1976. The significance of bacterial grazing and mineral cycling for the decomposition of particulate detritus. In: The role of terrestrial and aquatic organisms in decomposition processes. J.M. Anderson and A. Macfayden, eds. Blackwell Scientific.

FREDRICKSON, L.H. 1978. Lowland hardwood wetlands: current status and habitat values for wildlife. In: Wetland functions and values: the state of our understanding. P.E. Greason, J.R. Clark and J.E. Clark, eds. Amer. Water Resour. Assoc.

FREDRICKSON, L.H. and M.E. HEITMEYER. 1985. Use of southern forested wetlands by waterfowl. In: Waterfowl in winter. M.W. Weller, ed. Galveston, Texas. In press.

HEITMEYER, M.E. 1985. The relationship between wintering strategies of mallards and dynamics of lowland hardwood wetlands in the upper Mississippi Delta. Ph.D. Dissertation, University of Missouri, Columbia, Missouri, 488 pp.

HOLSINGER, J.R. 1976. The amphipod crustaceans (Gammaridae) of North America. EPA Identification Manual, Cincinnati, Ohio.

HUBERT, J.F. and J.N. KRULL. 1973. Seasonal flucuations of aquatic macroinvertebrates in Oakwood Bottoms greentree reservoir. Am. Midl. Natur. 90:177-185.

KORTE, P.A. and L.H. FREDRICKSON. 1977. Loss of Missouri's lowland hardwood ecosystem. Trans. N. Am. Wildl. Nat. Res. Conf. 42:31-41.

KRAPU, G.L. 1974. Feeding ecology of pintail hens during reproduction. Auk 91:278-290.

KRUSEKOPF, H.H. 1966. Delta soils of southeast Missouri. Univ. Missouri Agr. Expt. Stat., Columbia, Missouri. 38 pp.

MOORE, W.G. 1970. Limnological studies of temporary ponds in southeastern Louisiana. Southwest. Nat. 15:83-110.

MERRITT, R.W. and K.W. CUMMINS. 1978. An introduction to the aquatic insects of North America. Kendall/Hunt Publ. Co. 441 pp.

PARSONS, K. and C.H. WHARTON. 1978. Macroinvertebrates of pools on a Piedmont river floodplain. Ga. J. Sci. 36:25-33.

PENNACK, R.W. 1978. Fresh-water invertebrates of the United States. Second edition. John Wiley and Sons, Inc. New York. 803 pp.

REID, F.A. 1985. Wetland invertebrates in relation to hydrology and water chemistry. In: Water impoundments for wildlife: A habitat management workshop. U.S. Forest Service. Bemidji, Minnesota. In press.

RUDOLPH, R.R. and C.G. HUNTER. 1964. Greentrees and green heads. In: Waterfowl tomorrow. J.P. Linduska, ed. U.S. Dept. Interior, Bureau of Sport Fisheries, Fish and Wildl. Service.

SKLAR, F.H. and W.H. CONNER. 1981. Effects of altered hydrology on primary production and animal populations in a Louisiana swamp forest. In: Third coastal marsh and estuary management symposium. J.W. Day, Jr., D.D. Culley, Jr., R.E. Turner and A.J. Mumphrey, Jr., eds. Louisiana State University, Division of Continuing Education, Baton Rouge, Louisiana.

STEWART, E.M. 1983. Distribution and abundance of fishes in natural and modified bottomland wetlands. M.S. Thesis. University of Missouri, Columbia, Missouri. 90 pp.

SWANSON, G.A., M.I. MEYER and J.R. SERIE. 1974. Feeding ecology of breeding blue-winged teal. J. Wildl. Mgmt. 38:396-407.

WHARTON, C.H., H.T. ODUM, K. EWEL, M. DUEVER, A. LUGO, R. BOYT, J. BARTHOLOMEW, E. DEBELLEVUE, S. BROWN, M. BROWN and L. DUEVER. 1976. Forested wetlands of Florida: their management and use. Florida Dept. Admin., Tallahassee, Florida. 348 pp.

WHARTON, C.H., V.W. LAMBOUR, J. NEWSOM, P.V. WINGER, L.L. GADDY and R. MANCKE. 1981. The fauna of bottomland hardwoods in southeastern United States. In: J.R. Clark, J.E. Clark and J. Benforado, eds. Wetlands of bottomland hardwood forests. Proc. of the bottomland hardwood forest wetlands of southeastern U.S., Elsevier Scientific Publ., New York.

WHITE, D. 1985. Lowland hardwood wetland invertebrate community and production in Missouri. Arch. Hydrobiol. In press.

WIGGENS, G.B., R.J. MACKAY and I.M. SMITH. 1980. Evolutionary strategies of animals in annual temporary pools. Arch. Hydrobiol./Suppl. 58: 97-206.

WILLIAMS, W.D. 1972. Freshwater isopods (Ascellidae) of North America. EPA Identification Manual No. 7. Cincinnati, Ohio.

WYLIE, G.D. 1985. Limnology of lowland hardwood wetlands in southeast Missouri. Ph.D. Dissertation. University of Missouri, Columbia, Missouri. 146 pp.

ZIZER, S.W. 1978. Seasonal variations in water chemistry and diversity of the phytophilic macroinvertebrates of three swamp communities in southeastern Louisiana. Southwest. Nat. 23: 545-562.