Importance of Snag Habitat for Animal Production in Southeastern Streams


ABSTRACT

The Satilla River in southeastern Georgia is a low gradient coastal plain stream with large quantities of woody debris (snags) along its banks. The major objective of this study was to assess the relative importance of the snag habitat as a site of invertebrate production in comparison to benthic habitats. This was accomplished from quantitative sampling of invertebrate habitats, analysis of drifting organisms, and gut analyses of the major fish species. Invertebrate diversity, biomass, and production were considerably higher on snag surfaces than in either sandy or muddy benthic substrates. Although snags represented a relatively small habitat surface (4% of total habitat surfaces), snags supported 60% of total invertebrate biomass and 16% of the production for a stretch of river. Drift densities from night samples collected throughout the year were relatively high, and approximately 78% of drifting invertebrate biomass originated from the snags. Four of the eight major fish species obtained at least 60% of their prey biomass from snags, although all species utilized snags to some extent. Management practices involving wood removal (snagging) from rivers such as the Satilla could be devastating to the invertebrate community and consequently to the several fish species, particularly sunfishes, that depend upon them. The return of woody material to previously snagged streams may help restore their natural levels of animal productivity.

Fisheries biologists have long recognized the value of submerged woody substrates, or snags, as a source of habitat and food for fishes (e.g., Marzolf 1978), but there has been little quantitative documentation of the significance of such structures to the stream or its fishes. Indeed, it has been common practice to remove vegetative obstructions from streams of all sizes to improve navigation, reduce flooding, and enhance scenic characteristics. Marzolf (1978) summarized the wide range of potentially negative effects that clearing and snagging operations are likely to have on a stream and its inhabitants. Some investigators have begun to quantify snag habitats (Triska and Cromack 1980; Wallace and Benke 1984), and others have begun to characterize and quantify the community of aquatic invertebrates that colonize them (Nilson and Larimore 1973; Anderson et al. 1978; Cudney and Wallace 1980). Angermann and Karr (1984) recently conducted some snag manipulation experiments in a small stream to assess the effect of the fish community.

In this paper we will integrate and summarize our findings from a study of invertebrate production dynamics and trophic relations in a southeastern coastal plain blackwater river (Benke et al. 1979; Benke et al. 1984). We will show that quantitative analyses of invertebrate biomass and production, invertebrate drift, and fish feeding each provide a consistent picture of the importance of snag habitat to river systems. These findings have important implications for the management of low-gradient streams from both an ecosystem and a fisheries perspective.

Satilla River

The Satilla River is a blackwater river located on the lower coastal plain of southeastern Georgia. Our major study site was near Atkinson, Georgia, about 129 km upstream from the Satilla’s mouth near Brunswick, Georgia. The gradient at this site is only 8 cm/km; mean discharge during the study was about 87 m³/s; and current velocities generally ranged from 20 to 90 cm/s in the main channel. The river has poorly buffered waters, relatively high concentrations of dissolved organic carbon, and a low pH which fluctuates in the 4.3–6.7 range, depending on water level and degree of swamp inundation. Water temperatures average 19°C; they usually are above 26°C in summer and above 10°C in winter.

The Satilla River meanders among broad cypress-black gum swamps along much of its length. The three major invertebrate habitats of the river, as in many low-gradient streams, are (1) the shifting sandy substratum of the main channel, (2) the muddy, depositional substratum of the backwaters, and (3) the submerged wood, or snags. Some major snag removals occurred over 50 years ago and localized snagging has occurred periodically. Nonetheless, snags are still obvious all along the river banks, found primarily along outer bends. A fourth benthic habitat exists during flood stage, when the river inundates all or part of the adjacent swamp forest floor for as much as three or four months per year. However, no attempt to estimate swamp invertebrate production was made and fishes could not be collected easily during flood periods.
Invertebrate Biomass and Production

Biomass and production of all common invertebrate species were estimated from quantitative sampling of each of the three major habitats. Standing stock biomass refers to the mean biomass of animals on a single date, or an average value over some period of time (e.g., a year). Its units are usually presented as g dry wt/m². Invertebrate (secondary) production is the total amount of biomass produced over a period of time, regardless of its fate (e.g., emergence of adult insects, or consumption of invertebrates by predators), and is an important aspect of energy flow (Benke 1984). Production units are usually g dry wt m⁻² yr⁻¹.

In order to estimate invertebrate biomass and production per surface area of each habitat, replicated samples were collected every 2-4 weeks for a year. Nine benthic samples were collected on each date with a 15x15-cm Ponar grab. Six snag samples were collected on each date by cutting a short section (about 40 cm length) from submerged wood retrieved with a small boat. Invertebrates were carefully separated from benthic substrata and from wood samples. All animals were identified to at least the genus level (species level when possible), enumerated, and measured in order to obtain standing stock biomass from length-weight regressions (Benke et al. 1984). Production was estimated for each major species using the size-frequency method. Surface area of wood samples was measured after invertebrates were removed to obtain density, biomass and production per surface area of each snag. After estimating population parameters per habitat surface area, these values were converted to amounts per linear metre of river using habitat quantification data (see below).

Among the three major habitats, the snag habitat had by far the highest animal diversity, standing stock biomass, and secondary production per unit of habitat surface. At least 40 genera were commonly found on snags, often with several species per genus. There was good representation across several major taxonomic groups including midges, black flies, mayflies, stoneflies, caddisflies, beetles, hellgrammites, and dragonflies. There were only 20 or fewer genera in the sand and mud habitats, each of which contained a predominance of midges and oligochaetes.

The snag animals were on the average much larger than those in the benthic habitats and as a result, their standing stock biomass (5.8 g dry weight per m² of snag surface) was roughly 60 times greater than biomass in the sand (0.094 g/m²) and 10 times greater than in the mud (0.59 g/m²) (Fig. 1, top). Production analyses did not present as great a difference among habitats, although production per unit surface area of snags was still several times higher than in the benthic habitats (Fig. 1, top). The reason for the lesser degree of difference is that the smaller animals in the benthic habitats had faster growth rates (productivity) than the larger animals on snags.

All invertebrates were categorized according to functional feeding groups (Merritt and Cummins 1978; Cummins and Klug 1979). The major amount of snag production was contributed by filtering collectors, particularly net-spinning caddisflies (Trichoptera), black flies (Simuliiidae), and midges (Chironomidae) (Fig. 1). In the sand and mud benthic habitats, most of the production was by small gathering collectors.

The relative amounts of each of the three major habitats were estimated in two ways. The relative amounts of sandy (main channel) and muddy (backwater) habitats were estimated over a 40 km stretch of river from recent topographic maps. River width was also measured during invertebrate sampling periods. The amount of snag surface habitat was estimated during a period of low discharge by measuring diameters of all stems intersected by replicated transects along the shoreline (Benke et al. 1984). This provided an estimate of snag surface area per linear metre of river.

Quantification of habitat areas showed that snags comprised only about 4% of available habitat surfaces, whereas, sandy habitat was by far the most abundant (80%) (Fig. 1, bottom left). In spite of these large differences in habitat availability, the snag habitat contained 60% of total invertebrate biomass per linear metre of river (Fig. 1, bottom). However, with the combination of large habitat surface area and high growth rates of its small animals, the sandy habitat had the highest invertebrate production per linear metre of river. In considering the river as a whole, it can be seen that filter-feeding collectors comprise the greatest biomass of invertebrates in the rivers (from snags), and gathering collectors have the highest production (mostly from sandy habitat).

In conclusion, the snag habitat was by far the most biologically rich habitat in terms of diversity and production per unit of habitat surface area. The snag annual production of 57.4 g m⁻² yr⁻¹ is among the higher benthic secondary production values reported in the literature (e.g., Waters 1977). At another site on the Satilla, we found a comparable snag production of 72.2 g m⁻² yr⁻¹ (Benke et al. 1984). Cud-
ney and Wallace (1980) reported annual production of net-spinning caddisflies alone to be as high as 41.4 g ash free dry wt per m² of snag surface in the Savannah River. Our current work on the Ogeechee River, Georgia indicates similar levels of production on snags (Wallace and Benke 1984). Invertebrate production in the Satilla sand and mud habitats (about 14 g m⁻² yr⁻¹) is in the moderate range in comparison to other studies, but depends on a high productivity (growth rate) of low biomass. Clearly, from the viewpoint of higher trophic levels, the snags seem the best choice as a source of food.

**Invertebrate Drift**

One way to obtain an independent assessment of invertebrates in a lotic ecosystem is to study the composition of drifting animals. For some species there may be a positive relationship between drift and production (e.g., Waters and Hokenstrom 1980). However, relative numbers or biomass of species in the drift do not necessarily represent relative benthic numbers, biomass or productivity, since species have differential tendencies to drift.

Quantitative drift samples (n = 2) were collected at 2–4 week intervals with standard drift nets (net opening = 0.135 m²; mesh opening = 0.4 mm) over the same 12-month period as habitat sampling. Since the habitat location of most species was known from benthic habitat sampling, we could identify the habitat origin of most drifting animals. Approximately 25% of all drifting animals (using either numbers or biomass) could have come from more than one habitat. In these cases, animals were assigned in equal proportions to the habitats from which they originated.

Annual mean drift density for post-dusk samples (n = 36), the usual time of maximum drift, was almost 3 animals/m², although densities fluctuated greatly throughout the year. Peak drift densities were usually found in the summer for most invertebrate groups and reached a combined value of more than 15/m³ on at least one date in the summer. Such drift densities are relatively high in comparison to the literature, and are suggestive of a reasonably productive system. The biomass represented by these drifting animals averaged about .33 mg dry weight/m³.

Seventy percent of the numbers and about 78% of the biomass (Fig. 1, bottom right) of animals in the drift originated from snags. These results suggest, even more strongly than the production data (above), that snags are of immense importance as a habitat in a coastal plain river such as the Satilla. It is possible that snag animals in general tend to drift more readily than those from the benthos. However, the correspondence between the high representation of snag animals in the drift and their representation as biomass among all substrates for a stretch of river is particularly striking (Fig. 1, bottom).

**Fish Feeding**

While the production and drift analyses clearly suggest that the snag fauna are the best choice for insectivorous fish feeding, it remains to be shown more directly that this is indeed the case.

The fish community was sampled at about 2-month intervals with a boat-mounted electrofishing unit (Benke et al. 1979) over the same 12-month period as the other collections. We attempted to collect at least 15 individuals of each common species on each sampling date, but we were not always successful. Fish collections were restricted to times of intermediate discharge when water levels were not too low for effective navigation, and not too high for effective operations of our electrofishing unit.

Stomach contents were usually identified to at least the genus level, and head width or length was measured. Biomass of each prey item was estimated from known length-biomass relationships (Benke et al. 1984). We then calculated the percentage that each prey taxon contributed to the total biomass of food in each stomach. Since we knew the habitat origin of most prey, we determined the percentage of habitat contributions to total biomass in each stomach. The average of these biomass percentages was then calculated for each fish species across all dates (Wallace 1981).

Five of the eight fish species we examined in detail were centrarchids (sunfishes): warmouth (Lepomis gulosus), spotted sunfish (L. punctatus), redbreast sunfish (L. auritus), bluegill (L. macrochirus), and largemouth bass (Micropterus salmoides). The three others were pirate perch (Aphredoderus sayanus), spotted sucker (Munynxeta melanops), and pickerel. The chain pickerel (Esox niger) and redfin pickerel (E. americanus) were combined since numbers collected were relatively low.

The fish species are arranged from top to bottom in Fig. 2 according to a tendency to feed in benthic substrates (sand and mud) or on snag insects, crayfish, fishes, etc. The ‘‘other’’ category usually consisted of aquatic invertebrates which were found in more than one habitat, and they could not be assigned to a specific habitat with confidence. Furthermore, we were unable to assign crayfish to one specific habitat, so they were treated as a separate category. Thus, the percentages for snag and mud habitats, in particular, should be considered conservative.

All of the fish species except the largemouth bass and the pickerel were primarily insectivores. The bass and pickerel preferred larger prey, particularly small fishes (see below). Crayfish and snag insects also comprised a significant fraction of the bass diet.

All of the Lepomis species primarily consumed prey from the snag habitat. Snag fauna comprised at least 60% of the diet for redbreast, bluegill, and spotted sunfish. Snag fauna represented 46% of the warmouth diet which also included 34% crayfish and 6% fish. The snag fauna consumed by all Lepomis species consisted primarily of midges and caddisflies. These were two of the three most productive taxa on snags. The other productive snag taxon (black flies) was rarely consumed by any fish species.

Snag insects also made up more than 60% of the pirate perch diet, again mostly midges and caddisflies, but 29% of their diet was from the mud habitat. The spotted sucker was the only fish species that utilized all three habitats to any extent, and the only one in which mud fauna constituted the major portion of the diet.

The feeding of the insectivores, with the exception of the spotted sucker, is very consistent with the fact that the highest invertebrate biomass and production occurred on the snag habitat, and the highest percentage of drift organisms were from the snags. We have little direct evidence to indicate whether these species actually forage from the snags, or capture the organisms after they are part of the drift. However, the snag insects tend to drift in much higher numbers during the night than during the day (Benke et al.)
1979). If sunfish do feed on the drift, it is probably a crepuscular activity since they are typically visual feeders.

We should note that our fish samples are somewhat biased since we only collected fishes during intermediate water levels. During high discharge, the water spreads out into the floodplain swamps resulting in entirely new food resources for all of these fish species. However, most of the year, the river is well within its banks, and we feel our analyses are an accurate representation of food resources during these extensive periods of time.

**Summary and Management Implications**

Our production and drift analyses document the importance of the snag habitat as a site of invertebrate production for this coastal plain river. Snags provide a relatively stable habitat in comparison to the shifting sandy habitat, where many of the large snag species could not survive. The snag habitat contains a much greater concentration of invertebrate biomass and consequently has a higher production per substrate surface area (Fig. 1). Owing to the great differences in biomass concentrations among habitats, the snag animals represent the highest invertebrate biomass for a stretch of river. However, the benthic habitat, especially sandy substrates, have higher overall production due to rapid biomass turnover and large habitat surface area.

Since we estimated that animal numbers and production in the sand were higher than those on snags per linear metre of river, it might be expected that sand fauna would also be a larger component of the drift than snag fauna. We have interpreted the predominance of snag fauna in the drift as evidence that they tend to drift much more readily than benthic fauna. There are good reasons for such an interpretation: snag fauna are exposed to faster current, and falling water levels should result in emigration when surface snags become exposed to desiccation. However, there may be other reasons for the high percentage of snag organisms in the drift. It is possible that we have overestimated productivity rates of sand fauna, and thus overestimated their production. If this were the case, snag fauna would become a larger fraction of total invertebrate production than our current interpretation.

The discrepancy between production and drift may also be due to an underestimation of the relative amount of snag surfaces in the river. Wallace and Benke (1984) developed an improved technique for estimating wood in rivers and estimated that wood in the Ogeechee River, another Georgia coastal plain river, was about five times higher than we found in the Satilla. Thus, it is possible that we underestimated the relative amount of snag habitat in the Satilla. We may ultimately find that snag fauna contribute an even greater portion of biomass and total secondary production than indicated in Fig. 1.

The use of snag fauna by fishes is entirely consistent with the results discussed above. Several species, particularly the sunfishes, rely heavily on this snag fauna. The only large fishes we were unable to capture by electrofishing were

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**Figure 2.** The habitat origin or source of the major food items for the large fish species in the Satilla River. Percentages for each species are the average of biomass percentages in each stomach. Sucker = spotted sucker, perch = pirate perch, sp sunfish = spotted sunfish, bass = largemouth bass, pickerel = redfin or chain pickerel, other = unknown habitat origin, Terr = terrestrial invertebrates, N = number of fish stomachs analyzed.
catfishes (*Ictalurus natalis* and *I. punctatus*). However, we did collect 12 catfishes on a single date with gill nets and found that they consumed about 51% snag fauna and 23% crayfish, much like the warmouth.

Although most of the larger species (collected by electrofishing) consumed invertebrates from the snag habitat, several smaller species, primarily collected by seineing, did not consume snag fauna (Benke et al. 1979). Shiners (*Notropis* spp.), silversides (*Menidia* spp.), mosquitofish (*Gambusia affinis*), minnows (*Cyprinidae*), and darters (*Percidae*) tended to ingest either sand-dwelling midge larvae and pupae, or terrestrial insects from the water surface. It is primarily these fish species that are eaten by the piscivorous bass and pickerel. Thus, the sand fauna → small fish → piscivore food chain appears to represent a completely separate trophic pathway from the snag fauna → sunfish food chain.

The results of this paper have obvious implications for management of stream ecosystems. Wood has been removed from streams of all sizes for two centuries in the United States (e.g., Wallace and Benke 1984). The U.S. Army Corps of Engineers removed snags with snagboats from several Georgia rivers until the 1950s in order to improve navigation. For several years, the Soil Conservation Service removed snags as part of a range of channel-modification procedures designed to reduce flooding in agricultural areas. Even today, many state and local agencies encourage the removal of stream obstructions as a means of habitat improvement (Sedell et al. 1982). Our findings indicate that extensive snagging in low-gradient streams could be devastating to much of the fish community, especially the sunfishes, pirate perch, and perhaps the catfishes. There do not appear to be good alternative food sources for these species. If food is limiting, sunfish production could easily be reduced by 70% based on food availability alone (Fig. 2). One might envision a shift in the fish community to one dominated by suckers and the small fishes that feed on benthic fauna. Our suggestion is reasonably consistent with Angermeier and Karr (1984) who found that removal of woody debris from a small Illinois stream reduced the abundance of larger species, such as bluegill, but actually resulted in an increase of some smaller species. Our trophic analysis suggests that bass and pickerel might survive snag removal since they feed on the small fishes, but other environmental changes associated with snagging might adversely affect any of these species.

Marzolf (1978) has pointed out several other biological consequences of snagging besides loss of food organisms that might affect various species, such as removal of fish cover and shelter. Angermeier and Karr (1984) suggested that association between fish and woody debris in their small stream was related more to the advantage of camouflage than increased food availability. Woody debris can also have major indirect influences on stream animals since it can play a major role in ecosystem processes (Triska and Cromack 1980; Sedell et al. 1982; Wallace and Benke 1984). Snags tend to reduce mean stream velocity and function as partial debris dams, serving to retain organic matter which ultimately contributes to the organic energy budget of the stream community. Removal of snags can increase stream velocity, adversely affect stream channels and riparian vegetation, reduce frequency of floodplain inundation, and alter nutrient and organic matter pathways between the river and its floodplain. Clearly, the consequences of removing snags from streams could easily be greater than that implied by Fig. 1 and Fig. 2.

Biologists involved in stream management should be acutely aware of the important ecological role played by wood in stream ecosystems, especially low-gradient streams of all sizes. Although there are certain situations that may require wood removal to eliminate stream blockage, the wiser management practice is usually no "management" other than protection of the adjacent flood plain (Wallace and Benke 1984). In view of the long history of snagging in the U.S., it seems likely that many streams in this country have a small proportion of the snags they once contained. Rather than removing snags, a stream management practice of returning snag material to barren streams has the potential for enhancing the diversity, abundance, and production of invertebrates and the fishes that depend on them for food.

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