THE ROLE OF MACROINVERTEBRATES IN STREAM ECOSYSTEM FUNCTION

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ABSTRACT

This review focuses on some of the roles of macroinvertebrate functional groups, i.e. grazers, shredders, gatherers, filterers, and predators, in stream-ecosystem processes. Many stream-dwelling insects exploit the physical characteristics of streams to obtain their foods. As consumers at intermediate trophic levels, macroinvertebrates are influenced by both bottom-up and top-down forces in streams and serve as the conduits by which these effects are propagated. Macroinvertebrates can have an important influence on nutrient cycles, primary productivity, decomposition, and translocation of materials. Interactions among macroinvertebrates and their food resources vary among functional groups. Macroinvertebrates constitute an important source of food for numerous fish, and unless outside energy subsidies are greater than in-stream food resources for fish, effective fisheries management must account for fish-invertebrate linkages and macroinvertebrate linkages with resources and habitats. Macroinvertebrates also serve as valuable indicators of stream degradation. The many roles performed by stream-dwelling macroinvertebrates underscore the importance of their conservation.

INTRODUCTION

Consumers maintain and modify ecosystem function in ways that often transcend simple consumption of food (131). Chew (21) suggested that consumers

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benefit ecosystems as regulators rather than energy movers. Consumers' regulatory functions include regulation of rates of succession and nutrient cycling, transportation and mixing of materials, top-down influences (by predators and herbivores), and physical structuring of ecosystems [as "ecosystem engineers" sensu Jones et al (87)]. Macroinvertebrates are usually ignored in such discussions. Our purpose here is to underscore the important roles of macroinvertebrates in streams.

The macroinvertebrate assemblage of most streams is highly diverse, and many of the individual species may be redundant (98) in the sense that ecosystem functions can proceed if they are absent (191). Categorization of any stream macroinvertebrate as a keystone species would be difficult (119, 138), but as a group they perform essential functions and are critical to the maintenance of stream functional integrity (8). Even normally rare species may have a critical role that becomes evident only after a major disturbance (188).

Functional Groups

In the heterogeneous physical environment of streams, benthic invertebrates have evolved a diverse array of morphological and behavioral mechanisms for exploiting foods. Throughout this review, we follow the functional classification of Cummins, which is based on morpho-behavioral mechanisms used by invertebrates to acquire foods (32, 113). These groups include scrapers, animals adapted to graze or scrape materials (periphyton, or attached algae, and its associated microbiota) from mineral and organic substrates; shredders, organisms that comminute primarily large pieces of decomposing vascular plant tissue (>1 mm diameter) along with the associated microflora and fauna, feed directly on living vascular macrophytes, or gouge decomposing wood; gatherers (= collectors), animals that feed primarily on fine particulate organic matter (FPOM; <1 mm diameter) deposited in streams; filterers, animals with specialized anatomical structures (e.g. setae, mouth brushes, fans, etc) or silk and silk-like secretions that act as sieves to remove particulate matter from suspension (189, 206); and predators, organisms that feed primarily on animal tissue by either engulfing their prey or piercing prey and sucking body contents.

These functional feeding groups refer primarily to modes of feeding or to the food-acquisition system (sensu 31) and not to the type of food per se (e.g. as determined from gut-content analysis). For example, many filter-feeding insects of high-gradient streams are primarily carnivores (e.g. 13). Scrapers consume not only attached algae but also quantities of what must be characterized as epilithon (100). Likewise, although shredders may select those leaves that have been microbially conditioned by colonizing fungi and bacteria (e.g. 32), these shredders also ingest attached algal cells, protozoans, and various other components of the fauna during feeding (113). Some shredders appar-

ently obtain very little of their assimilated energy directly from microbial biomass (47), although enzymes derived from microbial endosymbionts or microbes ingested with leaf tissue may be important in cellulose hydrolysis (170). Although these mechanisms used to obtain foods seem valid criteria for separating taxa, many questions remain concerning the ultimate sources of protein, carbohydrates, fats, and assimilated energy for each of these functional groups.

Physical Template

The physical environment of streams places many constraints on organisms as well as on the type and form of food that is available. Most stream reaches are characterized by many diverse microhabitats (51), which result from physical factors, such as relief, lithology, runoff, and large woody debris, that generate an array of channel forms (15). Physical heterogeneity, including the substrate and the current velocity of a stream channel, is an important factor that may influence local biotic diversity (80, 120, 182), nutrient dynamics (117, 155), algae and macrophyte distribution (155, 156), retention and distribution of organic matter (78, 79, 96, 173, 175, 198), predator-prey interactions (61, 151), presence or absence of refugia during disturbance (96), and secondary production of invertebrates (12, 78, 172). Growns & Davis (58) demonstrated linkages between functional feeding groups and several near-bed hydraulic parameters, but such linkages are not surprising. For example, within the mosaic of habitat types in a southern Appalachian stream, secondary production by most filterers occurs in high velocity, low-retention habitats, whereas secondary production by gatherers and shredders dominate low-velocity, high-retention pools (e.g. 78). The linkages between flow parameters, resource availability, respiratory and thermal requirements, and biotic interactions such as competition and predation influence the structure and function of diverse stream ecosystems. These parameters (as well as others) presumably influence an organism's energy costs and gains as well as its ultimate success in a given habitat (59).

Despite the attractiveness of a habitat-based approach to studying stream ecosystems, many problems remain in its application for several reasons: (*a*) Many interacting factors influence biota; (*b*) an array of microhabitats may exist within and among streams; (*c*) boundaries among patches are often indiscreet and vary in space and time; and (*d*) the resolution and classification of such boundaries may vary with the research or management objectives (64).

Top-Down and Bottom-Up Influences on Stream Ecosystems

Top-down regulation by consumers can have an important influence on nutrient cycles, primary productivity, decomposition, and translocation of materials.

Despite the abundant evidence from both field and laboratory studies for either strong bottom-up or top-down influence by consumers in streams, many of the studies reviewed below (as well as many others) suffer from one or more deficiencies: (*a*) They were conducted at specific times of the year and were often of short duration. (*b*) They failed to consider indirect effects that may require several generations to detect. (*c*) Unnatural densities of primary and secondary consumers were used. (*d*) Enclosures or exclosures were used that did not allow sufficient exchange with the stream environment. (*e*) There was no replication (primarily a problem with ecosystem-level studies). (*f*) The study failed to consider or incorporate abiotic forces such as hydrologic regime (i.e. account for floods and drought). Hunter & Price (77) suggested that environmental heterogeneity may have influenced many of the classic debates on whether abiotic or biotic factors determine population change and that differences in results can be partly attributed to the relative stabilities of the various environments studied. They suggested that although top-down trophic cascades are dramatic in some instances, a bottom-up perspective seems more logical because "the removal of higher trophic levels leaves lower trophic levels present (if perhaps greatly modified), whereas the removal of primary producers leaves no system at all" (77, p. 725). Despite experimental limitations, many studies have demonstrated a significant role for stream-dwelling macroinvertebrates at intermediate levels of food webs, regardless of whether the results pointed to top-down or bottom-up effects. It is through these intermediate stages, incorporating macroinvertebrate populations, that the effects are propagated either up or down. In the following section, we focus on some of the ascribed roles of specific macroinvertebrate functional groups in stream ecosystem processes.

FUNCTIONAL ROLES OF INVERTEBRATES IN STREAMS

Grazers

Invertebrate herbivores in streams use various mechanisms to feed on plants: Some feed on aquatic vascular plants by shredding (shredder-herbivores) or piercing; others graze algal films attached to rocks or other submerged objects. In most streams, algal grazing is by far the most important. Mechanistically, these grazers are scrapers (32) because they feed by scraping the epilithon (100) from mineral and organic substrates.

The algae-grazers interaction in streams is tightly coupled; that is, algal production directly affects grazers and grazer feeding directly affects algae (158). Gregory (56) and Lamberti & Moore (94) noted that this interaction

had not been extensively studied. However, considerable research, perhaps stimulated by those reviews, has focused on this area in the past decade.

Gregory (56) noted that many studies have shown a correlation between algal and grazer abundance, which suggests food limitation. For example, following clear-cutting of stream-side vegetation, high grazer abundance is generally associated with increased light levels and high algal abundance (e.g. 65, 188). More compelling evidence for resource limitation emerges from studies showing the density dependence of grazer growth (73, 74, 95, 108). Moreover, other studies revealed that algal production is increased by the addition of nutrients, light, or both and that this increase is followed by enhanced grazer abundance, growth, and/or production (41, 63, 69, 71, 92, 120, 129, 146, 147, 160). Finally, light reduction has been shown to decrease grazer abundance (52) and nutrient reduction to decrease snail growth rates (128).

Gregory (56) reviewed studies demonstrating that grazers can greatly reduce algae abundance, showing that removal of grazers increased algae abundance. Yet other studies have revealed little or no grazer effect (43, 74, 130, 183). A grazing effect may not be seen when algae are light limited (43, 130) or when grazer abundance is low (85, 91). In recent studies, investigators have used raised platforms in natural streams (43, 85, 95, 108), enclosures and exclosures in natural streams (44, 45, 109, 110, 160), stream-side or in-stream channels (63, 71–74, 93, 129, 160), and laboratory streams (91, 92, 128, 176, 177) to examine grazer-algae interactions. The effects of insecticides (203, 207) or top-down effects induced by predator manipulation have also been studied (150, 151). Most of these authors reported that grazers reduce algal biomass.

Most studies have shown that algal primary production is lower when grazers are present than when they are absent (71, 85, 91, 95, 128, 160). However, Lamberti et al (91, 92) found evidence that grazing snails may increase primary production. Lamberti & Moore (94) suggested that at low densities grazers have no effect on algal production, at intermediate densities they may increase algal production by stimulating productivity (i.e. production per unit biomass, P/B), and at high densities grazers decrease algal production. Stimulation of primary production by grazers is controversial but has been demonstrated in some terrestrial ecosystems (e.g. 112) and been suggested for streams (40). Grazers might enhance algal productivity (P/B) by removing dead or senescent algal cells; shifting algal community composition to more productive species; decreasing the thickness of the algal film, which would allow light and nutrient penetration; and remobilizing nutrients (92, 94). Productivity may also be enhanced by mucus trails of grazing gastropods, which may provide a microenvironment rich in regenerated nutrients that stimulates growth of microalgae, as shown for marine habitats (141).

On the other hand, algal production increases caused by grazers may be

impossible to confirm because the loss of photosynthetic tissue may exceed any enhanced algal *P/B*. Grazer enhancement of algal *P/B* has often but not universally been demonstrated. Several studies (72, 91, 95) have shown that grazers may increase productivity per unit chlorophyll a (*P/*Chla), but other studies have shown decreases (71, 125, 160) or no change (85, 128). In general, grazing appears to increase the assimilation number (chlorophyll a per unit biomass) (56, 73, 85, 91).

Stream invertebrates may affect algal abundance by methods other than direct feeding. Hart (62) found that a grazing caddisfly reduced the overstory consisting of filamentous blue-green algae, and this promoted the growth of diatoms. Within deep water habitats, crayfish reduced *Cladophora* spp. and thereby indirectly aided diatoms and diatom-feeding grazing insects (26). Case-building chironomids increased the surface area for diatom growth and perhaps protected diatoms from grazing mayflies (153). In tropical streams, freshwater shrimp may enhance algal growth by clearing surficial sediment via their feeding activity (154). By reducing periphyton biomass, grazers indirectly influence localized hydraulic characteristics, zones of stationary water (transient storage), and nutrient cycling (110, 126). Several studies have also shown that grazing snails (92, 125) and insects (37) increase amounts of downstream export of FPOM from grazed surfaces, as well as the resistance of stream algae to disturbance from floods (127).

Shredders

Upland streams, especially those draining forested catchments, receive a large portion of their energy input as coarse particulate organic matter (CPOM) from terrestrial litter inputs. For example, in the eastern United States, average litter-fall inputs to streams are about 600 g (dry mass) m^{-2} $year^{-1}$, over half of which consists of leaves (200). This detrital material represents an important source of energy for many stream detritivores (6, 32), and food limitation to CPOM-consuming detritivores has been shown (36, 157).

In both laboratory studies (33, 111, 124, 145, 167) and stream manipulations (22, 29, 192), shredders increase conversion of CPOM to FPOM and dissolved organic matter (DOM) (118). CPOM-shredding insects generally have low assimilation efficiencies (55, 81, 111). Hence, a large portion of leaf litter inputs are transformed into FPOM, which is more amenable to downstream transport (e.g. 29, 34, 192).

In addition to facilitating downstream transfer of FPOM, some burrowing animals increase FPOM transfer to sediments. For example, larvae of the European sericostomatid caddisfly *Sericostoma personatum* feed on surficial CPOM at night and burrow into the stream bed during the day. Larval defecation by *S. personatum* increased subsurface sediment organic content by

75–185% over the organic content of control sediments in controls containing no sericostomatids (185). Presumably, similar increases may result from the presence of other sericostomatids such as the western North American species *Gumaga nigricula,* which also transfers case-associated algae that is subsequently lost via abrasion during burrowing (14).

WOOD FEEDING   Invertebrate shredders also promote wood decomposition by scraping, gouging, and tunneling wood (7, 38). These activities expose additional wood to further microbial colonization and decomposition (7). Also, the wood-gouging habits of net-spinning caddisflies during retreat formation over many decades may be important; these filterers were implicated in a 53–58% reduction in a cross-sectional area of untreated timber pilings and the subsequent collapse of a highway bridge (133).

SHREDDER HERBIVORES   Shredding and consumption of living macrophytes (by shredder herbivores) is another potential pathway of FPOM production in stream ecosystems. Although macrophytes are generally assumed to enter stream foodwebs as detritus during autumn senescence, invertebrate consumption of living macrophytes may also contribute detritus to the food web (101, 135, 163). Some floating-leaf macrophytes may be heavily grazed, and decomposition associated with grazing can contribute considerable amounts of organic matter to detrital foodwebs throughout the growing season (190). However, invertebrate consumption of submerged macrophytes in streams has not been well studied. Shredder herbivores such as some trichopteran larvae may rely on macrophytes for food during late spring and summer in downstream reaches where leaf inputs are reduced and CPOM standing crops are low (82). In a Danish stream, consumption of the macrophyte *Potamogeton perfoliatus* was low, ranging from 1.3 to 1.8% of annual plant production; however, consumption was higher (4–18% of macrophyte production) early in the growing season (83). Larval feeding and growth rates of the limnephilid caddisfly *Anabolia nervosa,* the dominant herbivore in this study, indicate that *Potamogeton* tissue is probably as suitable a food as any terrestrial leaf litter (84). Other than the results of these studies, little information is available on feeding ecology or the effects of aquatic invertebrates on macrophytes in streams, or on the ecosystem consequences of macrophyte feeding (135).

SHREDDER-GENERATED FPOM   Heard (66) described a "resource chain" in which consumers specialize on a resource and consequently influence the rate of transfer as the resource passes through different conditions. The processing of allochthonus inputs to streams is an example. Cummins et al (33) demonstrated that FPOM-feeding collectors exhibit faster growth rates in the presence of leaf-shredding invertebrates. Likewise, in short-term feeding studies with

[32]P-labeled leaves, two FPOM feeders accumulated significantly more radio-phosphorus when shedders were present to facilitate leaf breakdown (167). Transformation of organic matter by shredders is probably far more important than their ability to directly degrade organic material via metabolic respiration. Direct metabolic respiration by invertebrate fauna in Bear Brook, New Hampshire, was estimated at <1% of the annual flux of organic matter through the stream (49). However, when feeding activities, bioenergetic efficiencies, and secondary production of invertebrates were considered, the overall impact of shredders on conversion of CPOM to FPOM was 13–35% (e.g. 197).

Until recently, little direct evidence was available to quantify the importance of shredders (114). In southern Appalachian headwater streams, the application of an insecticide eliminated >90% of insect biomass and greatly reduced secondary production (104). This manipulation significantly reduced leaf litter breakdown and export of FPOM compared with adjacent, untreated reference streams (29, 186, 192). Restoration of the shredder functional group coincided with restoration of leaf-litter processing rates (22, 191) and FPOM export (186, 191). These studies demonstrated that macroinvertebrates accounted for 25–28% of annual leaf-litter processing (29) and 56% of FPOM export over a 3-year period (186). Thus, biological processes in small, high-gradient streams that exhibit high physical retention of CPOM inputs favor entrainment by processing CPOM to smaller, more easily transported particles (FPOM) (29, 186, 192).

The above studies were conducted in small first-order streams, and the extent to which these studies apply to larger streams, and/or other geographical areas where shredders may not be as abundant, has not been assessed. In addition to shredder activities, those of grazers, filterers, predators, and collectors contribute to the overall FPOM pool, as well as to detrital turnover (166). Wotton (204) reviewed many other mechanisms of FPOM generation, including mechanical breakage of CPOM, flocculation of DOM, direct inputs of bacteria from allochthonous sources, microbial degradation, breakdown of large woody debris, soil organic matter, and grazing and algal sloughing. The degree to which gatherers or filterers actually depend on FPOM generated from CPOM shredders vs FPOM derived from shredder-independent mechanisms remains unknown (67). Furthermore, how much shredders facilitate collectors' activities probably varies over time and space (67). Undoubtedly, physical forces associated with flow and deposition interact to form a much more dynamic suspended and deposited FPOM pool than commonly recognized.

Gatherers

Gatherers are adapted to feeding primarily on fine particles (<1 mm diameter) deposited on substrate surfaces or in depositional areas. Gatherers usually are

the most abundant stream macroinvertebrates (12, 78, 104, 121, 173), and many gatherers, such as chironomids, are among the most frequently reported prey in guts of predaceous insects (e.g. 2). Despite their obvious importance in stream food webs, their functional role is probably among the least studied.

To date, the role of gatherers in bioturbation and resuspension of organic matter has received little attention. Although surficial FPOM represents a small portion of the total FPOM standing crop in Idaho streams, it may contribute disproportionately to metabolism as it is readily available to gatherer organisms (34). Continuous deposition and resuspension of FPOM also may cause the impact of bottom-feeding gatherers on food resources to be felt downstream rather than local food depletion (34). Feeding activities of macroinvertebrates may also affect deposition. For instance, in a montane Puerto Rican stream, atyid shrimp reduce depositional organic matter as well as the abundance of smaller collectors (chironomid larvae) (154).

In Sycamore Creek, Arizona, gatherers exhibit low assimilation efficiencies (7–15%) and very high ingestion rates (food consumption equivalent to their body weight every 4–6 h) (48). As ingestion rates of collectors in Sycamore Creek exceed primary production, coprophagy is obviously an important component of gatherer feeding. Although they performed no actual measurements, Fisher & Gray (48) suggested that bactivory associated with fecal reingestion is an important component of collector diets. Using ^{13}C sodium acetate to label bacteria in a headwater spring seep in North Carolina, Hall (60) found that several FPOM-feeding gatherer taxa (chironomids and copepods) had a higher $\delta\ ^{13}$C than their FPOM food resources, which suggests preferential assimilation of bacterial carbon relative to FPOM.

MICROBE-DETRIVORE RELATIONSHIPS   Views concerning the relative roles of detritus, decomposer microbes, and detritivorous animals differ widely. Aquatic insects can be microbial predators or competitors or can depend on microbes as a link to detritus (70); however, clarification of conditions under which microbes are detrital consumers vs competitors awaits more data (115). Many stream ecosystems depend strongly on allochthonous inputs of DOM and bacteria. In low-gradient streams of the southeastern US, metazoans such as filter-feeding black flies can directly consume large numbers of bacteria, effectively short-circuiting several trophic transfers associated with the microbial loop (39, 115, 116). Fine particle–feeding meiobenthos assimilate a much larger proportion of microbial biomass (142) found on FPOM than that consumed by insects that shred larger leaves (46). The microbial "peanut butter" and detrital "cracker" usually associated with macroinvertebrate shredders (30) may be more applicable to microdetritivores (142).

In another study in Sycamore Creek, gatherers ingested (and reingested through coprophagy) an estimated 131% of the nitrogen retained during a

20-day, postflood recovery period (57). Most of the nitrogen was returned to the particulate nitrogen pool by gatherer egestion, excretion, and mortality. Gatherers recycled between 15 and 70% of the retained nitrogen back to primary producers as excreted ammonia. However, insects, even aquatic species, can excrete nitrogen in forms other than ammonia (20). The fate of organic nitrogen and other nutrients eliminated by invertebrates and the potential availability of this material to microbes and algae merits much more study.

Filter Feeders

Filter feeders, especially filter-feeding macroinvertebrates, have evolved various mechanisms for removing particles from suspension (189, 206). Although many trichopterans may be filter feeders based on their mode of capture, they are also predators, that rely primarily on animal drift (13, 53, 143, 144). Conversely, some ephemeropterans, trichopterans such as Philopotamidae, and dipterans such as Simuliidae and some Chironomidae (189) exploit minute particles (<1–50 μm in diameter), which dominate the seston in most streams. For bivalves, the range of particles consumed is generally smaller, ranging from <1 to 10 μm (181). Some filter feeders, such as the Philopotamidae, Simuliidae, and bivalves may actually increase particle sizes by ingesting minute particles and egesting compacted fecal particles larger than those originally consumed. Thus, these animals may perform two very important functions: (a) the removal of FPOM from suspension (which would otherwise pass unused through the stream segment) and (b) the supply of larger particles via their feces to a broad spectrum of deposit-feeding detritivores.

Filter feeders may retard downstream transport of suspended particulate organic matter (POM) (193). In doing so, they would significantly decrease spiraling distances of nutrients and organic matter (134, 199). Newbold et al (134) suggested that filter feeders have their greatest effect on nutrient spiraling length when particulate transport and nutrient limitation are high. Studies have indicated low rates of seston removal by filter feeders, i.e. generally well below 1% seston removal per meter of stream length (53, 67). The highest rates of seston removal were obtained in studies that incorporated fine-particle feeders such as Simuliidae. Morin et al (122) found that simuliid larvae ingested 0.8–1.4% of the seston per meter of stream below a Quebec lake outlet. This study took place during a late spring period when flows were low and standing stock of black flies was high, whereas other studies, performed on an annual basis, indicated lower rates of seston removal.

Larger particle–feeding hydropsychids (Trichoptera) select higher-quality food items such as diatoms and animal drift (13, 143, 144). This selectivity, and generally low rates of seston removal by hydropsychids, suggests that their major impact is on the quantity and type of POM in suspension (13, 53, 144).

Experimental studies such as that of Georgian & Thorp (53) are especially relevant to ecologists studying invertebrate drift in streams. They estimated that two *Hydropsyche* species in riffles of a New York stream removed 18% of drifting invertebrate prey per meter. Their results suggest that when large net-spinning caddisfly populations are present in shallow streams, their predation may suppress stream drift (53).

Streams with limited stable substrate, sufficient current velocity, and high-quality organic seston concentrations often support massive standing stocks of filter-feeding hydropsychids and/or black flies (50, 139, 184, 205). Filterer densities that are higher than those of other functional groups are possible because filterers use the kinetic energy of the current to exploit foods produced in upstream habitats (28). As a consequence, filterers expend less energy in search of food; consequently, the stream segment in which they occur can support a higher biomass per unit area (28). In addition, some of highest secondary production values reported per unit habitat space are those of filtering invertebrates in streams. The high filterer biomass or production found below impoundments or lake outflows is especially noteworthy (50, 105, 139, 159, 184), as is that on woody debris in low-gradient streams with unstable sandy bottoms (12, 28, 171). Thus, in habitats with a high degree of particle transport, filterers exploit the physical environment and increase particle retention. In contrast, as noted above, highest shredder densities are often found in CPOM-retentive reaches, where they exploit retained food resources, increase conversion of CPOM to more easily transported FPOM, and decrease particle retention.

In addition to their influence on suspended organic matter, filterers may modify local benthic community structure. For example, hydropsychid predation may have an important influence on community structure occurring near their retreats in lake outlets (42) and natural streams (35, 68). In a sandy-bottomed Australian stream, hydropsychid larvae appear to facilitate colonization by grazing *Baetis* spp. mayflies by increasing retention and abundance of food resources of *Baetis* species (algae and detritus) on the silken hydropsychid retreats (137).

Predators

As in other types of ecosystems, predators in streams have top-down effects on their prey through direct consumption and reduction of prey populations. During the past 15 years, numerous studies have examined various aspects of predator-prey interactions in streams. Many of these studies have been previously reviewed (3, 25, 169, 201, 205). For the purpose of this review, we focus on the impact of predation on benthic communities and specific processes.

Earlier reviews by Allan (2) and Thorp (180) suggested a lack of strong evidence that predators significantly influence lotic community structure. More recent studies have yielded mixed results regarding the impact of predators on prey populations: Many studies show significant effects of predators on prey, whereas others have shown little or no impact of predation on prey populations (25, 169). Results of a meta-analysis of 20 studies showed that, on average, predators deplete prey density by ~0.4 standard deviations from prey densities found in predator-free areas, which is a small-to-moderate, but significant, impact (204).

Cooper et al (25) suggested that the magnitude of prey exchange (i.e. immigration and emigration) among substrate patches has an overwhelming influence on the perceived effects of predators on prey populations in enclosure and exclosure studies conducted in streams. They suggest that this exchange may be a reason that lentic studies, or studies in isolated stream pools, show a greater proportion of significant predator impacts than stream studies. Sih & Wooster (169) extended the analysis by addressing predator impacts in patches surrounded by background environments lacking predators and having a constant or decreasing prey density. They then examined situations in which the per capita emigration rates of prey are altered by the presence of predators. Outcomes were also influenced by the presence or absence of predators and the degree of prey recruitment in the background environment, as well as by the ability of prey species to hide in refuges (169). Sih et al (168) found that approximately 25% of all prey populations showed negative predator impacts in studies involving experimental manipulations of predators. Invertebrate predators appear to have a greater impact on benthic prey than do fish predators, apparently because of different behavioral responses of prey (see references in 169). Vertebrate predators such as fish often cause invertebrate prey to reduce their movement rate and seek refuge in the substrate, whereas invertebrate predators increase prey movement and their propensity to drift (see references in 169, 204). Studies that examine the impact of both vertebrate and invertebrate predators simultaneously are difficult and require detailed knowledge of behavioral interactions between predators as well as between predators and prey. For example, stonefly and fish predation either interfered with or facilitated the other predator depending upon whether *Baetis* or *Ephemerella* species were the prey (174).

NONLETHAL EFFECTS OF INVERTEBRATE PREDATORS   Predators may also influence growth and reproduction of prey populations. For example, in the absence of predatory crayfish, snails (*Physella* spp.) reproduced earlier and grew to a terminal body size less than half of that of snails found in the presence of crayfish (27). By shunting more assimilated energy into rapid growth and delaying the onset of reproduction, snails achieve a larger terminal body size

and thereby decrease mortality resulting from size-specific predation, which is much greater for smaller than larger snails (27). Peckarsky et al (140) found that *Baetis* mayflies raised in the presence of stonefly predators matured at significantly smaller sizes, showed little or no growth, and had lower egg biomass per female than *Baetis bicaudatus* reared in the absence of plecopteran predators. Scrimgeour & Culp (165) reared *Baetis tricaudatus* in the laboratory under safe (no predation threat) and risky (model predator present) conditions. *B. tricaudatus* reared in safe environments matured earlier, reached a larger terminal size, and exhibited both greater fecundity and larger egg size than those reared under predation threat at each food level. Although these results suggest that predators can influence prey fitness under laboratory conditions, such effects under field conditions have not been demonstrated (165).

Evidence from one study shows that predaceous plecopterans and caddisflies can significantly decrease the rate of leaf-litter processing by reducing shredder populations in leaf packs (136). However, predator densities in this experiment were almost 10 times that of background. Malmqvist (106) used more realistic densities of predators and tested the effects of a predatory stonefly, *Diura nanseni*, confined in cages with and without predators on decomposition of leaf litter. He found that less leaf material was processed in cages with predators, even though no reduction in prey densities could be demonstrated. Furthermore, in laboratory feeding experiments, two of three shredder species produced less FPOM when exposed to predators (106).

MACROINVERTEBRATE-FISH INTERACTIONS   Hynes (80) stated that invertebrates are the most widespread and important food of running-water fish and that very few groups of fish do not feed on invertebrates. However, actually demonstrating and quantifying the importance of this energy flow is difficult. Perhaps the best evidence for the importance of macroinvertebrates to fish comes from studies showing higher fish production in response to nutrient or carbon addition. Richardson (158) reviewed several studies suggesting that moderate nutrient or organic enrichment enhances fish production. In a classic study, Warren et al (194) added sucrose to an Oregon stream and observed increased growth, biomass, and production of the bacterium *Sphaerotilus natans*, aquatic invertebrates, and trout. Peterson et al (146) found a strong bottom-up effect resulting from phosphorus fertilization of a tundra river. Stable isotope analyses allowed the enrichment to be traced through the food web from algae to insects and fish (146). Studies showing higher fish abundance in streams draining clear-cut watersheds can be interpreted similarly (e.g. 202). Clear-cutting increases sunlight to streams, resulting in higher autochthonous production; higher, or at least modified, invertebrate production; and higher fish abundance.

Evidence for the importance of the macroinvertebrate-fish trophic linkage

also comes from top-down studies. Strong top-down fish effects have been demonstrated in lakes (e.g. 18) and in some streams with piscivorous and algivorous fish (152). However, the results of studies of lotic invertebrate-feeding fish using enclosures or exclosures, fish removal, or fish addition have varied (3, 169). Except in a few studies, effects were seen only on some species or only on some substrates (e.g. 150, 151, 164), and most studies did not show dramatic effects. Several authors have discussed how these variations might be attributed to problems associated with enclosure and exclosure studies (e.g. 3, 25, 54, 169). Also, some macroinvertebrate-fish studies were done with drift-feeding salmonids, which may have little impact on benthos (19, 196).

Allen (4, 5) studied trout and invertebrates in a small New Zealand trout stream, the Horokiwi, and noted, "We find therefore, that the quantity of bottom fauna which the trout eat in a year, 14 tons, is seventy times as great as the average amount of fauna present at one time" (5, p. 34). Allen's classic study became widely known as the Allen paradox (80). However, more recent studies have shown that the ratio of fish ingestion to macroinvertebrate standing crop may not greatly exceed possible turnover ratios of the macroinvertebrates (195, 196).

SECONDARY PRODUCTION   The data required to document the linkage between benthic macroinvertebrate prey and their invertebrate and vertebrate predators are difficult to obtain. Measurements of macroinvertebrate abundance and biomass are not sufficient to estimate the quantity of food available to predators. Benke (10) argued that production is the most comprehensive measure of success of a population because it includes a composite of several features: abundance, biomass, growth, reproduction, survivorship, and generation time. Unfortunately, while secondary-production measurements of numerous taxa exist, in Benke's (10) extensive review, he found total invertebrate production for <50 streams worldwide. Moreover, few studies have estimated production of macroinvertebrate prey and their predators in the same stream. In some fishless first- and second-order streams at Coweeta, North Carolina, invertebrate predators are responsible for 25–36% of total benthic production (78, 104). Likewise, Smock et al (171) found that invertebrate predators represented 30% of macroinvertebrate production in a low-gradient South Carolina stream.

APPLIED ASPECTS OF MACROINVERTEBRATE FUNCTION IN STREAMS

Exotic Species

In streams, noninsects usually constitute the most notorious exotic invertebrate invaders. Some well-known examples include the Asiatic clam, *Corbicula*

fluminea; the zebra mussel, *Dreissena polymorpha;* and crayfish, e.g. *Orconectes rusticus. C. fluminea* were estimated to filter the entire water column of a reach of the Potomac River in 3–4 days (24) and that of the Chowan River, North Carolina, every 1.0–1.6 days, depending on chlorophyll concentrations (97). However, the extent to which this impact extends throughout the entire water column may depend on mixing at different flow regimes (97). In the lower Potomac, Phelps (148) implicated the invasion of the Asiatic clam as triggering a series of ecosystem changes such as decreased turbidity, which increased submerged aquatic vegetation. These changes in turn influenced alterations in biota including algae, fish, and birds.

Since its discovery in the Great Lakes in the late 1980s, the zebra mussel has spread rapidly throughout many lakes and connecting waterways, including the Mississippi River drainage (103). The spread was so rapid and documented impacts were so alarming that by 1993, at least one book was devoted entirely to the zebra mussel (132). Although the potential impacts on streams and rivers of North America are uncertain, in the Rhine, population densities of 30,000–40,000 per m^2 young zebra mussels have been observed (132). Its extended planktonic larval stage (lasting several days to weeks) has tremendous dispersal potential in running waters (132). The most obvious concerns are the mussel's high filtration rates and its reputation as a notorious fouler of various water works (103). However, some positive environmental impacts may include removal of nutrients and seston from the water column; use as sentinal organisms for various pollutants and trace metals (86); and conversion of various toxic wastes to consumable nutrients for other benthos and phytoplankton. Nevertheless, the degree to which potential benefits offset negative effects is, at best, uncertain. Negative impacts have been projected for some native biota, phytoplankton, and fisheries, although some benthos may benefit from the deposition of nutrients and organic matter.

Numerous species of crayfish have been introduced to lakes and streams worldwide (76). One native midwestern species, *O. rusticus,* has a grossly disjunct range, apparently the result of numerous multiple introductions (76); this species may have displaced native crayfish in some streams and lakes (17, 76, 107). Mechanisms of displacement may vary from locality to locality. Mather & Stein (107) suggested that slow displacement of *Orconectes sanborni* by *O. rusticus* in an Ohio stream is mediated in part by lower fish predation on the larger *O. rusticus.* Thus, indirect and direct effects of predation as influenced in part by body size seem to be important in the displacement process.

The introduced stream-inhabiting insects that have received the most attention are those used to control noxious aquatic plants (e.g. 16). Undoubtedly, stream insects have been much more successful invaders than commonly recognized. They are often readily assimilated into the local fauna, and the

extent to which they have altered food webs is unclear. A relatively recent introduction of two alien caddisfly species into Hawaiian Island streams has resulted in some long-term dietary shifts of an endemic goby away from the relatively few native aquatic insect species to these exotic species (90).

Fisheries

An important question for commercial and sports fisheries is, what limits productivity of aquatic ecosystems? Richardson (158) reviewed several lines of evidence and reached the conclusion that fish production, at least for salmonids, is limited by benthic production. Evidence also indicates that some habitats may contribute more than others to productivity of higher trophic levels such as fish. In a low-gradient, warm-water river lacking salmonids, Benke et al (11) found that woody-debris habitats represented only 4% of total benthic habitat but contributed 60% to total invertebrate biomass and 16% of total invertebrate production in a study reach of the Satilla River, Georgia. Four of the eight major fish species in the Satilla obtained at least 60% of their diet from snag-inhabiting invertebrates, and significant portions of the diets of piscivorous species relied on prey that used snag-inhabiting invertebrates in their diets.

A disproportionate contribution of specific habitats to invertebrate production and/or drift, which is subsequently available at higher trophic levels, can have far-reaching consequences for fisheries management. However, such contributions are rarely assessed. In some situations, analysis of various habitats will require a tremendous effort. For example, Baker et al (9) delineated about 13 different freshwater habitats along a reach of the lower Mississippi River. Obviously, biotic inventories in this large riverine system require tremendous effort, and assessing productivity and processes in such diverse systems demands even more effort and resources. Numerous direct and indirect linkages between habitats add another layer of complexity. As pointed out by Richardson (158), most models of stream ecosystem function have addressed flow of energy and materials without incorporating feedback mechanisms that regulate population and trophic interactions. Most of these studies have failed to identify feedback loops that may be strongly regulating in stream ecosystems. The task of identifying such feedback loops will be formidable. Clearly, unless outside energy subsidies are greater than in-stream food resources for fish, effective fisheries management must account for fish-invertebrate linkages and macroinvertebrate linkages with resources and habitats.

Pollutants

Many of the processes relating to translocation of nutrients and food resources in streams also influence translocation of industrial pollutants in streams. For

example, both grazers and shredders enhance downstream movement of radio-labeled organically bound toxicants from periphyton and leaf litter, respectively (162, 178). Furthermore, downstream populations of filter-feeding hydropsychids accumulated significantly greater amounts of a radiolabeled PCB in periphyton-dominated channels in the presence of grazing invertebrates, and the presence of shredders significantly increased release of radiolabeled PCB from leaf litter to downstream hydropsychid populations (162). Sallenave et al (162) suggested that modeling the fate and transport of lipophilic, organically bound compounds in streams will require an understanding not only of the physiochemical properties of the system, but of biotic processing as well. The potential role of biota in translocation and retention of contaminants in stream ecosystems deserves more attention than it has received to date.

Macroinvertebrates as Biological Monitors and Indicators

Macroinvertebrates have been used to monitor accumulation of heavy metals (86) and insecticides (123) in streams. Aquatic insects, as well as other components of the aquatic biota, have been used extensively to evaluate the degree of anthropogenic disturbance to both lotic and lentic ecosystems. In recent years, interest in this area has grown tremendously, as evidenced by several books devoted entirely to the subject (e.g. 1, 102, 149, 161). Invertebrates have been used in numerous biological-monitoring methods (e.g. 161). The most widely used are based on tolerance values for specific taxa, which normally range from 0 (very intolerant) to 10 (very tolerant) according to the ability of a taxon to inhabit streams differing in water quality (e.g. 23, 75, 99, 149). In view of the many roles performed by macroinvertebrates in streams, indices that incorporate concepts such as biological diversity and integrity are an important and economical means of assessing ecosystem health (88, 89), although other views have been expressed (179). Experimental manipulation of headwater streams has established a link between degraded biotic indexes for an insecticide-induced disturbance and ecosystem processes such as secondary production, detritus processing, and FPOM export (187). Large increases in algal standing crops after an insecticide reduced macroinvertebrate populations were also noted in a Japanese stream (207). However, the extent to which biotic indices and modified community structure indicate altered ecosystem-level processes for other types of anthropogenic disturbances (e.g. organic pollution, heavy metals, sediments, acid-mine drainage, and forest clear-cutting) remains unknown. This area of investigation deserves a much greater blend of basic and applied ecology than it has received to date and should be a rewarding and important area of future research.

SUMMARY

As consumers at the intermediate levels of lotic food webs, macroinvertebrates are influenced by both bottom-up and top-down forces in streams and serve as conduits by which these effects are propagated. Although the bottom-up role of macroinvertebrates is clear, the top-down impacts have been less well documented. Shredder detritivores can exercise strong top-down effects by depleting their food resources, but they do not influence CPOM renewal. Similarly, gatherers have little top-down effect on renewal of their foods, whereas feeding and fecal production by other groups influence FPOM availability.

The extent to which feeding by gatherers qualitatively modifies FPOM resources depends on nutrient-microbial-detrital-animal linkages. Despite their abundance and importance to higher trophic levels, the functional role of gatherers is poorly known. In contrast, algal-grazer interactions are tightly coupled, as grazers influence both standing crop and rate of renewal of their algal resource. However, filterers, with the exception of microfilterers in some localities, have minimal quantitative influence on their resources and on resource renewal, but they exert their strongest effect on seston quality. Filterers also link suspended particles and FPOM supply to gatherers.

Available evidence suggests the impact of invertebrate predators on their prey is probably at least as great, if not greater than, that of vertebrate predators in many streams. In addition to direct mortality, their impact includes nonlethal effects on prey feeding activities, growth rates, fecundity, and behavior. The long coevolution of invertebrate and vertebrate predators and their prey, coupled with the complex mosaic of stream habitats, demands that we use complex and innovative approaches to understand predator impact on benthic communities.

The many roles performed by macroinvertebrates in streams underscores the importance of their conservation. Macroinvertebrates have served as valuable indicators of degradation of streams, and as increasing demands are placed on our water resources, their value in assessments of these impacts will increase.

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