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Responses of stream benthic macroinvertebrates to fire

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Abstract

Synthesis of published research on the responses of stream benthic macroinvertebrates to fire in western United States indicates a consistent pattern of response that can guide resource management and future research. Direct effects of fire generally are minor or indiscernible. Indirect effects, resulting primarily from increased rates of runoff and channel alteration, have the greatest impacts on macroinvertebrate community metrics and foodweb responses. Postfire effects are variable in time and space, but in smaller size streams (first to fourth order) that are otherwise undisturbed, changes generally are restricted to the first 5–10 years following fire and are associated with the more intense burns (crown fires with ≥50% of the catchment involved). In unfragmented habitats, initially supporting intact, functioning stream ecosystems, recovery from fire appears to be relatively rapid and to contribute to enhanced aquatic productivity and biodiversity. However, in poorly managed watersheds and those subjected to indiscriminate salvage logging, impacts from fire are expected to be greater and recovery of the macroinvertebrate communities and stream ecosystems more protracted.

Keywords: Benthos; Salvage logging; Streams; Wildfire ecology; Forest management

1. Introduction

Macroscopic insects and other bottom-dwelling invertebrates are primary food resources for salmonids and other fishes and are sensitive indicators of overall aquatic ecosystem health. Prior to 1970, there was no published empirical evidence on the effects of fire on aquatic macroinvertebrates. At the time of the 1978 National Fire Effects Workshop, touted as "a state-of-knowledge review" of the "effects of fire on water" (Tiedemann et al., 1979), only three studies documenting the responses of macroinvertebrates to fire were recognized (Lotspeich et al., 1970; Hoffman and Ferreira, 1976; Wood, 1977[1]). All three studies were conducted shortly after fire and showed no adverse effects on the macroinvertebrates. Knowledge of longer-term effects was largely anecdotal, and/or inferred from responses to other types of disturbances, and strongly influenced by the prevailing equilibrium views of forest succession and recovery from disturbance. In the interim, a substantial body of information has accrued, extending over periods of 2–20 years postfire, which provides a broader perspective of the ways and extent to which fire affects aquatic ecosystems, particularly in flowing water. In addition, it is now possible to view the findings in the light of the widely accepted non-equilibrium view of nature in which ecological responses and relationships are seen as being mediated largely by disturbance and patch dynamics (Botkin, 1990; Pickett and White, 1985).

The purpose of this article is to provide a synthesis of existing knowledge concerning the responses of

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[1] Reference not seen, cited by Tiedemann et al. (1979).

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benthic macroinvertebrates to fire as indicators of overall stream ecosystem response, to examine the implications of these findings for present and proposed forest management practices (e.g. prescribed burning and salvage logging), and to indicate where additional information is needed. The focus is on flowing water (lotic) ecosystems because that is where the interface between land and water is greatest and the most dramatic influences of fire on physical and chemical conditions occur. The effects of fire on stream macroinvertebrates can be conveniently separated into direct and indirect influences. Direct effects are limited to the time of the fire and extending to the first major runoff event and include increased temperature, nutrients, ash, charcoal, and ammonia. Indirect effects of fire are largely associated with increased erosion, sediment transport and deposition, channel alteration, and turbidity that begin with the first runoff following fire. Major differences in impacts on the macroinvertebrates relate to stream size and extent of the catchment burned; thus size matters. In addition, time plays an important role in determining the response to the generally large-scale disturbance resulting from fire. Food-web responses of the macroinvertebrate community are of special concern because they affect the survival and growth of fish, an ecosystem service of direct interest to humans. Finally, a comprehensive view must also consider the condition of the stream macroinvertebrate community at the time of the fire and the extent to which the catchment is itself has been previously impacted and fragmented. These considerations also have important implications for salvage logging (Beschta et al., 1995).

2. Direct effects of fire

The direct effects of fire on macroinvertebrate communities generally are minor or indiscernible (Rinne, 1996; Minshall et al., 1997, 2001a). Prefire and immediately postfire attributes of the macroinvertebrate community probably are essentially identical, based on comparison of reference and various intensity burn streams. In the absence of prefire data, community structure prior to fire often can be reasonably inferred from collections made during or soon after a fire. However, important exceptions include: intense heating in areas of small water volume (e.g. small first- or second-order streams or shallow, sluggish margins of larger streams), extended exposure to dense smoke, and errant retardant drops. In isolated cases, each of these may cause high mortality of benthic macroinvertebrates and/or fish (Johnson and Sanders, 1977; Norris and Webb, 1989; Spencer and Hauer, 1991; Roby and Azuma, 1995). After a fire, loss of riparian vegetation and overloading of existing food resources by ash and charcoal may occur, especially where ice and snow cover inhibit growth of attached diatoms (Minshall et al., 2001c,d). Consequently, there may be short-term (e.g. over winter) decreases in macroinvertebrate total biomass resulting from mortality and weight loss.

3. Indirect effects of fire

The impact of fire on macroinvertebrate communities varies with burn intensity and extent; stream size and gradient; precipitation and amount of runoff; vegetative cover; geology; and topography. As a result, even closely associated streams in the same fire will be affected differently in timing and magnitude of disturbance (Minshall et al., 2001a,b). Usually the most dramatic impacts are associated with physical upheaval resulting from flooding and mass movement, with accompanying channel alteration and sediment transport and deposition (Rinne, 1996; Minshall et al., 1997, 2001a). In the Rocky Mountain and Intermountain areas, these events usually are associated with snowmelt runoff or intense mid-summer rainstorms following the July–early September fire season. In southwestern montane watersheds, flood events often occur during the July–August monsoon period immediately following the May–June fire season (Rinne, 1996). In some cases, hydrologic events may reduce macroinvertebrate density by 85–90% (Rinne, 1996). However, these episodes may not occur in, or be most severe in, the first year following a fire. Furthermore, not all streams within the fire perimeter are affected equally, or at all, regardless of proximity. Thus, macroinvertebrate community response to fire is often individualistic and related to the generally stochastic nature of disturbance and heterogeneity of environmental conditions.

4. Size matters

The size of both the stream and the fire influence the effects on stream macroinvertebrates. Headwater catchments tend to burn more intensely and completely than do those of larger size streams (Minshall and Brock, 1991). Beyond a certain threshold, the greater the extent of a catchment exposed to fire (especially canopy fire), the greater the impact on the macroinvertebrate community (Minshall et al., 2001b). Consequently, there often is gradual decrease in adverse impacts with increasing stream size, and substantial negative effects are unlikely in streams sixth order or larger (Mihuc et al., 1996; Minshall et al., 2001b). The limit of this threshold for initiation of effects is yet to be determined but probably varies with climate and topography and lies between 25 and 50% of the total area burned in areas of moderate gradient (Minshall et al., 2001b) and may be even less in steeper terrain (Minshall et al., 2001a).

5. Time heals

In terms of taxonomic richness, total abundance, and total biomass, the macroinvertebrate community may return to prefire conditions in a year or two following the physical disturbances associated with a fire, but wide variations may continue for 5–10 years postfire (Roby and Azuma, 1995; Minshall et al., 2001a,b). However, community composition shifts towards increases in dominance and in the relative abundance of disturbance-adapted strategists (Mihuc et al., 1996). Although the annual variations of most community measures tend to become attenuated (i.e. relatively stable) within 7–10 years after fire, they may continue to show greater within-year variability than unburned reference streams for an unknown number ($\geq$15 years) of additional years (Minshall et al., 2001a,b). Many ecologists (e.g. O'Neill et al., 1989) would interpret this result as reduced (incomplete return to full) stability. Albin (1979) concluded that a first-order stream in Yellowstone National Park (YNP) whose catchment had burned 45 and 36 years previously continued to differ from an adjacent unburned reference stream. The macroinvertebrate community in the burned stream had greater mean abundance, total richness, and mean Shannon–Weiner diversity than the reference stream. However, additional studies are needed to determine if this pattern can be generalized, because other studies (Roby and Azuma, 1995; Minshall et al., 2001a,d) indicate that the values for these attributes in burned streams tend to converge with those of reference streams within 10–15 years.

6. Food-web responses and adaptive strategies

Little is known about food-web dynamics in postfire streams. Qualitative changes in plant food resources following fire (e.g. loss of riparian leaf detritus or increase in algae) could be expected to alter the feeding guild composition of the macroinvertebrate community (Minshall et al., 1989). In burned streams in YNP, functional feeding group composition differed from that of reference streams and contained a greater proportion of trophic generalists (Minshall et al., 1997).

In general, shredders are expected to track the loss and subsequent recovery of allochthonous leaf detritus, and scrapers are expected to reflect the changes in autotrophic periphyton associated with the opening of the forest canopy and the release of nutrients. Molles (1982) found that the ratio of Trichoptera shredder:-grazer [scraper] biomass increased from 1:17 in aspen streams to 3:1 in conifer streams. This shift was attributed to greater amounts of food for shredders, in the form of leaf litter, associated with greater retention by woody debris in the conifer streams. These differences were believed to be due to long-term changes accompanying forest succession following fire; conifer stands were believed to be a later succession stage than aspen.

However, strict adherence to a patterned sequence of feeding group replacements generally has not been observed in subsequent research because physical factors, particularly turbidity, sedimentation, and scouring, have an overriding influence on macroinvertebrate occurrence, and furthermore, most stream invertebrates are not narrow food specialists (e.g. Mihuc et al., 1996). For example, following the 1979 Mortar Creek Fire in the Frank Church Wilderness of central Idaho, scraper biomass in five burned streams either exceeded those in the reference streams from the start (~2 months postfire), or exceeded reference stream values after a couple of years (Minshall et al., 2001b). However, shredder biomass followed the expected pattern only in one of the burned Mortar Creek study streams, Little Creek, where it initially declined coincidental with the destruction of the riparian vegetation and its conversion to charcoal; biomass remained low for several more years. Recovery of shredder biomass in Little Creek circa 1985, suggests that, at least in this relatively stable stream, deciduous riparian vegetation had recovered sufficiently by that time to begin providing a reliable food base for this functional feeding group. However, shredder biomass generally was low in all of the streams, including the reference ones, indicating that factors other than those associated with fire were limiting. Thus, shredder:scraper ratios based on the total macroinvertebrate biomass did not follow the pattern described by Molles (1982) for Trichoptera. A similar result was found for total density. Trichoptera were too sparse in Mortar Creek Fire streams to evaluate separately.

The only published study of food-web dynamics in postfire streams is for Cache Creek, YNP. Mihuc and Minshall (1995) examined the trophic ecology of 11 benthic macroinvertebrates in Cache Creek, including those accounting for one-third of the total community abundance and half of the eight most abundant species during the period of highest charcoal loading (1988–1992). They found that burned material is of little importance as a food resource for primary consumers in postfire streams. This is consistent with the observation that total macroinvertebrate biomass in first- to third-order YNP streams decreased between October and March immediately following fire, when ice and snow cover restricted their diets to particulate organic matter high in charcoal (Minshall et al., 2001c,d). Of the 11 taxa studied, only *Paraleptophlebia heteronea* exhibited growth. This finding was attributed to the relatively high ingestion rate of this species, which presumably adapts it for extracting nutrition from low quality food resources. In another study, the shredder, *Pteronarcella badia*, grew when fed only burned leaves and pine needles, although the materials were less intensively burned than those fed to the 11 Cache Creek representatives (MacRury, 2002). The results for *P. badia* raise the possibility that low intensity fires, such as those that might result from a prescribed or understory burn, may have less of an adverse effect on allochthonous detritus food resources than high intensity fires. Trophic generalists capable of using two or more resources for growth were common food-web components in Cache Creek and elsewhere in YNP. Thus, many lotic invertebrates, including two of the most abundant macroinvertebrates during postfire recovery in YNP (*Baetis bicaudatus* and *Zapada columbiana*), potentially can to switch foods as availability changes in postfire streams.

Individual taxa respond differently to the various physical changes and shifts in food resources (Mihuc and Minshall, 1995; Mihuc et al., 1996). Responses of species favored by fire appear to be largely opportunistic, not only with respect to food resources but also with regard to individual evolutionary strategies adapted for life in streams. Streams are inherently unstable, dynamic, heterogeneous environments in which disturbance is a regular occurrence (Resh et al., 1988). Opportunistic species, particularly those well suited for dispersal through drift and with multivoltine life cycles and high reproductive success (e.g. Chironomidae, *B. bicaudatus*), and tolerant species, with wide habitat preferences (e.g. *Z. columbiana*) and herbivore-detritivore food requirements, seem to be especially well-adapted to conditions following fire (Anderson, 1992; Mihuc et al., 1996; Minshall et al., 1997). Taxa that exhibit habitat requirements for stable riffles or slower current velocities tend to decline in abundance and biomass following wildfires (Mihuc et al., 1996). This relationship is evident in some Ephemeroptera genera (e.g. *Drunella*, *Ephemerella*, and *Paraleptophlebia*), especially those that are dorsoventrally compressed (e.g. *Cinygmula*, *Epeorus*, and *Rithrogena*; Mihuc et al., 1996). Many Ephemeroptera are sensitive to reduced water quality, and the flattened forms may be less mobile than streamlined forms (e.g. *Baetis*) and thus, more sensitive to sedimentation and scouring.

7. Implications for watershed management

Though often temporarily dramatic, the effect of fire on macroinvertebrates in otherwise intact, unfragmented stream ecosystems is not catastrophic (e.g. compared to the Mount St. Helens eruption; Anderson, 1992) nor is recovery exceptionally long term, even where extended periods of fire suppression have occurred (Minshall et al., 2001b,d). As noted above, the indirect effects of fire on stream macroinvertebrates and ecosystems generally are much greater than the direct ones, but when viewed in an appropriate ecological perspective of years to decades, both types of effects appear to be in the normal range of variation, or rapidly return to near prefire conditions. Macroinvertebrate community metrics and food-web rebound (this review); fish feed, grow, and reproduce (Rieman et al., 1997; Gresswell, 1999); and thus, the ecosystems that support these aquatic organisms remain intact. There is no fire crisis, and given the normal mosaic of a heterogeneous array of different-sized patches of varying degrees of burn intensity, no need for special action in natural, relatively unfragmented ecosystems. Even where mitigative or salvage actions are deemed necessary or desirable, there is sufficient time (i.e. at least a few years; Lowell et al., 1992; Lowell and Cahill, 1996) to act rationally and thoughtfully.

Results for macroinvertebrates generally support the belief that fire and similar natural disturbance events are not detrimental to the sustained maintenance of diverse and productive aquatic ecosystems (i.e. those found in undisturbed forests). However, in watersheds already adversely impacted by generations of resource extraction and short-sighted management, fire can be expected to have much more severe effects; this is because of the compounding effects that fire is expected to have on degraded watersheds. An example of cumulative negative consequences resulting from the combination of prefire resource management actions and postfire responses is provided by Rinne (1996) but research on this topic is needed in an array of geographic and management settings. Past and even current logging, grazing, mining, road building, and fire-salvage practices, both inside and outside of valley bottoms, have disarticulated landscapes and caused them to deteriorate even before the occurrence of fire (e.g. see Covich, 1993; Power et al., 1988, 1997; Resh et al., 1988 and references cited therein). Recovery of stream ecosystems from the effects of fire is likely to be slower, more sporadic, and potentially incomplete in cases where natural process already are impaired. Therefore, development and resumption of a more holistic practice (both spatially and temporally) of forest management and the restoration and/or maintenance of ecosystem integrity at the catchment scale and larger, is much more urgent than fire prevention or postfire stream channel protection and restoration.

The condition of stream ecosystems and their stabilization and recovery after wildfire is especially sensitive to the extent to which riparian and floodplain processes remain intact. The relatively rapid recovery of stream macroinvertebrates is associated with the more rapid recovery of the riparian vegetation (25–50 years to full canopy development) compared to that of the uplands (100–300 years) (Minshall et al., 2001a,b; Minshall, personal observation). This observation suggests that stream ecosystem recovery is more dependent on riparian vegetation and flood plain conditions than on the more-distant portions of its catchment. Therefore, road construction, log removal, and other anthropogenic disturbances or encroachments in the riparian-floodplain corridor should be avoided, severely restricted, or repaired. These general guidelines for all resource management actions also extend to salvage logging, fire fighting (e.g. dozer lines), and fire prevention activities (e.g. extensive thinning and fire break construction outside of residential areas) that expose soil to erosion, accelerate runoff, or alter natural hydrologic pathways.

In places where salvage logging occurs, the amount of snags that can be removed from the uplands without serious adverse effects on stream macroinvertebrate but ecosystem recovery is unknown and is likely to vary with forest type, geology, and topographical relief. However, it is known that virtually all forms of postfire logging can have various adverse effects on stream ecosystems (e.g. Megahan, 1983; Smith et al., 1993a,b; Stout et al., 1993; Ketcheson and Megahan, 1996). Based on results from watersheds having various proportions of their areas burned by wildfire (e.g. Minshall et al., 1995, 2001b; Minshall, personal observation), it is probable that the amount of timber removed should not exceed about 25% of the merchantable timber (unless contradictory information is available). In addition, postfire removal should be appropriately spaced across the landscape and should be in proportion to the size classes (DBH) of trees present at the time of the fire (see also Beschta et al., 1995). This proportional harvesting is necessary because of the important graded inputs (Lyon, 1984) that a mix of such large woody debris contributes to streams over the extended recovery period (Minshall et al., 1989). In addition, fire lines should be obliterated prior to logging, and road construction or other major ground-disturbing activities should be avoided in order to prevent additional runoff and erosion. Salvage harvest yields responses (e.g. ground disturbance, woody debris removal, interruption of normal infiltration pathways, and acceleration of surface flows) that interact with the direct and indirect effects of fire to make these actions so potentially damaging. In addition, the negative effects extend many years beyond the actual time of salvage activities because of the harvest of snags that normally fall and become incorporated into stream channels and forest floors over several decades or more (Lyon, 1984). These wood inputs are important to create habitat, increase nutrients, and retard runoff and channel alteration during what is normally the most critical stage of stream and riparian vegetation recovery (Minshall et al., 1989; Lawrence and Minshall, 1994).

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