[1982]

Ward, J. V. 1982. Ecological
aspects of stream regulation:
Responses in downstream lotic
reaches. Water Pollution
and Management Reviews
(New Delhi) 2:1-26.

1

Ecological Aspects of Stream Regulation: Responses in Downstream Lotic Reaches

JAMES V. WARD
Department of Zoology and Entomology
Colorado State University, Fort Collins, Colorado 80523, USA

INTRODUCTION

Stream regulation, the anthropogenic control of discharge in running waters, has profoundly influenced virtually all of the world's major river systems (Ward and Stanford, 1979a). In some regions, the total surface area occupied by impoundments is greater than that of natural lakes. Although the most obvious ecological alterations occur in the inundated portion behind the dam where the running water system is transformed into an artificial lake (see Ridley and Steel, 1975 and Baxter, 1977 for reviews), the structure and function of the remaining lotic reaches are also profoundly modified by stream regulation.

The regulation of running waters is manifest in a variety of forms, and each stream regulation scheme is to some extent a unique system. However, generalized responses occur, and broad types of stream regulation are apparent (Table 1). For example, the ecological implications of a storage reservoir distinctly differ from those of a hydroelectric facility, and a deep-release dam has quite different effects on the receiving stream than a surface-release reservoir. Environmental conditions in lotic reaches below dams are a function of (1) the quality of water entering the reservoir, (2) limnological phenomena within the reservoir, and (3) operational variables at the dam. Effects of stream regulation may extend tens or even hundreds of kilometers downstream.

This review paper addresses the ecological responses of lotic reaches and stream organisms to the influence of upstream impoundments. Consideration will be given to hydrologic, chemical and thermal modifications, and the resultant effects on aquatic and riparian flora, macroinvertebrates, and fishes. The term "regulated stream" as used herein applies to modified lotic reaches downstream from dams.

Table 1 SOME GENERALIZED QUALITATIVE RESPONSES OF DOWNSTREAM REACHES TO STREAM REGULATION (RELATIVE TO COMPARABLE UNREGULATED STREAMS).

	Receiving stream	
Variable	Surface-release	Deep-release
Turbidity	Clarification	Clarification
Nutrients	Reduced	Reduced less
Plankton	Enhanced	Present
Detritus	Reduced	Reduced
Discharge	Variable	Variable
Temperature range	Increased	Decreased
Dissolved oxygen	Saturated	Anoxic to supersaturated

HYDROLOGIC RESPONSES

When a dam is placed across a stream, a hydrodynamic disequilibrium is manifest in the downstream reach (Leopold et al., 1964; Dolan et al., 1974; Buma and Day, 1977; Simons, 1979; Petts, 1980). Hydrodynamic responses to stream regulation are primarily a function of alterations in the sediment load and the flow regime, and their interactions (Petts, 1980).

FLOW REGIME

The flow regime of regulated streams may differ in four major ways (Table 2) from natural (preimpoundment) conditions (Ward, 1976a). Short-term flow fluctuations characterize lotic reaches below hydroelectric dams; storage reservoirs may enhance flow constancy; reduced total discharge may result from interbasin transfer, conduit bypass, or increased evaporative loss from the reservoir surface; and increased total discharge occurs in streams receiving water abstracted from another catchment. A regulated stream may exhibit more than one of these alterations. For example, short-term fluctuations in discharge below hydroelectric dams may be accompanied by enhanced seasonal flow constancy (Müller, 1962; Pearson et al., 1968; Hoffman and Kilambi, 1971; Ward, 1976a; Fraley, 1979; Henricson and Müller, 1979).

Compared with free-flowing rivers, regulated reaches generally exhibit lower mean annual discharge maxima, and reductions in the magnitude and frequency of flood events with greater than annual recurrence intervals. For example, the mean annual flood of the Colorado River, 2436

Table 2 GENERALIZED TYPES OF FLOW REGIME MODIFICATION BELOW IDEALIZED SINGLE-FUNCTION RESERVOIRS.

	Function of reservoir			
Flow modification	Hydro	Storage	Irrigation	Diversion
Short-term flow fluctuations	×		×	
Seasonal flow constancy	×	×		
Reduced discharge				×
Increased discharge				×

m^3/sec, was reduced to 765 m^3/sec, and the 10-year recurrence interval flood dropped from 3483 to 850 m^3/sec following regulation by Glen Canyon Dam (Dolan et al., 1974).

CLARIFICATION

Large reservoirs reduce downstream sediment loads over 95% compared to preimpoundment levels (Leopold et al., 1964). Construction of Glen Canyon Dam reduced the median sediment concentration of the Colorado River from 1500 ppm to 7 ppm (Dolan et al., 1974). Prior to regulation by the Aswan Dam, the Nile River annually carried from 60–180 million tons of silt to the Mediterranean Sea (Mancy, 1979).

The downstream transport of organic detritus is also disrupted by stream regulation (Webster et al., 1979). Much of the detritus in stream systems is derived from headwater terrestrial communities and is sequentially processed downstream (Vannote et al., 1980). The truncation of detrital transport and processing significantly alters the energy base of the lotic system (Ward and Stanford, 1982a). Although few data are available, it is apparent that quantitative (total transport) and qualitative (particle size composition, nutritional quality, chemical diversity) components of organic detritus may be altered, and that temporal patterns are modified in regulated lotic reaches (Lind, 1971; Ward, 1974; Webster et al., 1979).

Turbidity plumes (which move through reservoirs under special conditions) and plankton blooms may reduce transparency in the receiving stream (Neel, 1963), but the overriding effect of impoundment is to greatly increase clarity in regulated segments.

CHANNEL MORPHOLOGY AND SUBSTRATE

The clear water released from most dams and the modified flow regime are responsible for adjustments of substrate and channel morphology in regulated streams. The erosive power of sediment-free water induces a variety of downstream changes (references in Buma and Day, 1977; see Simons, 1979, for a discussion of responses of the river channel and tributaries upstream from the impoundment).

Degradation (channel deepening) is the predominant channel response (Figure 1) immediately below dams (Buma and Day, 1977; Petts, 1980), although further downstream contributions of sediment from channel and floodplain erosion plus tributary inputs interact with the flow regime to alter channel morphology and substrate composition (Kellerhals et al., 1979; Petts, 1980).

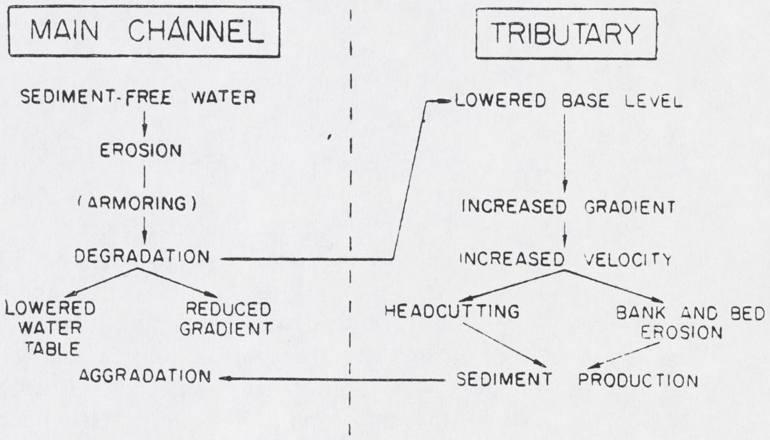


Figure 1. Some potential hydrologic responses of the main channel and a tributary to the release of sediment-free water from an upstream impoundment.

However, because of reduction in the magnitude and frequency of flood events, coupled with constraints to erosion (e.g., armoring, see Simons, 1979), the erosive potential of clear water releases may not be fully realized. Accommodation of regulated flow within the existing channel in the absence of competent discharges may restrict channel adjustments to rare periods of severe flooding. Simulated flooding may be necessary in some cases to remove fine sediments deposited during dam construction (Eustis and Hillen, 1954).

Because of reductions in the frequency and magnitude of competent discharges by regulation, sediment buildup may occur at the confluence of the main channel with unregulated tributaries (Baxter and Glaude, 1980). Hydrodynamic disequilibria will be established in downstream tributaries if their base levels are altered. Degradation of the main channel may thus induce erosion in tributaries by rejuvenation and supply additional sediment to the regulated river. Even without degradation, the base level may be effectively lowered by reduced discharge in the regulated channel at times of tributary flooding.

The types and extent of changes in channel morphology induced by stream regulation depend on the interactions between the flow regime, sediment quality and quantity, and the resistance of the channel boundary (Petts, 1980). Degradation is only one of several possible responses. Others include changes in cross-sectional area or channel patterns, and lateral movements of the channel. Hydrologic responses also vary spatially (downstream) in a given regulated river as tributaries add sediment and modify the flow regime in the main channel.

The downstream extent and degree of hydrologic modification by stream regulation depend on a variety of factors, but in general alterations in channel morphology are apparent downstream until "the proportion of non-regulated runoff reduces the proportion of catchment impounded to less than 40% of the total area draining into the stream-channel" (Petts, 1980, p. 328). Eventually, even highly regulated reaches establish a dynamic equilibrium with the altered sediment and flow regimes.

CHEMICAL RESPONSES

In this section concern is directed toward changes in chemical characteristics of influent water compared to outflow from the dam, and the effects of release depth on the quality of discharge water. The extent to which impounded water is chemically altered by limnological phenomena varies between reservoirs and within the same reservoir over time. See Golterman (1975), Wetzel (1975) and Cole (1979) for detailed descriptions of chemical dynamics in standing water bodies. The following discussion primarily applies to chemical modifications engendered by "on-stream, deep-storage reservoirs" (sensu Hannan, 1979). Increased salinity induced by evaporation is a major chemical response in "off-stream (closed) reservoirs", whereas "run-of-the-river reservoirs" may have minimal effects on river chemistry.

Under certain circumstances, the chemical characteristics of inflowing water may maintain integrity as a density current moving through the reservoir (Neel, 1963; Wunderlich, 1971; Soltero et al., 1974; Hannan, 1979; Krenkel et al., 1979). Generally, however, significant alterations occur within the reservoir, resulting in differences in the quality of water entering the reservoir and that discharged from the dam (Love, 1961; Symons et al., 1965; Wright, 1967; Soltero et al., 1973; Klomp, 1976; Hannan, 1979; Krenkel et al., 1979). Even reservoirs with relatively short retention times tend to act as sinks for certain substances (e.g., nutrients, some heavy metals), whereas other components (e.g., H_2S), not normally present in the inflow, may be produced within the reservoir and released downstream. Some authors emphasize a general improvement of water quality by impoundment (e.g., Klomp, 1976; Simmons and Voshell, 1978; Hannan et al., 1979); others report inducement of deleterious chemical conditions (e.g., Wright, 1967; Isom, 1971; Young et al., 1976). Obviously both beneficial and adverse effects occur (see Love, 1961); whether the overall result improves or degrades water quality depends on the river-reservoir system in question and the parameters examined.

Temporal patterns of river chemistry may be considerably altered by stream regulation (Soltero et al., 1973). For example, chemical conditions characterizing summer may be delayed until winter in the lotic reach below the dam (Neel, 1963). In addition, impoundment tends to reduce the sharp temporal variations which may characterize upstream reaches (Love, 1961; Soltero et al., 1973, Crisp, 1977). The influence of biological phenomena on chemical conditions in the reservoir "is often greater than the influence of the other factors combined" (Hannan, 1979, p. 80), and such effects vary with depth. In the epilimnion of a reservoir phytoplankton may rapidly deplete nutrients and CO_2, and photosynthesis may induce decalcification and elevate pH. The metalimnion may contain oxygen-supersaturated strata under some conditions, but oxygen-depleted waters at other times (Gordon and Morris, 1979). The hypolimnion is the primary site of decomposition processes which elevate CO_2 levels, and lower oxygen and pH.

SALINITY

Reservoirs may act as salinity traps under some conditions (Soltero et al., 1973). However, inundation of Tertiary marine sediments by impoundment exasperated an already serious salinity problem in the Murray-Darling River Basin in Australia (Walker, 1979). The absence of flooding under regulated flow regimes may increase salinification of floodplain pans by failing to provide a dilution effect (Davies, 1979).

Large impoundments, especially in tropical or arid regions, may increase salinity by evaporation. The salinity of Lake Nasser in Egypt is increasing due to evaporation of from 8–20 billion m^3 of water annually (Mancy, 1979; Ramadan, 1979).

Since salinity increases with depth in stratified reservoirs (Neel, 1963), surface-release should be employed where reductions in downstream salinity levels are desired (Wright, 1967; Martin and Arneson, 1978.)

DISSOLVED OXYGEN

The effects of impoundment on downstream oxygen levels are a function of the trophic status of the reservoir, retention time, release depth, and other factors. Air drafts in the release tunnel will generally ameliorate any oxygen deficits before water is discharged into the receiving stream

(Neel, 1963; see section on gas supersaturation). Oxygen problems arise when hypolimnetic waters from eutrophic reservoirs are released from the dam with little turbulence (Pfitzer, 1967; Ruggles and Watt, 1975; Davies, 1979; Krenkel et al., 1979; Walker, 1979). Hannan et al. (1979) have demonstrated a progressive down-reservoir movement of a hypolimnetic anoxic zone, which during low flow years may not reach the dam prior to autumnal overturn.

The rapidity of downstream recovery of oxygen-depleted water is primarily dependent upon turbulence, and photosynthesis by aquatic plants.

Ammonia, sulfides, and reduced forms of iron and manganese associated with anoxic hypolimnia may be discharged from deep-release dams (Neel, 1963; Wright, 1967; Hannan and Young, 1974; Davies, 1979; Krenkel et al., 1979). Such reduced chemical species may be toxic to aquatic biota, and increase the total oxygen demand in the tailwaters. Oxygen-depleted waters reduce the capacity of the stream to assimilate inputs of organic wastes (Ruggles and Watt, 1975).

NUTRIENTS

Reservoirs may act as nutrient traps such that net output at the dam is less than total nutrient input (Hannan et al., 1973; Soltero et al., 1973; Klomp, 1976; Hannan, 1979). For example, 25% of the total nitrogen entering a large impoundment in Montana, U.S.A., was retained within the reservoir, although there was an 11% increase in nitrate nitrogen (Soltero et al., 1973). Studies of another Montana reservoir showed that inorganic nitrogen was invariably higher in outflowing than inflowing waters (Rada and Wright, 1979). Although part of this difference may be due to precipitation inputs, the net increase in inorganic nitrogen was primarily attributed to nitrogen fixation by the blue-green alga *Aphanizomenon flos-aquae*. Despite considerable mineralization of combined phosphorus within the reservoir, total phosphorus inputs and outputs were similar (Rada and Wright, 1979). Soltero et al. (1973, p. 347), however, reported that only "14 per cent of the phosphorus that entered the reservoir was discharged," primarily due to sedimentation of particulate phosphorus. Other investigators have also reported a reduction in phosphorus by impoundment (Klomp, 1976), or no significant change (Hannan and Young, 1974).

Several authors provide useful summaries of alterations in specific nutrients and other chemical constituents induced by impoundment (e.g., Soltero et al., 1973; Klomp, 1976; Hannan, 1979; Hannan et al., 1979; Ramadan, 1979).

Because nutrient levels increase with depth in stratified reservoirs, surface-release accentuates nutrient accumulation in impounded waters, whereas deep-release supplies greater amounts to the receiving stream (Neel, 1963; Wright, 1967; Martin and Arneson, 1978; Davies, 1979).

Selective depth withdrawal capabilities thus allow some control over amounts and concentrations of nutrients discharged to downstream lotic reaches (Paulson et al., 1979).

Unlike the classical pattern of aging in natural lakes, many impoundments exhibit initially high levels of nutrients which decline over time as continued leaching from the substrate surface depletes nutrients from the reservoir basin (Neel, 1963; Balon, 1978; but see Pennak, 1949).

DISSOLVED GAS SUPERSATURATION

Lotic waters below dams may become supersaturated with atmospheric gases to the detriment of stream biota. Weitkamp and Katz (1980) recently reviewed conditions leading to dissolved gas supersaturation and effects on aquatic organisms. Although gas supersaturation may occur under natural conditions, it poses the most serious problems in the tailwaters of high-head hydroelectric dams where falling water mixes with air which is subsequently dissolved under hydrostatic pressure in deep plunge pools. Early data on supersaturation below dams are available from Sweden (Jarnefelt, 1948; Lindroth, 1957), but the most intensive and comprehensive research has been conducted in the Columbia River Basin (e.g., Ebel, 1969; Beiningen and Ebel, 1970; Meekin and Allen, 1974; Raymond, 1979). Dissolved gas levels above 120% saturation have been commonly recorded, with occasional values exceeding 140% (Weitkamp and Katz, 1980).

THERMAL RESPONSES

NATURAL THERMAL CONDITIONS

The temperature regime of a water body is a composite of the entire thermal pattern including absolute temperatures, amplitudes, and rates of change, superimposed upon temporal and spatial vectors (Ward and Stanford, 1982b). In addition to latitude and altitude, a variety of hydrological, topographical, and meteorological factors are responsible for thermal patterns in natural lotic system (Collings, 1969; Smith, 1972; Smith and Lavis, 1975).

In natural streams not greatly influenced by groundwater, close relationships between air and water temperatures have been observed in England (Smith and Lavis, 1975), Alaska (Sheridan, 1961), and the French Pyrenees (Thibault, 1971), although major discrepancies may occur during periods of ice cover, snowmelt, or spates. Because larger volumes of water are less responsive to atmospheric vagaries, the thermal conditions of source waters are carried further downstream during high discharge. The aspect of the drainage basin, streamside vegetation, and channel form influence the relative importance of direct solar radiation on stream temperature (Macan, 1958; Edington, 1965; Brown, 1971). Substrate type and degree of exposure to direct sunlight play major roles in determining temperature regimes of tropical streams (Geijskes, 1942).

Natural streams of mid- and high-latitudes normally have temperatures which vary from around 0–20°C, or less, annually. Rivers in regions of continental climates may exhibit slightly greater ranges (e.g., 0–26°C for the Volga River, U.S.S.R.; Mordukhai-Boltovskoi, 1978). Tropical streams rarely exceed about 32°C (see e.g., Bishop, 1973).

The diel range of temperature to which aquatic animals are exposed may be of considerable ecological significance (Ward, 1976b; Ward and Stanford, 1979b, 1982b; Vannote and Sweeney, 1980). Maximum diel ranges vary from less than 1°C at spring sources (Ward and Dufford, 1979) or under ice (Clifford, 1978), to well over 10°C in exposed streams (Mackichan, 1967; Smith and Lavis, 1975). Although tropical streams exhibit more constant thermal conditions, considerable diel (Bishop, 1973) and annual fluctuations (Harrison, 1965) have been documented.

Subsurface ice, which forms under special conditions in lotic waters (Ashton, 1979), may have major effects on stream organisms (Maciolek and Needham, 1951).

Middle reaches are often the most responsive to atmospheric temperatures. Headwaters which are well-canopied and receive substantial groundwater are thermally stable; the large volume of water is responsible for thermal stability in the lower reaches of river systems (Ward and Stanford, 1979b; Vannote and Sweeney, 1980).

REGULATED THERMAL CONDITIONS

The extent to which impoundment modifies lotic temperatures therefore depends not only on the characteristics of the reservoir and operational variables, but is also determined by the position of the dam along the longitudinal stream profile (Ward and Stanford, 1982a). Operational variables influencing downstream temperature include release depth and discharge pattern; thermal stratification patterns and retention times are major limnological variables (Ward and Stanford, 1979b).

Seven biologically significant components of the thermal regime may be altered by stream regulation (Table 3). Although models have been developed to predict downstream temperatures or to exert managerial control over thermal conditions below dams (Nielson, 1967; Beard and Willey, 1970; Adams, 1975), only specific portions of the total thermal pattern have been considered. Considerable modification of the total thermal pattern by impoundment may occur without appreciably changing mean annual stream temperatures (Templeton and Coutant, 1971; Lavis and Smith, 1972; Ward, 1976c). Shallow or surface-release reservoirs and natural lakes have similar effects on the thermal regime of the receiving stream (Martin and Arneson, 1978; Ward and Short, 1978;

Table 3 IDEALIZED THERMAL ALTERATIONS OF THE MIDDLE REACHES OF TEMPERATE STREAMS INDUCED BY UPSTREAM IMPOUNDMENTS WITH DIMICTIC PATTERNS OF STRATIFICATION.

Thermal alteration	Deep-release	Surface-release
Diel range	Reduced*	Variable
Annual range	Reduced	Expanded
Summer temperature	Decreased	Elevated
Winter temperature	Increased	Similar
Seasonal maximum	Delayed	Delayed
Vernal rise	Less rapid	Delayed
Autumnal decline	More rapid	Delayed

*Diel range may be increased in summer below hydroelectric dams.

Fraley, 1979). Release of warm surface waters during stratification decreases heat storage in the reservoir, and elevates summer temperatures downstream. In addition, there may be a delay in the vernal rise and autumnal decline in temperature irrespective of release depth (Neel, 1963; Spence and Hynes, 1971a; Mordukhai-Boltovskoi, 1978; Walker, 1979).

The most dramatic thermal alterations occur below stratified deep-release impoundments on temperate zone streams (Ward and Stanford, 1982a). Storage reservoirs which release water from the hypolimnion during the entire period of stratification produce a thermal regime in the receiving stream characterized by diel and seasonal constancy, winter warm and summer cool conditions, and alterations in the seasonal temperature pattern (Ward, 1976b, 1976c; Ward and Stanford, 1979b). Diel temperature fluctuations may be virtually eliminated immediately below deep-release dams. The annual range 5 km downstream from a Japanese reservoir was decreased from 21°C to 12°C (Nishizawa and Yamabe, 1970). A reservoir in England depressed downstream temperatures as much as 12°C in summer (Lavis and Smith, 1972). Penaz et al. (1968) found average summer temperatures 9.5°C lower and winter temperatures 4.5°C higher below a dam in Czechoslovakia, compared to thermal conditions above the reservoir. Water temperatures below a Colorado mountain reservoir ranged only from 3–13 °C and the seasonal maximum was delayed until October, the time of reservoir overturn (Ward, 1974). Armitage (1979) reported significant delays in the vernal rise (20–50 days) and autumnal decline (0–20 days) in temperature below an impoundment in the Pennine Moorland of England.

Streams below deep-release hydroelectric dams may exhibit enhanced summer diel thermal variations in conjunction with flow fluctuations, since small volumes of water during non-generation periods rapidly equilibrate with ambient air temperatures (Pfitzer, 1967; Ward and Stanford, 1982c). A falling water level in a stratified reservoir with a fixed outlet port, or changing release depth in a dam with selective withdrawal, may also produce abrupt temperature changes in the receiving stream.

Reduced flow, whether from diversion or during non-generation periods below hydroelectric dams, results in more extreme water temperatures. Low discharge in winter enhances formation of anchor ice, although ice-free conditions generally prevail for some distance below deep-release dams, even in regions normally having several months of ice cover (Ward, 1976b).

Recovery of a thermal regime altered by stream regulation may take tens or even hundreds of kilometers. For example, below Vir Dam on the River Svratka in Czechoslovakia, thermal recovery required over 40 km (Penaz et al., 1968). The rate of recovery with distance is a function of thermic slope (i.e., the difference between air and water temperatures) and discharge, among other factors (Bratranek, 1953; Nielson, 1967; Beard and Willey, 1970; Adams, 1975).

BIOTIC RESPONSES

The generalized responses of biotic components to upstream impoundment presented in Table 4 assume the absence of adverse environmental

Table 4 A SUMMARY OF COMMON RESPONSES OF RIPARIAN AND AQUATIC FLORA, AND MACROINVERTEBRATES TO STREAM REGULATION IN LOTIC REACHES WITH OTHERWISE FAVOURABLE CONDITIONS.

Biotic-Component	General Effects	Comments
Riparian vegetation	Variable	Dependent upon hydrologic regime
Periphyton	Enhanced standing crop	Filamentous chlorophytes and bryophytes favored
Submerged angiosperms	Enhanced	Increased densities; upstream range extensions
Macroinvertebrates		
Abundance	Variable	Dependent upon flow regime
Diversity	Reduced	Often due to thermal alterations
Composition	Altered	Trophic, thermal, and flow alterations

conditions such as pollution, oxygen depletion, and sedimentation, which would otherwise mask the effects of regulation. The responses indicated are therefore based primarily on the sublethal modifications of hydrologic, chemical, and thermal regimes by stream regulation discussed in preceding sections.

AQUATIC AND RIPARIAN FLORA

Riparian vegetation plays an important ecological role in stream ecosystems, especially in headwater reaches, by providing cover for stream fishes, by reducing bank erosion, by supplying energy in the form of allochthonous organic detritus, and through its influence on stream temperature.

The specific influence of stream regulation on riparian vegetation primarily reflects the complex interrelationships of several hydrologic variables (Buma and Day, 1975), making generalizations difficult. Reduced flow fluctuations may enhance riparian species already present or may allow invasion of the riparian zone by non-riparian species which are unable to tolerate flooding along natural streams (Dolan et al., 1974; Buma and Day, 1975, 1977; Grelsson and Nilsson, 1980). Reductions in discharge by diversion may facilitate encroachment of riparian vegetation to the extent of channel modification (Ward, 1976a). Severe water level fluctuations, induced by certain types of regulation, however, will reduce or eliminate the normal streamside vegetation. The erosive power of clear water releases may eliminate riparian habitats such as point bars and terraces (Dolan et al., 1974). The removal of silts and clays may, by reducing moisture (and nutrient?) holding capacity, render the soil of marginal areas unsuitable for rooting and growth of riparian plants (Simons, 1979). In addition, degradation below the dam may reduce the water table of the flood plains, thereby affecting riparian communities (Buma and Day, 1977; Simons, 1979).

Submerged angiosperms and attached aquatic plants (bryophytes and benthic algae) generally respond in a similar fashion to stream regulation (Table 4). Although aquatic plants may be adversely affected under some conditions, such as heavy siltation or extreme flow fluctuations (Neel, 1963; Kroger, 1973; Ward, 1976a), more commonly stream regulation imparts an overall favorable environment for stream flora (Penaz et al., 1968; Spence and Hynes, 1971a; Ward, 1976c; Holmes and Whitton, 1977, 1981; Lowe, 1979; Marcus, 1980). Conditions which may occur in regulated lotic reaches which tend to favour aquatic plants include (1) enhanced flow constancy, (2) increased bank and bed stability, (3) reduced scour, (4) increased water clarity, (5) higher winter temperatures, (6) absence of surface and anchor ice, (7) higher nutrient levels, and (8) reduced stream gradients. The negative effects of short-term flow fluctuations which occur below some dams are often more than compensated for by increased substrate stability induced by long-term reductions in flow variations, and the presence of other factors favourable to stream flora. Under certain conditions stream regulation results in nuisance growths of aquatic plants (see e.g., Walker, 1979).

Although fewer species of diatoms were recorded at a regulated site on a British river, the species richness of total phytobenthos was greater than at unregulated locations (Holmes and Whitton, 1981). Filamentous green algae and desmids were especially enhanced. The absence of certain algal species was attributed to the dense cover of bryophytes or to the upstream reservoir acting as a barrier to downstream movement of inocula. The more constant flow conditions are likely responsible for the invasion of the regulated lotic reach by species of aquatic angiosperms which were restricted to lower reaches prior to impoundment (Holmes and Whitton, 1977). Mountain streams in Colorado which normally lack higher plants may develop dense beds of submerged angiosperms in regulated reaches (Ward, 1976c).

Ross and Rushforth (1980) failed to detect any significant changes in the periphytic diatom communities of a Rocky Mountain Stream following upstream impoundment. In another Rocky Mountain stream, however, a more diverse diatom assemblage colonized glass slides immediately below a deep-release reservoir than at sites further downstream (Marcus, 1980). The site closest to the dam exhibited net periphytic productivity four times greater than at downstream locations, a response attributed to nutrient enrichment resulting from nitrogen fixation in the reservoir.

Total streambed coverage by phytobenthos nearly tripled below a Czechoslovakian reservoir compared to a lotic site upstream (Penaz et al., 1968). Bryophytes and filamenous chlorophytes were especially favoured at regulated sites.

MACROINVERTEBRATES

Studies of macroinvertebrate communities in regulated streams may provide considerable insight into the ecological requirements of the benthic fauna. The most productive locations for study are regulated lotic systems which are otherwise relatively pristine, and where severe conditions such as oxygen depletion do not occur. The abundance of macroinvertebrates in such waters may be elevated or depressed compared to natural streams of the region; species diversity is almost invariably reduced; and the taxonomic composition is greatly altered (Table 4). Entire groups (e.g., stoneflies, heptageniid mayflies) may be absent immediately below the dam (Ward, 1976c). Non-insects (e.g., snails, amphipods) tend to be favoured below deep release dams (Ward and Short, 1978). Such generalizations, however, have been based nearly exclusively on studies of the middle reaches of temperate zone streams (see Ward and Stanford, 1979a). Few comprehensive data are available for regulated streams of high or equatorial latitudes, and there is a general paucity of information on effects of impoundment in either headwaters or the lower reaches of large rivers.

The direct and indirect effects of thermal and flow modifications on environmental conditions in regulated streams are thought to account for much of the observed modifications in the zoobenthic community (Ward and Stanford, 1979b). In addition, truncation of detrital transport, increased autochthonous plant production, and contributions of limnetic seston, may greatly alter trophic dynamics in regulated streams (Ward and Short, 1978, Webster et al., 1979; Short and Ward, 1980; Kondratieff and Voshell, 1981).

The modified thermal regime below deep-release dams may be a major factor contributing to alterations of the macroinvertebrate community, especially in streams with otherwise favourable conditions (Pearson et al., 1968; Penaz et al., 1968; Hoffman and Kilambi, 1971; Spence and Hynes, 1971a; Lehmkuhl, 1972; Ward, 1974, 1976b; Gore, 1977). Ward (1976b; and Ward and Stanford, 1979b) developed a conceptual model relating the modified thermal regime below dimictic deep-release storage reservoirs to ecological interrelationships hypothesized as responsible for reduced species diversity of macroinvertebrates. Many lotic species in the temperate zone evolved in response to natural thermal heterogeneity (see Ward and Stanford, 1982b). For example, the temperature regime of regulated streams fails to provide appropriate stimuli to cue life cycle phenomena for some species (Lehmkuhl, 1972; Ward, 1976b). Such species will be eliminated, and only those species preadapted to regulated stream temperatures (e.g., Springbrook forms) will find favourable thermal conditions (Ward and Short, 1978). Other species for which the thermal regime is suboptimal may be eliminated by low growth efficiency, reduced fecundity, shifts in predator-prey interactions, or competitive exclusion (Ward, 1976b). Because the niche of a species may change throughout the life cycle, the temporal spacing of overlapping generations (resulting from extended emergence under more constant temperatures) may occupy niches that would have been available for other species. Shallow or surface-release reservoirs may elevate downstream summer temperature to the extent of endangering the indigenous cold water fauna (Fraley, 1979). Life histories below surface-release dams may exhibit subtle, but significant alterations (Kondratieff and Voshell, 1981).

The degree of flow constancy appears to largely determine macroinvertebrate abundance in regulated streams (Ward, 1976a; Ward and Stanford, 1979b). Extremely high densities have been recorded below deep-release (Ward, 1974) and surface-release (Ward and Short, 1978) reservoirs where flow constancy prevailed. Severe flow fluctuations may deplete the fauna directly or indirectly by effects on the substrate and the food base, and by reducing habital diversity (e.g., eliminating accumulations of sedimentary detritus). Macroinvertebrates exhibit considerable taxonomic differences in susceptibility to stranding and tolerence to exposure (Fisher and LaVoy, 1972; Brusven et al., 1974), which alters community structure in stream reaches subjected to short-term flow variation. Drift of stream organisms may be induced by both increasing and decreasing discharge (Anderson and Lehmkuhl, 1968; Minshall and Winger, 1968; Brooker and Hemsworth, 1978) which may conceivably deplete populations below dams, especially in stream reaches without tributaries to supply colonizers to the main channel.

Enhanced flow constancy generally leads to dense populations of zoobenthos due to increased bank and bed stability, and increases in the food base. Dense macrophyte beds which may develop under such flow conditions provide current refugia for species normally unable to maintain populations in high gradient streams (Ward, 1974, 1976a). A constant discharge pattern, especially if associated with reduced total flow, may have deleterious effects on the receiving stream (Eustis and Hillen, 1954). Aquatic plants may reach nuisance proportions. Conversely, the absence of flushing action by periodic high discharge may result in siltation with associated adverse effects on plant and animal components. Intragravel flow may be reduced as substrate interstices accumulate fine materials, thus reducing the hyporheic zone which provides an important habitat for benthic species as well as incubation sites for fish eggs and larvae. Reduced flow may result in extreme temperatures detrimental to the benthos. See Ward (1976a) for a detailed discussion of the interrelated effects of various flow modifications on stream conditions and lotic organisms. Ward and Stanford (1982c) specifically address the influence of discharge pattern on thermal conditions.

An enhanced community of filter-feeders characterizes streams below surface-release impoundments and natural lakes. Net-spinning caddisflies (Trichoptera) and blackflies (Simuliidae) may cover virtually the entire suitable substrate at certain seasons. Other filter-feeders such as bryozoans and sponges may attain high populations under certain conditions (Ward and Short, 1978). Shredder invertebrates which feed on coarse detritus (often terrestrial leaf litter) are reduced in abundance due to the elimination of detrital transport from upper reaches (Short and Ward, 1980).

Although invertebrates may be adversely affected by gas supersaturation (Weitkamp and Katz, 1980), aquatic insects appear relatively tolerant (Montgomery and Fickeisen, 1979). Insects exhibited increased buoyancy (by external adherence of entrained air bubbles) when exposed to conditions simulating gas supersaturated waters in stilling basins below dams (Montgomery and Fickeisen, 1979). Species specific differences in flotation induced by supersaturated waters could alter the taxonomic composition of benthos in regulated streams.

FISHES

In addressing the influence of stream regulation on fishes of running waters a distinction must be made between resident fishes, and migratory species for which dams pose additional problems. Fishes which regularly migrate between fresh water and the sea to spawn are of two types. Species such as salmon which enter fresh water to spawn are termed anadromous, whereas catadromous fishes, such as eels, migrate into salt water to spawn. The discussion herein will concentrate on the effects of stream regulation on anadromous migrants (Table 5) and resident fishes (Table 6). Dams are less of an obstacle for eels, the major catadromous species of economic importance, because of the vagility of upstream migrating elvers (Baxter and Glaude, 1980).

Table 5 SOME PROBLEMS PRIMARILY ASSOCIATED WITH MIGRATION OF ANADROMOUS FISHES, ENGENDERED BY STREAM REGULATION. PARENTHESES INDICATE SERIOUS LIMITATIONS TO AVAILABLE MITIGATIVE STRATEGIES (see text).

	Adults	Juveniles	Mitigative Strategies
Blockage	×	—	(×)
Increased passage time	×	×	(×)
Reduced spawning area	×	—	—
Inappropriate stimuli	×	×	×
Turbine mortality	—	×	×
Predation losses	×	×	(×)
Gas supersaturation	×	×	×
Stratified reservoirs	×	×	—
Stranding	×	×	×

Dams block upstream spawning migration and impoundments reduce the area of stream substrate available for spawning. For example, less than 30 per cent of the original habitat of the Columbia River Basin remains accessible to anadromous salmonids due to construction of mainstream dams (Robinson, 1978). If migratory movements are not completely blocked, the length of time required to reach spawning grounds is increased by stream regulation. Regulated streams may not provide the flow or thermal stimuli to appropriately cue migratory movements. If the flushing action of high flows is eliminated, the substrate may be rendered unsuitable for incubation of eggs or fry. Conversely, the erosive power of clear water releases may sometimes remove spawning substrate (Boles, 1981).

Juveniles may be significantly delayed in their downstream migration. Raymond (1979) attributed a nearly one-month delay in downstream migrating juveniles to the construction of dams on the Snake River, a major tributary of the Columbia River. Survival of juvenile chinook salmon has, over a given length of river, declined from 80-90% to 33% since the completion of additional dams. During low flow years, most juvenile mortality resulted from passage through the turbines, increased predation, and delays in passing through reservoirs, whereas gas supersaturation accounted for most of the losses during years of high discharge. Mitigation strategies may reduce such losses. Screens may be installed to prevent juveniles from passing through the turbines, and spillway deflectors and other devices are available to reduce losses from gas bubble disease (Weitkamp and Katz, 1980). Fish ladders have been only partially successful. In some instances, adults and juveniles have been captured and transported by truck around dams. Present methods, in some cases, may not be sufficient to preserve the anadromous fishery above the dam (Geen, 1975; Mundle, 1979). However, Atlantic salmon and American shad have been restored in the highly regulated Connecticut River (711 dams) after an absence of almost 200 years (Blakely et. al., 1979).

Resident stream fish communities are also modified by regulation (Table 6). Four species of cyprinids which occurred in a river upstream from an impoundment in Canada were absent below the dam, although some other species greatly increased in abundance in the tailwaters (Spence and Hynes, 1971b). Edwards (1978) also found a reduction in fish species diversity, compared to preimpoundment records, in a Texas river. A species of darter which formerly bred during the cold part of the year exhibited year-round breeding in the tailwater. Total fish biomass above the reservoir (848 g) was twice as great as in the tailwater (413 g) per collecting effort. Exotic (introduced) species comprised a greater percentage of total fish species below the dam (28%) than above the reservoir (14%).

Table 6 SOME EFFECTS OF STREAM REGULATION ON RESIDENT FISHES OF THE RECEIVING STREAM.

Standing crop	Variable
Species composition	Altered
Species diversity	Reduced
Exotic Species	Increased
Growth	Poor to excellent
Spawning Success	Temperature and flow dependent

Authors of the above studies attributed modifications in the thermal regime as largely responsible for the altered tailwater fish communities. The species eliminated from the downstream section of the Canadian River were those near the northernmost limits of their ranges. Spring and summer temperatures were not sufficient for spawning behaviour below the deep-release dam. Edwards (1978) also attributed alteration in tailwater fish communities to the thermal consequences of releasing water from the hypolimnion. Pfitzer (1967) refers to the failure of reproduction of warm water species in the cold tailwaters below TVA reservoirs. Richmond and Zimmerman (1978), using electrophoretic techniques, isolated a "cool-water" isozyme of malate dehydrogenase (MDH) in populations of red shiners in a tailwater in Texas. There is some evidence of selection for a more plastic genotype in populations occurring in tailwaters exhibiting unpredictable environmental conditions.

Impaired gametogenesis in sturgeon below a dam in Russia was attributed to excessive energy expenditures in winter necessitated by altered temperatures and discharge (Artyukhin et al., 1979). Grizzle (1981) reported a higher incidence of lesions in fishes below a hypolimnial release dam than in populations further downstream.

Acutely lethal conditions may also be induced by stream regulation. The release of oxygen depleted water and associated reduced substances (e.g., H_2S) may eliminate fishes from tailwaters. Thermal shock may result from shifting release depths from one temperature stratum to another. If, because of receding water levels in the reservoir, cold water is released only during spring and early summer, the tailwater will be unsuitable for either a trout or a warm-water fishery (Pfitzer, 1967).

Bishop and Bell (1978) documented high fish mortalities when water flow below a dam was terminated for short periods during construction. Up to 270 dead specimens per m^2 were collected from small temporary pools following flow cessation. In addition to directly affecting fishes, flow fluctuations may greatly reduce tailwater productivity, especially since the areas richest in fish food organisms (riffles) are the first to be exposed. These same riffle areas are used for spawning. Rainbow trout redds in the stream below a dam in Tennessee were invariably constructed in water less than 30 cm deep (Parsons, 1955). If spawning occurred during low water, the redds were destroyed during periods of high discharge; redds constructed during high water were exposed during low discharge. The use of small weirs, to maintain fish habitat during periods of flow reduction, is being investigated as a mitigation strategy for regulated Norwegian rivers (Lillehammer and Saltveit, 1979).

Nonetheless, highly productive put-and-take tailwater fisheries have been established, even below hydroelectric dams. Food for tailwater fishes may be primarily of reservoir derivation rather than from tailwater production (Walburg et al., 1971). Plankton discharged from the dam may provide an important food source for reservoir fishes, although not if water is released from the hypolimnion (Ward, 1975). Crisp et al.

(1978) found zooplankton in trout stomachs only when water was released from the dam at a depth of 11 meters or less below the reservoir surface. Pfitzer (1967) reported excellent growth of trout in tailwaters below reservoirs populated with threadfin shad. Large numbers of young-of-the-year shad pass through the penstocks during the winter months. By stocking trout in the tailwaters prior to the occurrence of the shad, the fish are able to utilize them as forage. Rapid winter growth and high survival provides an abundance of large trout for the spring fishing season.

MANAGEMENT IMPLICATIONS

Lotic systems and stream organisms have evolved in response to heterogeneous environmental conditions. Both predictable (e.g., the annual temperature pattern) and unpredictable (e.g., major flood events) variations are important in maintaining the structure and functions of stream ecosystems. Stream regulation tends to reduce environmental heterogeneity and temporally disrupt natural biotic and abiotic patterns in the receiving stream.

Management of regulated streams should, therefore, be predicated upon an understanding of natural lotic ecosystems, as well as knowledge of limnological phenomena occurring within impoundments and ecological responses of downstream reaches. The "Serial Discontinuity Concept" (Ward and Stanford, 1982a) provides a hypothetical framework to evince the basin-wide effects of impoundment in an attempt to attain a broad theoretical perspective of regulated lotic ecosystems. Because ecological processes vary as a function of position along the longitudinal stream profile (Vannote et al., 1980), an impoundment in the headwaters will have quite different effects on the receiving stream environment than a comparable impoundment on the middle or lower reaches of a river system (Ward and Stanford, 1982a). The cumulative effects of multiple impoundment remain virtually uninvestigated despite the presence of a series of dams on many river systems (Stanford and Ward, 1979).

The manager has only two operational variables, discharge and release depth, under his direct and immediate control. The ecological implications of either variable are, however, profound as stressed in the various sections of this paper. Varying release depth influences such factors as nutrients, seston, dissolved oxygen, toxins, and the temperature of water discharged from the dam. Control of the flow regime has a myriad of hydrodynamic and other ramifications which have major effects on downstream biota. Dams with selective depth withdrawal capabilities may be used to meet managerial objectives (e.g., eutrophication control), and provide systems amenable to experimental manipulation of factors controlling the structure and function of stream ecosystems. The plethora of stream regulation projects necessitates a fuller understanding of the ecological ramifications of various operational schemes, if conditions in the receiving stream environment are to be optimized within the limits posed by other managerial objectives.

ACKNOWLEDGEMENTS

Appreciation is extended to Dr. Robert W. Pennak, Department of Environmental Population and Organismic Biology, University of Colorado, for critically reviewing the manuscript. Thanks are due Miss Nancy Flaming and Mrs. Nancy Heisler for typing the manuscript. This paper was prepared while the author was supported by the Colorado Experiment Station.

REFERENCES

Adams, D.B. (1975) Predicted and observed temperature and water-quality changes of lakes and reservoirs. In: Publ. No. 117 de l'Association Internationale des Sciences Hydrologiques, Tokyo, 873–882.

Anderson, N.H. and Lehmkuhl, D.M. (1968) Catastrophic drift of insects in a woodland stream. *Ecology*, 49, 198–206.

Armitage, P.D. (1979) Stream regulation in Great Britain. In: Ward, J.V and Stanford, J.A. (eds.) *The Ecology of Regulated Streams*, Plenum Press, New York, 165–181.

Artyukhin, Ye. N., Sukhoparova, A.D. and Fimukhina, L.G. (1979) The gonads of the sturgeon, *Acipenser guldenstadti*, in the zone below the dam of the Volgograd water engineering system, *J. Ichthyology*, 78, 912–923.

Ashton, G.D. (1979) River Ice. *Am. Sci.*, 67, 38–45.

Balon, E.K. (1978) Kariba: The dubious benefits of large dams. AMBIO, 7, 40–48.

Baxter, R.M. (1977) Environmental effects of dams and impoundments. *Ann. Rev. Ecol Syst.*, 8, 255–283.

Baxter, R.M. and Glaude, P. (1980) Environmental effects of dams and impoundments in Canada: Experience and prospects. *Can. Bull. Fish. Aquat. Sci.*, No. 205, 34 pp.

Beard, L.R. and Willey, R.G. (1970) An approach to reservoir temperature analysis. *Water Resources Res.*, 6, 1335–1345.

Beiningen, K.T. and Ebel, W.J. (1970) Effect of John Day Dam on dissolved nitrogen concentrations and salmon in the Columbia River. *Trans. Am. Fish. Soc.*, 99, 664–671.

Bishop, J.E. (1973) *Limnology of a Small Malayan river Sungai Gombak*, Dr. W. Junk, The Hague, 493 pp.

Bishop, K.A. and Bell, J.D. (1978) Observations on the fish fauna below Tallowa Dam (Shoalhaven River, New South Wales) during river flow stoppages. *Austr. J. Mar. Freshwater Res.*, 29, 543–549.

Blakeley, L.B., Saunders, W.P. and Kirshen, P.H. (1979) Effects of historical and anticipated development on fish populations in the Connecticut River, Massachusetts. In: Driver, E.E. and Wunderlich, W.O. (eds.) *Environmental Effects of Hydraulic Engineering Works*, Tennessee Valley Authority, Knoxville, Tennessee, 103–114.

Boles, G.L. (1981) Macroinvertebrate colonization of replacement substrate below a hypolimnial release reservoir. *Hydrobiologia*, 78, 133–146.

Bratranek, A. (1953) Influence of water temperature regime in river valley reservoirs on the changes in temperature of outflowing water. *Vod. hospodar.*, 3, 350–352 (in Czech.).

Brooker, M.P. and Hemsworth, R.J. (1978) The effect of the release of an artificial discharge of water on invertebrate drift in the R. Wye, Wales. *Hydrobiologia*, 59, 155–163.

Brown, G.W. (1971) Water temperature in small streams as influenced by environmental factors and logging. In: Krygier, J.T. and Hall, J.D. (eds.) *Forest Land Uses and Stream Environment*, Oregon State University, Corvallis, 175–181.

Brusven, M.A. MacPhee, C. and Biggam, R. (1974) Effects of water fluctuation on benthic insects. In: *Anatomy of a River*, Pacific Northwest River Basins Commission Report, Vancouver, Washington, 67–79.

Buma, P.G. and Day, J.C. (1975) Reservoir-induced plant community changes: A methodological exploration. *J. Envir. Management*, 3, 219–250.

Buma, P.G. and Day, J.C. (1977) Channel morphology below reservoir storage projects. *Envir. Conserv.*, 4, 279–284.

Clifford, H.F. (1978) Descriptive phenology and seasonality of a Canadian brownwater stream. *Hydrobiologia*, 58, 213–231.

Cole, G.A. (1979) *Textbook of Limnology*, Mosby, St. Louis, 426 pp.

Collings, M.R. (1969) Temperature analysis of a stream. *U.S. Geol. Surv. Prof. Paper* 650–B, B174–B179.

Crisp, D.T. (1977) Some physical and chemical effects of the Cow Green (Upper Teesdale) impoundment. *Freshwat. Biol.*, 7, 109–120.

Crisp, D.T. Mann, R.H.K. and McCormack, J.C. (1978) The effects of impoundment and regulation upon the stomach contents of fish at Cow Green, Upper Teesdale. *J. Fish Biol.*, 12, 287–301.

Davies, B.R. (1979) Stream regulation in Africa: A review. In: Ward, J.V. and Stanford, J.A. (eds.) *The Ecology of Regulated Streams*, Plenum Press, New York, 113–142.

Dolan, R. Howard, A. and Gallenson, A. (1974) Man's impact on the Colorado River in the Grand Canyon. *Am. Sci.*, 62, 392–401.

Ebel, W.J. (1969) Supersaturation of nitrogen in the Columbia River and its effect on salmon and steelhead trout. *U.S. Nat. Marine Fisheries Service Fisheries Bull.*, 68, 1–11.

Edington, J.M. (1965) Some observations on stream temperature. *Oikos*, 15, 265–273.

Edwards, R.J. (1978) The effects of hypolimnion reservoir releases on fish distribution and species diversity. *Trans. Am. Fish. Soc.*, 107, 71–77.

Eustis, A.B. and Hillen, R.H. (1954) Stream sediment removal by controlled reservoir releases. *Prog. Fish. Cult.*, 16, 30–35.

Fisher, S.G. and LaVoy, A. (1972) Differences in littoral fauna due to fluctuating water levels below a hydroelectric dam. *J. Fish. Res. Board Can.*, 29, 1472–1476.

Fraley, J.J. (1979) Effects of elevated stream temperatures below a shallow reservoir on a cold water macroinvertebrate fauna. In: Ward, J.V. and Stanford, J.A., (eds.) *The Ecology of Regulated Streams*, Plenum Press, New York, 257–272.

Geen, G.H. (1975) Ecological consequences of the proposed Moran Dam on the Fraser River. *J. Fish. Res. Board Can.*, 32, 126–135.

Geijskes, D.C. (1942) Observations on temperature in a tropical river. *Ecology*, 23, 106–110.

Golterman, H.L. (1975) *Physiological Limnology*, Elsevier, Amsterdam, 489 pp.

Gordon, J.A. and Morris, J.W. (1979) Dissolved oxygen depletion mechanisms operating in the metalimnion of a deep impoundment. In: Driver, E.E. and Wunderlich, W.O. (eds.) *Environmental Effects of Hydraulic Engineering Works*, Tennessee Valley Authority, Knoxville, Tennessee, 29–38.

Gore, J.A. (1977) Reservoir manipulations and benthic macroinvertebrates in a prairie river. *Hydrobiologia*, 55, 113–123.

Grelsson, G. and Nilsson, C. (1980) Colonization by *Pinus sylvestris* of a former middle-geolittoral habitat on the Umealven River in northern Sweden, following river regulation for hydro-electric power. *Holarct. Ecol.*, 3, 124–128.

Grizzle, J.M. (1981) Effects of hypolimnetic discharge on fish health below a reservoir. *Trans. Am. Fish. Soc.*, 110, 29–43.

Hannan, H.H. (1979) Chemical modifications in reservoir-regulated streams. In: Ward, J.V. and Stanford, J.A. (eds.) *The Ecology of Regulated Streams*, Plenum Press, New York, 75–94.

Hannan, H.H. Barrows, D.B. Fuchs, I.R. Segura, R D. and Whitenberg, D.C. (1979) Limnological and operational factors affecting water quality in Canyon Reservoir, Texas. In: Driver, E.E. and Wunderlich, W.O. (eds.) *Environmental Effects of Hydraulic Engineering Works*, Tennessee Valley Authority, Knoxville, Tennessee, 39–48.

Hannan, H.H. Young, W.C. and Mayhew, J.J. (1973) Nitrogen and phosphorus in a stretch of the Guadalupe River, Texas, with five main-stream impoundments. *Hydrobiologia*, 43, 419–441.

Hannan, H.H. and Young, W.J. (1974) The influence of a deep-storage reservoir on the physicochemical limnology of a central texas river. *Hydrobiologia*, 44, 177–207.

Harrison, A.D. (1965) River zonation in southern Africa. *Arch. Hydrobiol.*, 61, 380–386.

Henricson, J. and Müller, K. (1979) Stream regulation in Sweden with some examples from central Europe. In: Ward, J.V. and Stanford, J A. (eds.) *The Ecology of Regulated Streams*, Plenum Press, New York, 183–199.

Hoffman, C.E. and Kilambi, R.V. (1971) Environmental changes produced by cold-water outlets from three Arkansas reservoirs. *Water Resources Research Center Publ.* No. 5., University of Arkansas, Fayetteville, 169 pp.

Holmes, N.T H. and Whitton, B.A (1977) The macrophytic vegetation of the River Tees in 1975: observed and predicted changes. *Freshwat. Biol.*, 7, 43–60.

Holmes, N.T.H. and Whitton, B.A. (1981) Phytobenthos of the River Tees and its tributaries. *Freshwat. Biol.*, 11, 139–163.

Isom, B.G. (1971) Effects of storage and mainstream reservoirs on benthic macroinvertebrates in the Tennessee Valley. In: Hall, G.E. (ed.) *Reservoir Fisheries and Limnology*, Am. Fish. Soc., Washington, D.C., 179–191.

Jarnefelt, V.H. (1948) Der Einfluss der Stromschnellen auf den Sauerstoff und Kohlensaueregehalt und das pH des Wassers im Flusse Vuoski. *Verh. Internat. Verein. Limnol.*, 10, 210–215.

Kellerhalls, R., Church, M. and Davies, L.B. (1979) Morphological effects of interbasin river diversions. *Can. J. Civil Eng.*, 6, 18–31.

Klomp, R. (1976) Limnological research for the management of water quality in storage reservoirs. *Hydrobiol. Bull.*, 10, 129–135.

Kondratieff, B.C. and Voshell, J.R. Jr. (1981) Influence of a reservoir on the life history of the mayfly Heterocloeon curiosum (McDunnough) (Ephemeroptera: Baetidae). *Can. J. Zool.*,59, 305–314.

Krenkel, P.A., Lee, G.F. and Jones, R.A. (1979) Effects of TVA impoundments on downstream water quality and biota. In: Ward, J.V. and Stanford, J.A. (eds.) *The Ecology of Regulated Streams*, Plenum Press, New York, 289–306.

Kroger, R.L. (1973) Biological effects of fluctuating water levels in the Snake River, Grand Teton National Park, Wyoming, *Am. Mid. Nat.*, 89, 478–481.

Lavis, M.E. and Smith, K. (1972) Reservoir storage and the thermal regime of rivers, with special reference to the River Lune, Yorkshire. *Sci. Tot. Environ.*, 1, 81–90.

Lehmkuhl, D.M. (1972) Change in thermal regime as a cause of reduction of benthic fauna downstream of a reservoir. *J. Fish. Res. Board. Can.*, 29, 1329–1332.

Leopold, L.B., Wolman, M.G. and Miller, J.P. (1964) *Fluvial Processes in Geomorphology*, Freeman, San Francisco, 522 pp.

Lillehammer, A. and Salveit, S.J. (1979) Stream regulation in Norway. In: Ward, J.V. and Stanford, J.A. (eds.) *The Ecology of Regulated Streams*, Plenum Press, New York, 201–213.

Lind, O.T. (1971) The organic matter budget of a central Texas reservoir. In: Hall, G.E. (ed.) *Reservoir Fisheries and Limnology*, Am. Fish Soc., Washington, D.C., 193–202.

Lindroth, A. (1957) Abiogenic gas supersaturation river water. *Arch. Hydrobiol.*, 53, 589–597.

Love, S.K. (1961) Relationship of impoundment to water quality. *J. Am. Water Works Assoc.*, 53. 559–568.

Lowe, R.L. (1979) Phytobenthic ecology and regulated streams. In: Ward, J.V. and Stanford, J.A. (eds.) *The Ecology of Regulated Streams*, Plenum Press, New York, 25–34.

Macan, T.T. (1958) The temperature of a small stony stream. *Hydrobiologia*, 12, 89–106.

Maciolek, J.A. and Needham, P.R. (1951) Ecological effects of winter conditions on trout and trout foods in Convict Creek, California, 1951. *Trans. Am. Fish. Soc.*, 81, 202–217.

Mackichan, K.A. (1967) Diurnal temperature fluctuations of three Nebraska streams. *U.S. Geol. Surv. Prof. Paper* 575–B, B233–B234.

Mancy, K.H. (1979) The environmental impact of the Aswan high dam. In: Driver, E.E. and Wunderlich, W.O. (eds.) *Environmental Effects of Hydraulic Engineering Works*, Tennessee Valley Authority, Knoxville, Tennessee, 422–434.

Marcus, M.D. (1980) Periphytic community response to chronic nutrient enrichment by a reservoir discharge. *Ecology*, 61, 387–399.

Martin, D.B. and Arneson, R.D. (1978) Comparative limnology of a deep-discharge reservoir and a surface-discharge lake on the Madison River, Montana. *Freshwat. Biol.*, 8, 33–42.

Meekin, T.K. and Allen, R.L. (1974) Nitrogen saturation levels in the mid-Columbia River, 1965–1971. *Washington Dept. Fisheries Techn. Report*, 12, 32–77.

Minshall, G.W. and Winger, P.V. (1968) The effect of reduction in stream flow on invertebrate drift. *Ecology*, 49, 580–582.

Montgomery, J.C. and Fickeisen, D.H. (1979) Tolerance and buoyancy of aquatic insect larvae exposed to gas supersaturated water. *Envir. Entomol.*, 8, 655–657.

Mordukhai-Bultovskoi, F.D. (ed.) (1979) *The River Volga and its Life*, Dr. W. Junk, The Hague, 473 pp.

Müller, K. (1962) Limnologisch-fischereibiologische Untersuchungen in regulierten Gewassern Schwedisch-Lapplands. *Oikos*, 13, 125–154.

Mundie, J.H. (1979) The regulated stream and salmon management. In: Ward, J.V. and Stanford, J.A. (eds.) *The Ecology of Regulated Streams*, Plenum Press, New York, 307–319.

Neel, J.K. (1963) Impact of reservoirs. In: Frey, D.G. (ed.) *Limnology in North America*, University of Wisconsin Press, Madison, 575–593.

Nielson, L.J. (1967) Evolution of pre-impoundment conditions for prediction of stored water quality. In: *Reservoir Fishery Resources Symposium*, Am. Fish. Soc., Washington, D.C., 153–168.

Nishizawa, T. and Yamabe, K. (1970) Change in downstream temperature caused by the construction of reservoirs. Part 1, *Tokyo Univ. Sci. Reps. Sect. C*, 10, 27–42.

Parsons, J.W. (1955) The trout fishery of the tailwater below Dale Hollow Reservoir. *Trans. Am. Fish. Soc.*, 85, 75–92.

Paulson, L.T., Baker, J.R. and Deacon, J.E. (1979) Potential use of hydroelectric facilities for manipulating the fertility of Lake Mead. In: *The Mitigation Symposium*, U.S. Dept. Agric., Fort Collins, Colorado, 296–300.

Pearson, W.D., Kramer, R.H. and Franklin, D.R. (1968) Macroinvertebrates in the Green River below Flaming Gorge Dam, 1964–65 and 1967. *Proc. Utah Acad. Sci. Arts Lett.*, 45, 148–167.

Penaz, M., Kubicek, F., Marvan, P. and Zelinka, M. (1968) Influence of the Vir River Valley Reservoir on the hydrobiological and ichthyological conditions in the River Svratka. *Acta Sc. Nat. Brno*, 2(1), 1–60.

Pennak, R.W. (1949) Annual limnological cycles in some Colorado Reservoir lakes. *Ecol. Monogr.*, 19, 233–267.

Petts, G.E. (1980) Long-term consequences of upstream impoundment. *Envir. Conserv.*, 7, 325–332.

Pfitzer, D.W. (1967) Evaluation of tailwater fishery resources resulting from high dams. In: *Reservoir Fishery Resources Symposium*, Am. Fish. Soc., Washington, D.C., 477–488.

Rada, R.G. and Wright, J.C. (1979) Factors affecting nitrogen and phosphorus levels in Canyon Ferry Reservoir, Montana, and its effluent Waters. *Northwest Sci.*, 53, 213–220.

Ramadan, F. (1979) The effect of the Aswan High Dam on the Nile water quality. In: Driver, E.E. and Wunderlich, W.O. (eds.) *Environmental Effects of Hydraulic Engineering Works*, Tennessee Valley Authority, Knoxville, Tennessee, 446–458.

Raymond, H.L. (1979) Effects of dams and impoundments of migrations of juvenile chinook salmon and steelhead from the Snake River, 1966–1975. *Trans. Am. Fish. Soc.*, 108, 505–529.

Richmond, M.C. and Zimmerman, E.G. (1978) Effect of temperature on activity of allozymic forms of supernatant malate dehydrogenase in the red shiner, *Notropis lutrensis. Comp. Biochem. Physiol.*, 61B, 415–419.

Ridley, J.E. and Steel, J.A. (1975) Ecological aspects of river impoundments. In: Whitton, B.A. (ed.) *River Ecology*, Blackwell, Oxford, 565–587.

Robinson, W.L. (1978) The Columbia: A river system under siege. *Oregon Wildl.*, 33, 3–7.

Ross, L.E. and Rushforth, S.R. (1980) The effects of a new reservoir on the attached diatom communities in Huntington Creek, Utah. U.S.A. *Hydrobiologia*, 68, 157–165.

Ruggles, C.P. and Watt, W.D. (1975) Ecological changes due to hydroelectric development on the Saint John River. *J. Fish. Res. Board Can.*, 32, 161–170.

Sheridan, W.L. (1961) Temperature relationships in a pink salmon stream in Alaska. *Ecology*, 42, 91–98.

Short, R.A. and Ward, J.V. (1980) Leaf litter processing in a regulated Rocky Mountain stream. *J. Fish. Aquat. Sci.*, 37, 123–127.

Simmons, G.M. Jr. and Voshell, J.R. Jr. (1978) Pre- and post-impoundment benthic macroinvertebrate communities of the North Anna River. In: Cairns, J. Jr., Benefield, E.F. and Webster, J.R. (eds.) *Current Prespectives on River-Reservoir Ecosystems*, N. Am. Benthological Soc., 45–61.

Simons, D.B. (1979) Effects of stream regulation on channel morphology. In: Ward, J.V. and Stanford, J.A. (eds.) *The Ecology of Regulated Streams*, Plenum Press, New York, 95–111.

Smith, K. (1972) River water temperatures—an environmental review. *Scott. Geogr. Mag.*, 88, 211–220.

Smith, K. and Lavis, M.E. (1975) Environmental influences on the temperature of a small upland stream. *Oikos*, 26, 228–236.

Soltero, R.A., Wright, J.C. and Horpestad, A.A. (1973) Effects of impoundment on the water quality of the Bighorn River. *Water Res.*, 7, 343–354.

Soltero, R.A., Wright, J.C. and Horpestad, A.A. (1974) The physical limnology of Bighorn Lake-Yellowtail Dam, Montana: Internal density currents. *Northwest Sci.*, 48, 107–124.

Spence, J.A. and Hynes, H.B.N. (1971a) Differences in benthos upstream and downstream of an impoundment. *J. Fish. Res. Board Can.*, 28, 35–43.

Spence, J.A. and Hynes, H.B.N. (1971b.) Differences in fish populations upstream and downstream of a mainstream impoundment. *J. Fish. Res. Board Can.*, 28, 45–46.

Symons, J.M., Weibel, S.R. and Robeck, G.G. (1965) Impoundment influences on water quality. *J. Am. Water Works Assoc*, 57, 51–75.

Templeton, W.L. and Coutant, C.C. (1971) Studies on the biological effects of thermal discharges from nuclear reactors to the Columbia River at Hanford. In: *Environmental Aspects of Nuclear Power Stations.* Internat. Atomic Energy Agency Symposium (IAEA–SM–146/33), 591–614.

Thibault, M. (1971) Ecologie d'un ruisseau a truites des Pyrenees-Atlantiques, le Lissuraga II.—Les fluctuations thermiques de l'eau; repercussion sur les periodes de sortie et la taille de quelques Ephemeropteres, Plecopteres et Trichopteres. *Ann. Hydrobiol*, 2, 241–274.

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J R. and Cushing, C.E. (1980) The river continuum concept. *Can. J. Fish. Aquat. Sci.*, 37, 130–137.

Vannote, R.L. and Sweeney, B.W. (1980) Geographic analysis of thermal equilibrium: a conceptual model for evaluating the effect of natural and modified. thermal regimes on aquatic insect communities. *Am. Nat.*, 115, 667–695.

Walburg, C.H., Kaiser, G.L. and Hudson, P.L. (1971) Lewis and Clark Lake tailwater biota and some relations of the tailwater and reservoir fish populations. In: Hall, G.E. (ed.) *Reservoir Fisheries and Limnology*, Am. Fish. Soc., Washington, D.C., 449–467.

Walker, K.F. (1979) Regulated streams in Australia: The Murray-Darling River system In: Ward, J.V. and Stanford, J.A. (eds.) *The Ecology of Regulated Streams*, Plenum Press, New York, 143–163.

Ward, J.V. (1974) A temperature-stressed stream ecosystem below a hypolimnial release mountain reservoir. *Arch. Hydrobiol.*, 74, 247–275.

Ward, J.V. (1975) Downstream fate of zooplankton from a hypolimnial release mountain reservoir. *Verh. Internat. Verein. Limnol.*, 19, 1798–1804.

Ward, J.V. (1976a) Effects of flow patterns below large dams on stream benthos: a review. In: Orsborn, J.F. and Allman, C.H. (eds.) *Instream Flow Needs Symposium*, Vol. II, *Am. Fish. Soc.*, Bethesda, Maryland, 235–253.

Ward, J.V. (1976b) Effects of thermal constancy and seasonal temperature displacement on community structure of stream macroinvertebrates. In: Esch, G.W. and McFarlane, R.W. (eds.) *Thermal Ecology II*, National Technical Information Service, Springfield, Virginia, 302–307.

Ward, J.V. (1976c) Comparative limnology of differentially regulated sections of a Colorado mountain river. *Arch. Hydrobiol.*, 78, 319–342.

Ward, J.V. and Dufford, R.G. (1979) Longitudinal and seasonal distribution of macroinvertebrates and epilithic algae in a Colorado springbrook-pond system. *Arch. Hydrobiol.*, 86, 284–321.

Ward, J.V. and Short, R.A. (1978) Macroinvertebrate community structure of four special lotic habitats in Colorado, U.S.A., *Verh. Internat. Verein. Limnol.*, 20, 1382–1387.

Ward, J.V. and Stanford, J.A. (eds.) (1979a) *The Ecology of Regulated Streams*, Plenum Press, New York, 398 pp.

Ward, J.V. and Stanford, J.A. (1979b) Ecological factors controlling stream zoobenthos with emphasis on thermal modification of regulated streams. In: Ward, J.V. and Stanford, J.A. (eds.) *The Ecology of Regulated Streams*, Plenum Press, New York, 35–55.

Ward, J.V. and Stanford, J.A. (1982a) The serial discontinuity concept of lotic ecosystems. In: Fontaine, T.D. and Bartell, S.M. (eds.) Proc. Symposium on *Dynamics of Lotic Ecosystems*, Augusta, Georgia (in Press).

Ward, J.V. and Stanford, J.A. (1982b) Thermal responses in the evolutionary ecology of aquatic insects. *Ann. Rev. Entomol.*, 27, (in press).

Ward, J.V. and Stanford, J.A. (1982c) Effects of reduced and perturbated flow below dams on fish food organisms in Rocky Mountain trout streams. In: Grover, J.H. (ed.) *Allocation of Fishery Resources*. Proceedings of a symposium Vichy, France (in press).

Webster, J.R., Benfield, E.F. and Cairns, J. Jr. (1979) Model predictions of effects of impoundment on particulate organic matter transport in a river system. In: Ward, J.V. and Stanford, J.A. (eds.) *The Ecology of Regulated Streams*, Plenum Press, New York, 339–364.

Weitkamp, D.E. and Katz, M. (1980) A review of dissolved gas supersaturation literature. *Trans. Am. Fish. Soc.*, 109, 659–702.

Wetzel, R.G. (1975) *Limnology*. Saunders, Philadelphia, 743 pp.

Wright, J.C. (1967) Effects of impoundments on productivity, water chemistry and head budgets of rivers. In: *Reservoir Fishery Resources Symposium*. Am. Fish. Soc., Washington, D.C., 188–199.

Wunderlich, W.O. (1971) The dynamics of density-stratified reservoirs. In: Hall, G.E. (ed.) *Reservoir Fisheries and Limnology*. Am. Fish. Soc., Washington, D.C., 219–231.

Young, W.C., Kent, D.H. and Whiteside, B.G. (1976) The influence of a deep storage reservoir on the species diversity of benthic macroinvertebrate communities of the Guadalupe River, Texas, *Texas, J. Sci.*, 27, 213–224.

Hydrobiologia
1982
missing

The influence of highway construction on the macroinvertebrates and epilithic algae of a high mountain stream

Leo D. Cline, Robert A. Short[1] & James V. Ward
Department of Zoology and Entomology, Colorado State University, Fort Collins, CO 80523, U.S.A.
[1] *Present address: Aquatic Station, Southwest Texas State University, San Marcos, TX 78666, U.S.A.*

Keywords: macroinvertebrates, epilithon, construction impact, mountain stream, Colorado

Abstract

The response of a high elevation Rocky Mountain stream to highway construction activities was investigated over a three-year period during the ice-free season. Suspended solids and the proportion of fine sediment in the substrate increased at impacted sites, but rapidly returned to levels similar to reference sites following cessation of construction activities. During snowmelt runoff when suspended solids levels increased, there was little or no sedimentation of fine particles, even in depositional areas. At impacted sites algal species diversity and the organic content of the epilithon were reduced, and the detrital component was increased. The epilithon recovered less rapidly than suspended solids or substrate. The macroinvertebrate community was altered by construction activities at some locations but not others, and was generally less severely affected than anticipated. However, where an alteration occurred, reduction in density, abundance, and diversity were apparent, and the taxonomic composition was modified. The severity of the response was a function of the flow regime and the timing and duration of the impact at a given site. The hydrologic regime and high gradient of the study stream appeared to ameliorate to some extent the potentially adverse effects of short-term perturbations engendered by highway construction activities.

Introduction

An understanding of the responses of biotic communities to perturbation is important not only in assessing man-induced changes, but also may provide insight into the structure and function of natural systems. Several recent volumes treat perturbation theory and processes of ecosystem recovery and restoration (e.g., Holdgate & Woodman 1978; Thorp & Gibbons 1978; Cairns 1980; Barrett & Rosenberg 1981). Virtually no data are available, however, on the responses of high elevation streams to anthropogenic alterations such as highway construction.

Paleolimnological evidence shows that road construction activities have had a demonstrable impact on aquatic organisms at least as long ago as Roman times (Hutchinson *et al.* 1970). Studies of contemporary activities have largely dealt with effects of logging roads on sediment production (e.g., Frederiksen 1970; Megahan & Kidd 1972). Few investigators have addressed the influence of highway construction on stream biota (King & Ball 1964; Burns 1972; Porter *et al.* 1974; Huckabee *et al.* 1975; Barton 1977; Extence 1978; Nixon 1978; Lenat *et al.* 1981), and even some of these studies treated biotic responses only secondarily. We know of no such previous study conducted on a high mountain stream.

In this paper we examine the effects of building a highway over a mountain pass in northern Colorado on the benthic algae and macroinvertebrates of a high elevation stream. It was our contention that the biotic components of such a lotic system would be especially sensitive to perturbation. Data on fishes were also collected, but because of special

Hydrobiologia 96, 149-159 (1982). 0018-8158/82/0962-0149/$02.20.

analytical problems related to the high mobility of these organisms, the results will be presented elsewhere.

Study area

Joe Wright Creek, a small tributary of the Cache la Poudre River, drains the east slope of Cameron Pass 113 km southwest of Fort Collins, Colorado. The stream segment studied ranges in elevation from 2 716 to 3 045 m a.s.l. with an average gradient of 3%. Cobble and boulder substrate predominate. Preconstruction riparian vegetation consisted of alder *(Alnus tenuifolia)*, willows (*Salix* spp.), englemann spruce *(Picea englemanni)*, and various grasses and sedges.

Stream waters were soft, low in total dissolved solids (TDS), and exhibited near neutral pH (Table 1). Waters were at least 90% saturated with oxygen at all locations. These variables, which were not appreciably affected by construction activities, exhibited values typical for headwater Rocky Mountain streams. A more detailed description of physico-chemical conditions is in preparation. The high discharge at Sites 7 and 8 resulted from withdrawal of impounded waters for irrigation during the sampling period.

Methods

Sampling was conducted biweekly over a three-year period (1975–1977) during the ice-free season (May–October). The sampling program was designed to follow the progressive upstream movement of construction activities.

Eight sites were sampled during the study (Fig. 1). Because of the sampling design, most sites were not sampled for the entire three year period. Study sites were located at riffles where sampling was conducted in fast water (erosional) areas. However, based upon results from the first two years, the sampling program was expanded during the third year to also include substrate and macroinvertebrate samples from slow water (depositional) areas at each location.

Construction activities crossed or paralleled Joe

Table 1. Mean values of selected physico-chemical variables during the ice-free season (May–October) for Joe Wright Creek, Colorado.

Variable	Study site							
	1	2	3	4	5	6	7	8
pH (mode)	7.3	7.2	7.2	7.2	7.2	7.2	7.2	7.3
Bound CO_2, mg/l	10.8	9.9	11.8	11.6	11.7	11.6	9.5	10.4
Dissolved O_2, mg/l	11.8	11.1	10.3	10.1	9.3	9.1	8.4	8.4
TDS, mg/l	33.2	30.6	25.4	30.5	27.0	30.9	36.8	31.9
Discharge, m^3/min	10.2	14.4	12.6	12.6	16.5	16.5	144.0	155.5

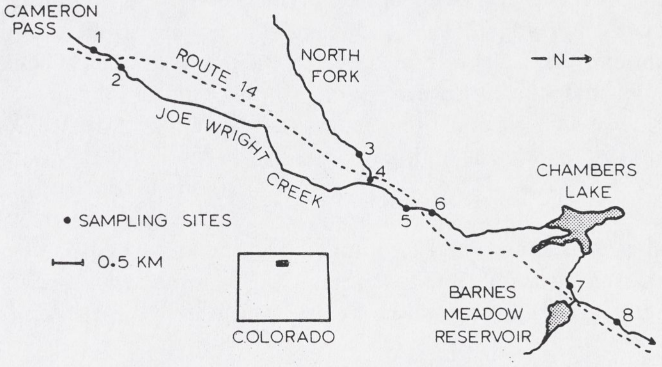


Fig. 1. Joe Wright Creek study area showing sampling sites.

Wright Creek over most of its 22 km length. Site pairs (a reference site and an impacted site) were sampled at locations of major perturbation. Construction activities included culvert installation (between Site pairs 1 and 2; and 3 and 4), bridge construction (between Site pair 5 and 6), channel realignment (between Site pairs 3 and 4; and 7 and 8). Even-numbered sites were affected by construction activities; odd-numbered sites served as reference locations.

Total suspended solids were sampled and analyzed according to *Standard Methods* (APHA *et al.* 1971). Substrate was collected by driving a 28 cm diameter core into the streambed and removing the upper 5 cm of substrate materials, which were dried and separated into size classes in the laboratory.

Epilithon, the attached plants and detritus associated with rock surfaces, was collected using a timed scraping technique (Ward 1974). The upper surfaces of at least ten cobble-sized rocks were scraped during a 5-min period. The percentage composition of the major epilithon components (algae, moss, lichen, detritus) was determined using a square petri dish with a gridded bottom. A Leitz phase contrast microscope, and a Leitz orthoplan microscope equipped with a Normarski phase interference attachment, were utilized for algal identification. Diatoms were cleared with 30% hydrogen peroxide prior to mounting on slides with Hyrax mounting medium. Diatoms, Chrysophyta, and Rhodophyta were identified to species level, or, in some cases, subspecies level; however, it was not always possible to distinguish the number of species within certain genera of Chlorophyta and Cyanophyta from preserved material. Epilithon dry weights were obtained after oven drying at 60 °C for 12 h and desiccating for at least 24 h. Loss on ignition values were determined by ashing the dried samples at 650 °C for 1 h followed by desiccation for at least 24 h prior to weighing.

Macroinvertebrates were collected with a Surber sampler 700 μm mesh) which enclosed 929 cm^2 of substrate. In 1975 and 1976, six samples were taken in fast water at each site on each date; in 1977 four replicates each were taken in fast and slow water areas. Biomass (wet weight) estimates were obtained by volumetric displacement, assuming a specific gravity of 1.0. No attempt was made to correct for loss of weight during preservation. Shannon diversity ($\bar{d}$) was computed from the formula:

$$\bar{d} = 3.3219/N - (N \log_{10}N - \Sigma N_i \log_{10}N_i),$$

where 3.3219 = conversion factor to base 2 logarithms,
N = total number of individuals,
N_i = total number of individuals of ith taxon.

Results

Suspended solids and substrate

Only two physico-chemical variables, suspended solids and substrate composition, were distinctly affected by construction activities. Increased discharge from snowmelt in June appreciably elevated suspended solids, except at Sites 7 and 8 below the storage reservoirs (Figs. 2 and 3). Levels were similar at Site pairs 1–2 and 5–6, but were 40 times higher at Site 4, where construction had already begun, than at reference Site 3. As runoff subsided, suspended solids decreased to less than 10 mg/l at reference Sites 1, 3 and 5; values were from 10 to 100 times greater at impacted Sites 2, 4 and 6. However, values at impacted sites approached reference levels within two weeks following cessation or major reduction of construction activities. Thus, recovery was relatively rapid, and apparently also persistent as exemplified by comparable mean suspended solids values at Sites 5 (23 mg/l) and 6 (17 mg/l) during 1976 when additional construction did not occur at this location. Clear water releases from Barnes Meadow Reservoir (which enters Joe Wright Creek between Sites 7 and 8) resulted in lower suspended solids levels at the impacted site than at the upstream reference location (Fig. 3). After construction ceased, values were again comparable at these two sites and remained so during 1976 when no construction occurred. The variations of suspended solids at impacted sites during construction resulted from the interactions of the flow regime and construction intensity, neither of which are indicated in Figs. 2 and 3.

At locations not regulated by impoundment (Sites 1–6), the proportion of fine sediment (defined as particles $\leqslant$2.0 mm diameter) in the substrate was generally lowest during snowmelt runoff. Site pairs exhibited comparable proportions of fine sediment during runoff and prior to construction. During construction, the relative contribution of fine sedi-

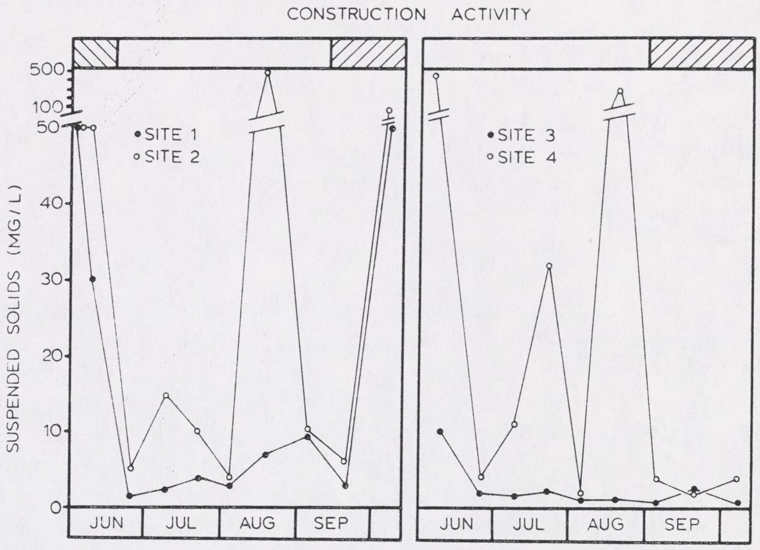


Fig. 2. Total suspended solids (mg/l) at impacted (Sites 2 and 4) and reference (Sites 1 and 3) locations on Joe Wright Creek, Colorado, 1977. Construction activity symbols: ▧ before construction; □ during construction; ▨ after construction.

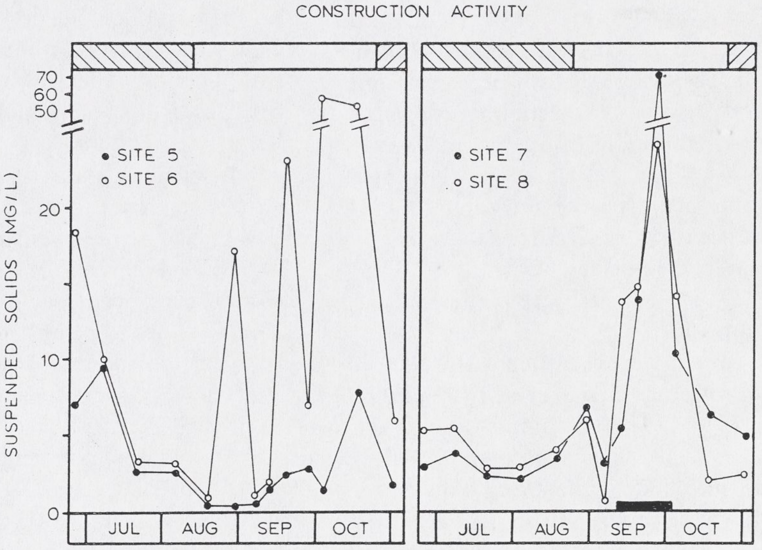


Fig. 3. Total suspended solids (mg/l) at impacted (Sites 6 and 8) and reference (Sites 5 and 7) locations on Joe Wright Creek, Colorado, 1975. (Solid bar on horizontal axis for Sites 7 and 8 indicates period of major discharge from intervening reservoir.) Construction activity symbols same as Fig. 2.

ments at impacted Sites 2 and 4 was twice that at reference Sites 1 and 3 (Fig. 4). Even greater disparities occurred between Site pair 5–6 (Fig. 5). However, by October 1976 (see Fig. 5), one year after construction at that location, the substrate of Site pair 5–6 exhibited comparable values indicative of relatively rapid recovery.

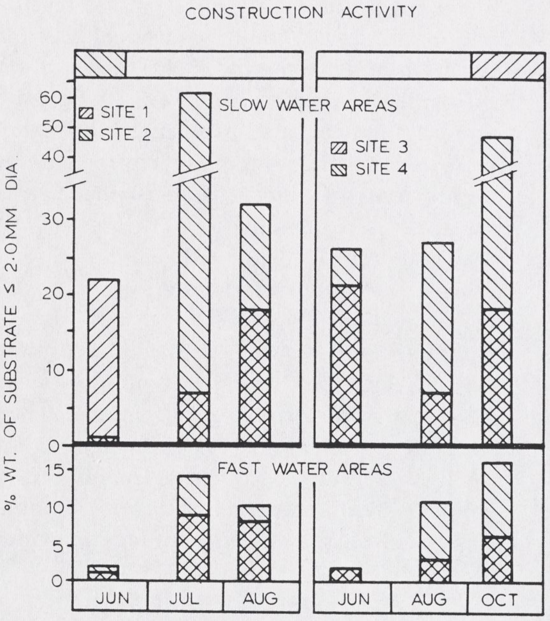


Fig. 4. Percentage dry weight of substrate less than 2.0 mm diameter from slow and fast water areas of Sites 1–4, Joe Wright Creek, Colorado, 1977. Construction activity symbols same as Fig. 2.

At Site pair 7–8 during 1975, the proportion of fine sediment in the substrate was twice as high at the reference location than at the downstream site prior to construction. Commencement of channel realignment reversed this pattern (Fig. 5). Subsequent reservoir releases, however, decreased the proportion of fine sediment at both of these sites. One year later, following a season without construction, the substrate composition was similar at Sites 7 and 8 (see Oct. 1976 on Fig. 5).

Substrate samples from slow water areas (Fig. 4) further elucidated the ameliorative role of current in cleansing the substrate. As discharge subsided during the 1977 season, the proportion of fine sediment in depositional areas at reference Site 1 progressively increased (1% in June, 7% in July, 17% in August). Impacted Site 2 contained 3–10 times more fine sediment than the depositional areas at Site 1; and 3–5 times more fine sediment than the erosional areas of Site 2. A similar relationship was found for Site pair 3–4, which began with comparable substrate in June (Fig. 4).

Therefore, the fine sediments suspended during snowmelt runoff were not deposited within the study reach, even in depositional areas, because of the high discharge at that time. As flow decreased, sedimentation occurred to a limited extent at refer-

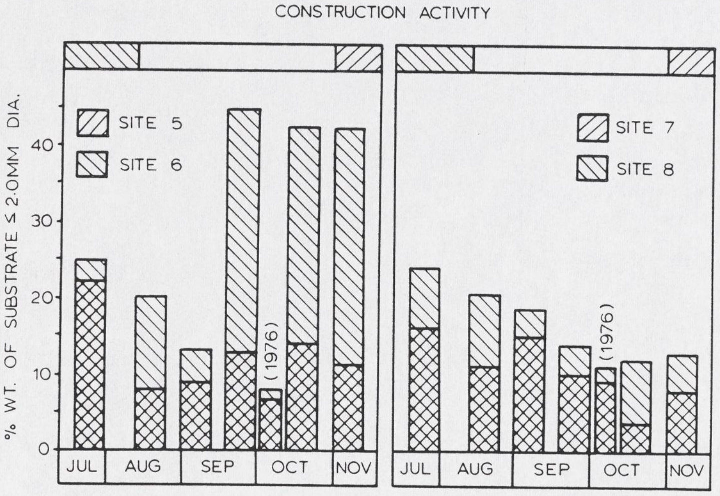


Fig. 5. Percentage dry weight of substrate less than 2.0 mm diameter from fast water areas of Sites 5–8, Joe Wright Creek, Colorado, 1975 and 1976. Construction activity symbols same as Fig. 2.

ence sites and to a greater extent at impacted locations, especially in slow water areas. A similar, but temporally displaced, pattern occurred at Sites 7 and 8 which were influenced by a regulated flow regime.

Epilithon

The living components (algae, moss, lichen) of the epilithon were generally less abundant, and the detrital component more abundant, at impacted sites than at the reference location of a given site pair (Table 2). The epilithon tended to collect fine sediment from the water column. Ash-free dry weight (AFDW), a reflection of the organic content of the epilithon, exhibited a general increase in absolute values downstream, with consistently lower values associated with the impacted location of each site pair (Table 2). The high values at Site 7 below the dam are a function of enhancement from stream regulation (see Ward 1976; Lowe 1979).

During the study 110 algal taxa in 5 divisions were collected. Diatoms (Bacillariophyta) accounted for 85 of the 110 algal taxa. The greatest number of total taxa (63) was collected at Site 1, the most upstream reference location. Fewer taxa were identified from the impacted site than from the reference location of each site pair except one (42 taxa at Site 5, 52 at Site 6).

The epilithon, while showing an effect from construction activities, exhibited a less dramatic response than expected. However, changes detected at impacted sites in 1975 persisted throughout the 1976 season, suggesting that recovery proceeds less rapidly than was the case for suspended solids and substrate.

Macroinvertebrate abundance

The general pattern of abundance exhibited by the total macroinvertebrate community was to begin at a very low density during snowmelt runoff in June, progressively increase through August or September, and subsequently decline (this pattern is undoubtedly partly a function of sampling efficiency as well as a reflection of life cycle phenomena).

Table 2. Summarized percentage compositon of major epilithon components and mean ash-free dry weight (mg) at study sites on Joe Wright Creek, Colorado, during 1975–1977[a]. Because of the sampling program, some sites were sampled in different years than other sites. Values from all site pairs are based on samples from the same years (see text).

		Study site							
		1	2	3	4	5	6	7	8
June	Algae	5	10	24	2	90(40)	50(30)	90(70)	90(25)
	Moss	0	0	0	0	0(50)	0(0)	0(0)	0(0)
	Lichen	0	0	0	0	0(0)	0(0)	0(0)	0(0)
	Detritus	95	90	76	98	10(10)	50(60)	10(30)	10(75)
July	Algae	22	22	15	10	85	30	75	75
	Moss	0	0	0	0	0	0	15	0
	Lichen	0	0	0	0	0	0	0	5
	Detritus	78	78	85	90	15	70	10	20
September	Algae	–	–	–	–	90	90	90	80
	Moss	–	–	–	–	0	0	0	0
	Lichen	–	–	–	–	0	0	0	0
	Detritus	–	–	–		10	10	10	20
October	Algae	85	80	50	85	70	25	–	–
	Moss	0	0	0	0	20	70	–	–
	Lichen	0	0	0	0	0	0	–	–
	Detritus	15	20	50	15	10	5	–	–
Mean AFDW[b]		5.0	3.7	7.7	7.0	9.3 (18.3)	8.1 (9.4)	13.5 (53.2)	7.3 (14.8)

[a] Values in parentheses are based on second year of study at that location.

[b] mg ash free dry weight per 5-min samples.

In fast water areas of Sites 1–4, density values were lower (but not invariably so) at impacted compared to reference sites, during and following construction (Figs. 6 and 7). For example, peak density at Site 1 (1 395 org/ m^2), was nearly three times higher than at Site 2 (500 org/ m^2), and mean density was double that at Site 2. In contrast, values at impacted and reference locations were similar for Site pairs 5–6 and 7–8 during 1975. Although Sites 7 and 8 were influenced by abrupt fluctuations in the regulated flow regime, the pattern and absolute density values responded similarly at both locations. Nor did macroinvertebrate abundance at Sites 5–8 exhibit any discernible effects of a longer term nature. One year after cessation of construction, values were comparable or even higher at previously impacted locations than at reference sites.

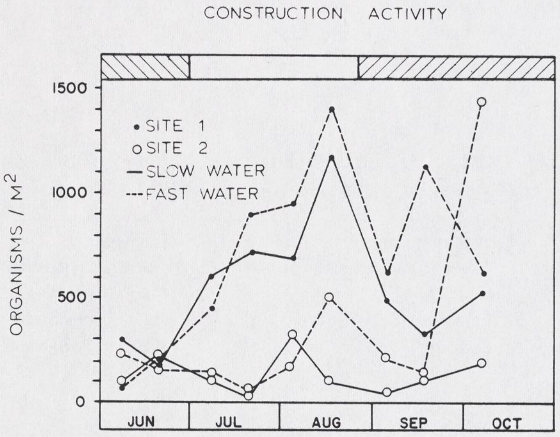


Fig. 6. Macroinvertebrate density (organisms/ m^2) in slow and fast water areas of Sites 1 and 2, Joe Wright Creek, Colorado, 1977. Construction activity symbols same as Fig. 2.

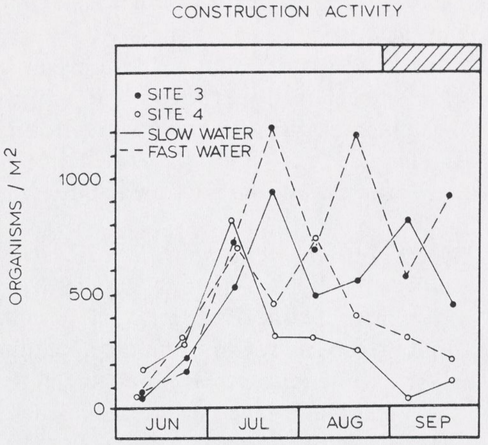


Fig. 7. Macroinvertebrate density (organisms/ m^2) in slow and fast water areas of Sites 3 and 4, Joe Wright Creek, Colorado, 1977. Construction activity symbols same as Fig. 2.

The effects of construction on macroinvertebrate abundance were sometimes more apparent in slow than fast water areas, despite the generally lower densities in the former habitat (Figs. 6 and 7).

Total macroinvertebrate biomass values (Table 3) support the results based on density. During 1975

Table 3. Mean total macroinvertebrate biomass (g/ m^2 wet wt) and percentage composition by biomass of major macroinvertebrate groups, Joe Wright Creek, 1975–77.

	Fast water areas												Slow water areas			
	1975				1976				1977				1977			
Site:	5	6	7	8	5	6	7	8	1	2	3	4	1	2	3	4
Mean biomass (g/ m^2)	4.1	5.2	2.5	3.4	2.4	2.7	1.0	1.5	4.3	1.1	2.7	1.5	3.9	0.7	1.6	0.9
Percentage composition																
Ephemeroptera	55	41	25	24	49	38	18	24	41	55	48	51	26	43	42	43
Plecoptera	11	16	35	52	12	25	10	28	9	13	19	4	8	4	27	25
Trichoptera	20	26	12	7	13	11	7	3	4	8	11	11	2	4	13	3
Diptera	13	16	24	14	19	20	41	21	31	16	18	22	52	31	10	16
Other[a]	1	1	4	3	7	6	23[b]	24[b]	15[b]	8	4	12	12	18[c]	8	13

[a] Oligochaeta, Coleoptera, Turbellaria, Nematoda, and Hydracarina.

[b] Oligochaeta 19%.

[c] Coleoptera 9%.

and 1976, when density was unaffected by construction activities, mean biomass values at impacted Sites 6 and 8 were comparable or even higher than at reference locations (Sites 5 and 7). In 1977 total mean biomass values were two to four times higher at reference Sites 1 and 3 than at Sites 2 and 4 which were affected by construction activities.

Macroinvertebrate composition

Ephemeroptera, Plecoptera, Trichoptera, and Diptera (especially Chironomidae, Simuliidae, and Blephariceridae) generally contributed the majority of total macroinvertebrate density and biomass (Tables 3 and 4), although stream regulation altered the composition at Sites 7 and 8 (see Ward & Short 1978; Ward & Stanford 1979). During 1975 and 1976, when there were no indications that total density or biomass values were influenced by construction activities, neither were there consistent differences in the composition of major groups between site pairs which could be attributed to construction. However, during 1977 Ephemeroptera and Diptera accounted for a greater proportion and Plecoptera a smaller proportion, of total density at impacted Sites 2 and 4 than at their corresponding reference locations. These differences were slightly greater in slow water than in fast water areas. Ephemeropterans contributed a larger proportion of total biomass at impacted sites during 1977, while other major groups did not exhibit consistent trends.

There were no discernible effects of construction activities on the abundance of individual macroinvertebrate taxa during the first two years of study. However, in 1977 when total density and biomass were affected by construction impacts, 16 taxa indicated an intolerance (consistently lower densities at impacted sites of each site pair) to the alterations engendered by construction (Table 5). Many taxa occurred in numbers too low to accurately assess their responses to perturbation. While the identification of taxa sensitive to construction activities is a significant finding, we do not know whether these results are applicable throughout the geographical range of the species, or even whether populations at lower elevations respond in a similar manner. In addition, the lack of suitable identification keys for the immature stages of many aquatic insects limits the value of these data.

Table 5. Macroinvertebrate taxa intolerant of the effects of construction activities on Joe Wright Creek, Colorado (see text).

Ephemeroptera
Ameletus sparsatus
Cinygmula sp.
Ephemerella coloradensis
E. doddsi
Rhithrogena robusta

Plecoptera
Alloperla (s.l.) spp.
Capnia sp.
Zapada oregonensis

Coleoptera
Heterlimnius corpulentus

Trichoptera
Arctopsyche grandis
Glossosoma sp.
Oligophlebodes sp.
Rhyacophila angelita

Diptera
Micropsectra sp.
Palpomyia sp.
Tipula sp.

Table 4. Percentage composition by density of major macroinvertebrate groups, Joe Wright Creek, 1975–1977.

	Percentage composition by density during and after highway construction															
	Fast water areas												Slow water areas			
	1975				1976				1977				1977			
Site:	5	6	7	8	5	6	7	8	1	2	3	4	1	2	3	4
Ephemeroptera	59	53	44	38	49	46	15	17	65	70	72	78	48	68	66	75
Plecoptera	15	15	14	27	10	13	11	13	11	10	11	4	16	5	14	9
Trichoptera	14	11	3	1	21	10	3	2	5	4	8	5	4	4	7	4
Diptera	10	19	37	33	15	27	47	58	4	6	7	9	6	12	9	10
Other[a]	2	2	2	1	5	4	24[b]	10	15	10	2	4	26[c]	11	4	2

[a] Oligochaeta, Coleoptera, Turbellaria, Nematoda, and Hydracarina.
[b] Oligochaeta 23.5%.
[c] Coleoptera 18%.

Macroinvertebrate diversity

Shannon diversity index values further support the macroinvertebrate response to construction previously indicated at impacted Sites 2 and 4, and the lack of a negative response at Sites 6 and 8. Prior to construction at Site 2, diversity values were higher than at reference Site 1, a pattern which reversed when construction activities commenced, and did so sooner and to a greater extent in slow water than fast water areas (Fig. 8). However, at Site pair 3–4, where commencement of construction preceded initial sampling, differences in diversity were apparent only for slow water areas (Fig. 9). Site pairs 5–6 and 7–8 displayed a similar range of Shannon diversity values as sites 1–4, but did not exhibit differences indicative of a construction impact at sites 6 and 8.

Discussion

Suspended solids at all impacted sites at times exceeded levels reported as being detrimental to aquatic biota (Cordone & Kelley 1961; European Inland Fisheries Advisory Committee 1965; Einstein 1972; Sorensen *et al.* 1977; Iwamoto *et al.* 1978). Why then were macroinvertebrates adversely affected only in 1977 when construction occurred at upstream locations? The answer appears related to the timing and duration of construction activities, and the lower discharge at upper sites which received less tributary inflow and did not derive flow supplements from impoundments (Table 1). Clear water releases from the reservoirs and tributary inflow, somewhat ameliorated high levels of suspended solids and reduced sedimentation at these downstream sites, especially Site 8. Barton

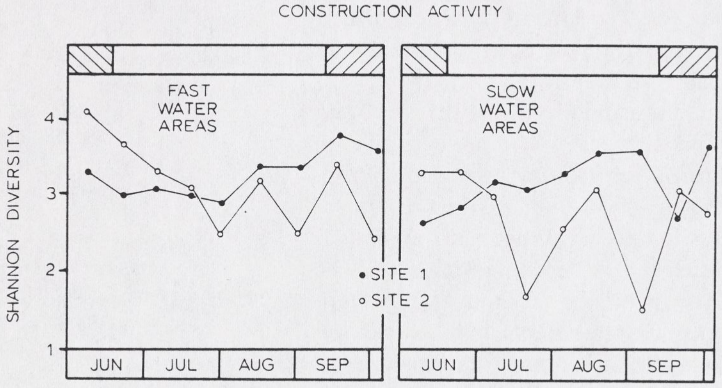


Fig. 8. Shannon-Weaver diversity index ($\bar{d}$) values for macroinvertebrate macroinvertebrate samples from slow and fast water areas of Sites 1 and 2, Joe Wright Creek, Colorado, 1977. Construction activity symbols same as Fig. 2.

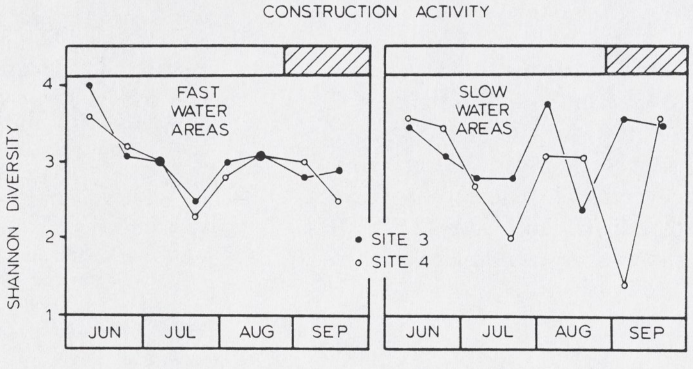


Fig. 9. Shannon-Weaver diversity index ($\bar{d}$) values for macroinvertebrate samples from slow and fast water areas of Sites 3 and 4, Joe Wright Creek, Colorado, 1977. Construction activity symbols same as Fig. 2.

(1977) and Hamilton (1961) concluded that severe and persistent sedimentation is required to induce distinct faunal changes. Impacts from stream-crossing during pipeline construction in British Columbia had only short-term, non-residual affects on macroinvertebrates (Tsui & McCart 1981). The extremely high snowmelt discharge which characterizes high mountain streams such as Joe Wright Creek, removes fine sediments which are not redeposited, even in depositional areas of high gradient reaches. Thus, snowmelt runoff (or high discharge from the reservoirs) cleanses the sediment and only increases suspended solids for a relatively short period. Deposition occurs in lentic water bodies or in low gradient lotic reaches father downstream.

At Sites 2 and 4 construction activities began earlier and continued about one month longer than at impacted locations downstream. This resulted in considerably higher levels of suspended solids over a longer period, and a greater proportion of fine sediment in the substrate of both erosional and especially depositional areas.

In conclusion, our original premise that the biota of high elevation streams would be sensitive to short-term perturbation from construction activities must be modified. Although distinct responses occurred at sites located in upper reaches, the effects were not nearly as severe as anticipated. The hydrologic characteristics and high gradient appeared to ameliorate the effects of construction activities. In addition, direct perturbations were of relatively short duration at all locations and were not annual events.

Acknowledgments

Research was supported by the U.S.D.A., Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO 80526, through The Eisenhower Consortium for Western Environmental Forestry Research. The authors wish to thank R. L. Bottorff, R. G. Dufford, and S. S. Hebein for field and laboratory assistance.

References

American Public Health Association, American Water Works Association, Water Pollution Control Federation, 1971. Standard Methods for the Examination of Water and Wastewater, 13th edn. American Public Health Assoc., New York. 874 pp.

Barrett, G. W. & Rosenberg, R., (Eds.), 1981. Stress Effects on Natural Ecosystems. Wiley-Interscience, Somerset, N.J.

Barton, B. A., 1977. Short-term effects of highway construction on the limnology of a small stream in southern Ontario. Freshwat. Biol. 7: 99–108.

Burns, J. W., 1972. Some effects of logging and associated road construction on northern California streams. Trans. Am. Fish. Soc. 101: 1–17.

Cairns, J. Jr. (Ed.), 1980. The Recovery Process in Damaged Ecosystems. Ann Arbor Science, Ann Arbor, Michigan. 250 pp.

Cordone, A. J. & Kelley, D. W., 1961. The influence of organic sediment on the aquatic life of streams. Calif. Fish Game 47: 189–228.

Einstein, H. A., 1972. Sedimentation (suspended solids). In: Oglesby, R. T., Carlson, C. A. & McCann, J. A. (Eds.) River Ecology and Man, pp. 309–318. Academic Press, New York.

European Inland Fisheries Advisory Commission, 1965. Water quality criteria for European freshwater fish. Report on finely divided solids and inland fisheries. (EIFAC Tech. Pap. No. 1). Air Wat. Pollut. 9: 151–168.

Extence, C. A., 1978. The effects of motorway construction on an urban stream. Envir. Poll. 17: 245–252.

Frederiksen, R. L., 1970. Erosion and sedimentation following road construction and timber harvest on unstable soils in three small western Oregon watersheds. USDA Forest Serv. Res. Pap. PNW-104, Pacific Northwest Forest & Range Experiment Station, Portland, Oregon. 15 pp.

Hamilton, J. D., 1961. The effect of sand-pit washings on a stream fauna. Verh. int. Verein. Limnol. 14: 435–439.

Holdgate, M. W. & Woodman, M. J., 1978. The Breakdown and Restoration of Ecosystems. Plenum Press, New York.

Huckabee, J. W., Goodyear, C. P. & Jones, R. D., 1975. Acid rock in the Great Smokies: unanticipated impact on aquatic biota of road construction in regions of sulfide mineralization. Trans. Am. Fish. Soc. 104: 677–684.

Hutchinson, G. E., Bonatti, E., Cowgill, U. M., Goulden, C. E., Leventhal, E. A., Mallett, M. E., Margaritora, F., Patrick, R., Racek, A., Robak, W. A., Stella, E., Wart-Perkins, J. B. & Willman, T. R., 1970. Ianula: an account of the history and development of the Lago di Monterosi, Latium, Italy. Trans. Am. phil. Soc. 60: 1–178.

Hynes, H. B. N., 1975. The stream and its valley. Verh. int. Verein. Limnol. 19: 1–15.

Iwamoto, R. N., Salo, E. O., Madej, M. A. & McComas, R. L., 1978. Sediment and water quality: a review of the literature including a suggested approach for water quality criteria. EPA 910/9-78-048.

King, D. L. & Ball, R. C., 1964. The influence of highway construction on a stream. Res. Rep. Mich. St. Agric. Exp. Stn. No. 19.

Lenat, D. R., Penrose, D. L. & Eagleson, K. W., 1981. Variable effects of sediment addition on stream benthos. Hydrobiologia 79: 187–194.

Lowe, R. L., 1979. Phytobenthic ecology and regulated streams. In: Ward, J. V. & Stanford, J. A. (Eds.) The Ecology of Regulated Streams, pp. 25–34. Plenum Press, New York.

Megahan, W. F. & Kidd, W. J., 1972. Effects of logging and logging roads on erosion and sediment deposition from steep terrain. J. Forestry 70: 136–141.

Nixon, R. A., 1978. Biogeochemical analyses of the impact of the Richard B. Russell Scenic Highway on Dukes Creek, White County, Georgia. Georgia J. Sci. 36: 16–24.

Porter, T. R., Rosenberg, D. R. M. & McGowan, D. K., 1974. Winter studies of the effects of a highway crossing on the fish and benthos of the Martin River, N.W.T. Env. Can., Fish. Mar. Serv., Tech. Rep. Ser. No. CEN/T-74-3.

Sorensen, D. L., McCarthy, M. M., Middlebrooks, E. J. & Porcella, D. B., 1977. Suspended and dissolved solids effects on freshwater biota: a review. Ecol. Res. Ser. EPA-600/3-77-042.

Thorp, J. H. & Gibbons, J. W. (Eds.), 1978. Energy and environmental stress in aquatic systems. DOE Symposium Series (CONF-771114), Springfield, Virginia.

Tsui, P. T. P. & McCart, P. J., 1981. Effect of stream-crossing by a pipeline on the benthic macroinvertebrate communities of a small mountain stream. Hydrobiologia 79: 271–276.

Ward, J. V., 1974. A temperature-stressed stream ecosystem below a hypolimnial release mountain reservoir. Arch. Hydrobiol. 74: 247–275.

Ward, J. V., 1976. Comparative limnology of differentially regulated sections of a Colorado mountain river. Arch. Hydrobiol. 78: 319–342.

Ward, J. V. & Short, R. A., 1978. Macroinvertebrate community structure of four special lotic habitats in Colorado, U.S.A. Verh. int. Verein. Limnol. 20: 1382–1387.

Ward, J. V. & Stanford, J. A. (Eds.), 1979. The Ecology of Regulated Streams. Plenum, New York.

Received 24 September 1981; in revised form 5 January 1982.

Hydrobiologic

[1982]
↑
missing issue

Effects of sediment releases from a reservoir on stream macroinvertebrates

Lawrence J. Gray & James V. Ward
Department of Zoology and Entomology, Colorado State University, Fort Collins, CO 80523, U.S.A.

Keywords: sediment, reservoir, stream, macroinvertebrates

Abstract

Effects of sediment release from Guernsey Reservoir on macroinvertebrates of the North Platte River, Wyoming, were investigated during summer 1981. Suspended solids concentrations during sediment release increased from <20 mg l^{-1} to >300 mg l^{-1}. Because fine particulates remained in suspension, mean particle size of substrates was unaltered. Densities of chironomids decreased 90% + during sediment release but recovered to initial levels in 3 weeks after the release ended. Densities of mayflies and oligochaetes increased. Changes in benthic populations were highly correlated with increases in suspended solids.

Introduction

Accumulation of sediment in reservoirs and subsequent reductions in storage capacity have become an increasingly serious problem (Brown 1975). One method of extending the useful life of reservoirs is flushing of profundal sediments (Simons 1979). Although the effects of reservoirs on many aspects of lotic ecosystem processes have been documented (Ward & Stanford 1979), effects of sediment release have received little attention despite potentially extreme consequences (Nisbet 1961).

Substrate type is a major determinant of macroinvertebrate distribution and abundance (Cummins & Lauff 1969; Cummins *et al.* 1966; Hynes 1970). Each species shows distinct preferences for particular substrates as a consequence of respiration requirements, food-gathering mechanisms, case-building behavior, and other life history characteristics (Cummins 1973; Cummins *et al.* 1966; Mackay 1977; Rabeni & Minshall 1977). Releases of reservoir sediments are expected to adversely affect macroinvertebrate communities by altering substrates, increasing suspended solids, and introducing potential toxins (e.g., dissolved sulfide).

Effects of settled sediment vary with amounts deposited. Slight deposition has little effect (Bjornn *et al.* 1977; Rabeni & Minshall 1977), whereas heavy amounts greatly decrease populations (Chutter 1968; Cordone & Kelly 1961; Gammon 1970; Nuttall & Bielby 1973).

Increases in suspended solids without deposition can affect benthic populations. Gammon (1970) found that increases of 20–80 mg l^{-1} above normal levels caused a 45–70% reduction in total numbers. Reductions occurred as organisms drifted downstream, and drift rates were linearly related to suspended solids concentrations. Rosenberg & Wiens (1975) also found increased rates of drift when bank sediments were experimentally introduced into a stream channel. However, the number of organisms drifting was independent of suspended solids concentrations. Hamilton (1961) found no change in numbers of organisms exposed to high concentrations of sand and silt in suspension.

Our study describes the effects of sediment release from Guernsey Reservoir, located on the North Platte River in southeastern Wyoming, on downstream populations of macroinvertebrates. Because downstream flows depend on irrigation

Hydrobiologia 96, 177–184 (1982). 0018-8158/82/0962-0177/$01.60.

demand, the river bed is dry from October to April. Thus diversity and density of macroinvertebrates are very low after flows resume in spring.

Since 1936, an annual flushing of reservoir sediments, known locally as the 'silt run,' has been conducted during July and August to reduce bank erosion and seepage losses in downstream irrigation canals. Because flows from an upstream reservoir are used to flush sediments from Guernsey Reservoir, discharge and most water quality parameters vary little from pre-silt run levels. The principal environmental effects of the silt run are an increase in suspended solids and potential deposition of fine particulates in stream channels. Objectives of the silt run study were to compare changes in densities of macroinvertebrates with *a priori* predictions, to quantify the relationship between biotic and environmental change, and to assess the relative contribution of suspended solids and settled solids to changes in abundance of macroinvertebrates.

Experimental design

Two study sites were selected after preliminary sampling in June (Fig. 1). Site 1 was located 4 km downstream from Guernsey Dam. Substrates consisted of cobbles one-half buried in a clay 'armor'. Site 2 was 3 km downstream from Whalen Dam, a low-head structure that diverts river flows into large irrigation canals. Substrates were cobble and gravel with little armor. Suspended solids concentrations were expected to decrease at Site 2 during the silt run as materials settled out behind Whalen Dam. A spatial control site was not present because of extreme flow fluctuations that occurred upstream from Guernsey Reservoir just before the silt run.

Five taxa of macroinvertebrates were chosen for intensive study: *Baetis insignificans* McDunnough (Ephemeroptera), *Tricorythodes minutus* Traver (Ephemeroptera), Orthocladiinae spp. (Diptera, primarily *Orthocladius* sp.), Chironomini spp. (Diptera, mostly *Limnochironomus* sp.), and Oligochaeta spp. These taxa comprised 95% of total numbers before the silt run.

B. insignificans is a small, streamlined mayfly that prefers upper surfaces of coarse substrates in moderate currents. Baetid mayflies in general are tolerant of high concentrations of suspended solids and moderate deposition (Bjornn *et al.* 1977; Gammon 1970; Hamilton 1961; Nuttall & Bielby 1973). Therefore, densities of *B. insignificans* were not expected to decrease during the silt run.

T. minutus is a sprawling mayfly on fine-coarse

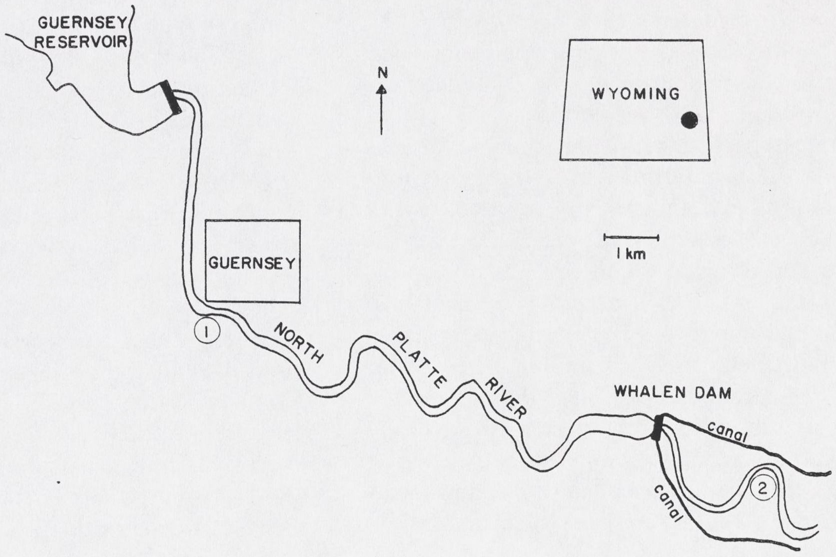


Fig. 1. Study area at Guernsey Reservoir-North Platte River, Wyoming. Circled numbers indicate sampling sites. The river is 50–100 m wide and 0.2–3.0 m deep during peak flows. Average river gradient is 1 m km^{-1}. Riparian vegetation consists of mature gallery forests and cultivated crops.

sediments. It is a characteristic mayfly of warm, turbid streams in western North America (Edmunds & Musser 1960). Gammon (1970) found that numbers of *Tricorythodes* sp. increased with high turbidities and build-up of sediments; thus, densities of *T. minutus* were expected to increase during the silt run.

Chironomids have exhibited variable responses to suspended and settled sediment. High turbidity alone may cause either a decrease, no change, or an increase in numbers (Bjornn *et al.* 1977; Gammon 1970; Hamilton 1961), although drift rates typically increase (Gammon 1970; Rosenberg & Wiens 1975). Heavy sedimentation with high turbidity may cause either decreased or increased densities (Gammon 1970; Nuttall & Bielby 1973). We expected a decrease in chironomid densities during the silt run. Although sediment deposition might eventually create favorable conditions for some species, chironomids colonizing the river in spring were more likely to be adapted to the clear flows and coarse substrates present at that time.

Populations of oligochaetes consistently increase in turbid, silted habitats (Hamilton 1961; Nuttall & Bielby 1973). Densities of these organisms were expected to increase during the silt run because of drift of organisms from Guernsey Reservoir and increases in silted substrates.

Benthic samples were collected with a modified Surber sampler that enclosed 320 cm^2 of substrate (net length = 50 cm, mesh = 0.5 mm). The sampler was secured in place with a support handle and 3-cm frame bolts. Substrate materials were either kicked or placed by hand into the net and returned to shore for elutriation. Organisms were preserved in Kahle's fluid and later transferred to ethanol for enumeration. Size classes of aquatic insects were based on measurements of total length (excluding cerci) at 10× with an ocular micrometer.

The set of environmental variables included concentration of total suspended solids (TSS) and substrate phi (ϕ) values. Phi values describe natural variation in substrate distribution caused by substrate patchiness and were expected to increase during the silt run (i.e., mean particle size decreases). TSS samples were collected with a US DH-48 sampler (U.S. Inter-Agency Committee on Water Resources 1965), filtered on Whatman® $_{GF/F}$ glass fiber filters, dried at 80°, and weighed to the nearest 0.1 mg on an analytical balance. Substrates were collected with a metal cylinder (900 cm^3) attached to a support rod. Samples were air-dried, placed on a series of standard sieves, and shaken mechanically (Ingram 1971). Mean phi values were calculated from moment statistics (McBride 1971). Average dry weight of substrate samples was 0.7 kg.

Fifteen samples were collected at each site on each date. A sample consisted of measurements of TSS concentration (taken as close to the streambed as possible), substrates (collected adjacent to Surber samples), and number of each macroinvertebrate taxon. Three random samples were taken in each of 5 locations at each site. A location was ≈ 200 m^2 of streambed from bank to thalweg in depths >20 cm. Locations were randomly selected on 6 July (pre-silt run) and sampled each time thereafter as a basis for temporal comparison. The 1981 silt run was conducted from 9 to 30 July. Three sets of samples were taken during the silt run (9, 16, and 23 July) and two sets were collected after (6 and 20 August).

Duplicate water samples for chemical analysis were collected in acid-washed, polyethylene bottles, transported on ice, and filtered immediately upon return to the laboratory (Whatman GF/F filters). Analyses were performed on refrigerated samples within 24 h. Nitrate-nitrogen was determined after reduction with cadmium to nitrite by a diazotization technique (Golterman *et al.* 1978). This method measures nitrate + nitrite. Soluble reactive phosphorus (SRP) was measured colorimetrically by the method of Murphy and Riley (1962). Conductivity was measured with a Hach® model 2 200 meter, pH by electrode, and alkalinity by titration with H_2SO_4. Dissolved oxygen and total sulfide samples were collected with 300-ml BOD bottles. Dissolved oxygen was determined by the Winkler method (azide modification). Total sulfide was measured idometrically after precipitation with $CdCl_2$ (Golterman *et al.* 1978).

Multivariate analysis of variance was used to test the null hypothesis of no overall change in each variable set for the period 6 July to 6 August (N = 75 per site). If the null hypothesis was rejected, then univariate tests were performed. Densities of macroinvertebrates may fluctuate from life history phenomena alone (e.g., synchronous emergence and recruitment). For example, the mayflies chosen for intensive study are known to have rapid life cycles. *T. minutus* completes larval development in 34d at 18° (Newell 1976), and *B. insignificans* has

Table 1. Physical–chemical parameters at sampling sites on the North Platte River downstream from Guernsey Reservoir, Wyoming, for the period 2 July to 20 August 1981. Upper rows are values for Site 1; lower, Site 2. Asterisks indicate silt run dates.

Parameter	2 July	6 July	9 July*	16 July*	23 July*	6 August	20 August
pH	8.25	8.33	8.30	8.13	8.28	8.30	8.15
	8.25	8.39	8.30	8.20	8.29	8.31	8.19
Conductance, μS cm^{-1}	690	820	690	780	750	700	530
	670	820	720	750	750	670	530
Total alkalinity, meq l^{-1}	2.9	2.9	3.0	2.9	2.9	2.8	2.6
	3.1	3.0	3.0	3.0	3.0	2.8	2.6
SRP, mg l^{-1}	0.01	<0.01	0.03	0.06	0.02	0.01	0.01
	0.01	<0.01	0.01	0.02	0.01	<0.01	0.01
Dissolved oxygen, mg l^{-1}	9.0	8.0	8.5	8.0	7.9	8.9	10.3
	9.0	7.9	8.1	7.6	7.9	8.8	10.4
Water temperture, °C (mean)	18.0	20.4	19.6	21.7	22.1	23.0	23.7
	18.6	22.8	19.3	21.0	22.1	22.9	23.2

several generations during summer in northwestern Colorado (Gray & Ward 1978). Thus acceptance or rejection of the null hypothesis was determined with additional information provided by size class distributions. Canonical correlations between rates of change in each set of variables were determined to further substantiate changes in biota caused by the silt run. Rates of change were calculated as the first derivative of the slope of a polynomial regression computed for each variable at each location for the period 6 July to 6 August ($N = 40$). This procedure eliminates within-location variation (mostly 'noise') and implies percentage rates of change that are linearly and additively related (Green 1979). All variables except substrate phi were log-transformed before analysis. Statistics were calculated with SPSS programs (Nie *et al.* 1975).

Results and discussion

The silt run had little effect on most water quality parameters (Table 1). The only chemical parameter to exhibit significant change was SRP which increased to 0.06 mg l^{-1} at Site 1. Nitrate-nitrogen was below the detection limit (0.05 mg l^{-1}). Dissolved oxygen remained high, and sulfide was not detected. Midday water temperatures were 19–23 °C throughout the study period at both sites.

Discharge from Guernsey Reservoir during the silt run varied from 109 to 150 m^3 s^{-1} with a mean of 136 m^3 s^{-1} (Fig. 2). Variations in flow did not affect sampling locations.

Concentrations of suspended solids increased 20-fold with peak values of 339 mg l^{-1} at Site 1 and 422 mg l^{-1} at Site 2 (Fig. 3). Lack of a downstream decrease in TSS indicates that materials can remain in suspension for long distances. Particle size analysis of suspended solids during past silt runs have shown that particulates are 75% silt and 25% clay (U.S. Geological Survey 1980). Because particulates remained in suspension, substrate phi values

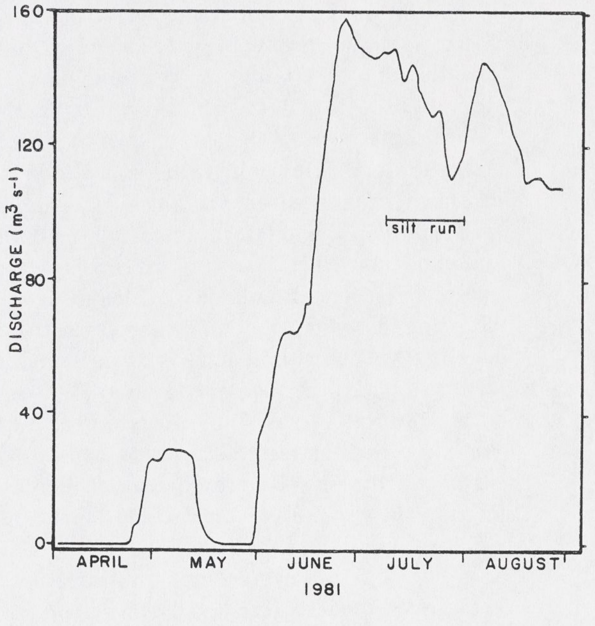


Fig. 2. Discharge from Guernsey Reservoir, Wyoming, for the period 1 April–31 August 1981. Flows depend on irrigation demand; thus, the river is dry from October to April.

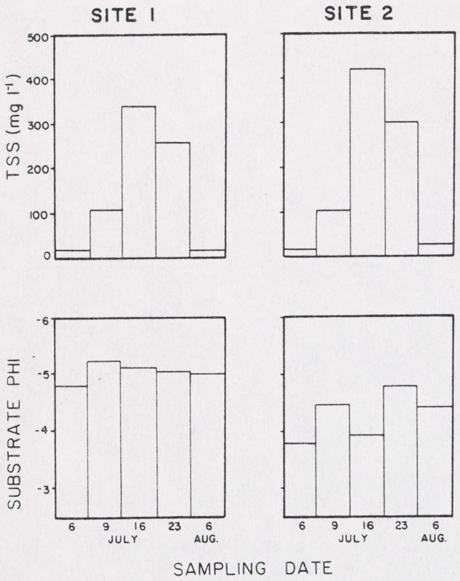


Fig. 3. Concentrations of total suspended solids and mean substrate particle size (ϕ) in the North Platte River downstream from Guernsey Reservoir, Wyoming. Overall differences in TSS and ϕ values between 6 July and 6 August were significant at both sites ($P < 0.01$), but ϕ values were not significantly different ($P = 0.49$ at Site 1, $P = 0.10$ at Site 2).

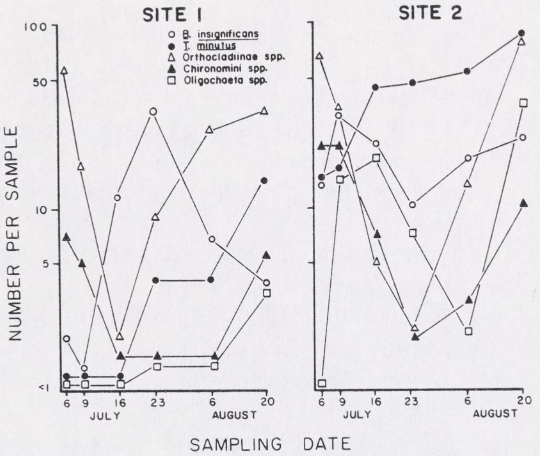


Fig. 4. Mean densities of macroinvertebrates downstream from Guernsey Reservoir, Wyoming. Overall differences in densities between 6 July and 6 August were significant at Site 1 ($P < 0.01$) and Site 2 ($P < 0.01$). Differences in densities during this period were significant for *B. insignificans* ($P < 0.01$, Site 1), *T. minutus* ($P < 0.01$, Site 1; $P < 0.01$, Site 2), Orthocladiinae spp. ($P < 0.01$, Site 1; $P < 0.01$, Site 2), Chironomini spp. ($P < 0.01$, Site 1; $P < 0.01$, Site 2), and Oligochaeta spp. ($P = 0.03$, Site 1; $P < 0.01$, Site 2). Differences were not significant for *B. insignificans* at Site 2 ($P = 0.12$).

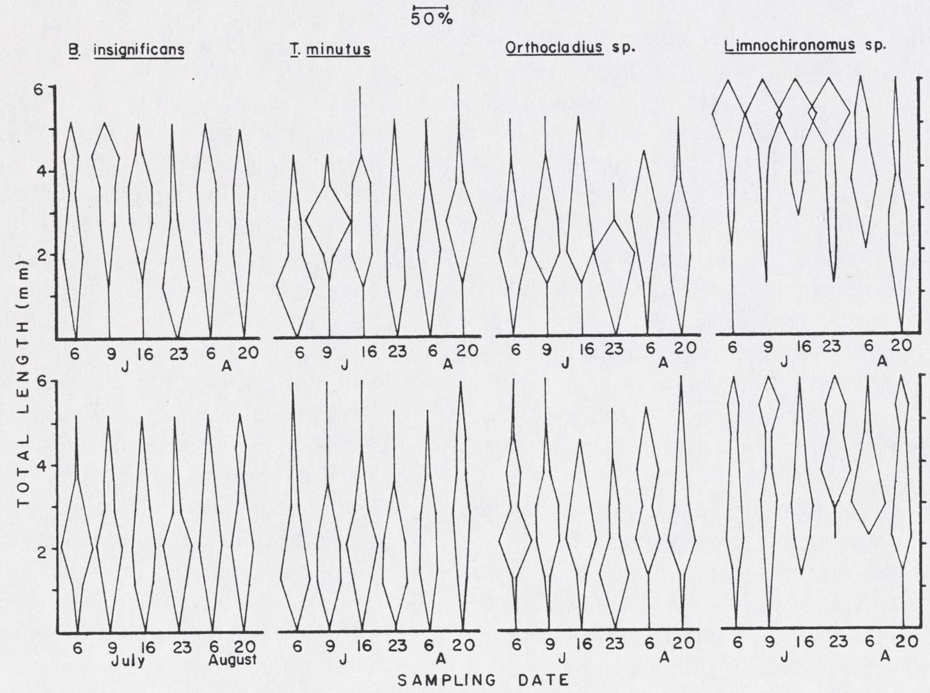


Fig. 5. Size class distributions of aquatic insects downstream from Guernsey Reservoir, Wyoming; top row, Site 1; bottom row, Site 2.

did not change (Fig. 3). Only slight deposition was observed on upper surfaces of substrates in most of the streambed. Overall, the silt-clay fraction comprised <1% of substrates. Heavy deposits (up to 3% silt-clay) were present only along shore (<5% of wetted perimeter), particularly around submerged vegetation.

Overall densities of macroinvertebrates significantly changed during the silt run at both study sites (Fig. 4). Individual taxa exhibited trends consistent with *a priori* hypotheses. Life history phenomena alone did not account for changes in densities except for mayflies at Site 1 (Fig. 5).

Densities of chironomids decreased 90%+ within 2 weeks after the silt run began. Although declines were similar for both taxa, the silt run affected different life stages. Recruitment of early instars was continuous for *Orthocladius* sp. during the silt run, but no recruitment occurred in populations of *Limnochironomus* sp. (Fig. 5). Unlike *Orthocladius* sp., *Limnochironomus* sp. constructed silk tubes throughout larval development. Suspended particulates may have interfered with feeding and respiratory mechanisms by either scouring or clogging the tubes. These effects could also explain the absence of chironomid pupae from 16 July to 23 July, because both species constructed tubes for pupation. Before and after the silt run, 5–10 pupae were collected per sample. Despite the high losses in July, densities of chironomids recovered to pre-silt run levels within 3 weeks after releases ended.

Density trends for mayflies at Site 2 followed initial predictions (Fig. 4). *T. minutus* increased from 14 individuals per sample on 6 July to 53 individuals per sample on 6 August. Densities of *B. insignificans* did not significantly change. At Site 1, densities of both species increased during the silt run, although these increases may have resulted from synchronous emergence on 9 July and subsequent recruitment during the next two weeks (Fig. 5).

Densities of oligochaetes increased at both study sites. The rapid, large increase at Site 2 at the start of the silt run suggests many organisms were derived from drift, although their point of origin is not known. Increased densities after the silt run resulted from large numbers of organisms collected in heavily-silted, shore habitats.

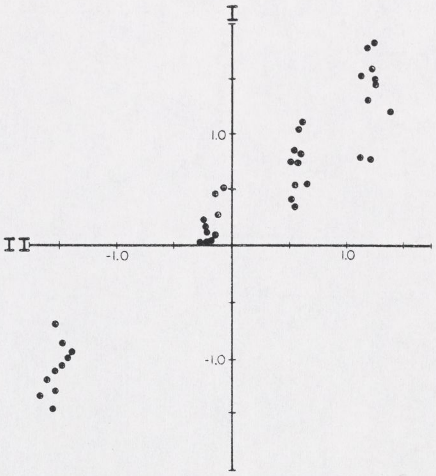


Fig. 6. Overall relationship between rates of change in densities of macroinvertebrates (Axis I) and environmental parameters (primarily total suspended solids, Axis II) during the Guernsey Reservoir silt run. Values are canonical variate scores calculated from the first correlation equation ($P < 0.01$): 0.16 △ log *B. insignificans* + 0.06 △ log *T. minutus* -0.70 △ log Orthocladiinae ssp. - 0.15 △ log Chironomini ssp. + 0.10 △ log Oligochaeta spp. = 1.01 △ log TSS + 0.03 △ ϕ. Other possible correlation equations were not significant ($P = 0.94$), indicating that biotic changes mainly resulted from silt run effects. The clustering of data points are a result of similar rates of change at both study sites during each time period, e.g., cluster at top right = change at beginning of silt run, cluster at bottom left = change at end of silt run.

Elevated nutrient levels during the silt run contributed to an increase in stream algae, especially *Cladophora* (Gray & Ward 1982). Algal mats trapped some sediment, thereby providing microhabitats and food materials for many macroinvertebrates (Williams & Winget 1979).

Overall, there was a strong correlation between changes in densities of macroinvertebrates and changes in environmental parameters (Fig. 6). Because substrates were unaltered by the silt run, nearly all of the biotic changes can be attributed to the increase in suspended solids with the possible exception of mayflies at Site 1.

The rapid response of macroinvertebrates in the North Platte River to environmental changes caused by the silt run reflects the highly perturbed conditions created by the reservoir throughout the year. Temporal contraction of stream discharge to brief periods in spring and summer combined with extreme fluctuations in releases select for species that are able to colonize and complete larval development between major disturbances (Henricson & Müller 1979). Warm stream temperatures, continuous recruitment, and rapid life cycles allow high population growth rates; thus, additional disturbance, such as the silt run, have only short-term effects on extant populations.

Summary

Increases in suspended solids caused by the flushing of sediments from Guernsey Reservoir had pronounced effects on densities of macroinvertebrates in the North Platte River. Chironomid densities greatly decreased, while densities of *T. minutus* and oligochaetes increased. Baetid mayflies are unaffected. Because flushed particulates were silt and clay that remained in suspension, changes in benthic densities occurred for many kilometers downstream. In general, the direction of change in individual populations was predictable from previous studies of sediment effects on related taxa. However, predictions of effects on some taxa, particularly chironomids, requires knowledge of past environmental conditions. The magnitude of effects and time required for recovery depend on reservoir operating procedures. In the North Platte River, sediment releases had short-term effects on benthic populations as a result of extreme annual flow variations and subsequent selection for organisms with rapid life cycles.

Acknowledgments

We wish to thank Mr. Dick Isler and Ms. Sharon Campbell (U.S. Bureau of Reclamation) for sharing unpublished data collected during previous silt runs; Mr. David Wilde (U.S. B.R.) kindly provided discharge data for Guernsey Reservoir, and Margaret L. D. Gray assisted with field collections.

The work upon which this publication is based was supported in part by funds provided by the Office of Water Research and Technology (Project No. B-266-COLO), U.S. Department of the Interior, Washington, D.C., as authorized by the Water Research and Development Act of 1978.

References

Bjornn, T. C., Brusven, M. A., Molnau, M. P., Milligan, J. H., Klamt, R. A., Chacho, E. & Schaye, C., 1977. Transport of granitic sediment in streams and its effects of insects and fish. Bull. No. 17, Forest, Wildlife and Range Exp. Sta., Univ. of Idaho, Moscow. 43 pp.

Brown, R. J., 1975. Reservoir and lake sedimentation. Nat. Tech. Infor. Serv., Springfield, Virginia. 110 pp.

Chutter, F. M., 1969. The effect of silt and sand on the invertebrate fauna of streams and rivers. Hydrobiologia 34: 57–76.

Cordone, A. J. & Kelly, D. W., 1961. The influence of inorganic sediment on the aquatic life of streams. Calif. Fish Game 47: 189–228.

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

Cummins, K. W. & Lauff, G. H., 1969. The influence of substrate particle size on the microdistribution of stream macrobenthos. Hydrobiologia 34: 145–181.

Cummins, K. W., Tryon, C. A., Jr. & Hartman, R. T. (Eds.), 1966. Organism-substrate relationships in streams. Spec. Publ. No. 4, Pymatuning Lab. Ecol., Univ. of Pittsburgh, Pennsylvania. 145 pp.

Edmunds, G. F. & Musser, G. G., 1960. The mayfly fauna of Green River in the Flaming Gorge Reservoir Basin, Wyoming and Utah, In: Ecological Studies of the Flora and Fauna of Flaming Gorge Reservoir Basin, Wyoming and Utah. Univ. of Utah Anthrop. Pap. No. 48, pp. 112–123.

Gammon, J. R., 1970. The effect of inorganic sediment on stream biota. U.S. Environ. Protect. Agency, 18050 DWC, Washington, DC. 141 pp.

Golterman, H. L., Clymo, R. S. & Onstad, M. A. M., 1978. Methods for Physical and Chemical Analysis of Fresh Waters. IBP Handbook No. 8, 2nd edn Blackwell Scientific, Oxford. 214 pp.

Gray, L. J. & Ward, J. V., 1978. Environmental effects of oil shale mining and processing, Part II: the aquatic macroinvertebrates of the Piceance Basin, Colorado, prior to oil shale processing. U.S. Environ. Protect. Agency, Environ. Res. Lab., Duluth, Minn., EPA-600/3-78-097. 40 pp.

Gray, L. J. & Ward, J. V., 1982. Response of lotic algae to sediment release from a reservoir. Southwest. Nat. (in press).

Green, R. H., 1979. Sampling Design and Statistical Analysis for Environmental Biologists. John Wiley, New York. 257 pp.

Hamilton, J. D., 1961. The effect of sand-pit washings on a stream fauna. Verh. int. Verein. Limnol. 14: 435–439.

Henricson, J. & Müller, K., 1979. Stream regulation in Sweden with some examples from Central Europe. In: Ward, J. V. & Stanford, J. A. (Eds.) The Ecology of Regulated Streams, pp. 183–199. Plenum Press, New York.

Hynes, H. B. N., 1970. The Ecology of Running Waters. Univ. of Toronto Press, Toronto. 555 pp.

Ingram, R. L., 1971. Sieve analysis. In: Carver, R. E. (Ed.) Procedures in Sedimentary Petrology, pp. 49–67. Wiley-InterScience, New York.

Mackay, R. J., 1977. Behavior of Pycnopsyche (Trichoptera: Limnephilidae) on mineral substrates in laboratory streams. Ecology 58: 191–195.

McBride, E. F., 1971. Mathematical treatment of size distribution data. In: Carver, R. E. (Ed.) Procedures in Sedinentary Petrology, pp. 109–127. Wiley-InterScience, New York.

Murphy, J. & Riley, J. P., 1962. Determination of phosphate in natural waters. Analyt. chim. Acta 27: 31–36.

Newell, R. L., 1976. The life history of a multivoltime mayfly Tricorythodes minutus (Traver) with special reference to the effects of temperature on growth and development. Ph.D. thesis, Idaho State Univ., Pocatello. 129 pp.

Nie, N. H., Hull, C. H., Jenkins, J. G., Steinbrenner, K. & Bent, D. H., 1975. Statistical Package for the Social Sciences, 2nd edn. McGraw-Hill, New York. 675 pp.

Nisbet, M., 1961. Un example de pollution de rivière par vidage d'une retenue hydroelectrique. Verh. int. Verein. Limnol. 14: 678–680.

Nuttall, P. M. & Bielby, G. J., 1973. The effectof china-clay wastes on stream invertebrates. Environ. Pollut. 5: 77–86.

Rabeni, C. F. & Minshall, G. W., 1977. Factors affecting microdistribution of stream benthic insects. Oikos 29: 33–43.

Rosenberg, D. M. & Wiens, A. P., 1975. Experimental sediment addition studies on the Harris River, N. W. T., Canada: the effect on macroinvertebrate drift. Verh. int. Verein. Limnol. 19: 1568–1574.

Simons, D. B., 1979. Effects of stream regulation of channel morphology. In: Ward, J. V. & Stanford, J. A. (Eds.) The Ecology of Regulated Streams, pp. 95–111. Plenum Press, New York.

United States Geological Survey, 1980. Water resources data for Wyoming, Water Year 1979, Vol. 1: Missouri River Basin. Nat. Tech. Infor. Serv., Springfield, Virginia. 642 pp.

United States Inter-Agency Committee on Water Resources, 1965. A study of methods used in measurement and analysis of sediment loads in streams. Rep. J. St. Anthony Falls Hydraulic Laboratory, Minneapolis, Minnesota. 5 pp.

Ward, J. V. & Stanford, J. A. (Eds.), 1979. The Ecology of Regulated Streams. Plenum Press, New York. 398 pp.

Williams, R.D. & Winget, R. N., 1979. Macroinvertebrate response to flow manipulation in the Strawberry River, Utah (U.S.A.). In: Ward, J. V. & Stanford, J. A. (Eds.) The Ecology of Regulated Streams, pp. 365–376. Plenum Press, New York.

Received 13 November 1981; in revised form 7 January 1982.

THE SOUTHWESTERN NATURALIST 28(2):125-135 MAY, 1983

AQUATIC MACROINVERTERBRATES OF THE PICEANCE BASIN, COLORADO: COMMUNITY RESPONSE ALONG SPATIAL AND TEMPORAL GRADIENTS OF ENVIRONMENTAL CONDITIONS

LAWRENCE J. GRAY, JAMES V. WARD, ROBERT MARTINSON,
AND ELIZABETH BERGEY

ABSTRACT.—A long-term study of the aquatic biotopes of the Piceance Basin has enabled analyses of macroinvertebrate communities along spatial (downstream) and temporal (year-to-year) gradients of environmental conditions. Cluster analysis indicates four distinct aquatic habitat types: spring sources, springbrooks, and the middle and lower reaches of Piceance Creek. Spatial differences in temperature and flow constancy influence habitat stability with respect to substrate, degree-day distribution, ice conditions, and the distribution and abundance of aquatic macrophytes. Despite great differences in thermal patterns, total annual degree-days were *ca.* 3000 in all four habitat types. The principal energy source for macroinvertebrates is autochthonous detritus. Trophic structure shifts from shredders—collectors—scrapers in the headwaters to collectors-predators in lower reaches. Year-to-year variations in discharge altered the density and composition of macroinvertebrates, and were reflected in the thermal regimes at mainstream locations. Data suggest that groundwater discharge from upper reaches is important in maintaining the structural and functional integrity of aquatic systems in the Piceance Basin.

Because of the seasonal distribution of precipitation and runoff, headwater streams in arid regions are highly dependent on groundwater discharge for permanent flow (Davis, 1974). Stream segments receiving proportionately large inputs of groundwater exhibit relatively constant thermal, chemical and, flow regimes. With progressive distance downstream these conditions are modified by climatic fluctuations, thus forming an environmental gradient that influences the distribution and abundance of aquatic organisms (Deacon and Minckley, 1974). Superimposed upon this spatial gradient is a temporal gradient engendered by year-to-year variations in precipitation which, in arid regions, is most directly reflected by differences in annual discharge.

Aquatic habitats in the Piceance Basin of northwestern Colorado (Northern Cool Desert) are structured by discharge from an extensive aquifer system; groundwater discharge accounts for 80% of surface runoff (Weeks et al. 1974). In desert streams the hydrologic extremes of drought and flooding are major determinants of macroinvertebrate distribution, abundance, and life history characteristics (Gray, 1981). Flow regimes have been suggested as an inportant factor affecting the abundance and composition of stream macroinvertebrates over long periods (Hynes, 1970; Ward, 1975). Spatial and temporal gradients in temperature, such as occur in the Piceance Basin, are also extremely important in structuring aquatic insect communities (Ward and Stanford, 1982).

From 1975-1980 a series of studies were conducted on aquatic habitats of the Piceance Basin to gather baseline data on water chemistry, macroinvertebrates, and fish before commencement of oil shale mining and processing

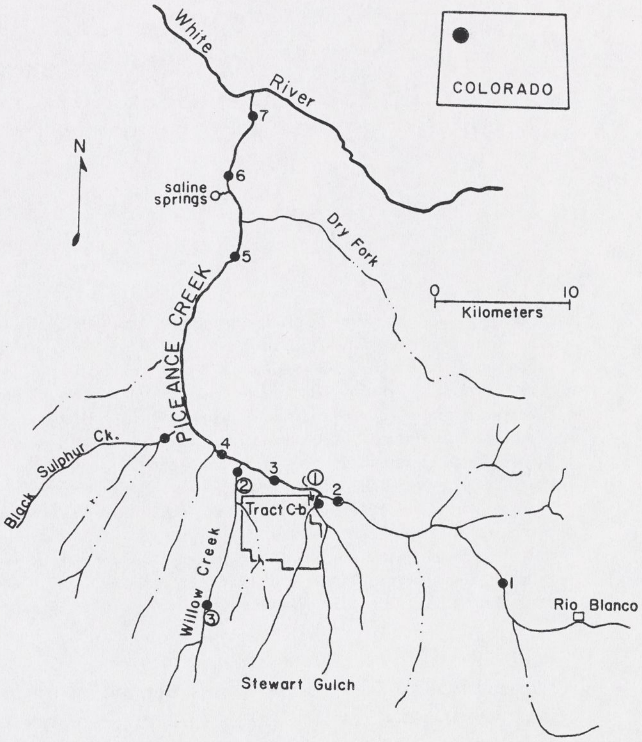


FIG. 1.—Map of the Piceance Basin, Colorado, showing locations of study sites. Circled numbers indicated springs. Tract C-b is one of two federal oil shale leases in the basin.

activities (Goettl and Edde, 1978; Gray and Ward, 1978; Martinson et al., 1982; Skogerboe et al., 1979). In this paper we synthesize data gathered on macroinvertebrate communities along spatial (downstream) and temporal (year-to-year) gradients of environmental conditions.

STUDY AREA.—The Piceance Basin is primarily underlain by rocks of the Green River Formation, the principal source of oil shale in the United States. The Green River Formation was formed by sedimentation processes in Lake Uinta during the Eocene (Bradley 1936). Predominant rock types are sandstones, shales, and marlstones.

Basin climate and vegetation are typical of the Northern Cool Desert. Annual precipitation is 20-40 cm (mean = 32 cm) with about one-half occuring as snow. Summer air temperatures may exceed 40°C, and winter temperature may be as low as −40°C (Weeks et al., 1974). Sagebrush (*Artemesia tridentata*) is dominant in valleys and on slopes, forming associations with other shrubs, such as black greasewood (*Sarcobatus vermiculatus*) and rabbitbrush (*Chrysothamnus viscidiflorus*), and various grasses. On ridges a pinyon (*Pinus edulis*)-juniper (*Juniperus osteosperma* and *J. scopulorum*) woodland predominates. The average plant coverage is only 25% of total surface area (Tiedeman and Terwilliger, 1978).

Piceance Creek, the largest of basin streams, begins in the White River National Forest (elevation = 2,440 m) and flows 80 km to enter the White River at 1,738 m (Fig. 1). Riparian vegetation consists of sagebrush, hay meadows, and occasional willows that do not form a complete canopy over the stream. Permanent flow is derived from groundwater discharge from the upper basin aquifer (Uinta and Green River Formations). The aquifer is recharged by snowmelt at elevations

[1983]

8

Citation: Stanford, J. A. and J. V. Ward. 1983. The effects of mainstream dams on physicochemistry of the Gunnison River, Colorado, p. 43-56. In: V. D. Adams and V. A. Lamarra (eds.), Aquatic Resources Management of the Colorado River Ecosystem. Ann Arbor Science Publ., Ann Arbor, Michigan.

CHAPTER 4

THE EFFECTS OF MAINSTREAM DAMS ON PHYSICOCHEMISTRY OF THE GUNNISON RIVER, COLORADO

J. A. Stanford
University of Montana Biological Station
Bigfork, Montana

J. V. Ward
Colorado State University
Fort Collins, Colorado

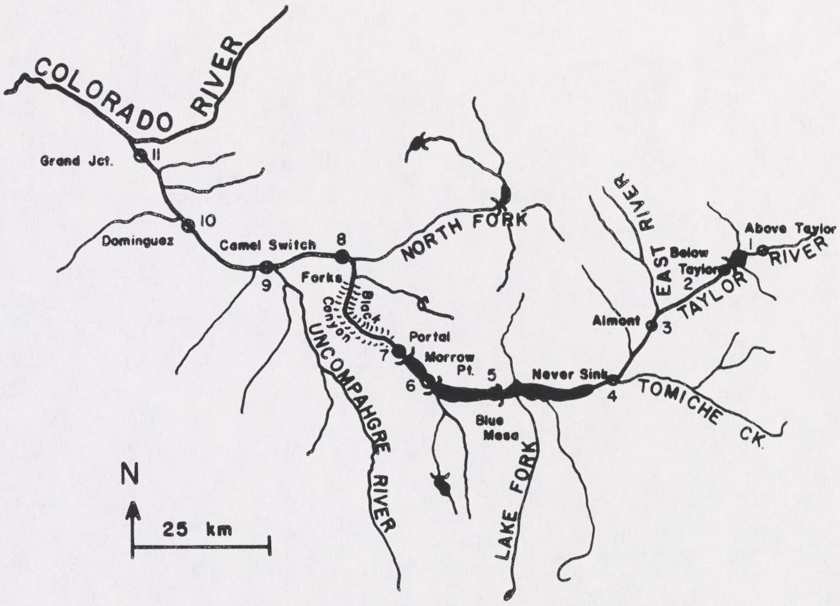
INTRODUCTION

The ways by which dams and diversions impact ecological processes in rivers have received increasing scientific inquiry in recent years [1]. However, almost all knowledge of effects of hydrologic regulation on riverine physicochemistry is based on measurements made at one or a few locations immediately downstream from the point of regulation. While it is obvious that dams alter downstream physicochemical regima profoundly, such impacts have not usually been placed in the context of an entire river system (see [2] for a notable exception).

As a part of a holistic approach to assess the ecology of stream regulation in the Gunnison River, Colorado, we report herein the physicochemical impacts of four mainstream dams on the river system from headwaters to mouth. The changes manifested by this intense regulation greatly influenced patterns and processes within the biotic communities extant in the various river segments [3]. Results reported here are limited to a physicochemical description of this major tributary of the Colorado River before and after regulation.

STUDY AREA

The Gunnison River flows westerly from the Continental Divide in central Colorado to its confluence with the Colorado River near Grand Junction, Colorado. The 20,533 km^2 drainage basin may be divided into two parts, based on basin geology. The upstream portion, above the confluence of the Cimarron River (Figure 1), lies primarily in mountainous terrain and drains granitic soils and relatively insoluble crystalline



GUNNISON RIVER SYSTEM

Figure 1. Location of the mainstream dams and eleven sampling sites on the Gunnison River, Colorado.

bedrock. Downstream from the Cimarron, the river drains a variety of mineral-rich sedimentary formations (especially gypsum shales), which characterize the semi-arid, high plateau of western Colorado.

The average monthly extremes in discharge of the Gunnison River at Grand Junction in the last 25 years have varied between a low of <1 m^3/sec to a high of >230 m^3/sec. However, the annual hydrograph is intensely regulated by hydropower and irrigation demands. Four mainstream reservoirs, Taylor Park, Blue Mesa, Morrow Point and Crystal (Figure 1), are impounded behind high dams and severely influence riverine hydrology. All four dams are deep-release (i.e., hypolimnial drain) systems. Taylor Park is an irrigation storage reservoir built in 1936, while the other three comprise the Aspinal Unit of the Colorado River Storage Project. Blue Mesa Dam was finished in 1965; Morrow Point Dam was closed in 1969. Crystal Reservoir began operation in 1975 as a re-regulation dam to dampen the extreme flow fluctuations below Morrow Point Reservoir. Considerable irrigation return flow occurs in the downstream river segment, especially via the lower Uncompahgre River and adjacent areas.

Few data are available concerning the limnology of these mainstream reservoirs. They are impounded within deep, granite walled canyons at ca. 2200 m elevation, where winter temperatures prevail from October - April. Consequently, these impoundments have a low heat budget. All, except Crystal, apparently stratify seasonally; surface temperatures may exceed 20°C for short periods during summer, but the majority of the stored water volume remains below 8°C year around (see Methods).

METHODS

We established eleven sampling sites along the Gunnison River from a headwater location above Taylor Park Reservoir to a point just upstream from the confluence with the Colorado River (Figure 1). Sampling was conducted on eleven occasions during the period September 1979 to October 1980.

Water samples for analyses of ion concentrations were collected in high-density polyethylene bottles, while grab samples for analyses of carbon fractions were collected in acid-washed teflon or glass bottles. All samples were stored on ice and air-freighted to the University of Montana Biological Station for analysis in the Freshwater Research Laboratory. Conductivity (YSI meter) and pH (Corning meter) measurements and alkalinity titrations (as $CaCO_3$) were made in the field. We installed Ryan© thermographs at two locations to augment records provided by Colorado Division of Wildlife.

Ions (Ca^{++}, Mg^{++}, K^{+}, Na^{+}, $NO_3^{=}$ and $SO_4^{=}$) were quantified by raw water injection into a model 16 Dionex© Ion Chromatograph with output integrated and digitized on a Hewlitt-Packard Model 3388 terminal.

Organic carbon present in water samples was separated into two fractions, particulate organic carbon (POC) and dissolved organic carbon (DOC), with glass-fiber filters (Gelman© 0.2 μm pore size). Organic carbon in filtrates was considered to be in the DOC fraction. POC and DOC were converted to CO_2 by hot persulfate digestion in sealed ampules and concentrations subsequently determined by quantification of the liberated CO_2 using an Oceanography International© infrared detector.

Every fifth analysis (ions or carbon) was replicated (i.e., multiple determinations, usually three, of the same parameter on the same sample) and samples were duplicated (i.e., two samples from the same location and time) to permit calculation of analytical precision and natural variation within sample locations. Reagent spikes were utilized (again every fifth analysis) to check accuracy of analytical technique. Standard deviations of replicates and duplicates were consistently less than one percent of the mean (i.e., high precision) and 90-110 percent of the sample spikes were recovered in analyses leading to the data reported herein.

Some chemical data were available in the STORET file of the U.S. Environmental Protection Agency for comparison to those generated during the present study. Discharge data were provided by the U. S. Geological Survey for various river sites and the U. S. Bureau of Reclamation for the dam sites. Available time-series flow data enabled us to compare discharge regima during the study period, with pre- and post-impoundment regimes (i.e., 1900-64 and 1965-present) on the mainstream river. Time-series temperature data were derived from unpublished literature, such as theses and various agency reports. Thermograph records for Sites 8 and 9 were provided by the Colorado Division of Wildlife, while data for Site 11 were provided by the U. S. Bureau of Reclamation. Relationships between discharge and thermal regima were established with the use of polynomial regression analyses and simple plots of annual degree days (a sum of mean daily temperatures over an annual period, [4]) along the river profile.

RESULTS AND DISCUSSION

The pre-regulation discharge regime of the Gunnison River varied from minimum flows during autumn and winter to spring maxima as a result of melting snowpack in the headwaters (Figure 2). The post-regulation flow has been considerably higher in winter and lower during spring (Figure 2), as runoff is stored in the reservoirs and discharged primarily from November to March. Greater than 90 percent of the average annual discharge is derived from precipitation in the headwaters; downstream side flows (i.e., below the North Fork River) in the lowland sedimentary formations contribute significant amounts of water only during short spates in spring and after heavy summer thunderstorms.

Historically, the upstream segment carried substantial sediment and bed loads during spring runoff which were deposited in the lower gradient downstream segment. Thus, for much of the year, the upstream segment flowed low and clear over a cobble and boulder bottom that was annually scoured and re-distributed by the spring freshet. The downstream segment was also fairly clear at base flow, but the bottom was predominantly silt. Occasional rubble riffles occurred in areas where side flows carried large materials into the river channel (Dolan et al. [5] describe this process of riffle or

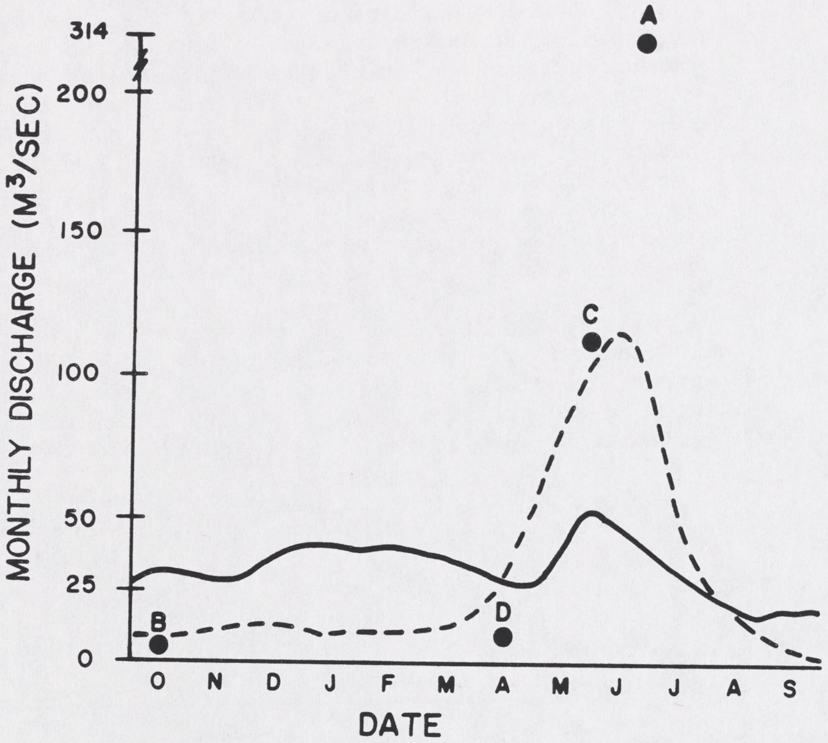


Figure 2. Discharge measured at Site 7, the U.S.G.S. gauging station below Crystal Dam, before regulation (broken line: monthly means 1948-1964) and after construction of mainstream dams (solid line: monthly means 1965-1980). Points A and B identify maximum and minimum pre-regulation discharge (monthly means 1934 and 1957); points C and D represent the maximum (1974) and minimum (1977) monthly flows since regulation (based on U. S. Geological Survey data).

rapids building by side flows on the mainstream Colorado River). Since regulation, silt loads accompanying runoff have been retained in the reservoirs. Thus, discharge below the dams is continually without significant amounts of suspended solids; the river from Taylor Park Reservoir to the East River and from Crystal Dam to the Colorado River is being continually sluiced by clear-water discharges that are of a higher mean volume July to March than prior to impoundment. The result is considerable armoring of the river bottom, the substrata being composed of firmly imbedded large rocks [6]. This situation presently characterizes the Taylor River and Black Canyon segments downstream from the dams to the East River and North Fork River, respectively. Although considerable sediment is contributed to the mainstream river in its lower segment as a result of irrigation return flow via the North Fork River, Uncompahgre River and smaller tributaries, the once silty bottom has now been sluiced to the extent that cobbles and larger rubble predominate in the thalweg from the Black Canyon reach downstream to the Colorado River confluence. In several locations (e.g., Dominguez Canyon), rapids are growing in length and wave height due to the inability of the regulated flow to move large boulders deposited in the mainstream channel by side flow spates.

Daily and annual temperature patterns in the river have also been strongly influenced by regulation. The tailwater segments immediately below the dams are several degrees warmer in winter and 7-20°C colder in summer than before regulation (Figure 3; Table I), because water is discharged

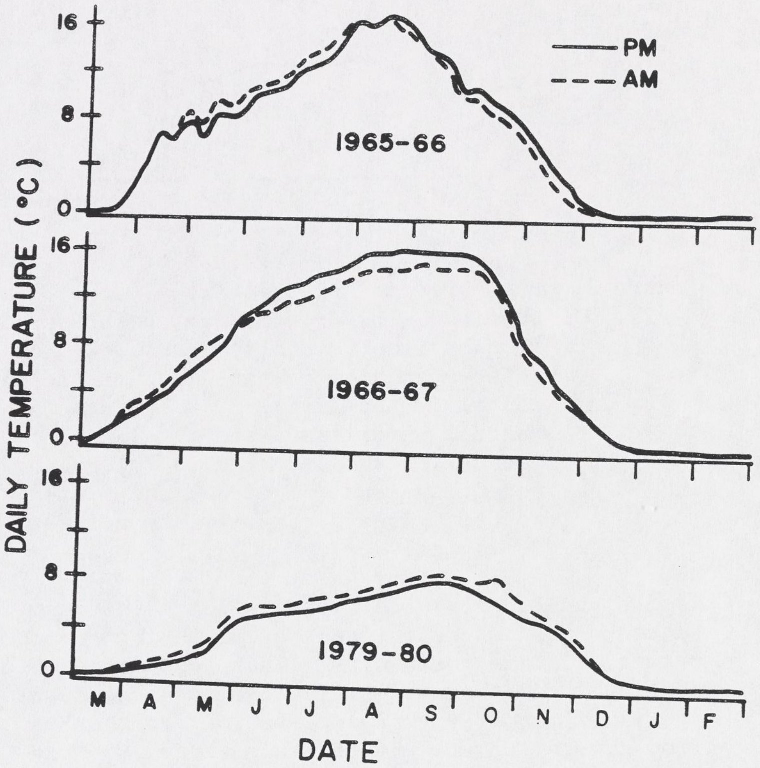


Figure 3. Pre- (1965-66, 1966-67 [from 7]) and post-regulation (1979-80) temperature patterns measured at Site 7, three km downstream from Crystal Dam.

Table I. Comparison of temperature patterns along the Gunnison River continuum before and after construction of the mainstream dams (modified from [3]).

Station No.	Km from Headwaters	Before Regulation		After Regulation	
		Annual Degree Days (Annual Thermal Range)	Daily[a] ΔT	Annual Degree Days (Annual Thermal Range)	Daily[a] ΔT
1	18	1950 (0-15.0)	-	1950 (0-15.0)	-
2*	24	2000 (0-15.0)	+0.1	1000 (2.5-7.2)	-2.6
3	54	2250 (0-16.5)	+0.7	2150 (0-15.5)	+3.2
4	81	2550 (0-18.8)	+0.8	2250 (0-18.8)	+1.1
5*	115	2650 (0-19.0)	+0.3	2323 (3.3-11.1)	-0.6
6*	130	-	-	-	-
7*	144	2895 (0-20.0)	+0.7	1361 (0-9.4)	-3.8
8	195	-	-	-	-
9	228	3606 (0-24.0)	+2.0	3694 (2.8-21.7)	+6.5
10	271	-	-	-	-
11	290	4132 (0-26.6)	+1.5	3432 (0-23.3)	-0.7

[a] calculated mean daily thermal gain or loss from upstream site (see text).
*tailwater area.

from near the bottom of the reservoirs. Prior to regulation, the annual mean temperature of the river progressively increased downstream (Table I). The daily thermal gain (averaged over 12 months) between the headwater site and the Colorado River was about 6°C. In the Black Canyon National Monument the granite walls and shading greatly influenced the daily thermal regime. Kinnear [7] observed that vernal temperatures in the Black Canyon were actually warmer during the night, than during daytime (Figure 3), due to differential heating and cooling of the canyon walls. Since regulation, this daily cycle has been eliminated by the high-volume, cold discharge from Crystal Reservoir. The post-regulation river thermal regime is summarized in Table I. The major conclusion from these data is that the Taylor River and lower mainstream segments are much colder than before regulation and the thermal gain in Black Canyon is more dramatic (simply because the water is so cold at the head of the canyon during the warmest time of the year). Rhithron conditions [8] now extend well into the lower river segment.

The negative thermal gain of -0.7°C observed between Sites 9 and 11 remains largely inexplicable and may be an artifact of limited time-series data (the post-regulation thermal regima at this site were based only on data for one year, 1978), or a response to groundwater input. Several warm springbrooks (e.g., Tongue and Buttermilk Creeks) flow into the river between Sites 8 and 9. The lower Uncompahgre River is also apparently fed by considerable flow from surface aquifers. These side flows may warm the Gunnison River slightly; a subsequent thermal loss could then eventuate in downstream areas not influenced by groundwaters. Thus, the thermal gain estimate at Site 9 could be slightly high.

A strong correlation (r = .87) between the flow rate from Crystal Dam and river temperatures below the Black Canyon (Sites 8 and 9) was observed. At minimum flows (ca. 16 m^3/sec), which occurred only during spring and summer during the period for which thermograph records exist (1978-81), thermal gain in the canyon was 10-12°C; whereas, high flows (ca. 30 m^3/sec and greater) limited thermal gain to 2-3°C. Thus, a very predictable relationship exists between discharge temperature, discharge volume and temperature of the river at any point downstream, given some knowledge of seasonal trends in air temperature. However, heat storage in the granite walls of the Black Canyon undoubtedly limits variance in this relationship; river channels in more open, low-gradient terrain probably exhibit greater diurnal fluctuations.

The observed significant difference between pre- and post-impoundment temperature minima at Site 9 (0° vs. 2.8°, Table I) may be related to the flow-thermal gain relationship within the Black Canyon. Even though the midwinter thermal gain is generally low, high volume discharge limits heat loss. The canyon walls apparently absorb enough heat to ameliorate heat loss. Prior to regulation, low flows coincided with cold, midwinter air temperatures. Thus, the river froze over for periods of a few days to several weeks until air temperatures moderated to the extent that a thermal gain occurred relative to flow rate.

Concentrations of major ions in solution were highest at the downstream sites, indicating substantial salt loading in the lower river segment. Ion concentration was inversely related to seasonal trends in flow at the least regulated sites during 1979-80 (Figure 4). Dissolved solids in tailwater segments were consistently lower than at upstream sites and concentrations were much less variable (i.e., influenced by flow volume) over all sampling dates (Figures 5 and 6).

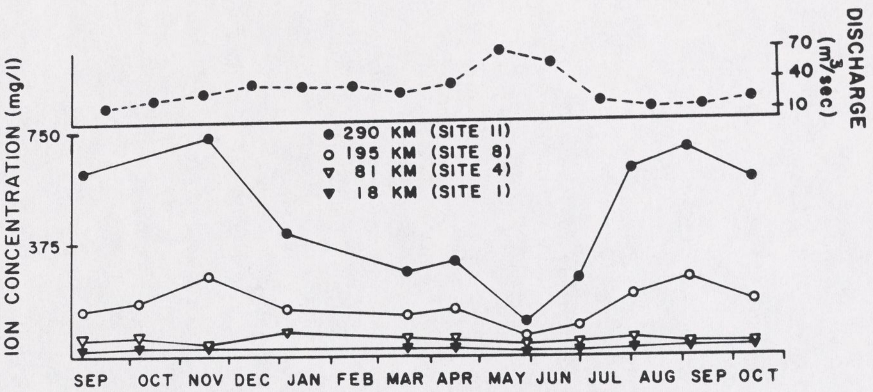


Figure 4. Concentration of the major ions (i.e., sum of Ca^{++}, Mg^{++}, Na^{+} and $SO_4^{=}$ concentrations) in water samples taken in time-series during 1979-80 at four locations along the Gunnison River profile. Flow rates (monthly means) are plotted only for Site 11 located near the confluence with the Colorado River.

Calcium was the dominant ion by percentage composition in the upper river (above the Black Canyon), while sulfate loading from side flows draining gypsum formations characterized the lower river segment (Figure 5). Sulfate-containing salts were observed in high concentrations (e.g., > 3000 mg/l) in the side flows (especially springbrooks and irrigation return flows) between Sites 7 and 9. The propensity of the reservoirs to sediment or precipitate dissolved solids was evinced in our data, but this loss was countered by loading rates nearly two orders of magnitude greater in the lower river segment (Figure 5).

Nitrate concentrations also increased in a downstream direction over the river continuum, but values were consistently elevated in tailwaters in comparison to sites above the reservoirs (Figure 6). The mobilization of nitrate is attributed to mineralization of organic matter (i.e., nitrification) and perhaps nitrogen fixation within the water column of the reservoirs. Nitrates were apparently utilized by autotrophic processes in riverine segments downstream from the dams (Figure 6). This was particularly evident in the Black Canyon, which is the segment least influenced by side flows. Benthic algae, particularly *Cladophora* spp., grow in profusion in all tailwater segments and are a dominant feature of the river bottom from Crystal Dam to Site 8. Tributary effects and turbid irrigation return flows apparently limited excessive growths of filamentous algae below Site 8, even though nutrient loading was apparent (Figure 6). However, thick accumulations of aufwuchs were present at the Dominguez Canyon Site (10) where we measured 3-5 cm accumulations of algae, fine silts, clays and organic detritus firmly attached to cobbles in riffle areas.

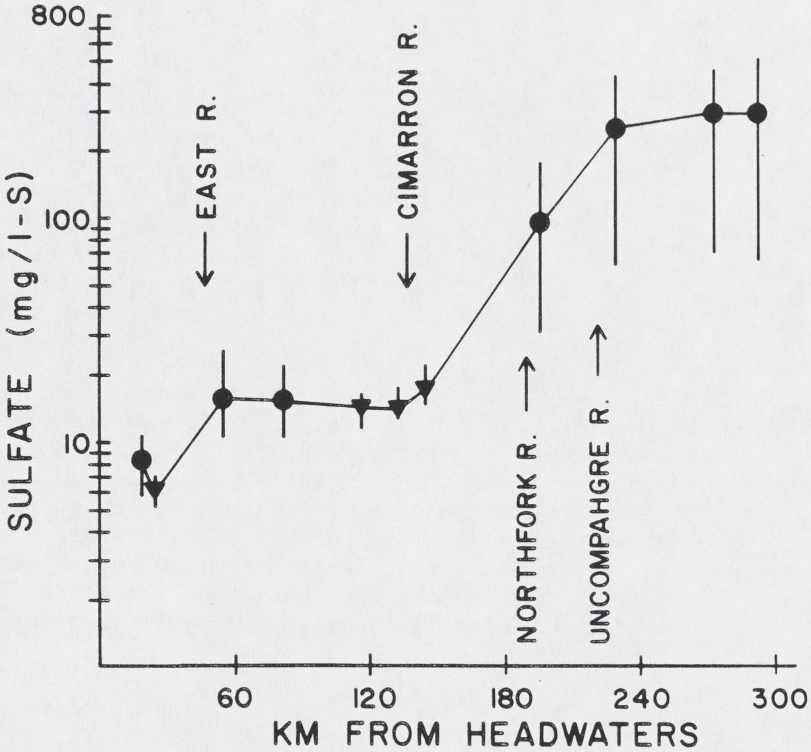


Figure 5. Mean annual sulfate concentrations (mg/l as S) measured at 11 sites on the Gunnison River. Inverted triangles indicate tailwater sites below mainstream dams; bars indicate ranges of values for 11 sampling periods during 1979-80. Location of major side flows are indicated by arrows.

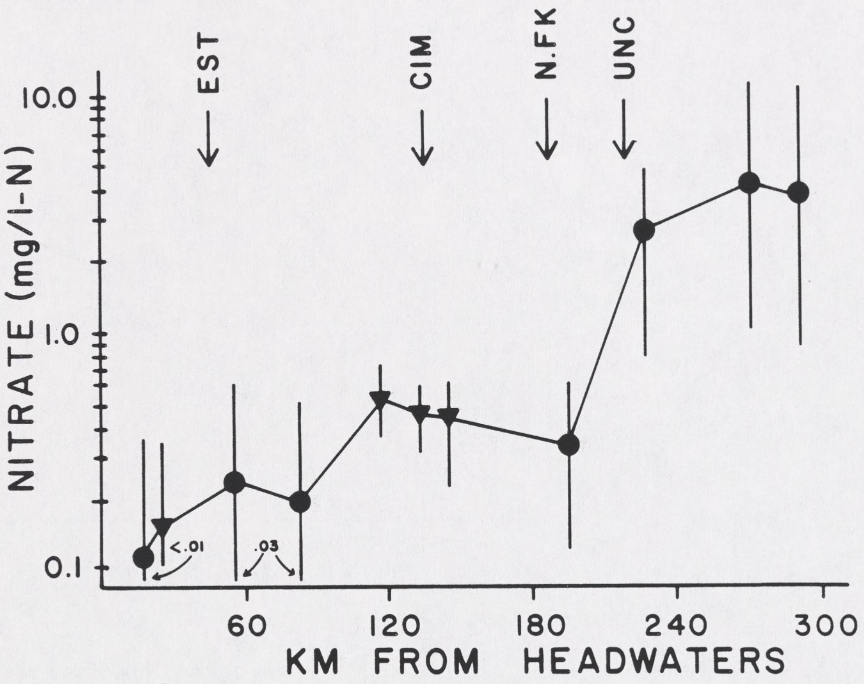


Figure 6. Mean annual nitrate concentrations (mg/l as N) measured at 11 sites on the Gunnison River. Inverted triangles indicate tailwater sites below mainstream dams; bars indicate ranges of values for 11 sampling periods during 1979-80. Location of major side flows are indicated by arrows.

The mineralization effect of the reservoirs was very evident in time-series measurements of particulate and dissolved organic carbon. Despite exports of plankton from the reservoirs, POC levels below the dams were consistently lower than in river segments immediately upstream from the impoundments and vice versa for DOC values. The total organic carbon pool in the river increased from ca. 1.0 to 10.0 mg/l, on the average from headwaters to the mouth (Figure 7). Agglutination processes (i.e., demobilization of dissolved solids by conversion to particulate carbon forms) were responsible for progressively increasing POC values downstream from Taylor Park and Crystal Dams. Much of the seston drift in these segments was due to

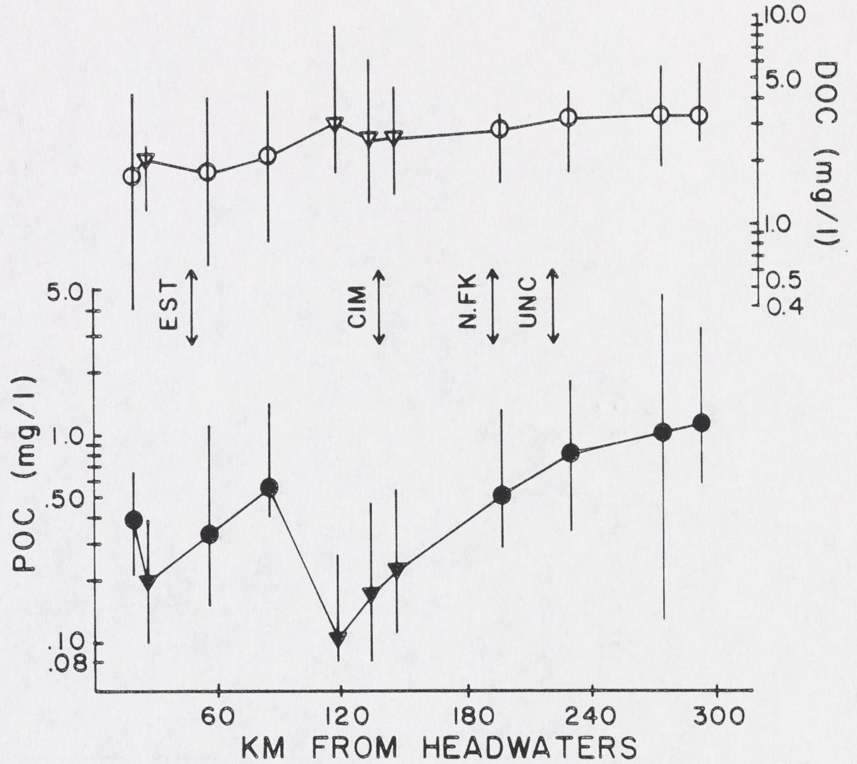


Figure 7. Mean annual dissolved (DOC) and particulate organic carbon (POC) concentrations (mg/l as C) measured at 11 sites on the Gunnison River. Inverted triangles indicate tailwater sites below mainstream dams; bars indicate range of values for 11 sampling periods during 1979-80. Location of major side flows are indicated by arrows.

sloughed filaments of *Cladophora* and other benthic algae. In lower river segments, side flows contributed significant amounts of allochthonous particulates; however, agglutination by autotrophic and micro-heterotrophic activity undoubtedly played a major role in size fractions and POC concentrations in this river segment, except during the spring freshet.

Thus, during 1979-80 the dissolved solids and organic carbon pool increased dramatically in a downstream direction; but, concentrations in the intensely regulated segments were greatly influenced by mineralization and precipitation within the reservoirs and, by agglutination as materials moved downstream in riverine segments. Time-series chemical data for periods previous to our study were limited to Site 4, upstream from Blue Mesa Reservoir. Our data were remarkably similar to these measurements (Table II) indicating that the trends reported here have been the norm since the Gunnison River was regulated. Dissolved and particulate solids loading undoubtedly occurred prior to regulation, but concentrations exported to the Colorado River were likely much lower and more erratic before irrigation return-flows were a significant feature of the lower river.

Table II. Comparison of data in the U. S. Environmental Protection Agency's STORET file to those obtained in the present study. Both data sets were generated from samples collected in time-series at the same location on the Gunnison River 5 km west of Gunnison, Colorado.

	STORET File 1968-1980		This Study 1979-1980	
	Mean (Range)	N	Mean (Range)	N
Magnesium	8.7 (4.0-18.0)	68	7.8 (5.0-12.9)	11
Sodium	5.4 (1.0-15.0)	63	4.0 (2.3-7.4)	11
Sulfate	19.0 (3.0-31.0)	69	15.6 (10.8-22.3)	11
Nitrate	0.19 (*-1.60)	59	0.19 (0.04-0.50)	11

*less than detection limit.

CONCLUSIONS

Hypolimnial-release impoundments on the Gunnison River have altered the physicochemistry of the riverine environment, mainly by reducing seasonal variability. Summer-cold, winter-warm conditions prevail in the river downstream from the dams. Dissolved solids (except $NO_3^=$) and particulate organic matter (POM) are reduced in concentration within reservoir tailwaters in comparison to concentrations in river segments above the reservoirs. Mobilization of $NO_3^=$ and other nutrients in reservoir effluents has stimulated thick growths of periphyton thalweg substrata, which has stabilized (armored) in response to elimination of spring flood flows. Inherent biophysical processes (e.g., communition and agglutination of POM; thermal gain via insolation) and side flows ameliorate or reset the consequences of regulation, as distance downstream from impoundments increases. Although the dissolved solids pool increases down the river profile, conditions 30-40 km downstream from the last dam (i.e., at Site 8) mimic the rhithron environment 115 km upstream (i.e., at Site 4). Physicochemistry of the Gunnison River near its confluence with the Colorado River is similar to pre-regulation, except that annual variance in discharge has decreased and dissolved solids increased.

REFERENCES

[1] Ward, J. V. and J. A. Stanford (Eds.) 1979. The Ecology of Regulated Streams. Plenum Press, New York. 398 pp.

[2] Penáz, M., F. Kubícek, P. Marvan and M. Zelinka. 1968. Influence of the Vír River Valley Reservoir on the hydrobiological and ichthyological conditions in the River Svratka. Acta Academiae Scientiarum Hungaricae 2(1): 1-60.

[3] Stanford, J. A. and J. V. Ward. 1981. Preliminary interpretations of the distribution of Hydropsychidae in a regulated river. pp. 323-328. *IN*: Moretti, G.P. (Ed.) Proceedings of the Third International Symposium on Trichoptera. Series Entomologica, Volume 20. Dr. W. Junk. The Hague.

[4] Baskerville, G. L. and P. Emin. 1969. Rapid estimation of heat accumulation from maximum and minimum temperatures. Ecology 50(3): 514-517.

[5] Dolan, R., A. Howard and A. Gallenson. 1974. Man's impact on the Colorado River in the Grand Canyon. American Scientist 62: 392-401.

[6] Simons, D. B. 1979. Effects of stream regulation on channel morphology. pp. 95-112. *IN*: Ward, J. V. and J. A. Stanford (Eds.) The Ecology of Regulated Streams. Plenum Press. New York. 398 pp.

[7] Kinnear, B. 1967. Fishes of Black Canyon. M. S. Thesis, Colorado State University. 45 pp.

[8] Hynes, H. B. N. 1970. The Ecology of Running Waters. University of Toronto Press. Toronto. 555 pp.

Environment International, Vol. 9, pp. 135–138, 1983
Printed in the USA. All rights reserved.

0160-4120/83 $3.00 + .00

[1983]

LEAF LITTER BREAKDOWN IN STREAMS RECEIVING TREATED AND UNTREATED METAL MINE DRAINAGE

L. J. Gray and J. V. Ward
Colorado State University, Department of Zoology and Entomology, Fort Collins, Colorado 80523, USA

(Received 29 October 1982; Accepted 13 December 1982)

Rates of alder leaf decomposition were used as an ecosystem-level measure of effects of untreated and treated acid mine drainage on two Colorado mountain streams. Untreated mine effluents had low pH and high concentrations of metals, particularly iron. Deposition of ferric hydroxide on leaf surfaces inhibited colonization by decomposers, such as fungi and aquatic insects, and thus little leaf breakdown occurred. Treated effluents had improved water quality (basic pH, low metal concentrations), but suspended flocs released by the treatment process buried leaves and reduced consumer activity. The rate of leaf breakdown was not significantly different from the rate with untreated effluents; thus improvement in water quality alone was insufficient to restore this important pathway of energy flow in headwater streams.

Introduction

Terrestrial plant litter is an important source of energy for consumers in many headwater streams. The dynamics of its decomposition, particularly the leaf fraction, has been a focal point of contemporary research in stream ecology (Anderson and Sedell, 1979).

The breakdown of whole leaves in streams involves rapid leaching of soluble compounds and subsequent fragmentation to fine particulates (Cummins, 1974). Fragmentation results from physical and biological agents, including abrasion caused by turbulence, microbial metabolism, and the feeding activities of benthic invertebrates. The relative contribution of each factor varies with leaf species, geographic region, and composition of biotic communities (Anderson and Sedell, 1979).

Because of its importance in the flow of energy in streams, leaf decomposition provides an ecosystem-level measure of pollution effects. In this study we used rates of leaf breakdown as an indicator of the response of lotic consumers to effluents of treated and untreated acid mine drainage in two Colorado mountain streams. In Colorado, many of the estimated 30,000 abandoned metal mining operations significantly affect local water quality (Wentz, 1974).

In a previous examination of the study streams, Boyne *et al.* (1982) found greatly reduced numbers and biomass of benthic invertebrates downstream from the entrance of untreated mine drainage. However, concentrations of heavy metals were below toxic levels for some species, particularly "shredders" that consume whole leaves. They hypothesized that the absence of shredders resulted from deposition of ferric hydroxide on leaf surfaces, which inhibited microbial colonization and thus lowered food quality (Cummins, 1974). Treatment of effluents to remove iron and eliminate deposition of ferric hydroxide would presumably allow microbial colonization and subsequent feeding by shredders, and thus increase rates of leaf breakdown. The present examination was performed to determine whether an improvement in water quality following treatment is sufficient to restore the pathways of energy flow, as evidenced by rates of leaf breakdown.

Study Areas

The two study streams were Kerber Creek (38°18′N, 106°08′W), a third-order tributary of San Luis Creek near Villa Grove (3000 m a.m.s.l., gradient = 3%), and Coal Creek (38°53′N, 107°01′W), a third-order tributary of the Slate River near Crested Butte (2830 m, gradient = 3%). The two sites at Kerber Creek were located upstream (Site K-1) and downstream (Site K-2) from the entrance of untreated mine drainage that severely degraded water quality (Ingwersen, 1982; Wentz, 1974). Control (Site C-1) and impact (Site C-2) sites on Coal Creek were located above and below the entrance of treated mine effluents. Sites C-1 and K-1 were similar in physical-chemical characteristics: pH = 7.5–7.7; conductivity = 90–100 μS cm^{-1}; mean temperature = 2.0 °C; dissolved oxygen at or near saturation, and concentrations of heavy metals below detection limits (0.01 mg L^{-1}). Characteristics at Site K-2 were pH = 6.1–6.4; conductivity = 460–510 μS cm^{-1}; mean temperature = 3.8 °C; dissolved oxygen at 83%–90% saturation. Mean concentrations of selected metals were 9 mg L^{-1} for total iron, 16 mg L^{-1} for total zinc, and 11 mg L^{-1} for total manganese. Extensive deposits of ferric hydroxide were present on stream substrates. At site C-2, mean values of physical-chemical parameters were pH = 7.2–7.4; conductivity = 430–560 μS cm^{-1}; temperature = 3.8 °C; dissolved oxygen at or near saturation; and concentrations of metals below detection limits. However, effluents carried larger quantities of a flocculent material consisting of a synthetic polymer. The polymer is used to precipitate metals and was apparently released accidentally during operation of the treatment plant. This floc settled on the streambed, forming a layer several centimeters thick.

Materials and Methods

Alder leaves were used as the test species because of their rapid rate of breakdown (Short *et al.*, 1980) and abundance along both study streams. Leaves were collected just before abscission in September 1981 and preleached in the laboratory using filtered stream water. Weight loss from leaching was determined by placing 0.1 g of leaf material in a beaker with stream water and incubating at 2 °C (24 h). After leaching, leaves were air dried, oven dried (60 °C, 48 h), weighed into 5-g packs, and strung on monofilament line (Short *et al.*, 1980). Each leaf pack was then lashed to a brick and placed in the study sites on 10–11 October (approximately 4 months after treatment of effluents into Coal Creek had begun). Five packs were recovered from each site at 2-, 5-, and 8-week intervals. Remaining packs were recovered in April 1982 (28 weeks). During collection, the pack was cut free from its brick and placed in a plastic bag with 5% formalin. In the laboratory each pack was rinsed with tap water to remove sediments, oven dried, weighed to the nearest 0.1 g, and combusted at 550 °C (4 h) to determine ash-free mass.

Shredders associated with the leaf packs were stored in 80% ethanol until identified and enumerated. Total biomass was determined by drying at 60 °C (48 h).

Results and Discussion

Leaf processing in streams follows an exponential decay model: $Y_t = Y_0 e^{-kt}$, where Y_t = leaf mass remaining after t days; Y_0 = initial mass (= 5.0 g DW or 4.6 g AFDW); and k = rate loss coefficient (Petersen and Cummins, 1974). After allowing for losses from leaching (=18.4% ±4.4% of DW, 1 S.D., $N = 20$), loss rate coefficients were calculated for each study site from the percent remaining data in Fig. 1. All regressions were significant ($P \leq 0.01$). Loss rate coefficients and the time required for 50% loss of leaf material were $k = 0.0147$, 48 days at site K-1; 0.0032, 217 days at site K-2; 0.0109, 64 days at site C-1; and 0.0037, 187 days at site C-2. Packs recovered in April from sites K-1 and C-1 show that these rate loss coefficients are representative of long-term rates of leaf breakdown. Only veins and petioles remained of packs at site K-1 after 196 days, and the calculated time for 90% processing was 157 days. At site C-1, a mean of 24% of the leaf mass remained from two packs, and this percentage is within calculated 95% confidence limits (5%–27% remaining after 196 days).

Rates of alder leaf breakdown at the two control sites are similar to rates reported for other streams at similar

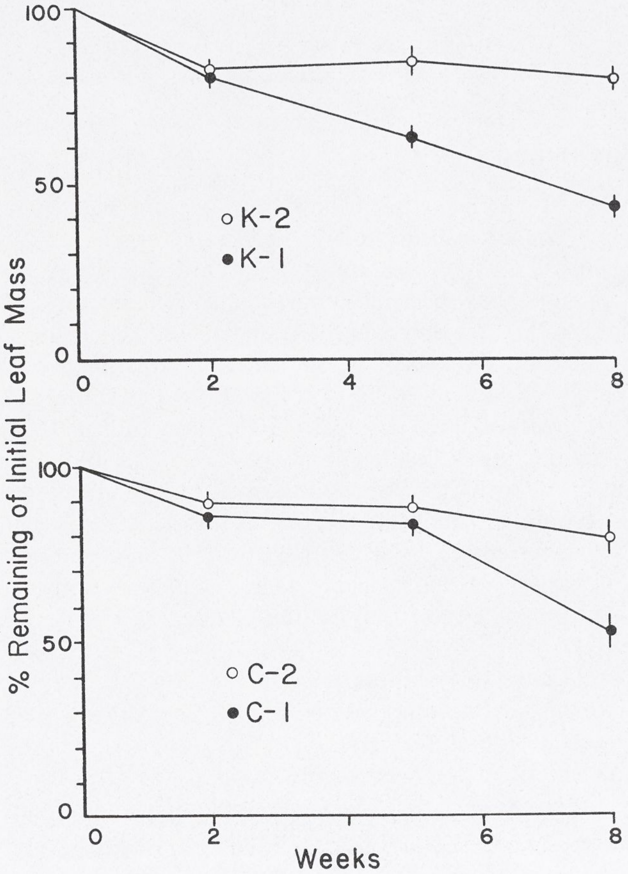


Fig. 1. Loss of leaf mass during fall 1981 in Kerber and Coal Creeks, CO, at control sites (K-1 and C-1), a site receiving untreated mine effluents (K-2), and a site receiving treated effluents (C-2). Vertical bars indicate ±1 S.E.

temperatures (Sedell *et al.*, 1975; Short and Ward, 1980). Microscopic examination of unpreserved leaf fragments after 8 weeks in-stream showed extensive growths of fungal mycelia and surface bacteria (Fig. 2). Hyphae of Basidiomycetes fungi were common, but further identification was precluded by the absence of reproductive structures. The higher rate loss coefficient at site K-1 compared to C-1 can be attributed to a greater abundance of shredders. Shredder abundance averaged 18 individuals and 14.1 mg DW per leaf pack at K-1, whereas values at C-1 were 3 individuals and 1.8 mg DW per pack. These differences reflected the species present and their life cycles. Shredder activity in Kerber Creek resulted from late-instars of *Pteronarcella badia* (Plecoptera) and *Dicosmoecus* sp. (Trichoptera). In Coal Creek the dominant shredders were winter stoneflies (*Zapada* spp.) present mainly as early instars.

The loss rate coefficient at site K-2 was significantly lower than the coefficient for site K-1 ($F = 92.9403$, d.f. = 1, 35, $P < 0.01$; analysis of covariance from Sokal and Rohlf, 1969). Extensive coatings of ferric hydroxide on leaves at site K-2 inhibited microbial colonization and feeding by shredders (Fig. 2). The only mechanism of leaf breakdown was mechanical disruption by current. These results concur with previous studies that have shown greatly reduced decomposition rates in aquatic habitats with low pH and high metal concentrations (Forbes and Magnuson, 1980; Giesy, 1978; Guthrie *et al.*, 1978).

The loss rate coefficient at site C-2 was significantly lower than the coefficient at site C-1 ($F = 29.0985$, d.f. = 1, 35, $P < 0.01$) but was equivalent to the coefficient at site K-2 ($F = 0.3149$, d.f. = 1, 34, $P = 0.58$). The low rate at C-2 resulted from several factors: (1) within 2 weeks, all leaf packs were buried by the floc released in the treated effluent, and buried leaves have been shown to lose mass slower than leaves on the surface (Herbst, 1980); (2) little microbial colonization occurred due to adherence of floc to leaf surfaces (Fig. 2); (3) as at site K-2, only a single shredder was collected among all leaf packs. The loss of mass that occurred probably resulted from abrasion by shifting floc.

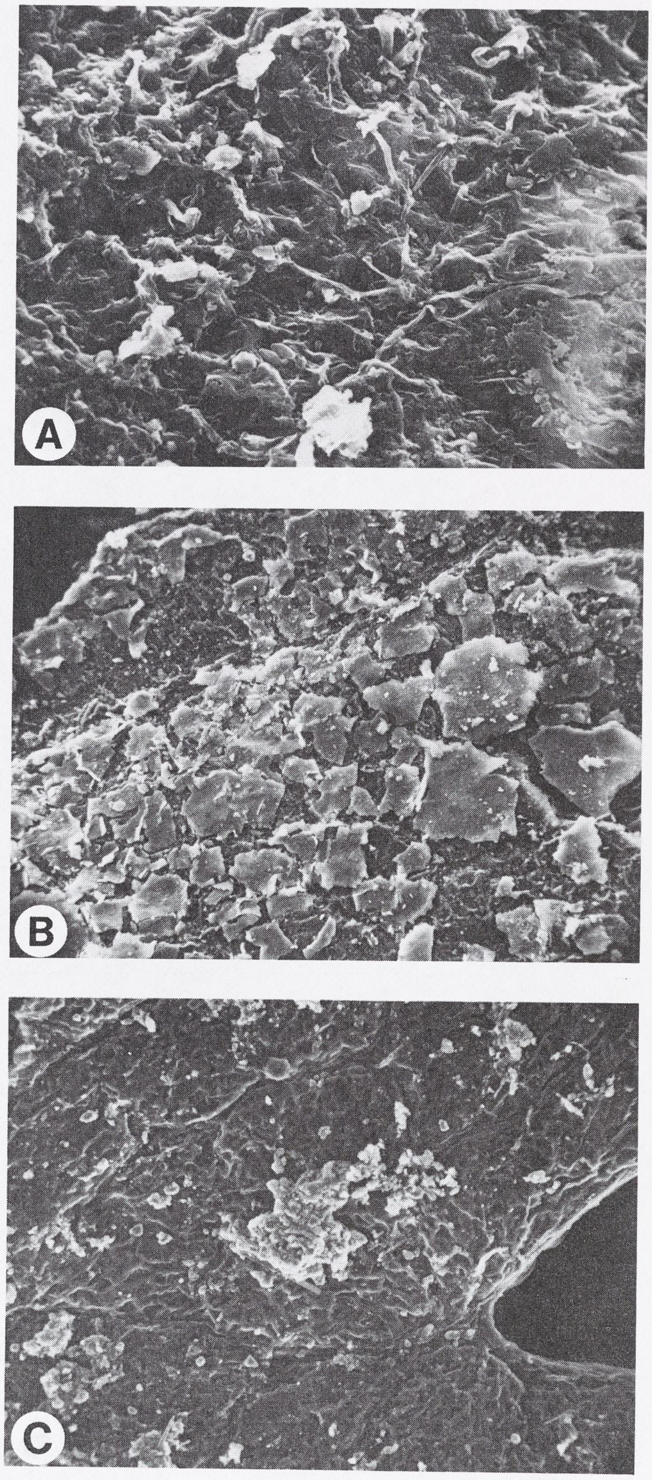


Fig. 2. Scanning electron micrographs of leaf surfaces at sites K-1 (A, 400×), K-2 (B, 80×), and C-2 (C, 100×). Note deposits of ferric hydroxide on leaves in B and polymer floc from treatment on leaves in C.

Conclusions

Operation of a treatment plant, while greatly improving the overall water quality of a stream receiving metal mine effluents, released flocculent materials which were deposited on the stream substrate. This deposition reduced the breakdown of leaf litter to a rate equivalent to that occurring in a stream receiving untreated mine effluents. The mechanism lowering rate loss coefficients was the same in both cases—inhibition of microbial colonization by surface deposits and subsequent lack of feeding by shredder insects. Thus the pathways of energy flow within the treated system were not restored despite improvements in overall water quality.

Acknowledgements—The authors thank J. H. Harvey for field assistance and M. J. Packard for assistance with electron microscopy. Research was conducted under the auspices of G-5115001 (CSM703) funded by the Office of Surface Mining, U.S. Department of the Interior.

References

Anderson, N. H. and Sedell, J. R. (1979) Detritus processing by macroinvertebrates in stream ecosystems, *Ann. Rev. Entomol.* **24,** 351–377.

Boyne, H. S., Ingwersen, J. B., Ward, J. V., Gray, L. J., Harvey, J., and Ponce, S. L. (1982) Environmental assessment of stream pollution by mine drainage as a function of geologic type and reclamation success. Colorado School of Mines, Golden, CO.

Cummins, K. W. (1974) Structure and function of stream ecosystems, *Bioscience* **24,** 631–641.

Forbes, A. M. and Magnuson, J. J. (1980) Decomposition and microbial colonization of leaves in a stream modified by coal ash effluent, *Hydrobiol.* **76,** 263–267.

Giesy, J. P., Jr. (1978) Cadmium inhibition of leaf decomposition in an aquatic microcosm, *Chemosphere* **7,** 467–476.

Guthrie, R. K., Cherry, D. S., and Singleton, F. L. (1978) Responses of heterotrophic bacterial populations to pH changes in coal ash effluent, *Water Res. Bull.* **14,** 803–808.

Herbst, G. N. (1980) Effects of burial on food value and consumption of leaf detritus by aquatic invertebrates in a lowland forest stream, *Oikos* **35,** 411–424.

Ingwersen, J. B. (1982) Downstream recovery of selected Colorado streams subject to acid drainage from abandoned metal mines. M. S. Thesis, Colorado State University, Fort Collins, CO.

Petersen, R. C. and Cummins, K. W. (1974) Leaf processing in a woodland stream, *Freshwater Biol.* **4,** 343–368.

Sedell, J. R., Triska, F. J., and Triska, N. M. (1975) The processing of conifer and hardwood leaves in two coniferous forest streams. I. Weight loss and associated invertebrates, *Verh. Int. Verein. Limnol.* **19,** 1617–1627.

Short, R. A. and Ward, J. V. (1980) Leaf litter processing in a regulated Rocky Mountain stream, *Can. J. Fish. Aquat. Sci.* **37,** 123–127.

Short, R. A., Canton, S. P., and Ward, J. V. (1980) Detritus processing and associated macroinvertebrates in a Colorado mountain stream, *Ecology* **61,** 727–732.

Sokal, R. R. and Rohlf, F. J. (1969) *Biometry.* W. H. Freeman, San Francisco, CA.

Wentz, D. A. (1974) Effect of mine drainage on the quality of streams in Colorado, 1971–72. Water Res. Circ. No. 21, U.S. Geological Survey, Denver, CO.

[Living in Flow of Water]
1999

Dynamics of Lotic Ecosystems

Edited by

Thomas D. Fontaine, III
Savannah River Ecology Laboratory
University of Georgia

Steven M. Bartell
Environmental Sciences Division
Oak Ridge National Laboratory

ANN ARBOR SCIENCE
THE BUTTERWORTH GROUP

230 Collingwood, P.O. Box 1425, Ann Arbor, Michigan 48106

Library of Congress Catalog Card Number 82-048641
ISBN 0-250-40612-8

Manufactured in the United States of America

Butterworths, Ltd., Borough Green, Sevenoaks
Kent TN15 8PH, England

17. THE INTERMEDIATE-DISTURBANCE HYPOTHESIS: AN EXPLANATION FOR BIOTIC DIVERSITY PATTERNS IN LOTIC ECOSYSTEMS

James V. Ward
Department of Zoology and Entomology
Colorado State University
Fort Collins, Colorado

Jack A. Stanford
University of Montana Biological Station
Bigfork, Montana

ABSTRACT

The intermediate-disturbance hypothesis predicts that biotic diversity will be greatest in communities subjected to moderate levels of disturbance. It is consistent with diversity patterns observed in natural and altered lotic ecosystems. Species diversity is suppressed in stream habitats exposed to disturbances that are severe (organic loading or acid mine drainage) or frequent (diel flow fluctuations). In addition, habitats with enhanced environmental constancy (spring sources or streams below storage reservoirs) exhibit suppressed diversity even if adverse conditions (e.g., oxygen deficits) are not apparent. It is postulated that "undisturbed" lotic systems are in fact "disturbed" and that the high biotic diversity of natural streams is a function of moderate perturbation. Diversity is enhanced by the spatio-temporal heterogeneity resulting from intermediate disturbance, which maintains the community in a nonequilibrium state. This theory may account for much of the diversity variance within stream systems and between different types of lotic habitats.

INTRODUCTION

The intermediate-disturbance hypothesis (Connell, 1978) predicts that a greater biotic diversity will be maintained in communities subjected to intermediate levels of disturbance than in those undergoing either greater or lesser perturbation. As stated by Osman (1977), "There appears . . . to be an optimal frequency of disturbance at which diversity is maximized." Support for the intermediate-disturbance hypothesis can be derived from terrestrial (e.g., Harper, 1969), marine (e.g., Paine, 1971), or lentic (e.g., Dodson, 1970) systems. There is a relatively rich literature relating the concept to intertidal and subtidal communities (Paine, 1966; 1969; 1971; Osman, 1977; Dayton, 1971; Menge, 1979).

It is postulated here that the intermediate-disturbance hypothesis largely explains patterns of biotic diversity observed in natural and altered lotic ecosystems. After a brief review of the salient features of the hypothesis, this paper explores the relationships between disturbance level and the diversity (species richness) of stream communities. Diversity is viewed primarily in an ecological time frame, i.e., "the maintenance of diversity, as opposed to the generation of diversity" (Huston, 1979), unless otherwise stated.

THE INTERMEDIATE-DISTURBANCE HYPOTHESIS

The intermediate-disturbance hypothesis is diagrammed in Figure 1. Simply stated, a certain level of "disturbance" results in a higher biotic diversity than greater or lesser perturbation. Disturbance level may be roughly equated with environmental heterogeneity if the latter is viewed broadly in a spatio-temporal context. The initial disturbance can be biotic (e.g., predation or disease) or abiotic (e.g., fire, storms, or wave action). The severity of the disturbance can be considered from the standpoint of intensity [e.g., intensity of predation (Paine, 1966)], frequency [e.g., frequency of fire (Taylor, 1973)], or both.

Connell (1978) presented evidence that the high diversity of trees in tropical rain forests and corals on tropical reefs is a function of disturbances, such as storms, which have an intermediate frequency of occurrence. Connell postulated that these systems exist in a "non-equilibrium state which, if not disturbed further, will progress toward a low-diversity equilibrium community." Examining burned areas in Yellowstone National Park, Taylor (1973) found that areas burned 25 years previously had the greatest diversity of plant, bird, and mammal species. Areas burned with greater or lesser frequency exhibited lower

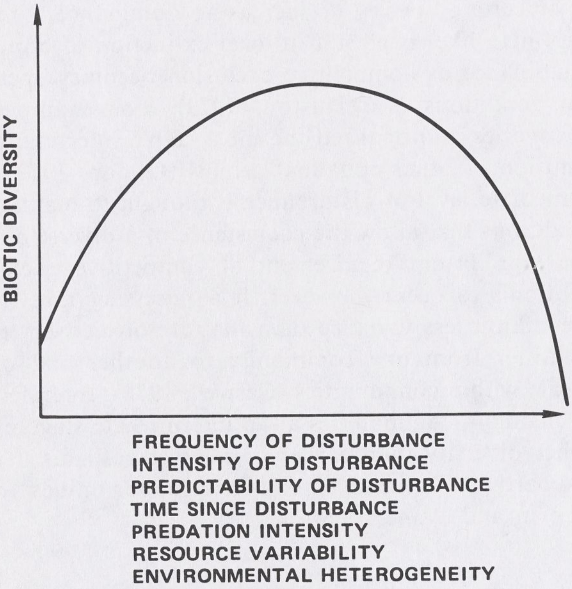


Figure 1. Theoretical relationship between biotic diversity and various measures of "disturbance" (modified from Connell, 1978).

biotic diversity. Loucks (1970) suggested that the natural tendency for random environmental perturbation in temperate forests maintains peak diversity in the vegetation community. Intermediate levels of disturbance or physiological stress have been shown to result in the greatest diversity of plant species in pastures (Grime, 1973). Osman (1977) reported a low diversity of epifaunal marine species on large rocks (high stability) and small rocks (low stability) but a high diversity on intermediate-sized rocks of moderate stability. Moderate predation pressure may maintain a high level of diversity of prey species, as Paine (1966) showed by comparing intertidal areas containing starfishes with those from which these predators had been removed. Many additional examples could be drawn from studies of terrestrial and especially marine systems (see Fox, 1979, and Huston, 1979, for additional references).

What accounts for the enhanced diversity associated with moderate disturbance? Disturbances that are too frequent (e.g., annual burning or low stability intertidal rocks) or too intense (e.g., toxic inputs or severe predation) are thought to suppress biotic diversity by causing local extinction of certain species or increasing dominance. Environmental homogeneity may likewise result in local extinction of populations and shifts in dominance as competitive exclusion becomes operative under equilibrium conditions (see Huston, 1979). For example, the most competitive species monopolized the most stable intertidal rocks to the virtual exclusion of other epifaunal groups (Osman, 1977).

An intermediate level of disturbance is thought to maintain nonequilibrium conditions that allow the coexistence of a diverse assemblage of species; the equilibrium requirement of competitive exclusion is not fulfilled. For this to occur, however, it is necessary that the extent of disturbance exhibit less variance than the rate of recovery (Fox, 1979), which will differ from one community to another and on a spatio-temporal scale within communities (Caswell, 1978). Intermediate disturbance may maintain communities at an intermediate stage of succession with a higher diversity than earlier or later stages; this in some communities is partly a function of enhanced opportunities for potential invaders (Levin and Paine, 1974).

EVIDENCE FROM LOTIC ECOSYSTEMS

It has been suggested that the intermediate-disturbance hypothesis may apply to a variety of systems (Levin and Paine, 1974). Although the concept has not previously been specifically related to lotic ecosystems, there is evidence supporting the applicability of the hypothesis to running waters. Patrick (1970), for example, considered competition among benthic plants to be relatively unimportant in determining the community structure of natural streams. She contended that unpredictable fluctuations in nutrients maintain diversity by preventing monopolization of resources by one or a few species. Biotic diversity is maintained partly by species replacement, as changing environmental conditions favor different assemblages of species. Ward (1976a; 1976b) postulated that the diversity of many natural streams is maintained by their nonequilibrium conditions and that anthropogenic alterations that enhance environmental constancy may increase coactive patterns and cause a shift toward an equilibrium community, accompanied by a reduction in diversity. Species diversity of stream organisms has also been associated with the extent of seasonal (Ide, 1935) and diel (Vannote et al., 1980) thermal variation, which may be partly responsible for the maintenance of life-cycle diversity (Ward, 1976a). Moderate predation pressure has been implicated in the maintenance of biotic diversity in streams (Patrick, 1970), and the "keystone species" concept (Paine, 1969) has been postulated as influencing diversity in stream systems (Fox, 1977; Ward and Stanford, 1979). Gray (1980) presented evidence suggesting that desert stream macroinvertebrate communities may respond to flood events in a manner consistent with the intermediate-disturbance hypothesis.

The species richness of selected stream macroinvertebrate communities is plotted against "extent of disturbance" in Figure 2. Examples were drawn from lotic systems ranging from small brooks to mid-sized rivers. Data points for natural streams (i.e., those relatively unaffected by man's activities) are plotted in the center of the figure; the (+) indicates a "normal" level of disturbance. It is not implied that all natural streams exhibit the same degree of environmental variance; habitats with lesser (–) and greater (++) than normal disturbance are likewise somewhat arbitrarily positioned on the horizontal axis. Because of variations in collecting efforts, sampling techniques, and levels of taxonomic resolution, species diversity values from different studies are of only rough comparative value. However, habitats indicated with solid circles have reference plots with corresponding numbers to indicate different sites from the same study. For example, number 6 in the center (130 species) is

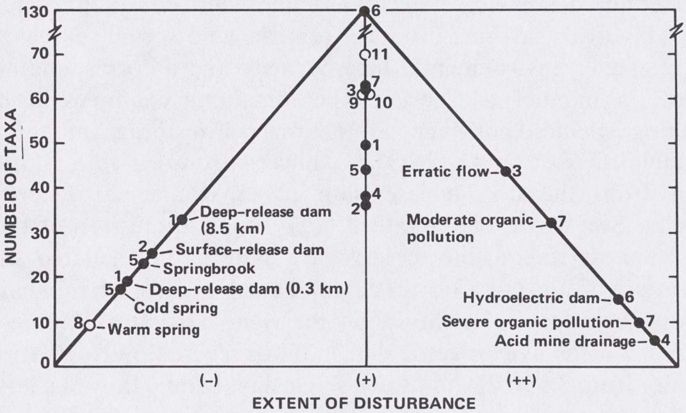


Figure 2. Taxonomic diversity of selected stream macroinvertebrate communities and extent of disturbance. Lotic habitats with minimal anthropogenic impact and "normal" environmental variability are plotted in the center (+) to indicate a moderate extent of disturbance. Habitats exhibiting lesser (–) and greater (++) than normal disturbance are also shown (see text for further explanation). Arabic numerals indicate citations: 1, Ward, 1974; 1976b. 2, Ward and Short, 1978. 3, Ward and Short, 1978. 4, Herricks and Cairns 1974. 5, Gray and Ward 1979; Martinson and Ward, unpublished. 6, Stanford, unpublished. 7, Gaufin and Tarzwell, 1956. 8, Ward, unpublished. 9, Ames, 1977. 10, Ward, 1975. 11, Ames, 1977.

the Middle Fork of the Flathead River, Montana, which exhibits considerable natural environmental heterogeneity, whereas number 6 on the right (15 species) is the South Fork of the Flathead River below a hydroelectric dam, where diel flow fluctuations are extreme. The reference plots enable comparisons of species richness between differentially disturbed sections of the same stream (or stream system), thus reducing other differences that influence diversity, such as stream type and zoogeographical factors. In some instances species richness does not fully elucidate the differences between disturbance levels because of the more even distribution of taxa in the natural systems. For example, although 25 taxa occurred below the surface-release dam, in contrast to 36 at a station above the reservoir (Figure 2), Shannon index values (1.7 vs. 4.1) better contrast the diversity differences. It was not possible in all cases to calculate diversity indices from the data available, however.

Several lotic habitats with enhanced environmental constancy are exemplified in Figure 2 (see figure legend for citations). Habitats were selected in which the low biotic diversity is not attributable to low oxygen or toxic substances. Extreme physico-chemical constancy characterizes the warm (25° C) and cold (8° C) spring sources. Explanations for reduced diversity in springs (relative to environmental homogeneity) have been addressed in detail elsewhere (Ward and Dufford, 1979). The spring brook (Figure 2), a short distance from the cold spring source, exhibits slightly greater environmental heterogeneity and a corresponding slight increase in number of species. The remaining examples of habitats exhibiting enhanced constancy are streams below storage impoundments. A notable increase in diversity is exhibited from 0.3 to 8.5 km downstream from the deep-release dam as environmental heterogeneity increases. See Ward and Stanford (1979) for a discussion of the interrelated factors responsible for diversity patterns in regulated streams.

A variety of lotic systems that exhibit excessive disturbance caused by anthropogenic factors is shown on the right portion of Figure 2. The stream below the hydroelectric dam exhibits severe flow fluctuations that may vary from 7.5 to 260 m^3/s in a single day. Erratic flow of a less severe nature downstream from an irrigation reservoir suppresses biotic diversity to a much lesser degree. A significant, but incomplete, recovery of macroinvertebrate diversity is shown from the septic zone to the recovery zone of a stream stressed by organic pollution. On the basis of species diversity, the stream receiving acid mine drainage indicates the most severe disturbance (Figure 2).

DISCUSSION AND CONCLUSIONS

It is our contention that "undisturbed" lotic systems are in fact "disturbed" and that the high biotic diversity of certain natural streams is a function of moderate perturbation. We propose that the diversity of natural lotic systems is maximized by the spatio-temporal heterogeneity resulting from moderate disturbance, which maintains the community in a nonequilibrium state. We feel that the concept of resource variability itself behaving as an abstract resource (Levins, 1979) is applicable to lotic ecosystems, especially as related to species packing.

It must be emphasized that biotic diversity varies greatly from one natural stream to another and longitudinally in the same stream system (Vannote et al., 1980). This variation in diversity in natural streams is generally consistent with the intermediate-disturbance hypothesis, however. The middle reaches of the steam continuum, the region of greatest environmental heterogeneity, also exhibit the highest biotic diversity (Vannote et al., 1980). Headwater reaches and the lower portions of rivers have lower diversity values associated with more constant environmental conditions (but see Horwitz, 1978). The unsuspected magnitude and unpredictability of environmental variance in tropical streams (Stout and Vandermeer, 1975) may, at least partly, account for the higher diversity of tropical than temperate stream insects, just as Connell (1978) used environmental inconstancy to explain the high diversity of trees and corals in tropical regions. To confirm or refute the relationship between disturbance level and biotic diversity, we must examine specific lotic ecosystems displaying variability in the frequency and severity of disturbance. In addition, a more precise and objective method of determining the extent of disturbance is needed.

Community structure is shaped by a myriad of physical, chemical, and biological variables acting synergistically. A single ecological measure of disturbance, such as the efficiency of energy flow or the rate of species replacement, may serve to integrate the biologically significant environmental variables in running waters. Until controlled experimental treatments are explicitly designed to quantify spatio-temporal heterogeneity, however, it is perhaps premature to attempt a rigorous mathematical description of disturbance in lotic ecosystems.

ACKNOWLEDGMENTS

Appreciation is extended to R. W. Pennak, University of Colorado, and V. H. Resh, University of California, Berkeley, for reading the manuscript. Discussions with R. T. Paine, University of Washington, and M. L. Rosenzweig, University of Arizona, were most helpful. Additional intellectual stimulation was provided by the students in the Graduate Limnology Seminar, Colorado State University, fall 1979. This manuscript was prepared while J. V. Ward was supported by the Colorado Experiment Station.

REFERENCES

Ames, E. L., 1977, Aquatic Insects of Two Western Slope Rivers, Colorado, M. S. Thesis, Colorado State University, Fort Collins.

Caswell, H., 1978, Predator-Mediated Coexistence: A Nonequilibrium Model, *Am. Nat.,* 112: 127-154.

Connell, J. H., 1978, Diversity in Tropical Rain Forests and Coral Reefs, *Science,* 199: 1302-1310.

Dayton, P. K., 1971, Competition, Disturbance, and Community Organization: The Provision and Subsequent Utilization of Space in a Rocky-Intertidal Community, *Ecol. Monogr.* 41: 351-389.

Dodson, S. I., 1970, Complementary Feeding Niches Sustained by Size-Selective Predation, *Limnol. Oceanogr.,* 15: 131-137.

Fox, L. R., 1977, Species Richness in Streams—An Alternative Mechanism, *Am. Nat.,* 111: 1017-1021.

Fox, J. F., 1979, Intermediate-Disturbance Hypothesis, *Science,* 204: 1344-1345.

Gaufin, A. R., and C. M. Tarzwell, 1956, Aquatic Macroinvertebrate Communities as Indicators of Pollution in Lytle Creek, *Sewage Industr. Wastes,* 28: 906-924.

Gray, L. J., 1980, Recolonization Pathways and Community Development of Desert Stream Macroinvertebrates, Ph.D. Thesis, Arizona State University, Tempe.

———, and J. V. Ward, 1979, Food Habits of Stream Benthos at Sites of Differing Food Availability, *Am. Midl. Nat.,* 102: 157-167.

Grime, J. P., 1973, Control of Species Density in Herbaceous Vegetation, *J. Environ. Manag.,* 1: 151-167.

Harper, J. L., 1969, The Role of Predation in Vegetational Diversity, *Brookhaven Symp. Biol.,* 22: 48-62.

Herricks, E. E., and J. Cairns, Jr., 1974, *Rehabilitation of Streams Receiving Acid Mine Drainage,* Virginia Water Resources Research Center, Bulletin 66, Virginia Polytechnic Institute and State University, Blacksburg.

Horwitz, R. J., 1978, Temporal Variability Patterns and the Distributional Patterns of Stream Fishes, *Ecol. Monogr.,* 48: 307-321.

Huston, M., 1979, A General Hypothesis of Species Diversity, *Am. Nat.,* 113: 81-101.

Ide, F. P., 1935, The Effect of Temperature on the Distribution of the Mayfly Fauna of a Stream, *Publs. Ont. Fish. Res. Lab.,* 50: 1-76.

Levin, S. A., and R. T. Paine, 1974, Disturbance, Patch Formation, and Community Structure, *Proc. Nat. Acad. Sci.,* 71: 2744-2747.

Levins, R., 1979, Coexistence in a Variable Environment, *Am. Nat.,* 114: 765-783.

Loucks, O. L., 1970, Evolution of Diversity, Efficiency, and Community Stability, *Am. Zool.,* 10: 17-25.

Menge, B. A., 1979, Coexistence Between the Seastars *Asterias vulgaris* and *A. forbesi* in a Heterogeneous Environment: A Non-Equilibrium Explanation, *Oecologia,* 41: 245-272.

Osman, R. W., 1977, The Establishment and Development of a Marine Epifaunal Community, *Ecol. Monogr.,* 47: 37-63.

Paine, R. T., 1966, Food Web Complexity and Species Diversity, *Am. Nat.,* 100: 65-75.

______, 1969, The *Pisaster-Teguia* Interaction: Prey Patches, Predator Food Preferences, and Intertidal Community Structure, *Ecology,* 50: 950-961.

______, 1971, A Short-Term Experimental Investigation of Resource Partitioning in a New Zealand Rocky Intertidal Habitat, *Ecology,* 52: 1096-1106.

Patrick, R., 1970. Benthic Stream Communities, *Am. Sci.,* 58: 546-549.

Stout, J. and J. Vandermeer, 1975, Comparison of Species Richness for Stream-Inhabiting Insects in Tropical and Mid-Latitude Streams, *Am. Nat.,* 109: 263-280.

Taylor, D. L., 1973, Some Ecological Implications of Forest Fire Control in Yellowstone National Park, Wyoming, *Ecology,* 54: 1394-1396.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing, 1980, The River Continuum Concept, *Can J. Fish. Aquat. Sci.,* 37: 130-137.

Ward, J. V., 1974, A Temperature-Stressed Stream Ecosystem Below a Hypolimnial Release Mountain Reservoir, *Arch. Hydrobiol.,* 74: 247-275.

______, 1975, Bottom Fauna-Substrate Relationships in a Northern Colorado Trout Stream: 1945 and 1974, *Ecology,* 56: 1429-1434.

______, 1976a, Effects of Thermal Constancy and Seasonal Temperature Displacement on Community Structure of Stream Macroinvertebrates, in G. W. Esch and R. W. McFarlane (Eds.), *Thermal Ecology II,* ERDA Symposium Series, CONF-750425, pp. 302-307, NTIS.

______, 1976b, Comparative Limnology of Differentially Regulated Sections of a Colorado Mountain River, *Arch. Hydrobiol.,* 78: 319-342.

______, and R. G. Dufford, 1979, Longitudinal and Seasonal Distribution of Macroinvertebrates and Epilithic Algae in a Colorado Springbrook-Pond System, *Arch. Hydrobiol.,* 86: 284-321.

______, and R. A. Short, 1978, Macroinvertebrate Community Structure of Four Special Lotic Habitats in Colorado, U.S.A., *Verh. Internat. Verein. Limnol.,* 20: 1382-1387.

______, and J. A. Stanford, 1979, Ecological Factors Controlling Stream Zoobenthos with Emphasis on Thermal Modification of Regulated Streams, in J. V. Ward and J. A. Stanford (Eds.), *The Ecology of Regulated Streams,* pp. 35-55, Plenum Press, New York.

Dynamics of Lotic Ecosystems

Edited by

Thomas D. Fontaine, III
Savannah River Ecology Laboratory
University of Georgia

Steven M. Bartell
Environmental Sciences Division
Oak Ridge National Laboratory

ANN ARBOR SCIENCE
THE BUTTERWORTH GROUP

230 Collingwood, P.O. Box 1425, Ann Arbor, Michigan 48106

Library of Congress Catalog Card Number 82-048641
ISBN 0-250-40612-8

Manufactured in the United States of America

Butterworths, Ltd., Borough Green, Sevenoaks
Kent TN15 8PH, England

2. THE SERIAL DISCONTINUITY CONCEPT OF LOTIC ECOSYSTEMS

James V. Ward

Department of Zoology and Entomology
Colorado State University
Fort Collins, Colorado

Jack A. Stanford

University of Montana Biological Station
Bigfork, Montana

ABSTRACT

Recent theoretical concepts of lotic ecosystems deal primarily with origins and fates of organic resources and inorganic nutrients as prescribed by the stream continuum and nutrient spiraling concepts. These concepts are based on gradient analysis in which stream systems are, of necessity, viewed as uninterrupted continua. Few riverine ecosystems, however, remain free-flowing over their entire course. Rather, regulation by dams has typically resulted in an alternating series of lentic and lotic reaches. The serial discontinuity concept is an attempt to attain a broad theoretical perspective of regulated lotic ecosystems. Discontinuity distance (DD), defined as the longitudinal shift of a given parameter by stream regulation, may be positive (downstream shift), negative (upstream shift), or near zero. The direction and intensity of DD vary as functions of the specific parameter examined and the position of the dam(s) along the longitudinal stream profile. The serial discontinuity concept can be applied to physical parameters (e.g., temperature summation) and biological phenomena at the population (e.g., species abundance patterns), community (e.g., biotic diversity), or ecosystem levels (e.g., Photosynthesis/Respiration). Regulated streams, according to the serial discontinuity concept, are viewed as large-scale experimental systems in which disruptions in continuum processes and nutrient spirals create conditions amenable to testing and developing basic theories of stream ecology.

INTRODUCTION

During the past decade two important theoretical concepts of lotic ecosystems have emerged. The river continuum concept (Vannote et al., 1980) describes the gradient of physical conditions and resulting biotic responses from the headwaters to the mouths of river systems. The nutrient spiraling concept (Webster, 1975; Wallace et al., 1977; Webster and Patten, 1979; Elwood et al., this volume) is concerned with the unidirectional and biologically mediated recycling (spiraling) of nutrients, including fixed carbon, along the river continuum. These concepts are based on gradient analysis (*sensu* Whittaker, 1967) in which stream systems are, of necessity, viewed as uninterrupted continua. Few riverine ecosystems, however, remain free-flowing over their entire course. Rather, regulation by dams has typically resulted in an alternating series of lentic and lotic reaches.

The effects of impoundments on lotic reaches immediately downstream from dams were recently summarized by Ward and Stanford (1979a). The serial discontinuity concept presented here is an attempt to attain a broad theoretical perspective of regulated lotic systems over the entire longitudinal stream profile. The concept treats physical parameters (e.g., thermal regima) and biological phenomena at the population (e.g., species abundance patterns), community (e.g., biotic diversity), and ecosystem levels (e.g., photosynthesis/respiration). According to this concept, regulated streams are viewed as large-scale experimental systems in which disruptions in continuum processes and nutrient spirals create conditions amenable to testing and developing basic theories of stream ecology.

THE SERIAL DISCONTINUITY CONCEPT

The serial discontinuity concept, at this initial stage of its derivation, contains the following presuppositions: (1) The river continuum and nutrient spiraling hypotheses are conceptually sound and their underlying assumptions are valid. (2) The watershed is free of pollution and other disturbance, except impoundment. (3) The remaining lotic reaches were not disturbed during reservoir construction (e.g., riparian vegetation and substrate were not modified). (4) Unless otherwise stated, the impoundments are assumed to be deep-release storage reservoirs, which thermally stratify and which do not release oxygen-deficient or gas-supersaturated waters. We intend to present the hypothesized ramifications of modifying thermal and flow regimes by impoundment as major disruptions of continuum processes, without additional complicating factors.

In Figures 1 and 2 the solid lines represent hypothetical curves of various parameters as functions of distance along the uninterrupted stream continuum. These idealized curves were derived from data contained in various sources (especially, Vannote et al., 1980; Cummins, 1975; 1977; 1979). According to such conceptualizations, natural headwater streams are characterized as heavily canopied, light-limited heterotrophic systems with low-amplitude thermal regimes and coarse substrates. Of course, not all headwater streams are canopied by terrestrial vegetation (Minshall, 1978), nor do they all receive substantial groundwater inputs to moderate temperature and flow patterns. The fact that the majority of research on natural streams in North America has been conducted in the eastern deciduous forest has fostered such generalizations since many undisturbed lotic ecosystems for which the most intensive data are available do indeed exhibit these general characteristics.

The dashed lines in Figures 1 and 2, which synthesize our present understanding of regulated streams, indicate hypothesized modifications of those parameters when dams are placed on upper, middle, and lower reaches. Impoundments are viewed as theoretical dimensionless points on the longitudinal stream profile (i.e., only the modification of the downstream lotic ecosystem is shown; the limnological dynamics within the reservoir are not). It must be stressed that the curves presented are highly idealized. The vertical axes are intentionally presented without scales. It is probably not possible to quantify precisely any of the parameters along the entire stream continuum. The best data are available for stream orders 1 through 5. Much additional research is needed to confirm or refute even the relative changes postulated here as resulting from impoundment. Further refinements will be required to account for geographical differences and synergistic effects engendered by other disturbances to watersheds.

The differential effects of dam position on parameter modification are illustrated in Figures 1 and 2. We postulate that a parameter that may be greatly modified in the lotic reach below a dam placed at one point on the longitudinal stream profile may be little affected by impounding a different reach. A major impoundment at any position on a river system

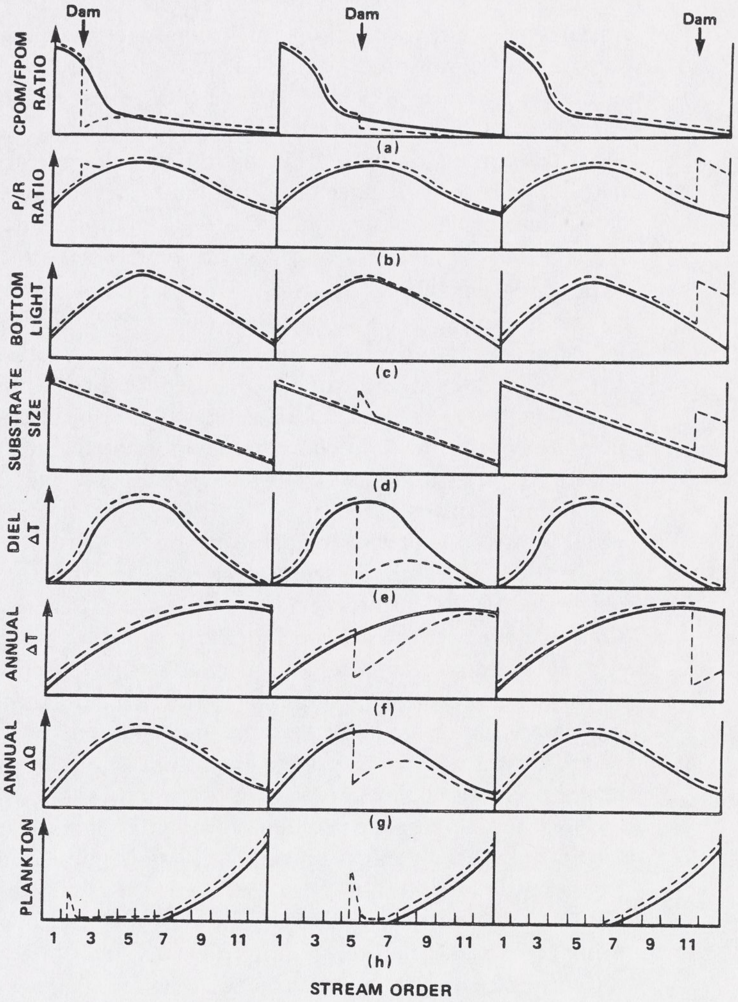


Figure 1. Relative changes in various parameters as a function of stream order, based on our interpretation of natural stream continua theory (solid lines) and postulated effects (dashed lines) of damming headwaters (left column), middle reaches (center column), and lower reaches (right column) of a river system. See text for further explanation.

will directly and indirectly affect all ecological aspects of the downstream lotic ecosystem at some level of resolution. Some, however, will be more severely influenced than others, and gross measurements may be little affected in some instances. For example, a headwater dam (Figure 1a) will greatly depress the ratio of coarse particulate to fine particulate

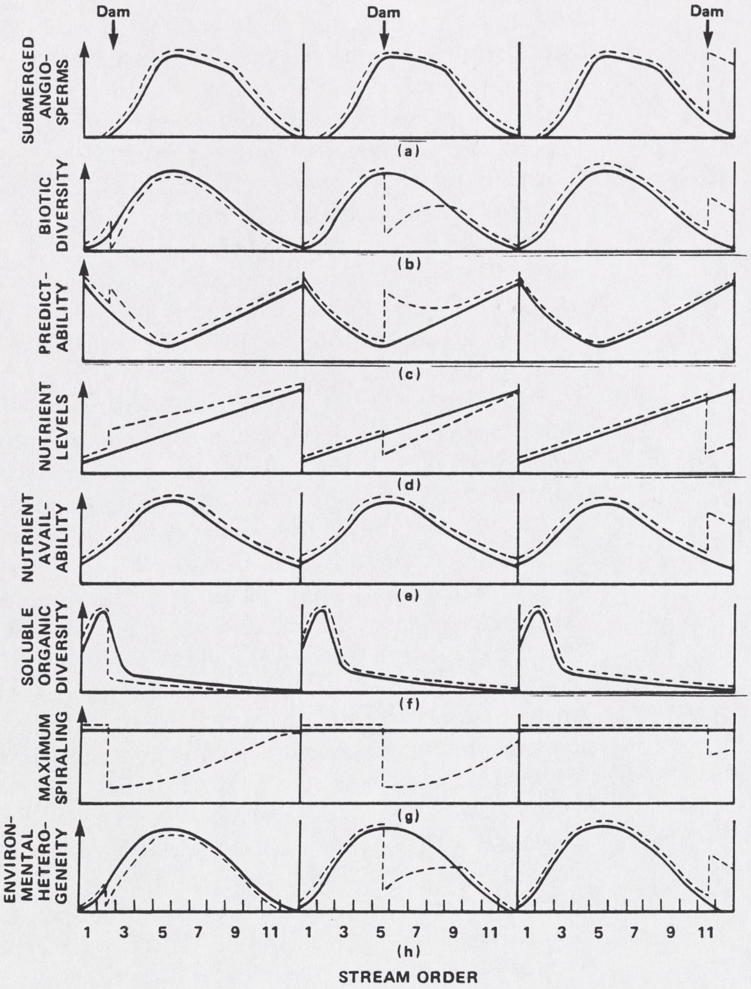


Figure 2. Relative changes in additional parameters (see Fig. 1 legend).

organic matter (CPOM/FPOM) below the impoundment because instream transport of detritus is blocked, whereas impounding the lower reaches of a river system will have little effect on the size composition of detritus. Invertebrate functional feeding groups will reflect changes in the CPOM/FPOM ratios (Short and Ward, 1980). Because of the importance of direct allochthonous inputs (primarily leaf litter) in the energy budgets of the upper reaches of forested streams, a headwater dam would be expected to modify functional composition most severely (shredders would be greatly reduced). In contrast, a dam on the lower reaches may not greatly alter the trophic relationships of the receiving stream.

Light intensity at the stream bottom (Figure 1c) will not be greatly changed by a headwater impoundment unless the downstream riparian vegetation is disrupted, but the clarification effect of impounding a formerly turbid river will greatly increase light penetration. This accounts for the hypothesized increase in photosynthesis-to-respiration ratio below dams in lower reaches (Figure 1b), especially if water clarity is accompanied by increased substrate stability. Clear water released from dams creates a hydrodynamic disequilibrium resulting in removal of fine sediment particles (see Simons, 1979). The effect on substrate size composition would be greatest in lower reaches (Figure 1d) where the majority of particles are small. Damming the Brazos River in Texas changed a sand-bottom stream into one with a predominantly rubble substrate (Stanford and Ward, 1979). Although few data are available, the effect of impoundment on the composition and quality of sedimentary detritus of downstream reaches (see Webster et al., 1979) may be biologically significant at all points on the stream profile.

It is unlikely that damming either the headwaters or lower reaches will have much effect on the maximum diel temperature range (diel ΔT) of the receiving stream (Figure 1e). The suppression of the diel range will be considerable below a dam in the middle reaches, where the greatest daily thermal range is normally exhibited, and will profoundly influence the biotic community structure (Ward and Stanford, 1979b). The annual thermal range (Figure 1f) would remain similar below a deep-release dam in the headwaters but would be reduced by impounding middle, and especially lower, reaches. Interpretation is complicated by shifts in latitude. The Mississippi River, for example, is exposed to quite a different climatic regime at its origin in Minnesota than at its mouth in Louisiana. Since water near 4° C is discharged from deep-release dams in winter and summer, the annual thermal amplitude may be greatly constricted. Surface-release reservoirs, especially if shallow, may significantly modify the receiving stream biota by raising summer temperatures (Fraley, 1979). Other thermal modifications engendered by stream regulation and their biological implications are discussed in detail in Ward (1976a) and Ward and Stanford (1979b).

In a pattern not unlike temperature, the flow regime of natural streams often exhibits maximum variation in middle reaches. The relative flow constancy of headwaters is attributed to their spring-fed nature and the moderation of precipitation by terrestrial watershed processes, whereas the discharge pattern of large rivers is dampened by the cumulative variations of many tributaries (Hynes, 1970). The middle reaches are most influenced by local meteorological events and hence exhibit the most variable and unpredictable flow regimes.

Storage reservoirs may moderate flow fluctuations (ΔQ) in the middle reaches (Figure 1g) by storing water during spates and major runoff periods and releasing additional water during periods of normally low flow. Storage reservoirs have a lesser influence on the already relatively constant flow regime of headwaters and lower reaches. The downstream flow regime is largely a function of the purpose of the reservoir. See Ward (1976b) for a discussion of the types of flow regulation and effects on stream biota.

True plankton communities (Figure 1h) occur only in the lower reaches of river systems except below impoundments and natural lakes. Plankton released from surface-release impoundments typically result in greatly enhanced populations of filter-feeding stream invertebrates immediately below the dam (Simmons and Voshell, 1978; Ward and Short, 1978). Lentic plankton are rapidly eliminated downstream, with concomitant major shifts in the invertebrate functional feeding-group composition. Plankton are also released from deep-release dams, but apparently not in sufficient numbers or with sufficient temporal predictability to greatly influence the trophic structure of the receiving stream biota (Ward, 1975).

Impoundment will not allow development of submerged angiosperms (Figure 2a) in the headwaters unless the canopy is disrupted, nor will major changes occur in the middle reaches where dense populations normally occur. In contrast, damming lower reaches may greatly enhance rooted aquatic plants, since the high nutrient levels can be used in the clear water and more stable substrate below the dams. High-gradient mountain streams lacking angiosperms may develop dense beds in regulated sections (Ward, 1976c). Attached algae exhibit a similar response (see Lowe, 1979).

It is postulated that biotic diversity, relative to unregulated lotic systems, will be modified irrespective of the position of the impoundment along the stream profile (Figure 2b). Regulation of the headwaters will suppress the biotic diversity in the receiving stream, primarily because of the disruption of detrital transport and the spiraling of nutrients and organic matter. The severe reduction of biotic diversity induced by damming middle reaches has been attributed primarily to the altered thermal regime. For example, it has been suggested (Ward, 1976a; Ward and Stanford, 1979b; Vannote et al., 1980) that daily variation in temperature, which is suppressed below dams in middle reaches, is partly responsible for maximizing species diversity in natural lotic systems by providing a wide range of thermal optima, even though suboptimal conditions occur over a portion of the diel cycle for each species.

Although few biological data are available for lower reaches, enhanced environmental heterogeneity below dams would likely lead to an increase in biotic diversity. The only known record of enhanced zoobenthic diversity below a dam occurs in a river that exhibited increased substrate and thermal heterogeneity in the regulated section (Ward and Stanford, 1979b).

The high biotic diversity in the middle reaches of natural streams may result not only from spatial heterogeneity but also from temporal heterogeneity (i.e., low predictability, Figure 2c). Lind (1971), for example, contrasted the relatively constant supply of organic matter discharged from a reservoir in Texas with the seasonal variations in organic transport which typify unregulated streams. Within limits, low predictability (high temporal heterogeneity) in flow and temperature regimes (and other factors) may enhance species packing of lotic organisms by several mechanisms (Patrick, 1970; Ward, 1976a); increased predictability resulting from impoundment may contribute to the reduced biotic diversity of regulated streams in middle reaches.

Although total nutrient levels (Figure 2d) generally increase along the stream continuum (Cummins, 1977), availability (Figure 2e) is probably greatest in middle reaches where the light regime and substrate are most suitable for plant growth. If the residence time of headwaters is increased, deep-release impoundments could conceivably raise nutrient levels downstream, but availability would not be altered. In middle and lower reaches, reservoirs generally act as nutrient sinks, but nitrate may be greater in outflowing than inflowing water (see Soltero et al., 1973). Greater nutrient availability induced by impoundment in lower reaches, because of increased clarity and substrate stability, may compensate for reduced levels in the receiving stream.

The relative diversity of soluble organic compounds (Figure 2f) is highest in headwaters of natural streams (Vannote et al., 1980), and impoundment of upper reaches would likely exert the greatest effect on this parameter. If residence time is increased, limnological phenomena within the reservoir (including biotic uptake and transformations) may reduce the chemical diversity below a headwater dam. Such a conclusion must, however, remain highly speculative at this time.

The homeostatic feedback mechanisms which control in situ nutrient cycling in autotrophic ecosystems (the "circular causal systems" of Hutchinson, 1948) are not directly applicable to stream ecosystems because of the unidirectional movement of water. If we view the stream on a spatio-temporal scale, however, a storage–cycle–release phenomenon, termed "nutrient spiraling" (Webster, 1975; Wallace et al., 1977; Webster and Patten, 1979, Elwood et al., this volume), becomes apparent. As stated by Cummins (1979), "communities in each successive stream order are dependent upon the inefficiency or 'leakage' from the preceding orders."

Vannote et al. (1980) emphasized the adjustments made by the biotic community along the river continuum which "are structured to process materials . . . thereby minimizing the variance in system structure and function." They further "propose that biological communities, developed in natural streams in dynamic equilibrium, assume processing strategies involving minimum energy loss. . . ," which is equated with maximum spiraling. From this we have deduced that maximum spiraling is maintained throughout the natural stream continuum (Figure 2g) by biotic adjustments to continually changing physical conditions. We propose that the disruption of nutrient spiraling by impoundment will be severely manifested in upper and middle reaches but less severely altered in large rivers where dissolved and particulate matter entering the reservoir will not differ greatly from that passed through the dam. There is some indication that the "food quality" of detritus may vary as a function of stream order (Naiman and Sedell, 1979). It is probable that limnological phenomena within reservoirs alter the food quality (as well as the amount and the chemical and size composition) of detritus, but no data are available.

Finally, we propose that environmental heterogeneity (viewed broadly to include both spatial and temporal components) exhibits a pattern along the stream profile (Figure 2h) which is similar to biotic diversity (see, e.g., Hedrick et al., 1976) and that the response to regulation will also be similar.

Multiple Impoundment

Figures 1 and 2 consider the differential effects on a given parameter of single dams positioned in the headwaters, the middle, or the lower reaches of a river system. Many river systems, however, are alternating series of lentic and lotic reaches because of multiple impoundment. For example, eleven main-stem dams have been constructed on the Snake River, a tributary of the Columbia (Robinson, 1978). The few data available on cumulative effects of multiple impoundment (e.g., Denisova, 1971) deal primarily with physico-chemical changes within the reservoirs. Virtually nothing is known regarding cumulative effects of multiple impoundment on the remaining lotic segments. If, for example, a factor modified by an upstream impoundment has not been returned to normal levels before reaching the next reservoir, will the interaction be neutral, cumulative, or ameliorative, and to what extent? Not only are precise answers to such questions generally unknown but the questions themselves have rarely been asked.

We have developed a hypothetical framework to visualize the basin-wide effects of impoundment (Figure 3) in an attempt to attain a broad theoretical perspective of regulated lotic ecosystems. The approach is applicable to smaller drainage basins (e.g., fifth-order systems) or portions of larger watersheds. The framework may also be used as a submodel to investigate the effects of individual dams in a series.

Two components are apparent (see Figure 3). Discontinuity distance (DD), defined as the longitudinal shift of a given parameter by stream regulation, has a length variable (X), which is the displacement of the parameter in stream-order units (kilometers may be more useful than stream-order units, especially in xeric regions). An upstream shift is indicated by X_{neg} and a downstream shift by X_{pos}; X_o indicates that no major longitudinal shift is apparent. The theoretical example in Figure 3 shows a downstream shift of the parameter A maximum by five stream orders (DD = +5).

The second component is parameter intensity (PI), defined as the difference in absolute parameter units between the natural and the

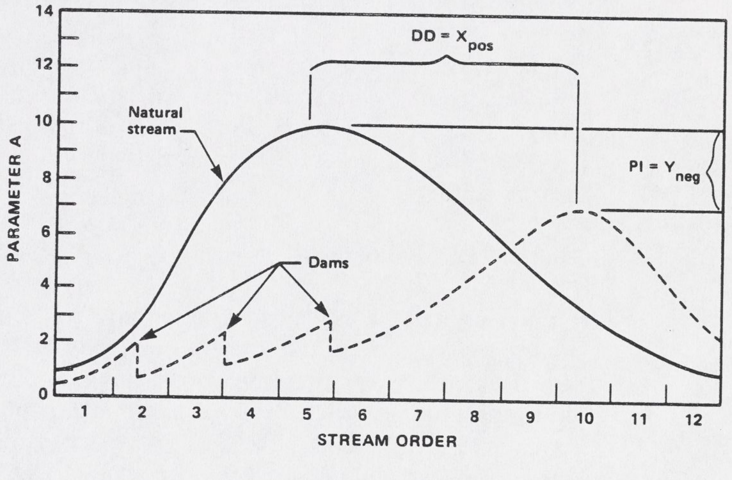


Figure 3. Theoretical framework for conceptualizing the influence of impoundment on ecological parameters in a river system. Discontinuity distance (DD) is the downstream (positive) or upstream (negative) shift of a parameter a given distance (X) due to stream regulation. PI is a measure of the difference in the parameter intensity attributed to stream regulation. See text for further explanation.

regulated lotic system. Parameter intensity can be elevated (Y_{pos}), depressed (Y_{neg}), or unchanged (Y_o) in comparison with the natural lotic system. For parameter A (Figure 3), PI is -3.

We contend that the conceptual framework exemplified in Fig. 3 provides a structure for designing and interpreting research on regulated lotic ecosystems. It is intentionally simplistic and general in this initial formulation, not only as a reflection of our inability to quantify precisely the effects of regulation but also so that it may be applicable to a variety of physical and biological parameters at different levels. For example, regulation of a river system may cause the distribution pattern of a lotic species to shift three stream orders downstream where mean annual abundance is depressed from 3000 to 2000 organisms/m^2 (DD = +3 and PI = -1000 organisms/m^2), or the position of the maximum photosynthesis-to-respiration ratio may not shift longitudinally but may be elevated from 1.1 to 1.3 at that point (DD = 0 and PI = +0.2).

One contribution of the model may be simply to focus conceptually on the basin-wide ramifications of stream regulation. The temporal shift of maximum temperatures in the Columbia River as additional dams were constructed (Jaske and Goebel, 1967), for example, could have been predicted and the biological implications better understood given a comprehensive view of the watershed. From a preliminary analysis of the distribution of hydropsychid caddisflies over nearly 300 km of a river with four mainstream impoundments (Stanford and Ward, 1981), it appears that the thermal regime and particulate organic carbon dynamics have undergone major downstream shifts since regulation of the river system. A simple mathematical model incorporating a variable number of reaches and impoundments should be initially developed and tested to examine trends in single parameters before attempting to apply this framework to the interactions of multiple factors. We hesitate to speculate further on the potential utility of the model without the results of experimental field research designed specifically within this framework. The ultimate goal of such a scheme is to stimulate research leading to the causal relationships essential to a fuller understanding of basic and applied aspects of stream ecology, and its success should be judged by that criterion.

ACKNOWLEDGMENTS

We wish to thank K. W. Cummins and J. R. Webster for suggestions regarding the manuscript. We gratefully acknowledge the support provided for our plenary presentation by the Savannah River Ecology

Laboratory and the Institute of Ecology, University of Georgia. This manuscript was prepared while J. V. Ward was supported by the Colorado Experiment Station.

REFERENCES

Cummins, K. W., 1975, The Ecology of Running Waters; Theory and Practice, in D. B. Baker et al. (Eds.), *Proceedings of the Sandusky River Basin Symposium*, pp. 277–293, International Joint Commission on the Great Lakes, Heidelburg College, Tiffin, OH.

———, 1977, From Headwater Streams to Rivers. *Am. Biol. Teacher*, 39: 305-312.

———, 1979, The Natural Stream Ecosystem, in J. V. Ward and J. A. Stanford (Eds.), *The Ecology of Regulated Streams*, pp. 7-24, Plenum Press, New York.

Denisova, A. I., 1971, The Effect of the Position of a Reservoir in a Cascade on Its Hydrochemistry, *Hydrobiol. J.*, 7: 8-15.

Fraley, J. J., 1979, Effects of Elevated Stream Temperatures Below a Shallow Reservoir on a Cold Water Macroinvertebrate Fauna, in: J. V. Ward and J. A. Stanford (Eds.), *The Ecology of Regulated Streams*, pp. 257-272, Plenum Press, New York.

Hedrick, P. W., M. E. Ginevan, and E. P. Ewing, 1976, Genetic Polymorphism in Heterogeneous Environments, *Annu. Rev. Ecol. Systemat.*, 7: 1-32.

Hutchinson, G. E., 1948, Circular Causal Systems in Ecology, *Ann. N. Y. Acad. Sci.*, 50: 221-246.

Hynes, H. B. N., 1970, *The Ecology of Running Waters*, University of Toronto Press, Toronto.

Jaske, J. T., and J. G. Goebel, 1967, Effects of Dam Construction on Temperature of the Columbia River, *J. Am. Water Works Assoc.*, 59: 935-942.

Lind, O. T., 1971, The Organic Matter Budget of a Central Texas Reservoir, in G. E. Hall (Ed.), *Reservoir Fisheries and Limnology*, pp. 193-202, Special Publication No. 8, American Fisheries Society, Washington, D.C.

Lowe, R. L., 1979, Phytobenthic Ecology and Regulated Streams, in J. V. Ward and J. A. Stanford (Eds.), *The Ecology of Regulated Streams*, pp. 25-34, Plenum Press, New York.

Minshall, G. W., 1978, Autotrophy in Stream Ecosystems, *BioScience*, 28: 767-771.

Naiman, R. J., and J. R. Sedell, 1979, Benthic Organic matter as a Function of Stream Order in Oregon, *Arch. Hydrobiol.*, 87: 404-422.

Patrick, R., 1970, Benthic Stream Communities, *Am. Sci.*, 58: 546-549.

Robinson, W. L., 1978, The Columbia: A River System Under Siege, *Ore. Wildl.*, 33: 3-7.

Short, R. A., and J. V. Ward, 1980, Leaf Litter Processing in a Regulated Rocky Mountain Stream, *J. Fish. Aquat. Sci.*, 37: 123-127.

Simons, D. B., 1979, Effects of Stream Regulation on Channel Morphology, in J. V. Ward and J. A. Stanford (Eds.), *The Ecology of Regulated Streams,* pp. 95-111, Plenum Press, New York.

Simmons, G. M., Jr., and J. R. Voshell, Jr., 1978, Pre- and Post-Impoundment Benthic Macroinvertebrate Communities of the North Anna River, in J. Cairns, E. F. Benfield, and J. R. Webster (Eds.), *Current Perspectives on River–Reservoir Ecosystems,* pp. 45–61, North American Benthological Society, Roanoke, VA.

Soltero, R. A., J. C. Wright, and A. A. Horpestad, 1973, Effects of Impoundment on the Water Quality of the Bighorn River, *Water Res.,* 7: 343-354.

Stanford, J. A., and J. V. Ward, 1979, Stream Regulation in North America, in J. V. Ward and J. A. Stanford (Eds.), *The Ecology of Regulated Streams,* pp. 215-236, Plenum Press, New York.

Stanford, J. A., and J. V. Ward, 1981, Preliminary Interpretations of the Distribution of Hydropsychidae in a Regulated River, in G. P. Moretti (Ed.), *Proceedings of the Third International Symposium on Trichoptera* pp. 323–328, Dr. W. Junk, Publishers, The Hague.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing, 1980, The River Continuum Concept, *Can. J. Fish. Aquat. Sci.,* 37: 130-137.

Wallace, J. B., J. R. Webster, and W. R. Woodall, 1977, The Role of Filter Feeders in Flowing Waters, *Arch. Hydrobiol.,* 79: 506-532.

Ward, J. V., 1975, Downstream Fate of Zooplankton from a Hypolimnial Release Mountain Reservoir, *Verh. Internat. Verein. Limnol.,* 19: 1798-1804.

______, 1976a, Effects of Thermal Constancy and Seasonal Temperature Displacement on Community Structure of Stream Macroinvertebrates, in G. W. Esch and R. W. McFarlane (Eds.), *Thermal Ecology II,* ERDA Symposium Series CONF-750425, pp. 302-307, NTIS, Springfield, VA.

______, 1976b, Effects of Flow Patterns Below Large Dams on Stream Benthos: A Review, in J. F. Orsborn and C. H. Allman (Eds.), *Instream Flow Needs Symposium,* Vol. II, pp. 235-253, American Fisheries Society, Bethesda, MD.

______, 1976c, Comparative Limnology of Differentially Regulated Sections of a Colorado Mountain River, *Arch. Hydrobiol.,* 78: 319-342.

______, and R. A. Short, 1978, Macroinvertebrate Community Structure of Four Special Lotic Habitats in Colorado, U.S.A., *Verh. Internat. Verein. Limnol.,* 20: 1382-1387.

______, and J. A. Stanford (Eds.), 1979a, *The Ecology of Regulated Streams,* Plenum Press, New York.

______, and J. A. Stanford, 1979b, Ecological Factors Controlling Stream Zoobenthos with Emphasis on Thermal Modification of Regulated Streams, in J. V. Ward and J. A. Stanford (Eds.), *The Ecology of Regulated Streams,* pp. 35-55, Plenum Press, New York.

Webster, J. R., 1975, Analysis of Potassium and Calcium Dynamics in Stream Ecosystems on Three Southern Appalachian Watersheds of Contrasting Vegetation, Ph.D. Thesis, University of Georgia, Athens.

Webster, J. R., and B. C. Patten, 1979, Effects of Watershed Perturbation on Stream Potassium and Calcium Dynamics, *Ecol. Monogr.,* 49: 51-72.

Webster, J. R., E. F. Benfield, and J. Cairns, Jr., 1979, Model Predictions of Effects of Impoundment on Particulate Organic Matter Transport in a River System, in J. V. Ward and J. A. Stanford (Eds.), *The Ecology of Regulated Streams,* pp. 339-364, Plenum Press, New York.

Whittaker, R. H., 1967, Gradient Analysis of Vegetation, *Biol. Rev.,* 42: 207-264.