The Ecology of Regulated Streams

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ECOLOGICAL FACTORS CONTROLLING STREAM ZOOBENTHOS WITH EMPHASIS ON THERMAL MODIFICATION OF REGULATED STREAMS

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INTRODUCTION

A myriad of factors, including temperature, flow, substrate, aquatic and riparian vegetation, dissolved substances, food and biotic interactions, determine the composition and abundance of stream zoobenthos (Macan, 1961, 1974; Hynes, 1970a,b). The influence of the watershed on many of these factors has only recently been fully appreciated (e.g., Hynes,, 1975; Cummins, this volume).

A much more exhaustive list of controlling factors could be developed, and each of those listed may be further subdivided. However, for the vast majority of unpolluted streams, temperature, flow, and substrate, and their ramifications, may be considered the major factors controlling the macroinvertebrates. These major controlling factors are, of course, often interrelated. For example, current influences substrate and substrate influences the composition and abundance of aquatic plants, all of which directly or indirectly affect zoobenthic organisms. Little is known regarding biotic interactions in streams, but even these are influenced by temperature, current and substrate (Pattee and Bournaud, 1970, Edington and Hildrew, 1973).

Because the substrate of streams in a given region is largely a function of the flow regime, temperature and flow (and their ramifications) remain perhaps the two most important controlling factors for zoobenthos of unpolluted streams. Therefore, following a brief overview of the general effects of reservoirs on the receiving stream, the major thrust of this review paper deals with effects of thermal and flow phenomena on benthic macroinvertebrates in lotic reaches downstream from impoundments, with special emphasis on the influence of temperature regime alterations. Discussion concentrates on results of comprehensive investigations of the zoobenthos of regulated streams in temperate latitudes, although only occasional reference is made to the numerous investigations conducted in the Tennessee Valley, USA (reviewed by Krenkel, et al., this volume).

GENERAL ENVIRONMENTAL MODIFICATIONS

Although the literature on reservoirs is voluminous, the few reviews dealing broadly with the ecological effects of damming rivers (Baxter, 1977; Ridley and Steel, 1975; Neel, 1963; Ackermann et al., 1973) primarily treat conditions in the reservoir, giving only brief general consideration to downstream effects.

Impoundments may result in a variety of downstream modifications of significance to stream zoobenthos (Table 1). The specific changes depend on a complex series of interactions resulting from operation and construction variables (e.g., position of outlet ports, purpose of the reservoir) and limnological variables (e.g., trophic state, extent of stratification), and are a function of geographical, climatic, geochemical and topographic factors.

Some effects, such as clarification (sedimentation of particles in the reservoir), generally occur irrespective of the mode of operation or additional variables. Other modifications of the receiving stream depend, at least in part, on the release depth. The influence of surface-release dams, for example, may be similar to that of natural lakes, which rarely release water low in dissolved oxygen; whereas anaerobic waters may be discharged from the hypolimnion of stratified reservoirs. However, not all reservoirs develop anoxic hypolimnia; and, even if they do, air drafts in the release ports or turbulent conditions below the dam function to raise dissolved oxygen levels in the receiving stream (Young et al., 1976). There are exceptions to all of the generalizations presented in Table 1. Turbidity currents in the reservoir, for example, may maintain high levels of turbidity in the receiving stream (Neel, 1963). Under some conditions most dissolved constituents may decrease in concentration during passage through a deep-release reservoir, despite the higher values in bottom waters (Soltero et al., 1973). Additional perturbation, such as thermal and organic pollution, and acid mine drainage, have confounded the interpretation of effects of regulation on some stream systems (e.g., Simmons and Voshell, 1978).

ZOOBENTHOS OF REGULATED STREAMS

Examination of the results of studies of zoobenthos in regulated streams reveal some common features despite vast differences in geographical locale, limnological conditions in the reservoir, release depth, flow modification, and a variety of other factors

Table 1. Some General Effects of Deep-Release Storage Reservoirs on Conditions in the Receiving Stream, Exclusive of Temperature, Flow, and Substrate. D = Decrease, I = Increase, V = Variable Effects

	Modification[a]	Selected References
Turbidity	D	Wright, 1967; Soltero et al. 1973; Ward, 1974
TDS, hardness	I	Neel, 1963; Wright, 1967
Nutrients	I	Neel, 1963; Hilsenhoff, 1971; Hall et al., 1976
Dissolved oxygen	V	Neel, 1963; Isom, 1971; Crisp, 1977
Hydrogen sulfide	V	Wright, 1967; Hannan and Young, 1974
Submerged angiosperms	I	Hall and Pople, 1968; Ward, 1976a, Holmes and Whitton, 1977
Periphyton	I	Spence and Hynes, 1971; Armitage, 1976; Ward, 1976a
Plankton	I	Müller, 1962; Ward, 1975; Armitage and Capper, 1976
Transport detritus	D	Ward, 1976a; Armitage, 1977

[a]Relative to unregulated lotic reaches or surface-release.

(Table 2). Macrobenthic diversity is generally reduced compared with that of the stream above the reservoir, unregulated tributaries, or locations farther downstream. The Brazos River in Texas is the only regulated stream known to the authors in which zoobenthic diversity is increased downstream (McClure and Stewart, 1976; Coulter and Stanford, unpublished). Deep releases from Possom Kingdom reservoir have sluiced the stream bottom, changing a warm sandy-bottom river into a cooler river with a rubble substrate. The former conditions and associated impoverished zoobenthic community prevail above the reservoir and downstream after ca. 80 km.

Table 2. Some effects[a] of stream regulation on lotic zoobenthos and controlling factors. I = Increased, D = Decreased, S = Similar, L = Lower level release depth, U = Upper level release depth.

Study and Location			Relative Abundance											Controlling Factors Modified[b]											Temperature					
	Standing Crop	Diversity	Amphipoda	Isopoda	Mollusca	Turbellaria	Oligochaeta	Plecoptera	Ephemeroptera	Trichoptera	Coleoptera	Diptera	Release Depth	Angiosperms	Algae	Plankton	Biotic Interaction	Substrate	Transport Detritus	Sediment Detritus	Chemistry	Dissolved Oxygen	Constant Flow	Fluctuating Flow	Diel Constancy	Seasonal Constancy[c]	Summer Cool	Summer Warm	Winter Warm	Pattern
Armitage 1976, 1978 (England)	I	S	I		I		I	D	D	S	I	S	U L	X	X	X		X	X				X		X		X		X	
Briggs 1948 (California)	I							D	D	I			L					X					X			X			X	
Stewart & Stanford, unpubl. (Texas)	I	I			I			I	I	I	I	I	L		X	X		X			X	X	X	X			X			X
Chutter 1963 (S. Africa)	I	D				I		D	D	I			L		X	X	X	X					X							
Fraley, this volume (Montana)	I	D		I				D	S	I			U			X							X	X	X			X		
Gore 1977 (Montana)	D	D			I	I		D	D	S	I		L		X				X							X	X			
Henricson & Müller, this volume (Sweden)	S	D		S	S	S	S	S	S	S			L										X	X	X	X			X	X
Hilsenhoff 1971 (Wisconsin)		D	I						D	D	D	I	L					X			X	X	X				X		X	
Hoffman & Kilambi 1971 (Arkansas)	I	D	I	I	D		I		D	D	D	I	L		X	X		X					X	X		X	X			
Isom 1971 (Tennessee Valley)	D	D		I	*			D	D	D		I	L		X			X			X	X		X			X			
Lehmkuhl 1972 (Saskatchewan)	D	D			D			D	D	D	D	I	L														X		X	X
Merkley 1978 (Iowa)	D	D							D	I		D	L								X			X						
Müller 1962[d] (Sweden)	D	D		S	D	D		D	D	D	D	D	L					X					X	X	X	X			X	X
Pearson et al. 1968 (Utah)	I	D	I				I	D	D	D	D	I	L		X			X					X	X			X			
Penáz et al. 1968 (Czechoslovakia)	I	D	I		I		I	S	I	I	D	I	L	X	X	X	X	X	X		X		X			X	X		X	X
Radford & Hartland-Rowe 1971 (Alberta)	D	D						S	I	D			L		X	X		X		X				X						
Simmons & Voshell 1978 (Virginia)	I	D			I			D	S	I		I	U		X	X					X	X								
Spence & Hynes 1971 (Ontario)	I	D	I		D			D	S	I	I	I	L		X	X	X	X		X		X	X				X			X
Trotsky & Gregory 1974 (Maine)	D	D						S	S	D	D	I	L											X						
Ward 1976a (Colorado)	I	D	I		I	I	I	D	S	D		I	L	X	X		X		X	X	X		X		X	X	X		X	X
Ward & Short 1978 (Colorado) (JWC)	D	D				D	I	S	S	D	D	I	L			X			X	X				X						
Ward & Short 1978 (Colorado) (TC)	I	D	I		I			D	D	I		I	U	X	X	X	X		X	X			X					X		
Young et al. 1976 (Texas)	I	D			I							I	L								X		X			X	X			

[a]Relative to unregulated streams or stations farther downstream. Missing taxonomic data indicate either that the taxon is not present or abundant, or that the author(s) made no mention of the effect.
[b]Factors indicated by the author(s) as significantly modified by regulation.
[c]Increased seasonal constancy was associated with increased diurnal fluctuation in some cases.
[d]Dam construction phase.
*Gastropods increased; pelecypods decreased.

The standing crop in the receiving stream may be enhanced or reduced compared to unregulated locations, reductions being characteristic of tailwaters with rapid flow fluctuations. However, standing crop may be enhanced in tailwaters with rapid daily flow fluctuations if regulation reduces the high flows associated with spring runoff (Pearson et al., 1968, Hoffman and Kilambi, 1971). Merkley (1978) reported decreased zoobenthic numbers, but increased biomass and production, downstream from a dam on an organically polluted prairie river.

All investigators report major alterations in macroinvertebrate composition at regulated sites. Table 2 shows the changes reported for major taxa; Ward and Short (1978) address the more specific taxonomic and functional group modifications induced by upstream impoundments. The relative abundance of some major groups (e.g., Ephemeroptera) may not change appreciably, although composition within the group will be greatly modified in the receiving stream. For example, heptageniid mayflies are generally reduced or absent in regulated sections. Some major taxa vary in their response to regulation (e.g., Trichoptera), whereas others exhibit a fairly consistent response irrespective of operational schemes or other variables. Amphipods, for example, are invariably enhanced by regulation, often appearing in streams lacking amphipods in unregulated sections (Ward, 1974, 1976a). Plecopterans are normally reduced or eliminated for some distance below dams, although certain hyporheic forms (e.g., chloroperlids) may increase in relative abundance under conditions of rapid flow fluctuations (Ward and Short, 1978; Trotsky and Gregory, 1974; Radford and Hartland-Rowe, 1971). The type of life cycle may largely determine whether a species can withstand the modified conditions (see Henricson and Müller, this volume).

Changes in the composition and abundance of zoobenthos have been attributed to a variety of factors resulting from regulation (Table 2). The enhancement of Trichoptera in lake outfalls (e.g., Müller, 1962) has been attributed to the contribution of lake plankton as a food source for filter-feeding species. Trichoptera and other filter feeders, such as Simuliidae, are enhanced in the receiving stream if surface water is released. Streams below dams that release deep water throughout the year may have reduced populations of filter feeders if reduction of transport detritus by clarification and mineralization in the reservoir is not rectified by the release of plankton (Ward, 1975). Many more data are needed on the dynamics of organic carbon in regulated streams.

The factors important to stream zoobenthos that are influenced by flow modification are shown in Figure 1. Submerged angiosperms and benthic algae are enhanced by decreased turbidity, increased nutrients, and increased bank and bed stability resulting from

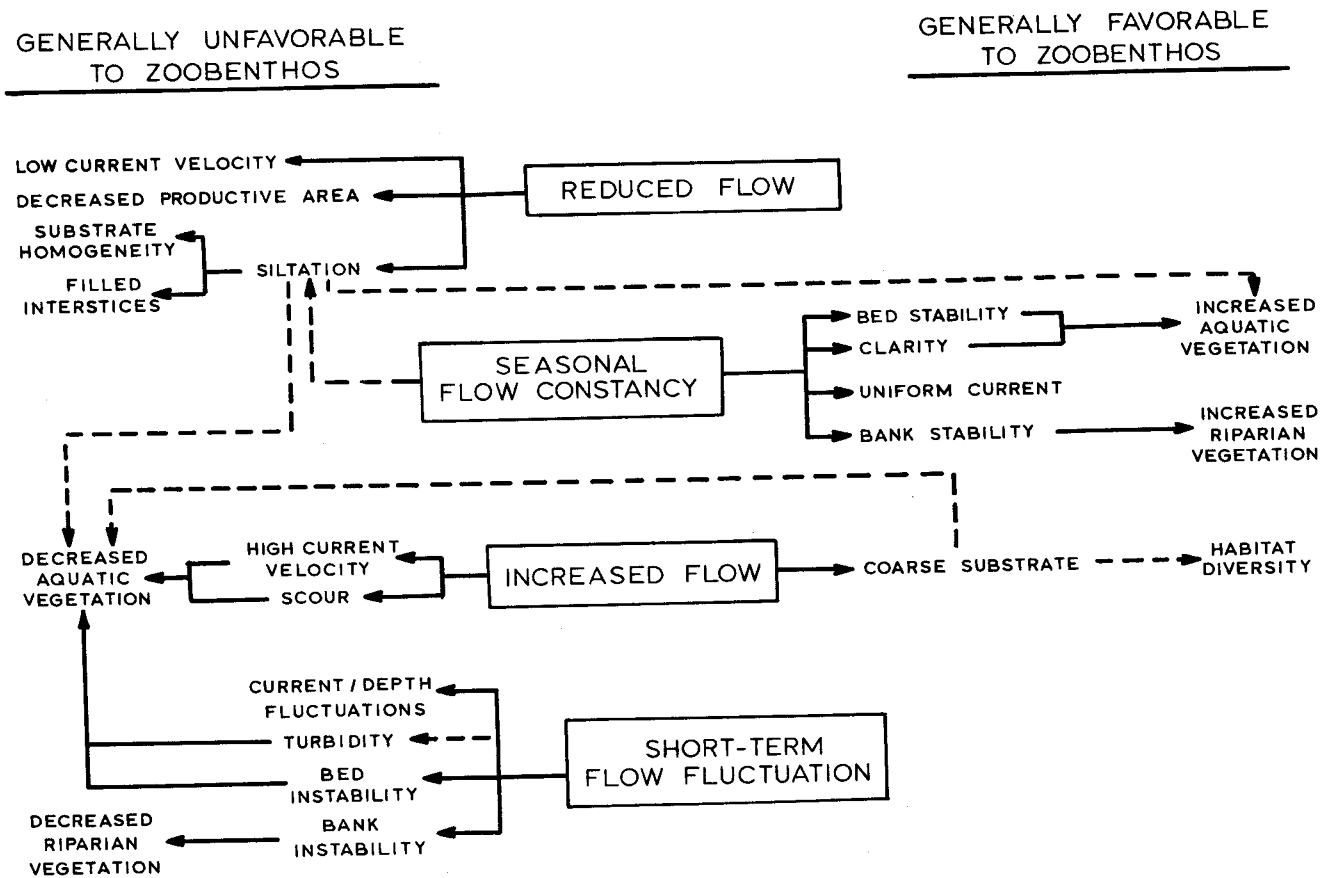

Figure 1. Potential effects of flow regime modifications below dams on ecological factors important to erosional zone zoobenthos. Dashed lines indicate less definite relationships (modified from Ward, 1976b).

increased flow constancy. Angiosperms and algae provide current refugia for species not otherwise able to maintain populations in rocky streams. Dense mats of epilithic algae may increase the availability of food to detritus feeders (Spence and Hynes, 1971), although forms utilizing holdfasts may be reduced or eliminated by the absence of smooth rock surfaces (Ward, 1976a). Flow constancy may also enhance riparian vegetation, with thermal and trophic implications for the stream system. Flow constancy combined with reduced flow may result in stream habitat alteration by vegetation encroachment and siltation. Riparian species that are adapted to fluctuating stream levels could be replaced by other vegetation under conditions of long-term flow constancy; the ecological implications of this are unclear.

Rapid short-term fluctuations reduce algae and macrophytes and deplete sedimentary detritus. Species restricted to pools, as well as those requiring rapid water, may be eliminated. Large areas may be alternately dewatered and flooded. Species requiring relatively constant flow or a narrow range of current velocity for efficient feeding are eliminated directly or placed at a competitive disadvantage.

The chemical effects in Table 2 primarily refer to the release of hydrogen sulfide and to changes in nutrient and oxygen levels. Simmons and Voshell (1978) studied a stream influenced by thermal pollution, acid mine drainage and heavy-metal pollution and concluded that an impoundment significantly improved conditions in the receiving stream. Other authors (e.g., Isom, 1971; Young et al., 1976) have reported inducement of deleterious chemical conditions. Many of the effects are site-specific. For example, higher levels of nutrients resulting from deep release may be beneficial in an oligotrophic stream, whereas eutrophication, depleted oxygen and toxic compounds may result in the stream below a highly productive reservoir. Henricson and Müller (this volume) report that, for Swedish rivers, downstream chemical changes are important mainly during the first 5-10 years after impoundment, but eventually return to near-normal values

UNREGULATED STREAM TEMPERATURE

Stream temperatures under natural conditions have been reviewed by Smith (1972), who includes important Japanese investigations rarely cited by European or North American workers. The following account only briefly summarizes thermal conditions of unregulated streams (see also Hynes, 1970a; Cummins, this volume).

Thermal changes downstream from the source are determined by meteorological conditions, topography, riparian vegetation, and hydrological conditions. The seasonal thermal range is positively correlated with stream order. Small streams are subject to considerable influence from local factors, such as shading by canyon walls and riparian vegetation, or from short-term changes in meteorlogical conditions, such as cloud cover (Kamler, 1965). Therefore, in upper reaches, the diel thermal range increases downstream as the small volume of water responds to atmospheric vagaries and local conditions. However, as discharge increases, a point is reached where the greater heat capacity of the river increases thermal stability, resulting in increased thermal constancy of lower reaches. During higher discharge, the thermal conditions of the headwaters extend farther downstream.

Small streams in temperate latitudes often exhibit annual ranges of more than 20°C. Diurnal ranges of around 6°C are fairly common during summer (Hynes, 1970a); changes as great as 14°C have been reported (Mackichan, 1967). Temperature extremes are reduced by shading from riparian vegetation and by groundwater inputs. Reduced flows result in more extreme temperatures, enhancing the formation of anchor ice in winter.

THERMAL MODIFICATION BY DAMS

The extent to which impoundments modify the temperature regime of the receiving stream depends primarily upon the release depth (which changes relative to the water surface as a function of reservoir level), the thermal stratification pattern of the reservoir, the retention time, and dam operation.

Thermal modification of the receiving stream may be considered under six categories (Table 2): (1) increased diurnal constancy, (2) increased seasonal constancy, (3) summer depression, (4) summer elevation, (5) winter elevation, and (6) thermal pattern changes. Despite great modification of the thermal regime, mean annual stream temperatures may not be greatly modified by impoundment (Jaske and Goebel, 1967; Lavis and Smith, 1971; Ward, 1976a).

The influence of surface-release dams on the temperature of receiving streams is similar to that of natural lakes, although reservoir retention times are often less. Despite great differences in stream size, zoobenthic communities below dams with upper-level release in Montana (Fraley, this volume) and Colorado (Ward and Short, 1978) were similarly modified by regulation. At regulated locations in both streams, increased density was associated with reduced zoobenthic diversity, plecopterans were severely reduced, and hydropsychid caddisflies comprised the majority of the macroinvertebrates. Elevated summer temperatures of these previously cold-water streams were partly responsible for the altered zoobenthic communities.

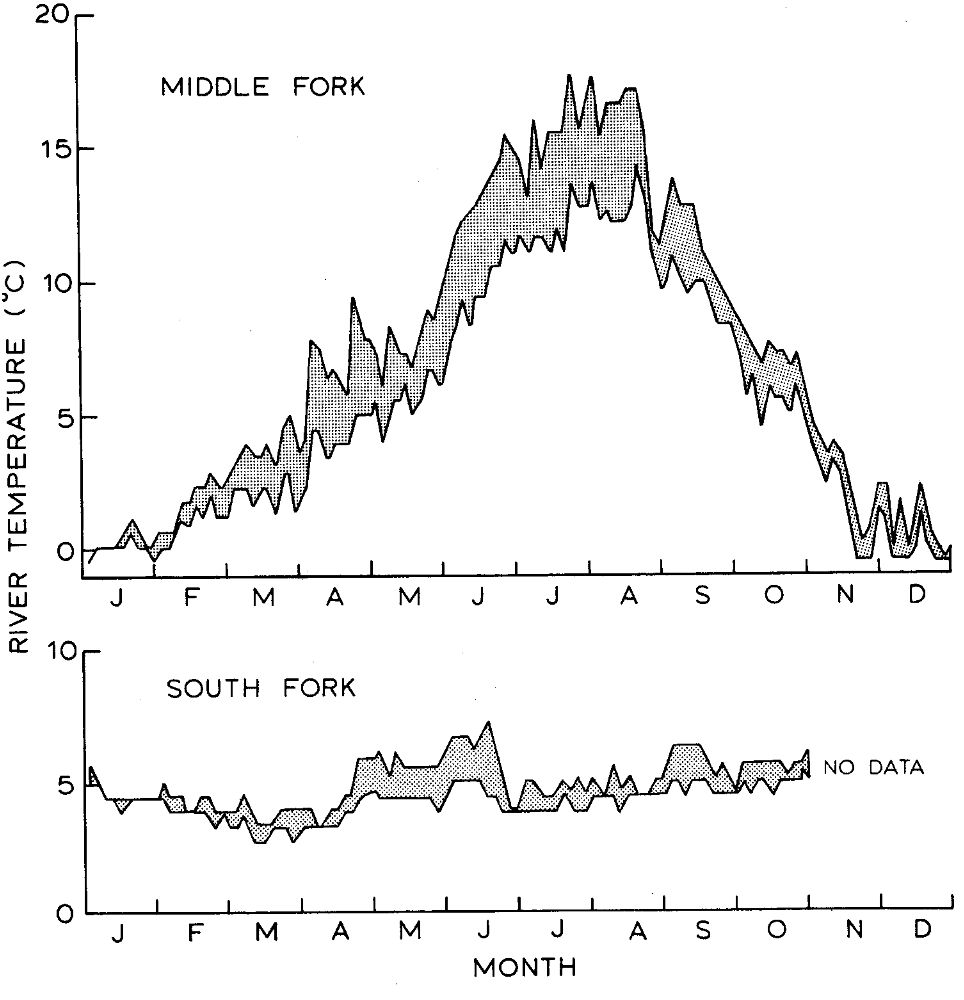

Figure 2. Thermal regimes of the unregulated Middle Fork and the regulated South Fork of the Flathead River during 1977 (Stanford, unpublished).

Severe thermal fluctuations over short periods may occur in streams below dams. Because of rapid heating during low flow periods, summer tailwater temperatures below deep-release dams may fluctuate 6-8°C as power releases peak and wane, which may occur two or three times each day (Pfitzer, 1967). Thermal shock may be induced below stratified reservoirs as the water level drops and release is shifted to the epilimnion. A combination of lower and upper outlet ports may have the same effect if discharge is shifted to the lower outlet as the reservoir level drops. Comprehensive data are not yet available relating the operation of dams with multilevel outlet structures to ecological conditions in the receiving stream.

The remainder of this paper will deal primarily with thermal effects of deep-release reservoirs that draw water from the hypolimnion during the entire period of stratification and thus do not produce rapid temperature fluctuations in the receiving stream. The thermal regime of such streams is characterized by diurnal and seasonal constancy and winter warm and summer cool conditions. Figure 2 contrasts the thermal pattern of the unregulated Middle Fork of the Flathead River, Montana, with the South Fork, which is regulated by Hungry Horse Reservoir (Stanford, Unpublished). The annual range 5 km downstream from a Japanese reservoir was reduced from 21 to 12°C (Nishizawa and Yamabe, 1970). A reservoir in the British uplands depressed downstream temperatures as much as 12°C in summer (Lavis and Smith, 1971). The stream temperature below a Colorado mountain reservoir ranged from 3-13°C and the seasonal maximum was delayed until late October, the time of reservoir overturn (Ward, 1974). Despite two release depths, some discharge from the spillway, and weak stratification of short duration, Crisp (1977) reported a marked reduction in diurnal range, and a delayed spring rise (20-50 days) and autumn decline (0-20 days) in the stream below a British impoundment. The seasonal range, however, was reduced only 1-2°C.

EFFECTS OF THERMAL ALTERATIONS ON ZOOBENTHOS

The modified thermal regime downstream from deep-release impoundments may be a major factor contributing to modifications of the zoobenthos community, especially in streams with otherwise favorable environmental conditions (Briggs, 1948; Pearson et al., 1968; Hoffman and Kilambi, 1971; Spence and Hynes, 1971; Lehmkuhl, 1972; Ward, 1974, 1976c; Gore, 1977).

Figure 3 shows the interrelationships, resulting from thermal regime modifications, hypothesized as responsible, in part, for the selective elimination of macroinvertebrate species in streams below deep-release dams.

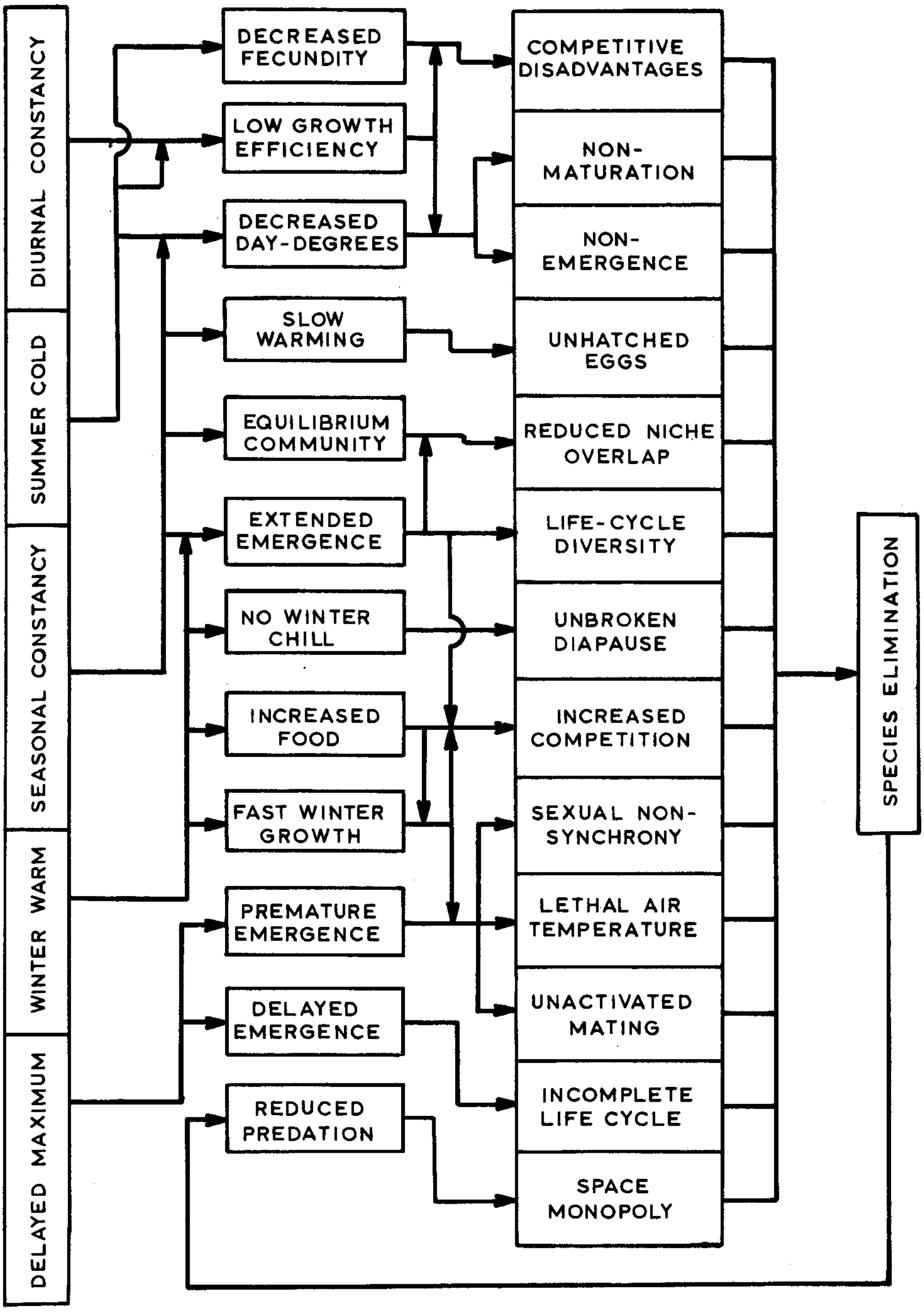

Figure 3. Thermal modifications below deep-release dams and resulting interrelationships hypothesized as partly responsible for selective elimination of zoobenthic species (modified from Ward, 1976c).

Diurnal Constancy

Streams below deep-release dams are characterized by a high degree of diurnal thermal constancy (Ward, 1976c, Crisp, 1977). Kamler (1965) emphasized the importance of diurnal thermal changes in controlling stream fauna, and Hubbs (1972) stated "...a steady-state environment is deleterious to most of the fauna and flora." However, because virtually no experimental data were available when Figure 3 was originally formulated (Ward, 1976c), the relationships are based upon information from related fields. For example, early work with codling moths (Shelford, 1929) and grasshoppers (Parker, 1930) showed that eggs and immatures developed more rapidly under fluctuating thermal regimes than under constant temperatures with the same mean values. The importance of daily temperature fluctuations as controlling factors for stream flora has recently been substantiated (Wong et al., 1978), and the postulated link between diurnal constancy and low growth efficiency of lotic zoobenthos (Fig. 3) has recently received empirical support. The development rate of eggs and the growth of immature Ephemeroptera (Sweeney, 1978) and Hemiptera (Sweeney and Schnack, 1977) were positively correlated with the degree of diel temperature fluctuation, but the reasons for the response have not been elucidated. Various physiological processes may have different thermal optima within the same organism (Hochachka and Somero, 1973), perhaps based upon enzyme temperature preferenda; and the relatively constant diurnal temperatures below some dams fail to provide the thermal range necessary to allow all metabolic pathways to operate optimally, at least for a time. Species with body processes requiring a wide daily temperature range for optimal energetic efficiency would have a competitive disadvantage in regulated steams.

The biological significance of daily thermal variations, and underlying mechanisms, still remain virtually uninvestigated. The following statement by Kinne (1964) is still valid: "Practically all information on non-genetic adaptation to temperature available to date has been obtained under conditions of constant temperature. There is great need for experiments conducted under temperature fluctuations - particularly where organisms from temperate latitudes are concerned."

Seasonal Constancy

Many natural streams in temperate latitudes are especially good examples of what Hutchinson (1953) calls nonequilibrium communities, since temporal fluctuations in environmental conditions are great and often unpredictable. Different species are favored as environmental conditions change, which allows considerable niche overlap, since competitive exclusion is not given sufficient time to eliminate species. Ide (1935) reported that stream mayfly diversity was positively correlated with the temperature range, and Paine (1966) found that the most diverse benthic intertidal community was associated with the greatest annual temperature fluctuation.

The relatively constant environmental conditions of streams below deep-release dams may cause a shift toward an equilibrium community, especially if factors in addition to temperature (e.g., chemical parameters, flow, turbidity, and the concentration and particle size of transport detritus) exhibit increased constancy and predictability. Thermal constancy also has indirect effects on zoobenthos. For example, epilithic algae may be abundant year-round in regulated streams, in contrast to the great temporal variability exhibited in unregulated streams resulting from ice and sediment abrasion and other controlling factors.

Whereas species such as *Gammarus lacustris*, which are able to complete their life cycle under constant thermal conditions (Smith, 1973), are favored below dams, species that depend upon seasonal cycles of temperature to cue various life cycle phenomena will be eliminated. The eggs of some organisms require a rapid rise of water temperature in spring to initiate hatching (Britt, 1962), and the spring rise in temperature is important in synchronizing emergence in some species (Lutz, 1968). The very gradual rise in temperature throughout the spring and summer below a dam on a Colorado mountain river contrasted greatly with the rapid spring increase at a location farther downstream, which was characterized by a much more diverse faunal assemblage (Ward, 1976a). Except for the unusual situation in the Brazos River referred to earlier, the only regulated stream known to the present authors in which zoobenthic diversity was not lowered was located below a dam that simultaneously draws water from upper and lower levels, thus reducing the seasonal range by only 1-2°C (Table 2).

Summer Cold Conditions

Water released from the hypolimnion of a deep stratified reservoir may result in summer temperatures below dams that are up to 20°C lower than those of unregulated streams of the region. According to Illies' (1952) "Entwicklungsnullpunkt" theory, growth is not only temperature dependent, but it ceases altogether if the temperature falls below the minimum critical temperature (the Entwicklungsnullpunkt) for a given species. Total degree days may not be adequate for the completion of the life cycle of some species, or the temperature may not attain the level necessary for nymphal maturation or emergence. For example, growth and maturation of the stonefly *Pteronarcella badia* is based on thermal summation, although emergence in dependent upon the attainment of an absolute water temperature (Stanford and Gaufin, unpublished). The failure of most stoneflies in the tailwaters below Hungry Horse Reservoir can be explained by lack of appropriate thermal criteria. The time between oviposition and hatching and the length of the hatching period may be greatly extended by low summer temperatures (e.g., Elliott, 1972). Reduced growth efficiency at low temperatures may eliminate species even though the temperature is within the tolerance range of the organism (Edington and Hildrew, 1973), presumably by causing a competitive disadvantage. Delayed emergence caused by slower growth could eliminate species, although this would depend on the particular life-cycle pattern. The emergence period may be lengthened under summer-cold conditions (Macan, 1957), or adult longevity may be increased (Nebeker, 1971a). Sweeney (1978) found that reduced temperatures during spring and summer lowered fecundity of winter and summer subimagos, apparently because of a reduction in the size of adults (Sweeney and Vannote, 1978). Species specific differences in the effects of summer cold conditions on fecundity would place some species at a competitive disadvantage. Species capable of metabolic adaptation to a wide range of thermal conditions (see, e.g., Fahy, 1973) would be favored in streams below deep-release dams.

Winter Warm Conditions

Increases in winter stream temperatures below deep-release dams may be of considerable ecological significance, especially in regions where streams normally develop an ice cover.

Species requiring winter chill (temperatures at or near 0°C) to break egg or larval diapause will be eliminated if winter temperatures are elevated (Lehmkuhl, 1972). Enhanced growth and resulting premature emergence (as much as five months early) from increased winter temperatures has been well documented (Coutant, 1968; Nebeker, 1971b; Lillehammer, 1975; but see Langford, 1975). Fey (1977) found that warming of a river by a power station eliminated the quiescent stage of *Hydropsyche pellucidula* larvae so that accelerated growth in February advanced emergence by 3-4 months.

Premature emergence may eliminate species if air temperatures are lethal to the adults (Nebeker, 1971b). Surviving adults may not reproduce, because mating mechanisms are not activated at low air temperatures (e.g., drumming in stoneflies; Rupprecht, 1975) or because of nonsynchronous emergence of males and females (Nebeker, 1971b). It may be significant that groups without aerial adults, such as amphipods, isopods, gastropods, oligochaetes, and turbellarians, often increase in relative abundance in streams below dams (Ward and Short, 1978) and in springbooks (Ward and Dufford, in press).

Winter warm conditions and seasonal constancy may cause extended emergence and thus increased life cycle diversity and increased and more constant productivity in regions with warm winter air temperatures (Ward, 1976c). Because the niche of a species may change throughout the life cycle, the temporal spacing of overlapping generations may occupy niches that would have been available for other species. Newell and Minshall (1978) found that a normally bivoltine mayfly exhibited multivoltinism in a stream section that was 18°C year-round, due to warm springs. Coactive patterns may increase under conditions of increased population density and more constant resource availability (Hutchinson, 1953; Yount, 1956; Patrick, 1970), resulting in reduced niche overlap and elimination of rare species.

Effects of increased winter temperatures will likely be of less ecological import in regions with more equable climates, such as Great Britain, where 0°C temperatures do not normally occur in streams and thus the fauna has not evolved a requirement for winter chill to break egg or larval diapause. This may explain, at least in part, some of the geographical differences in faunal response to stream regulation.

Delayed Thermal Maximum

In addition to the thermal modifications discussed, the seasonal maximum temperature may be greatly delayed (Jaske and Goebel, 1967; Ward, 1976a,c). The delayed seasonal maximum may conceivably delay or cause precocious emergence, depending on specific life history requirements. However, because empirical data are lacking, the effects of the delayed thermal maximum must rest on speculation. Research is badly needed in this area.

Reduced Predation

Predation often exerts a major role in determining the structure of stream communities (Patrick, 1970). A reduction of predation pressure may reduce the number of species in a community; even those not directly preyed upon are affected (Paine, 1966).

If one of the species eliminated by regulation is a "keystone species" (sensu Paine, 1969), that is, a top carnivore that prevents the monopolization of resources by a few species, zoobenthos diversity may be further reduced.

CONCLUSIONS

Although our understanding of the effects of reservoirs on biota of downstream lotic reaches has increased substantially in recent years, it has not kept pace with the proliferation of dams. Only a handful of investigators have published comprehensive ecological data on a relatively few regulated streams. Dams with multilevel outlet structures offer nearly unlimited potential for experimental manipulations as a means to more fully understand the structure and function of stream ecosystems. In addition to the great need for experimental research, much descriptive work remains to be done. The differential response to regulation of streams along latitudinal or altitudinal gradients could provide considerable insight into ecological phenomena, but too few sites have been intensively studied to offer valid comparative data.

Ward and Short (1978) stressed the value of benthic organisms as integrators of ecological conditions and developed a preliminary classification system based upon species response to regulation. An understanding of why certain taxa are affected in a given way would contribute not only to knowledge of ecological requirements of species but ultimately would provide data of predictive value in assessing impacts and beneficial modification of future stream regulation projects.

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