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Effects of Suspended Solids and Sediment on Reproduction and Early Life of Warmwater Fishes

A Review

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EFFECTS OF SUSPENDED SOLIDS AND SEDIMENT ON REPRODUCTION AND EARLY LIFE OF WARMWATER FISHES: A REVIEW

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FOREWORD

Effective regulatory and enforcement actions by the Environmental Protection Agency would be virtually impossible without sound scientific data on pollutants and their impact on environmental stability and human health. Responsibility for building this data base has been assigned to EPA's Office of Research and Development and its 15 major field installations, one of which is the Corvallis Environmental Research Laboratory (CERL).

The primary mission of the Corvallis Laboratory is research on the effects of environmental pollutants on terrestrial, freshwater, and marine ecosystems; the behavior, effects and control of pollutants in lake and stream systems; and the development of predictive models on the movement of pollutants in the biosphere.

This report presents a review of literature and a critical evaluation of what is known about the effects of sediment and suspended solids on the reproduction and early life of warmwater fishes.

James C. McCarty
Acting Director, CERL

ABSTRACT

Review of published literature and research reports revealed limited data for a few warmwater fish species concerning the impacts of suspended solids and sediments on reproductive success. Laboratory and field studies during the 1930-50's examined direct mortality as the result of extremely high levels of suspended solids. Controversy ensued in the 1940-60's over the impacts of turbidity on fish populations in the Great Lakes and midwestern rivers. Variations in year-class strength of important fishes have not been correlated with sediment loading, concentrations of suspended solids, nor sedimentation rates. Renewed interest in suspended solid impacts on aquatic ecosystems was evident in 1970's as indicated by published literature and symposia reporting laboratory bioassays and ecological field studies.

Species and stages of warmwater fishes are not equally susceptible to suspended solids. Only limited circumstantial evidence was found on the potential effects on gonad development in fish. There was substantial evidence that reproductive behavior was variously affected by suspended solids and sediment relative to spawning time, place of spawning, and spawning behavior. The more adaptively successful species' reproductive activities were not carried on at times of highest turbidity. Fishes with complex patterns of reproductive behavior are more vulnerable to interference by suspended solids at a number of critical behavioral phases during the spawning process. Incubation stage is particularly susceptible to adverse effects from sediment, especially among those species which do not fan their nest. Cluster analysis of reproductive behaviors of 110 warmwater fish species produced relationships which are intuitively logical.

Larval stages of selected species are reported to be less tolerant of suspended solids than eggs or adults. Lethal levels for suspended solids are interrelated with age-specific and species-specific differences as well as suspended solid particle size, shape, concentration, and turbulence in the environment. Increased suspended solids reduce sight-feeding distances, disrupt activity and respiratory patterns, and change orientation responses of some larval and juvenile warmwater fishes. Several species have successfully circumvented the adverse effects of sustained high levels of suspended solids in their environment through functional and behavioral adaptations conducive to survival in turbid habitats.

Although unequivocal experimental evidence demonstrating causal relationship between suspended solids and sediment on reproduction of warmwater fishes was scarce, generalizations from the overwhelming body of independent observations suggested that most warmwater fish assemblages have been affected and species composition have been altered because of sediment effects on the more sensitive species. Aquatic communities in total; plankton, macroinvertebrates, as well as fish; have been altered.

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SECTION I

CONCLUSIONS

The relationship between specific kinds and quantities of suspended solids or sediments and biological effects such as egg or larval mortality has been described for only a few warmwater fishes of North America. Searches of the literature base generally revealed laboratory and tank studies during the 1930-40's, limited field studies and speculation on the ecological effects of turbidity on fish populations in the 1950-60's, and laboratory bioassays and field studies in 1970's as the result of renewed interest in the effects of dredging, shoreline erosion, quarrying, and stream alteration.

Variations in year-class strength of important fishes have not been correlated with sediment loading, concentration of suspended solids, or sedimentation rates. Not all species of warmwater fishes are equally susceptible to suspended solids. Long-term ichthyofaunistic surveys show that sensitive species have been extirpated already from some impacted ecosystems.

The specific effects of suspended solids and of sediments (deposited solids) were not usually distinguished. Inferences by many authors were not supported by evidence and cause-and-effect relationships were not well documented. There is virtually no empirical foundation for suspended solid standards relating sensitivity of warmwater fish eggs and larvae to suspended sediment.

Several potential effects of suspended solids on gonad development in fish were reviewed but only limited circumstantial evidence was found in the literature that would elevate any one potential effect to a real effect. However, to conclude that suspended solids do not limit maturation or fecundity may be premature since the project has not been adequately investigated.

There is substantial evidence indicating that the reproductive behavior of warmwater fishes is variously affected by suspended solids and sediment relative to seasonal time of spawning, the place of spawning, and the nature of spawning behavior. Under conditions of increasing sediment loads in all forms of water bodies, the more adaptively successful species include those whose reproductive activities are carried on largely outside of times of highest turbidity. Species which protect their developing eggs from siltation by behavioral or other means have a reproductive advantage over those which afford no such protection. Reproductive failure among many species is also attributable to direct loss of spawning habitat through siltation of formerly clean bottoms and loss of vegetation due to reduction of the photic zone by turbidity. Fishes with complex patterns of reproductive behavior are vulnerable to interference by suspended solids and sediment at a number of critical behavioral phases of the spawning process. Species that have a strong visual component in their spawning behavior are particularly susceptible to such interference. Short-term exposure to high levels of suspended solids probably does not seriously impede reproductive movements of most warmwater fishes, but chronic exposures could produce physiological effects that are disruptive to reproductive behavior.

Natural occurring concentrations of suspended solids and sediment are sometimes sufficiently high to cause significant mortality to embryos of warmwater species, as reported for walleye, northern pike, and yellow perch. Death is attributed to smothering when sediment deposition is sufficient for complete burial of the egg which interferes with gas exchange across membranes. Timing of exposure to sediment may be an important factor. Even though embryos may suffer no effect from sediment at water hardening, during later stages of development when oxygen demand is greater, similar concentrations of sediment could be detrimental. The small size of many warmwater fish eggs makes smothering by settling sediment a real possibility in shallow wind-swept reservoirs or lakes and unstable streams where bank sloughing and soil erosion are common. Therefore, incubation -- that stage from fertilization to hatching -- is particularly susceptible to adverse effects from sediment, especially among those species where fanning of the nest does not occur.

Laboratory bioassays indicate that larval stages of selected species are less tolerant of suspended solids than eggs or adults. Although the cause of death was not always apparent, available evidence suggests that lethal levels for suspended solids are determined by interaction between biotic factors, including age-specific and species-specific differences, and abiotic factors, such as particle size, shape, concentration, and the amount of turbulence in the environment. Larvae hiding within the interstices of rocky substrate (lithophils) may be smothered or exposed to predation by loss of bottom cover from excessive sediments.

Limited studies have shown suspended solids to impact larval and juvenile fishes at sublethal levels by reducing sight-feeding distances, disrupting activity and respiratory patterns, and changing orientation responses. Indirect impacts of suspended solids on larval and juvenile fishes are more difficult to evaluate. Many species rely upon visual detection of planktonic organisms during the initial feeding stages. Rapid attenuation of light in turbid water may influence survival of these forms by reducing planktonic food mass or providing protection for prey organisms. Larvae and juveniles employing tactile senses for food detection are more suited for existence under low levels of illumination and possibly derive benefits from the concealing properties of suspended solids. Ascertaining the importance of turbidity as a cause of larval fish drift, and the influence of drift on larval survival, demands more understanding of the mechanics and ecological significance of drifting movements in riverine systems. Reduced standing stocks and growth rates of fishes reported for turbid waters have been confounded by the presence of species such as carp. Finally, there is evidence that larvae and juveniles of several species have successfully circumvented the adverse effects of sustained high levels of suspended solids in their environment through acquisition of functional and behavioral adaptations which are conducive to survival in highly turbid habitats.

Cluster analysis of reproductive behavior of 110 warmwater fish species produced relationships which are intuitively logical. Refinements of the clustering technique are possible, and additional characteristics could be employed so as to reflect overall reproductive strategies rather than primarily behavioral characteristics. To date, our literature survey has concentrated on a limited number of references concerning behavioral characteristics. A large body of literature on this topic remains to be examined.

Although unequivocal experimental evidence demonstrating causal relationship between suspended solids and sediment on reproduction of warmwater fishes is scarce, generalizations from an overwhelming body of independent observations suggest that most warmwater fish assemblages have been affected and species composition altered because of sediment effects on the more sensitive species. Aquatic communities in total; plankton, macroinvertebrates, as well as fish; have been altered. Populations and communities have been seriously affected and species diversity diminished. Overall faunal impoverishment has taken place, contributing to the expanding lists of endangered and threatened fauna and flora.

SECTION II

INTRODUCTION*

THE PROBLEM

Each year millions of metric tons of solids reach waterways from snow melt and rainfall runoff from crop- and rangelands, forests, surface mines, roadsides, and urban pavement. Holeman (1968) estimated the annual sediment yield of the major rivers of the world at 20 billion metric tons, five times more than the dissolved load. Runoff from non-point sources (NPS) transports soil, animal manure, acid mine wastes, nutrients, salts, pesticides, heavy metals, oils and grease and other toxic substances. In the U.S., erosion from cropland contributes 1.8 billion metric tons of soil to lakes, streams and rivers each year (Mayo 1975). This is approximately 50% of the total erosional sediment (Wadleigh 1968). However, the proportion of sediment from urban construction may overtake the total agricultural erosional rate in the near future (Wolman and Schick 1967). The most erosive watershed (tons sediment load/km) in the U.S. is the East River basin above Scotia, California (Judson and Ritter 1964).

Suspended solids and sediment cause increased drainage maintenance costs, reduced capacities of river and stream channels (thereby contributing to flooding), loss of reservoir capacity, direct damages from suspended sediment, transport of pollutants, increased water treatment costs, and negative impacts on fish, wildlife, and recreational demands (Harmon and Duncan 1978). In 1966, the total annual damage from sediment in streams, not including loss of agricultural productivity of farm land to erosion has been estimated to be 262 million dollars (Stall 1966). Pollution from NPS is recognized nationally and internationally as an important water quality problem that grows in importance as site specific, industrial and municipal inputs are reduced.

Impacts of NPS solids on aquatic life vary with the organism and the quality and quantity of the solids, their solubility, and with the kind of compounds transported with them. Organisms are affected by solids in suspension, after deposition as sediment ("silt"), or both. Also, the inorganic and organic components (salts, nutrients, pesticides, heavy metals, and other toxic substances) have direct and complex indirect effects on aquatic life, some known and others inferred. The European Inland Fisheries Advisory Commission Working Party on Water Quality Criteria for European Freshwater Fish (EIFAC 1964) listed four ways in which suspended solids might be harmful to fish:

> "(1) By acting directly on the fish swimming in water in which solids are suspended, and either killing them or reducing their growth rate, resistance to disease, etc.
>
> (2) By preventing the successful development of fish eggs and larvae.
>
> (3) By modifying natural movements and migrations of fish.
>
> (4) By reducing the abundance of food available to the fish."

*By Robert C. Summerfelt

The general effects of inorganic sediment on aquatic biota -- the preponderance of the citations emphasized effects, mainly effects of logging and road construction, on salmonids and aquatic insects of trout and salmon streams of Alaska, California, Colorado, Idaho, Oregon, and Washington -- have been reviewed, several times (Cordone and Kelley 1961, Hollis et al. 1964, Everhart and Duchrow 1970, Phillips 1971, Koski 1972, Gibbons and Salo 1973, McKee and Wolf 1963, Meehan 1974, Mortensen et al. 1976, Iwamoto et al. 1978). Iwamoto et al. (1978) has summarized sedimentation effects on aquatic organisms as follows:

"1) clogging and abrasion of gills and other respiratory surfaces;

2) adhering to the chorion of eggs;

3) providing conditions conducive to the entry and persistence of disease-related organisms;

4) inducing behavioral modifications;

5) entombing different life stages;

6) altering water chemistry by the adsorption and/or absorption of chemicals;

7) affecting utilizable habitat by the scouring and filling of pools and riffles and changing bedload composition;

8) reducing photosynthetic growth and primary production;

9) affecting intragravel permeability and dissolved oxygen levels;

10) affecting the fishing for and catchability of sport fishes."

Field and laboratory studies have shown that advanced life stages of most fishes are quite tolerant, to a direct toxic effect, of suspended solids. The most critical impacts on fish may be those which impair their reproductive processes: adult maturation and reproductive behavior, and egg and larval growth, development, and survival. The most serious impact of sediment on salmonids occurs from sedimentation of the gravel used for spawning but fishes in lakes and ponds are affected as well because most deposit their eggs on the bottom, making them part of the benthos during a critical period in their life histories. In the Great Lakes, all fishes, except freshwater drum (Aplodinotus grunniens), have demersal eggs, and many have been affected by changes taking place in the sediment because of the tremendous amounts of allochthonous materials entering the lakes (Beeton 1969).

SCOPE OF REVIEW

We systematically investigated current literature on the effects of sediment and suspended solids on aspects of the reproductive biology and early life history of warmwater fishes. The objectives of this study are: 1) to

critically review the literature on the impacts of sediment on spawning success of warmwater fishes; and 2) to determine fish species which are sensitive to impacts of sediment on spawning. Knowledge of the comparative reproductive strategies of warmwater fishes as a mechanism to provide inferences of potential effects of sediment from the limited number of species for which effects have been documented to species with similar reproductive adaptations for which impacts of NPS sediment have not heretofore, been evaluated. We focused on the general impact of suspended solids and sediment without getting into specific search to evaluate runoff from feedlots, sewage effluents, mining wastes or other industrial effluents although some references are included.

Sediment is the transport mechanism whereby chlorinated hydrocarbons begin their pathway from the application site, through the food web, to lipid storage in fish. The biomagnification and transovarian movement of pesticides has had negative effects on the hatching success and survival of larval salmonids in Michigan fish hatcheries using adult salmon captured in tributary streams of Lake Michigan (Johnson and Pecor 1969, Willford et al. 1969). The special role of bacteria in formation of methyl mercury in lake sediment is also a major sediment-fish related problem, since methyl mercury is highly soluble and transferable to fish by diffusion across the gills and through the food chain (Jensen and Jernelov 1969). Regulations against sale of methyl mercury contaminated fish in the U.S. caused economic losses to sport and commercial fisheries. However, toxicant related interactions with sediment opens an expansive literature base aside from the thrust of our review, thus, they were not reviewed.

Our attention is on the direct physical effects (molar action, or abrasion, suffocation) of suspended or sedimented solids. There exist some problems relating to terminology because certain words have different usage in the vernacular and because sediments are difficult to define physically and chemically. The words sediment and suspended solids are often interchanged and although suspended matter is usually measured as mg of solids/liter (ppm), suspended solids concentration is sometimes expressed by measurement of turbidity or light transmission. Turbidity is the degree of opaqueness produced by suspended particulate matter, which limits light transmission. This optical property cannot be uniformly equated with concentration of suspended solids (Everhart and Duchrow 1970).

We have attempted, where possible, to distinguish between effects caused by suspended solids and sediment. The former refers to the solids in suspension (i.e., the non-filterable residue--American Public Health Association 1976) and sediment the solid matter (soil, sand, gravel, and detrital matter) that has been deposited on the substrate. The latter is synonymous with alluvium or mud. Golterman (1975) defines mud as composed mainly of silicates, carbonates, and organic matter. "Resuspended solids" is often used in reference to recently resuspended sediments, however, in this form ("resuspended") it is more accurately called suspended solids.

Not uncommonly, silt is used to mean either suspended solids, sediment, and both, but technically, silt as a specific particle size grouping of sediments intermediate between sand and clay. On the Wentworth grade-scale,

there are five grades of sand with particle sizes ranging from 0.125 to 2.0 mm, silt ranges between 0.0039 to 0.0625 mm (3.9 to 62.5 microns), and clay particles are less than 3.9 microns (Selley 1976). The U.S. Department of Agriculture defines silt as particles between 5 and 50 microns (Berger 1972), but others use particle sizes 2-63 mincrons, or less than 16 microns (Golterman 1975).

Stream load consists of the dissolved load, suspended solids, and bedload. The latter is the part of the suspended solids which moves by rolling, or sliding on the bed of the stream, while the suspended solids is the sediment kept in the main body of the flow by the upward momentum of turbulent eddies (Beaumont 1975). Investigators of river ecology have not distinguished effects of bedload and suspended solids.

LITERATURE SEARCH*

Computerized Search

Completed computerized searches of current researches secured from the Smithsonian Science Information Exchange, Inc. (SSIE) included "LA64-78 Sedimentation in Streams, Lakes, and Reservoirs" dated 6/78; "LA13-78 Turbidity in Oceans, Bays, Streams, and Lakes" dated 6/78; and "BA15 Effects of Turbidity on Aquatic Organisms," dated 4/77. Investigators selected from current notices of research projects were contacted by mail requesting any publications, reports, or additional suggested sources of information on effects of sediment on freshwater aquatic biota.

National Technical Information Service bibliographies related to sediment examined included: (1) "Sediment water interaction and its effect upon water quality", NTIS/PS-78/0015 (Jan. 1978): 140 abstracts; (2) Sediment transport in rivers", NTIS/PS-77/1039 (1977): 203 citations; (3) "Stream erosion and scouring processes", NTIS/PS 77/0437 (June 1977): 97 abstracts; and (4) "Reservoir and lake sedimentation", NTIS/PS-78/0021 (Jan. 1978): 56 abstracts. These four NTIS bibliographies included very few references offering information on sediment-biota aspects.

Iowa State University Library's Automated Retrieval Service (ISU/LARS) assistance was secured in using two sets of linked keywords for searching: Biological Abstracts and Bioresearch Index (BIOSIS), 1970 to present, covering over 8,458 serials; Pollution Abstracts, 1970 to present, for over 2,500 sources; Comprehensive Dissertation Index, 1861 to present; and Science Citation Index (SCI), 1974 to present, for over 2,600 journals.

A primary key word set with words silt ($), sediment ($), turbidity ($), suspended solid, and water quality ($) was matched with a secondary key words consisting of fish ($), pike ($), sunfish ($), Lepomis, bass ($), Micropterus, aquatic ($) and bottom fauna. The term "$" permitted the computer program to utilize expansions of the root word. A separate secondary key word listing using stream, river, pond, lake, and reservoir was matched with primary word set for permuted pairs of words as two level indexing entries for a search of titles, enrichment words (BIOSIS), or key words resulted in approximately 3 to 5 times as many matches. However, the numbers of references related to the scope of the present study were much greater with the biological-tiered listing.

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*By R. J. Muncy

A computerized search of Science Citation Index (SCI) using the author-title of four major early review papers concerning the effects of sediments on fishes (Ellis 1936, Buck, 1956, Cordone and Kelley 1961, and Wallen 1951a) was extremely effective in locating 23 recent citations, compared with 15 citations using two-level biological key-word listings. Updated searches of SCI were made using issues published after computerized search (July 1978) rather than ISU Current Awareness Reference Service (CARES).

Computerized search of 12,000+ reports in the reference base at the Fish and Wildlife Reference Service, Denver, Colorado by library staff using "effects of water quality on fish" yielded 122 references and using the terms "sedimentation, silt, and turbidity" yielded 191 references from federal aid reports and theses. Dr. Menzel found that about one-third of the references were related to and useful for our topic concerning the effects of sediment on the spawning of warmwater fishes.

Bibliographies

Bibliographies and review papers searched as reference sources included Iwamoto et al. (1978), Sorensen et al. (1977), Alderdice et al. (1977), Morton (1977), Gammon (1970), Cairns (1968), European Inland Fisheries Advisory Commission (1965), McKee and Wolf (1963), Cordone and Kelley (1961), and Ellis (1944). Most of the earlier papers containing experimental data were repeatedly included in the more recent review papers and bibliographies.

SECTION III

GENERAL ECOSYSTEM EFFECTS OF SUSPENDED SOLIDS AND SEDIMENT*

INTRODUCTION

Reproduction, year-class strength, survival and growth of fish may be affected by:

1) sediment transport of nutrients and toxicants (heavy metals and pesticides),

2) light-limiting effects of suspended solids,

3) sediment accumulation, and

4) decomposition of organic matter.

The purpose of this section is to identify and evaluate the nature and extent of sediment and suspended solids related effects on aquatic ecosystems that indirectly affect fish reproductive success through the dependence of fish on other members of the aquatic community and trophic processes.

The productive process in aquatic ecosystems is reviewed to determine effects of sediment and suspended solids on fish food resources and the special impact of allochthonous organic matter. This section complements and expands on a similar review by Sorensen et al. (1977). The synthesis on river ecology provided by the contributions to the books edited by Oglesby et al. (1972) and (Whitton 1975a), and the thorough review given the macroinvertebrates and other topics by Hynes (1970) provide valuable insight into river ecology and effects of suspended solids and sediment on lotic ecosystems. Although they did not focus on the problem considered here, they were valuable sources of original literature. Watershed inputs of carbon and nutrients have traditionally been considered in terms of their effects on primary productivity, but a recent comprehensive team effort using watershed input-out model, tracing inputs throughout four lake ecosystems from British Columbia to New Hampshire, demonstrates causal relations to productivity of zooplankton, insects and fish (Richey et al. 1978). There is need for further research at the community level on the quantitative response of freshwater biota to suspended and dissolved solids (Sorensen et al. 1977).

INFLUENCES ON PRIMARY PRODUCTIVITY

In central Oklahoma, where soil erosion contributes Permian red clay of a particle size 0.5 to 5 microns in diameter, many ponds are permanently muddy because the clay particles settle slowly, and are resuspended easily by wind action (Irwin and Stevenson 1951). Colloidal turbidity in central Oklahoma ponds has limited algal populations (Claffey 1955). In the same area, Butler (1964) observed an inverse relationship between turbidity and primary productivity; gross primary productivity in a clear pond was three-fold greater than

* By Robert C. Summerfelt

in an adjacent turbid pond. Also, in central Oklahoma, Toetz (1967) found that clarity of pond water was positively correlated with mean depth, pH, dissolved solids and conductivity; shallow ponds with large surface areas tended to be turbid. Toetz found that pigment diversity in 29 farm ponds was lower in turbid ponds than in clear ponds, suggesting that phytoplankton populations in turbid ponds are always in the initial stages of algal succession. Suspended solids scatter and absorb light, rapidly absorbing radiant energy in the upper layers of water, reducing the depth of effective photosynthesis (Bartsch 1960). The reduced light transmission light-limits photosynthesis by algae and macrophytes, and also harms algae and macrophytes by abrasion, coating and smothering.

Cairns (1968) reviewed a substantial body of literature demonstrating a negative relation between concentration of suspended solids and light penetration. There is a direct relationship between the depth distribution of vascular aquatic plants and algae and the depth of light penetration. Greatly reducing light penetration may shift algal composition from green to bluegreen since the latter are tolerant to higher levels of ultraviolet light which is rapidly extinguished with depth. Aside from certain exceptions such as the central Oklahoma Permian red clay area, transparency in most natural lakes is controlled by algal biomass and Secchi disk transparency is a useful measure of trophic conditions (Brezonik 1978). In a survey of 50 Iowa lakes, Jones and Bachmann (1978a) found that reduced transparency was related more to algal density than to suspended inorganic matter; transparency generally decreased as the summer progressed corresponding to an increase in algal population.

In the Missouri River impoundments, turbidity was regarded as the strongest limiting factor to plankton abundance. and plankton is of great importance to fish growth and survival (Benson and Cowell 1967). In the last downstream reservoir, Lewis and Clark Lake, most inorganic turbidity was attributed to fine sand, silt, and clay particles. Current velocities of about 10 cm/sec were "adequate" to keep the clay fraction (<62 microns) in suspension. Hudson and Cowell (1967) reported an inverse relationship between net phytoplankton abundance and turbidity in sections of Lewis and Clark Lake.

In rivers, the photosynthetic rate (g $O_2 l^{-1} h^{-1}$) is linearly proportional to available light, except when the light intensity fluctuates rapidly (Kelly et al. 1976). Turbidity increases the attenuation coefficient at all wavelengths, especially the red end (Westlake 1966). Low transparency is also produced in rivers and lakes by algal blooms and low transparency is characteristic of eutrophy. However, the more general case in rivers is for photosynthetic productivity to be more limited by turbidity than nutrient levels (Swale 1964, Lund 1969, Angino and O'Brian 1968). A moving bedload has a strong molar action that scours away periphyton communities (Ball and Bahr 1975). Epipelic (attached to the surface of the sediment, i.e., one component of the benthic algae) algae can be swept into the plankton by strong currents (Whitton 1975b).

Turbidity from colloidal clay in central Oklahoma may greatly alter the distribution of heat--the temperature in surface water in turbid ponds often exceeds that of non-turbid ponds of similar size and morphometry -- consequently, summer stratification tends to be more pronounced in turbid situations (Butler 1963). Differences in turbidity affect the depth distribution of solar radiation such that in shallow areas where solar radiation reaches the bottom, much energy

is used in heating the bottom mud and the water mass has a much more uniform temperature, but in turbid ponds of similar depth, a greater amount of radiation is absorbed in the water column, especially near the surface, and less near the bottom, and the sediment warms to a lesser extent: "Unless there is mechanical mixing, pronounced stratification occurs (Butler 1964)." Wallen (1951b) also found a greater difference between the surface and bottom temperature in turbid than in clear ponds.

Suspended solids and sediment interfere with the trophic process of energy and mass transfers from producer through consumer levels. Moore (1937) expressed concern over the effects of silt deposits on fish food organisms and the negative effects of reduced light transparency on phytoplankton.

Post impoundment water quality studies on rivers invariably show reduced suspended solids loads downstream of the dam. Sediment trapped behind Clark Hill Dam on the Savannah River reduced the sediment load downstream from the dam, increased the depth of the photosynthetic zone, increased the abundance of periphytic algae, and produced a larger number of species of benthic organisms (Patrick 1976). The review by McKee and Wolf (1963) cites sources that show turbidity decreases primary productivity and reduces abundance of fish food organisms. Jones (1964) stated that suspended coal dust cuts off the light from streambed, preventing photosynthesis by plants, and reducing abundance of invertebrate fish food. King and Ball (1964) found a 61% reduction in primary production and 68% reduction in autotrophic aufwuchs production in a 30-mile section of Red Cedar River, Michigan as the result of two-fold increase of inorganic sediment originating from highway construction. Iwamoto et al. (1978) presented an extensive summary of negative impacts of suspended solids on attached and plankton algae. Cordone and Kelley (1961) pointed out the difficulties of measuring impact of turbidity on stream algae.

In lotic systems, the majority of the total organic input comes from outside the river, and the diet of fish often contains a high proportion of items of direct terrestrial origin; thus, in streams the role of macrophytes lies more in their role in modifying and diversifying habitats than in the supply of organic matter (Westlake 1975). Silt and organic materials accumulate in macrophytes, and rivers with macrophytes contain larger and more varied invertebrate life than are found in bare areas; macrophytes also provide shelter and spawning sites for fish and invertebrates and emergence routes for invertebrates (Westlake 1975). There is "very much" lower biomass of macrophytes in turbid waters--"The more turbid the water the smaller the proportion of river-bed receiving sufficient light and the fewer the species that can survive (Westlake 1975)." Adaptive response of some macrophytes to seasonal changes in turbidity may result in atypical phenological patterns such as growth in early winter when this coincides with occurrence of clear water (Edwards 1969). Though the main effect of suspended solids is through reduction in light intensity, some macrophytes may be buried and eliminated by rapid accumulation of silt (Edwards 1969). The most widespread effect on aquatic macrophytes is probably through increased turbidity and depostion of silt on the leaves which will reduce the light reaching the leaves and hence decrease photosynthesis.

Morton (1977) cited two references showing a detrimental effect of dredging and dredge spoil on rooted aquatic plants. Robel (1961) reported inverse

correlation between turbidity (colorimetric units) and production of sago pondweed (Potamogeton pectinatus). Langlois (1941) attributes the loss of lotus beds in St. Clair River and Sandusky Bay of Lake Erie to "increased silt loads". Martin and Uhler (1951:120-121) reported the increased impact of sediment turbidity and stains on aquatic vascular plants. In the Cedar River, Michigan, a large influx of inorganic solids decreased light, reduced autotrophic photosynthesis, scoured organisms from the stream bed, suffocated many organisms, filled pools, and modified the channel (Ball and Bahr 1975).

NUTRIENT RELATIONSHIPS

Nutrient input affects the rate of photosynthetic productivity per unit biomass and the standing crop of plant biomass. Trophic status of aquatic ecosystems is responsive to inputs of carbon and nutrients from their watershed. Research findings from the Hubbard Brook Experimental Forest, New Hampshire, show that a deciduous forest ecosystem has a marked control on downstream water quality; clear-cutting increased nitrate nitrogen runoff, causing eutrophication of the streams (Beaumont 1975). A high community photosynthesis rate and abundant plant biomass indicates a state of eutrophication; increases in nitrogen and phosphorus concentrations and decreases in dissolved oxygen are accepted indices of eutrophication (Hasler 1947). In lotic environments, the sudden appearance of a large growth of Cladophora spp. is an indication of nutrient eutrophication (Whitton 1975b). Excessive nutrient input promotes algal blooms, accumulation of particular organic matter, and an excessive nocturnal respiratory demand, leading to fish kills. Before the latter occurs, there are progressive changes in species composition (National Academy of Sciences 1969).

Nutrients from agricultural drainage are transported by surface runoff, subsurface runoff (flow from drainage tile), and ground water (base flow). The type of nutrient carried by each component varies with the chemical, the soil and seasons. Loess soils, which have particles in the silt and clay range, have greater adsorptive capacities than alluvial soils with a high sand content. Whereas, loss of dissolved NO_3-N from tile drainage and shallow subsurface flows can be substantial, loss of PO_4-P is mainly associated with surface runoff events. For central Iowa rivers draining fields intensively rowcropped for corn and soybeans, surface runoff seems to play the major role in contributing nutrients (Kilkus et al. 1975). Phosphorus associated with sediments, either adsorbed to clay or a component of organic matter, is usually present in greater quantity than dissolved P in surface runoff. Laboratory studies by Toetz (1967) indicate that clay particles in suspension do not adsorb NH_4-N and thus do not play an important role in nitrification.

Although both N and P are important contributors to eutrophication, the ability of heterocystous blue-green algae to fix atmospheric nitrogen suggests that blue-green algae would still occur if phosphorus was available (Fitzgerald 1971). The majority of eutrophication research, exemplified by the papers in two major symposia (National Academy of Sciences 1969, Golterman 1977), has focused on sources and biochemistry of phosphorus. Bachmann and Jones (1976) have called phosphorus the "key element" in eutrophication control. Some authors have portrayed lake condition as a continuous function of phosphorus

loading rates (Uttormark and Wall 1976). Vollenweider (1968) indicated that P-loading rates in excess of 0.13 $g/m^2/yr$ tended to produce eutrophic conditions in lakes with mean depths of less than 5 m. Watershed outputs in Iowa average 0.035 g/m^2, and P-loading rates of lakes range from 0.11 to 2.06 g/m^2 (Jones and Bachmann 1978b).

The most ecologically sound approach to eutrophication control is to prevent introduction of phosphorus, because after introduction and deposition as sediment, phosphorus recycling from sediment can contribute to long periods in recovery after external loading is restricted (Golterman et al. 1977). The largest proportion of contributions to the 1976 international symposium on interactions between sediment and freshwater dealt with various aspects of phosphorus transfers from and to the sediments (Golterman 1977). It has been suggested by Uttormark and Wall (1976) that the immediate focus of management of fertile lakes receiving high input should be to ease the symptoms of fertility.

Because of the light limitation of turbidity coinciding with nutrient inputs from erosional sources, periods of high nutrient loading often correspond to times of reduced primary productivity (Ball and Bahr 1975).

EFFECTS ON FISH FOODS -- THE ZOOPLANKTON AND BENTHOS

Quantity and quality of food may affect survival at a "critical stage", such as the transition from endogenous to exogenous food resources (Toetz 1966). At any age, however, limited food may reduce growth, decrease resistance to disease or toxic substances, and increase mortality.

In nature, growth of fish is usually less than genetic potential as demonstrated in the laboratory or fish hatchery where fish are fed to repletion. Although fish growth may be rapid in certain natural conditions before carrying capacity is reached, such as in a newly impounded, or in chemically renovated lake, growth of fish in nature is usually limited by availability of food (Lewis 1967, Doudoroff 1976).

The benthic macroinvertebrates have been shown to be a major source of food for fishes and another feature of biological productivity that is negatively impacted by sediment. Suspended matter and sediment can limit both the quantity and quality of food resources, and foraging efficiency of the fish (Doudoroff 1976). Eutrophy, caused by nutrient transport with sediments, changes the benthos to organisms--like oligochaetes and midges that are tolerant to severe oxygen depletions related to high oxygen demand of the sediments--that are less suitable as fish foods.

Many investigators have shown that suspended solids and settled solids have a negative impact on food available to fish (Cairns 1968, Cleary 1956, Cordone and Kelley 1961, European Inland Fishery Advisory Commission 1964, Gammon 1970). Ellis (1936) demonstrated that many species of fresh-water mussels were killed by a blanketing effect from 6.3 to 25.4 mm of "very fine erosion silt, chiefly adobe clay with very little organic matter." The experimental design seemed to distinguish the blanketing effect from oxygen depletion; silt appeared to interfere with the feeding activity of mussels and accumulated in their mantle cavity and in the gill chambers.

The EIFAC 1964 report cited a study of the Mondsee, in Austria, where production of whitefish was affected as a result of an 80% reduction in Daphnia production resulting from high clay turbidities produced by runoff from road construction. Winner (1975) reports that turbidity from agricultural runoff indirectly affects zooplankton productivity, inhibiting algal production, which eliminates certain filter feeders such as the Cladocera and Copepoda, and directly by interfering with the feeding process itself. Winner cited a report by Rylov (1940) where under turbid conditions, silt that accumulated in the digestive tract of Cladocera caused them to sink. Increased turbidity in Lake Erie is reported to have affected the depth distribution of zooplankton (Doan 1942). Claffey (1955) studied plankton productivity in relation to turbidity in 10 clear (<25 ppm) and 10 turbid (>25 ppm) ponds in Oklahoma. Numbers of phytoplankton, zooplankton, and bacteria, and volume of net plankton were larger in ponds with <25 ppm, intermediate in ponds with turbidity 25-50 ppm, and least in ponds with turbidity 51-350 ppm.

Benthic organisms are smothered and damaged by sediment causing mortality and depopulation. The highest concentration of suspended sediment within a river is found closest to the bed, and bedload moves and slides along the bed of the stream (Beaumont 1975). Thus, stream invertebrates and benthic algae are in a highly vulnerable habitat. In lentic environments, shading can cause macrophyte die-off, reducing the amount of structural support for invertebrate life. Reduction in suspended solids in the Savannah River following construction of the Clark Hill Dam resulted in improvement of the food base, benthic, algae, arthropods (benthos), and fish (Patrick 1976). Dredging in the Savannah River increased suspended solids load, caused a decrease in benthic algae, insects (especially the filter feeders), and fish. In one case, sand deposition in a river caused an impoverishment of invertebrates. The effect was related to the unstable shifting nature of the sand deposits rather than to turbidity or abrasion by the particles in suspension (Nuttall 1972). In the Red Cedar River, Michigan, species diversity of benthic macroinvertebrates was reduced by silt and organic sediment (Ball and Bahr 1975).

Generally suspended solids and sediment input are regarded as detrimental to benthic organisms which live in or on the substrate, deriving energy by feeding on the organic matter contained in the sediment. However, in some turbid lotic systems, the high density of particulate organic matter--caused by the extensive interface with the terrestrial system and physical factors keeping particles in suspension (Cummins 1972)--serves as an abundant food supply for detrital feeders (Winner 1975). Moderate siltation (organic detritus) may enhance production of certain important fish food organisms. Silt bottom areas are needed by burrowing mayfly nymphs (Carlander et al. 1967) because they construct U-shaped respiration tubes in the muddy bottoms where they ingest mud, organic detritus, algae, and bacteria. The Upper Mississippi River, from St. Paul, Minnesota to St. Louis, Missouri, is a series of navigation pools which are affected by sediments and other pollutants. Although municipal and industrial effluents are believed to have severely reduced the numbers of burrowing mayflies (Hexagenia bilineata, H. limbata, and Pentagenia vittigera) for 30 miles below Minneapolis, and for over 300 miles below St. Louis (Fremling 1970), the other navigation pools of the Upper Mississippi, with silty bottoms, were very productive of large Hexagenia mayflies (Fremling 1960).

"Enrichment and siltation" has increased the carrying capacity for H. limbata which now dominates areas formerly dominated by H. bilineata. In Pool 19 above Keokuk, Iowa, Hexagenia spp. composed over 50% by volume of the food of channel catfish (Ictalurus punctatus), freshwater drum, mooneye (Hiodon tergisus), goldeye (Hiodon alosoides), and white bass (Morone chrysops), and over 40% by volume of the food of paddlefish (Polyodon spathula) and white crappie (Pomoxis annularis) (Hoopes 1960). In the polluted areas cited above, burrowing mayflies tolerate anaerobic conditions for as long as 11 hours (Fremling 1970). Unfortunately, total productivity of the Upper Mississippi navigation pools is being reduced by filling of the pools by sand (Fremling 1970), and other components of the sediment load.

Beeton (1969) implicates severe oxygen depletion as the major factor in change in the benthos in western Lake Erie; where nymphs of the mayfly Hexagenia were formerly dominant, they almost disappeared, and pollution-tolerant sludge worms became the dominant organism.

Gammon (1970) reported effects of suspended solids on macroinvertebrates and fish from a crushed limestone quarry. Discharges with less than 40 mg/l part of each day caused a 25% reduction in macroinvertebrate population, and inputs of more than 120 mg/l with sediment accumulation caused a 60% reduction. Fish emigrated from pools when heavy sediment input occurred in the spring, but vacated pools in the summer only after deposits of sediment accumulated. Forshage and Carter (1974) reported 97% reduction of macroinvertebrates on multiple-plate samples at dredge sites as result of physical and sedimentation effects.

Forester and Lawrence (1978) reported a decrease in the standing crop of bluegill (Lepomis macrochirus) in ponds caused by carp (Cyprinus carpio) roiling the sediments.

Ellis (1931) reported erosion silts destroying mussel population in Mississippi, Tennessee, and Ohio rivers and Ellis (1936) experimentally demonstrated silt deposits of 6.3 to 25.4 mm killed freshwater mussels.

Increased silting, which reduced transparency by one-half, decreased bottom fauna in a reservoir by one-half (Moore 1937). Cordone and Kelley (1961) reported extensively on the impacts of sediments on bottom fauna of coldwater trout streams and they concluded that substantial quantities of inorganic sediment entering a flowing stream can seriously reduce the abundance of bottom-dwelling invertebrates. Iwamoto et al. (1978) in an extensive review with emphasis on freshwater salmonid habitats, indicated inconclusive effects of various amounts of deposited sediments on benthic faunas.

Fingernail clams (family Sphaeriidae), found in major rivers, irrigation pools, and man-made and natural lakes, are important links in food chains from algae, bacteria and detritus to fish and ducks. They are widely utilized by bottom-feeding fish such as channel catfish, carp, and bullheads (Ictalurus spp.) (Paparo and Sparks 1976). "Erosion silt" in water reduced mussel feeding time by 75%. Rogers (1976) indicated that fingernail clams could withstand heavy deposits of silt but less sand. Carp in the Illinois River, where fingernail clams disappeared, were measurably thinner and smaller than carp caught

downstream (Mills et al. 1966). In sections unaffected by the dieoff, Starrett (1972) reported that fingernail clams formed 50.2% by volume of the food items of carp, but only one clam was found in carp collected in the affected section. Hambric (1953) found 21 genera of benthic macroinvertebrates in clear ponds (less than 25 ppm turbidity units) that were not found in turbid ponds (more than 25 ppm), but a greater volume of organisms were collected from the turbid ponds than the clear ponds.

Swenson (1978) demonstrated that light penetration along the western edge of Lake Superior is reduced significantly by even low levels of turbidity created by erosion of a band of red clay as a result of wave action on the shore line. Zooplankton concentrated near the surface in red clay plumes also concentrated rainbow smelt (Osmerus mordax), but the smelt also preyed on larval lake herring (Coregonus artedii). Swenson proposed that smelt may be more predacious on the young lake herring in turbid water than in clear water, and that turbidity is having an adverse effect on the herring population through enhanced smelt predation contributing to the declines of the formerly abundant western Lake Superior lake herring population.

IMPACT OF ALLOCHTHONOUS ORGANIC MATTER

The importance of allochthonous organic inputs as a food source in lotic ecosystems was reviewed by Hynes (1970) and Jones (1975). Water quality degradation due to excessive oxygen demand caused by decomposing organic matter--produced in situ, because of excessive nutrients, or produced outside (allochthonous) the system--is a widespread cause of summer and fish kills in both lotic and lentic environments. Exaggerated diurnal dissolved oxygen concentration is one of the earliest detectable results of stream eutrophication (Ball and Bahr 1975). Sediment and resuspended sediment (suspended solids) exert an oxygen demand in rivers, the amount of resuspension determines the degree of oxygen depletion (Isaac 1962). Suspended solids may directly interfere with surface reaeration of streams (Alsonso et al. 1973). Westlake (1975) reported a model which predicts an increase in the daily oxygen output of a river upon removal of turbidity from an effluent.

Organic matter covered with silt may comprise 8 to 12% of the dry weight of mud of navigational pools (Ellis 1936); these organic deposits may cause a high mortality of young mussels (Ellis 1931). In lentic environments, insects are favored over zooplankton by higher inputs of allochthonous particulate organic matter (POM) than of autochthonous POM; increases in magnitude of autochthonous carbon sources result in progressively greater respiratory decomposition in the sediments (Richey et al. 1978). In Lake Erie collapse of the blue pike and sauger populations were found to occur during the period when extensive oxygen depletion and change in the benthos were first reported (Beeton 1969).

In the U.S., animal wastes total 1.7 billion tons annually, and in terms of human population waste equivalents, they are ten times greater than that produced by the U.S. human population (Robbins et al. 1971). Fortunately most of these wastes do not enter aquatic systems, but Henderson (1962) reported that oxygen demand of runoff from animal-growing areas are substantial, and much greater than municipal sources. Oxygen depletion from decomposition

has caused major fish kills (Robbins et al. 1971). Winterkills are "one of the most widespread catastrophes to befall shallow northern waters" (Threinen 1970), therefore, they have been a focus of considerable research (Schneberger 1970). Organic matter with its biological oxygen demand, either produced *in situ* or from allochthonous sources carried to lakes and ponds by runoff, is the major problem causing oxygen depletion.

SECTION IV

CRITICAL REPRODUCTIVE PERIODS

INTRODUCTION

Numerous ichthyofaunistic surveys have been carried out, followed by data comparison with earlier, similar studies done in the same areas (Cross 1967, Durham and Whitley 1971, Larimore and Smith 1963, Trautman 1957). Based on these comparative data, inferences have been drawn on the causes of species disappearance. Often increased suspended and sedimented solids are cited as causes of species composition changes. Examples are probably available for most states, but to illustrate the nature of this type of data base, the report by Durham and Whitley (1971) is used. They compared the stream fish fauna in Coles County, Illinois found in their 1967-1970 collection with an earlier study of Hankinson (1913). Their comparison showed that five species, found in the earlier study (presumably indigenous species which were intolerant to substantial water quality change) were not found in the recent collections. They concluded: "Many of these changes can be attributed to change in land usage and greater siltation occurring in the streams." However, the authors also cite many other recent types of water quality change including additions of fertilizers, insecticides, herbicides, domestic sewage, and industrial wastes. This report is indicative of the circumstantial nature of our "sediment effects" information base.

To adequately assess the impact of sediment and suspended solids (or any other environmental variable or stressor) on fish reproductive success, all phases of the reproductive cycle must be examined. Those particular aspects that are critical to overall spawning success and that are most sensitive to the particular environmental alteration in question need to be identified. Failure of any one important link in the cycle can have a major impact on the success of a particular year class. We have attempted to evaluate, through a review of the available literature, the sensitivity of each life period to the effects of suspended solids and sediment in warmwater, freshwater ecosystems. For each life stage, potential direct and indirect effects are considered and discussed. Observations and experimental results derived from studies on coldwater, estuarine and marine species are occasionally included in order to introduce findings which may apply to warmwater, freshwater forms.

GONAD MATURATION AND FECUNDITY*

Gonadal development generally is a very complex physiological process of long duration, whereas actual spawning, involving the release and fertilization of ova, often is limited to a relatively brief period of time (June 1977, Schwassmann 1971). The factors involved in the process of gonad maturation have been extensively investigated (deVlaming 1972, 1974; deVlaming et al. 1978, Hoar 1969, Peter and Hontela 1978, Schreck and Scanlon 1977), yet many aspects are still not understood.

Spawning seasons of fish are adjusted in time to a particular phase of the seasonal cycle which is suitable for rearing of the offspring. Schwassmann (1971) suggested that the entire annual sexual cycle is subject to synchronization by external factors. deVlaming (1974) pointed out that among the teleosts there is evidence that temperature, photoperiod, food availability, salinity changes and environmental flooding can activate neuroendocrine centers which regulate reproductive cycling. Thus, the endocrine system of fish can translate environmental cues into biochemical cues which activate and maintain reproductive organs. Environmental alteration that interferes in some way with overall endocrine system functions may have important implications in reproductive functions. Fish endocrinology has received a great deal of attention recently as seen in the reviews of that subject (deVlaming 1972, 1974; Fontaine 1976, Hoar and Randall 1969 [volumes II and III], Donaldson 1973, Schreck and Scanlon 1977).

In addition to investigations directed at reproductive endocrinology, an interest in the role of the endocrine system in the response of fish to stress is also apparent. Beginning with the hypotheses of Selye (1950, 1976), Christian (1975), and Christian and Davis (1964), investigators have sought to discover the full extent of the effects of environmental stressors on the behavior, physiology and biochemistry of organisms. Donaldson and Dye (1975), Mazeaud et al. (1977), Schreck and Lorz (1978), Schreck and Scanlon (1977) and Strange et al. (1977) have demonstrated that a variety of stressors cause measurable stress reactions, as determined by secretion of hormones (primarily corticoids and catecholamines), in fish. These primary effects of stress may have widespread secondary effects (Mazeaud et al. 1977) including potential impacts on reproductive success (Bagenal 1969, Christian 1975, Kipling and Frost 1969). Many environmental stressors have been shown to have a negative impact on reproduction but the exact mechanisms for these effects and whether the endocrine system is directly involved have not been determined (Brungs et al. 1978 and previous annual literature reviews in the June issues of the Journal of the Water Pollution Control Federation). Nonetheless, extracting information from a widely dispersed literature, a potential involvement of endocrine disfunction in reproductive failure brought on by diverse environmental alterations is indicated.

The literature provides very few clues on the effects of suspended solids on gonad maturation and fecundity in warmwater fish. However, a hierarchy of potential effects can be outlined and supportive evidence for each sought in the literature.

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* By Gary J. Atchison

Lethal Effects

Several authors have indicated that adult fish can die as a direct result of exposure to elevated suspended solid levels (Cairns 1968, Trautman 1957, Wallen 1951a). For such a direct effect, generally gill passages must be clogged to the extent that fish suffocate. Wallen (1951a) concluded from his experimental evidence that direct mortality due to montmorillonite clay suspensions was not likely to occur at the levels found in nature. In his experiments, most fish survived for at least one week at concentrations of clay below 100,000 mg/l. Rapid lethal effects did not occur until levels as high as about 175,000 mg/l were reached. Pumpkinseed sunfish (*Lepomis gibbosus*) seemed to be the least tolerant of the 16 species tested with an average fatal suspended clay level of 69,000 mg/l. Cairns (1968) pointed out that some rivers in Kansas carried suspended solid loads in excess of 70,000 mg/l yet supported rather diverse fish faunas. He did not comment on whether these species formed a community similar to the one historically occurring in those rivers. As Trautman (1957) clearly pointed out, species of fish are quite variable in their tolerance to suspended solids.

Good experimental evidence has not been reported supporting direct mortality due to suspended solids as a critical factor in the adult stage of warmwater fish. Only circumstantial evidence is currently available.

Suspended solids may, however, contribute indirectly to adult mortality through a reduced resistance to disease (European Inland Fishery Advisory Commission 1965). Herbert and Merkens (1961) found that concentrations of 207 mg/l diatomaceous earth caused an increase in the incidence of fin rot in rainbow trout (*Salmo gairdneri*). Cairns (1968) suggested that the sloughing off of mucus associated with high levels of suspended solids may expose the epithelium of fish, resulting in an increased incidence of parasitism. He presented no evidence in support of this contention.

Resistance to disease is a function of the physiological state of a fish and if biochemical defenses have been depleted by the reaction of the fish to another stressor, disease defense is greatly lessened (Wedemeyer 1970). Selye (1950) defined stress as the sum of all the physiological responses by which an animal tries to maintain or re-establish a normal metabolism in the face of a physical or chemical force. Suspended solids are a stressor and may elicite a stress response from fish. Many other environmental stressors have been implicated in causing increased incidences of disease including the following: low dissolved oxygen, changing temperature, metabolic waste build-up, crowding, industrial wastes, and pesticides (Haley et al. 1967, Meyer 1970, Snieszko 1974). Meyer (1970) also pointed out that handling and reproduction can elicite stress responses and increase susceptibility to disease.

Again, the role of suspended solids in reducing disease resistance is only weakly supported by experimental evidence yet its potential role cannot be discounted entirely.

Sublethal Effects

Sublethal effects of suspended solids are probably of greater long term significance to adult fish in sustaining populations than is adult mortality. Maturation may be blocked entirely or only delayed depending on the extent of suspended solids loading. If fish mature, fecundity may be reduced. Any of these sublethal impacts could have long term detrimental effects on fish populations. No experimental evidence was found in the literature directly implicating suspended solids as a cause of any of the effects suggested above; only circumstantial evidence is available. Decreased light penetration into water or decreased food availability and growth due to suspended solids may indirectly contribute to these sublethal effects.

Light Penetration

A growing body of evidence supports the role of photoperiod in hormone production and maturation of gonads in fish (deVlaming 1972, 1974, 1975; Vodicnik et al. 1978). However, little emphasis has been placed on the role of light intensity on gonad maturation. An extensive literature exists demonstrating that suspended solids can reduce light penetration, and therefore, reduce intensity at greater water depths, to the extent that photosynthesis can be reduced or eliminated (see Section III).

Swingle (1956) provides the only evidence found in the literature suggesting that suspended materials might affect fish reproductive processes by reducing light penetration. He stated it has been repeatedly noted that largemouth bass (*Micropterus salmoides*) spawn earlier in clear water than in waters colored by phytoplankton or suspended clay. He found that spawning in muddy ponds had been delayed as much as 30 days in the spring as compared to clear ponds.

No evidence was found to suggest that light penetration blocks maturation of gonads or reduces fecundity.

Feeding and Growth

One of the well documented ecosystem effects of suspended solids and sediments is the negative impact on food available to fish (see Section III).

Doudoroff (1976) suggested that an environmental stressor might reduce available food to the extent that all the energy and materials in the food consumed by fish would be needed for maintenance of normal activity and other body functions, leaving insufficient energy and materials for growth and reproduction. Bulkley (1975) found that high suspended solids reduced available food for largemouth bass to the extent that growth of maturing fish was reduced enough that they were physically incapable of reproduction. Buck (1956) found that fish growth was better in clear ponds than ponds with elevated suspended solids. He stated that largemouth bass was the species most affected.

Even if food is available, suspended solids may create problems for fish in locating that food. Vinyard and O'Brien (1976) demonstrated that the reactive distance of bluegill to Daphnia was significantly affected by increased turbidity (produced by suspended clay) and reduced light intensities. At high turbidities (about 30 JTU) the reactive distance became nearly independent of prey size. A 50% reduction in reactive distance reduced the actual volume of water searched by a factor of 4 to 8 depending on assumptions of searching patterns. Therefore, in turbid waters, a bluegill must search a much greater volume of water in a given time compared to clear water to obtain an equal amount of food, providing that food density is equal in the two situations. When this finding is compared with the data presented by Heimstra et al. (1969) the effect of suspended solids on sunfish feeding becomes potentially even greater. They found that juvenile largemouth bass and green sunfish (Lepomis cyanellus) exposed to "silt" turbidity tended to reduce their activity levels. Their highest turbidity levels were only 14-16 JTU, much below levels often found in nature. This reduction in activity coupled with the reduced reactive distance places these sight feeders at an even greater disadvantage under conditions of high suspended solids. Others have supported the contention that predators find it more difficult to obtain food in turbid waters (Cross 1967, Ginetz and Larkin 1976, McKee and Wolf 1963, Ritchie 1972).

The decreased ability of fish to obtain an adequate food supply, of course, has implications in growth processes. Many studies have indicated that food intake and growth can affect many aspects of the reproductive cycle, including age at maturity, timing of gonad maturation, fecundity and whether or not spawning occurs at all.

LeCren (1965) emphasized that maturation in fish is a function of size rather than age and that fish with high growth rates mature earlier than slower growing fish. He also found that the fat content of eggs and subsequent size of the 0 age fish varied with feeding conditions for the females over the previous year. Nikolsky (1963) pointed out that reduced food supply can cause a retardation of growth, later onset of maturity, an extension in the size range of the first-time spawners and a reduction in the fecundity of fish of the same size.

Wootton (1973) showed that decreased food ration decreased the percentage of female three-spined stickleback (Gasterosteus aculeatus) that matured, their weight at maturity, the average number and weight of eggs per spawning and increased the interval of time between spawnings. Scott (1962) demonstrated that variations in egg numbers in rainbow trout were attributable to fish size, egg size and adequacy of diet. Lack of food lowered the rate of maturation and fecundity and caused atresia and resorption of eggs.

Bagenal (1969) showed that brown trout (Salmo trutta) that had more adequate diets grew faster, had higher water content in their eggs indicating earlier spawning times, had more and smaller eggs and had a higher percentage of matured eggs. He suggested that stress due to food competition leads to lower fecundity through altered endocrine activity.

Alm (1954) showed that perch (Perca fluviatilus) under less crowded conditions, and thus more adequate diet, grew better and matured earlier than fish under crowded conditions. Wilkins (1967) demonstrated reduced spawning in herring (Clupea harengus) brought on by emaciation and lack of food.

deVlaming (1971) found that food deprivation induced gonadal regression in a relatively short period of time in gobiid fish (Gillichthys mirabilis) which were in phases of active gametogenesis. Clemens and Reed (1967) reported that goldfish (Carassius auratus) testes could be regressed through diet limitation.

The evidence suggests that suspended solids, through effects on food availability and subsequent reduced fish growth, could indirectly affect several aspects of maturation and fecundity in fish. The long term effects of changes in maturation or fecundity on fish population are dependent on a complex set of population and environmental conditions. Doudoroff (1976) suggested that a moderate reduction in the role of reproduction could actually result in an increase in fish production as fewer young are produced to compete for the same, limited food supply. He pointed out that natural production of young is generally more than sufficient for full utilization of the available habitat and food resources. However, based on current knowledge, we have only limited abilities to judge when a decline in reproduction of warmwater species is moderate and when it is severe. Often this is not discovered until populations have declined significantly, at times to extinction.

In some cases where maturation of gonads does occur, spawning is blocked and mature ova are reabsorbed by the female. The exact causes of atresia and resorption have not been identified nor have elevated levels of suspended solids been implicated.

LeCren (1965) found that after severe winters fish may not shed eggs that had matured. June (1977) found for many species that atresia and resorption of eggs were high due to unsuitable spawning conditions that developed at times in a reservoir. Il'ina and Gordeyev (1970) reported that a good indicator of the lack of suitable spawning substrate for several species of fish in a reservoir was an increase in the percentage of females with eggs undergoing resorption. Suspended solids were not discussed in these studies.

Starrett (1951) suggested that the combination of floods and heavy "silt" loads can be an important limiting factor for minnows and other species; that they cause an elimination of possible spawning sites which may postpone spawning or result in the resorption of eggs and a disinclination to spawn. Again, mainly circumstantial evidence suggests that suspended solids can block spawning and thus be a critical factor in the adult stages of the reproductive cycle.

Generalized Stress Reaction

One fact that becomes apparent in searching the literature on environmental variables controlling fish reproduction is that many diverse chemical, physical and biological factors can act in a negative way to influence maturation and fecundity. Many authors discuss the stress associated with certain environmental variables including crowding, food availability, toxic substances, oxygen depletion, temperature, and to a limited extent suspended solids. The role of stress in disease resistance has been discussed above.

Only limited experimentation has occurred on stress reactions of fish to suspended solids. Certain behavior patterns can be used as indicators of stress. Elevated suspended solids levels can cause effects on the respiratory system of fish eliciting coughing (Bulkley 1975, Heimstra et al. 1969) and increased ventilation rates (Horkel and Pearson 1976). Cairns (1968) suggested that suspended solids can damage fish gills and result in widespread metabolic effects.

Mazeaud et al. (1977) pointed out that diverse biochemical and physiological effects in fish are caused by a variety of environmental stressors. These effects included the primary response of increased corticosteroids and catecholamines which generate such secondary effects as immunosuppression, declines in white blood cells, muscle protein, liver glycogen, and melanocytes and increases in blood glucose, blood lactate, heart rate and gill blood flow. Even stress reactions due to social interactions produce at least some of these changes (Erickson 1967, Noakes and Leatherland 1977).

Others have suggested that an additional and important secondary effect of the stress reaction is a reduction in endocrine activities associated with reproduction as other hormones are preferentially mobilized to confront the stressor (Bagenal 1969, Christian 1975). This area of research is only now developing and no studies have been reported dealing with suspended solids associated stress reactions and their impact on reproduction. Future research on this subject should be rewarding.

Conclusions

Several potential effects of suspended solids on gonad development in fish were reviewed but only limited circumstantial evidence was found in the literature that would elevate any one potential effect to a real effect. However, to conclude that suspended solids do not limit maturation or fecundity may be premature since the subject has not been adequately investigated.

REPRODUCTIVE BEHAVIOR*

Introduction

The reproductive behavior of the temperate, warmwater ichthyofauna is enormously complex, and the literature on the subject is widely scattered. To date, no single review has adequately related the major reproductive patterns to ecological interrelationships within the warmwater community. In attempting to assess the impact of turbidity and sedimentation on reproductive behavior, therefore, it has been necessary initially to identify the major behavioral components, discuss their general adaptive significance, and finally to characterize the fauna accordingly. The organization of this review has been primarily influenced by Breder and Rosen's (1966) monumental account of the Modes of Reproduction in Fishes and by Balon's (1975) recent proposal of reproductive guilds of fishes. Tables 1 - 4 summarize the major elements of reproductive behavior among most native warmwater families of the U.S. and Canada. Several families were excluded from these tables because of insufficient information (cavefishes), their failure to reproduce in freshwater (freshwater eels), or their only peripheral occurrence in U.S. or Canadian waters (characins and cichlids). All salmoniform families, the burbot and sculpins have been regarded as coldwater forms in terms of their reproductive behavior although some species exist in warmwater communities as well. Usage of common and scientific names follows Bailey et al. (1970). There has been no attempt to cover introduced groups or to survey the non-North American fauna or literature.

Detailed information on reproductive behavior was obtained from numerous sources, and it would serve little purpose to cite all references here. A number, however, deserve mention for their broad utility. Breder and Rosen (1966) remains the single most comprehensive treatment of the subject. Several regional ichthyofaunistic studies also provided valuable species accounts: Cross (1967) - Kansas; Eddy and Underhill (1974) - Upper Mississippi Valley; Moyle (1976) - California; Scott and Crossman (1973) - Canada; and Trautman (1957) - Ohio. Carlander (1969, 1977) was another useful source of summary information. The data base is weakest for warmwater fishes of the Intermountain West and the Pacific Slope but this reflects the general paucity of information on western species.

In a brief review such as this which attempts to cover a large and diversified fauna, it is not possible to provide detailed taxonomic accounts even at the family level. Thus in the material that follows, behavioral characteristics of families are condensed into brief phrases or included in large topical categories. These descriptions should be regarded as representing only the most typical or widespread conditions among the various groups. Particularly among the larger families, a great variety of reproductive behaviors has evolved in response to ecological niche specialization.

There is only a small body of literature providing direct evidence on the impact of turbidity and sedimentation upon reproductive behavior. Most accounts are observations of an incidental nature, and therefore subject to

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individual interpretation. Experimental evidence is almost entirely lacking. There is substantial indirect evidence contained in regional faunal analyses which associate changes in community composition with historical environmental alterations. Although some authors of such studies hold strong opinions on the ecological impact of turbidity and sedimentation on fish populations, it is often difficult to separate this factor from other forms of environmental change. Even in cases clearly implicating suspended solids and sediments, it may not be a simple matter to identify the affected life history stages. Nevertheless, when a number of investigators independently make similar observations in nature and reach similar conclusions on this question, the strength of their combined opinions is considerable. For the most part, the present review concentrates on families and ecological groups of warmwater fishes but tables in Section VI focus on the tolerances of individual species.

Reproductive Timing

With few exceptions, the spawning seasons of temperate, warmwater fishes are definable in timing and duration, most commonly occurring under lengthening day and warming conditions. Efforts to precisely define the spawning seasons of the various species are complicated, however, by the extent of climatic variation within their respective geographical ranges. Thus among widespread forms, the spawning period can be characterized only rather imprecisely according to general stages of seasonal progression, as in Table 1. While a more accurate definition might be achieved employing temperature criteria, reliable data on thermal requirements for reproduction are available for relatively few species. Because hydrological factors also have an important bearing on reproductive success, local and regional timing adjustments are often encountered as well. In warmwater fluvial environments, especially, peak annual sediment loads frequently coincide with and significantly affect reproductive activities. In the material that follows, therefore, an effort has been made to distinguish the several major patterns of reproductive timing among warmwater fishes and to explain their ecological significance.

Recently the term "coolwater" has been applied in reference to a variety of northern fishes to emphasize their ecological intermediacy between the mass of warmwater species, on the one hand, and coldwater fishes on the other. Comprised of the pikes (Esocidae) and perches (Percinae), the coolwater group is of great importance to northern fisheries. In general, the coolwater community spawns during a brief interval in early spring (Table 1) under conditions of low but slowly rising temperatures, meltwater elevated water levels, and seasonally low turbidity. As a group, coolwater forms are intolerant of elevated temperature, turbidity and siltation during their reproductive and early life history stages, as documented throughout this report. Their strategy of early spring spawning, therefore, is adaptive through avoidance of deleterious environmental conditions that often follow later in spring, particularly in more eutrophic waters. A similar reproductive strategy is practiced by a small group of "pioneer" fishes which are especially well adapted to the harsh, unstable environments of small northern headwater streams. Among typical species such as the stoneroller (*Campostoma anomalum*), creek chub (*Semotilus atromaculatus*), and orangethroat darter (*Etheostoma spectabile*), reproductive success is keyed to completion of spawning activities prior to late spring rains and ensuing conditions of high, often muddy waters (Cross 1967).

TABLE 1. PATTERNS OF REPRODUCTIVE TIMING AND MOVEMENTS AMONG WARMWATER FISHES.

Family	Spawning Season	Duration of Season	Movement
Petromyzontidae	Late spring	Brief	Upstream to tributaries
Acipenseridae	Early to late spring	Brief	Upstream, often extensive
Polyodontidae	Late spring	Brief	To shoal areas within large rivers
Lepisosteidae	Late spring	Brief	Inshore to weedy places
Amiidae	Late spring	Brief	Inshore to weedy places
Clupeidae	Late spring	Brief	Some anadromy
Hiodontidae	Late spring	Brief	Inshore?
Umbridae	Late spring	Brief	Limited movement to streams, ponds, marshes
Esocidae	Early to late spring	Brief	Inshore to flooded areas
Cyprinidae	Primarily early to late spring, some in summer	Brief for most, protracted for some	Upstream among fluviatile species, inshore movement among others
Catostomidae	Early to late spring	Brief	Upstream in many
Ictaluridae	Late spring to summer	Usually brief, protracted for some	None or limited inshore movement
Aphredoderidae	Early spring	Brief?	Not known
Percopsidae	Late spring	Brief	Limited upstream or inshore movement
Cyprinodontidae	Late spring to summer, perhaps year-around in some	Extended	Very limited, if any
Poeciliidae	Most warmer months?	Extended	Very limited, if any
Atherinidae	Late spring & summer	Probably brief	Not known
Gasterosteidae	Late spring & summer	Extended	None or very limited
Percichthyidae	Late spring	Brief	Inshore, some anadromy
Centrarchidae	Late spring & summer	Brief to extended	Inshore
Percidae			
Etheostomatinae	Early to late spring	Brief	To shallow water
Percinae	Early spring	Brief	To shallow water
Sciaenidae	Late spring to summer	Often lengthy	Not known

Although the unstable, mineral laden, turbid warmwaters of the Western Plains and Intermountain regions have presented inhospitable habitat for most fishes throughout geologically Recent time, to the well-watered East favorable conditions prevailed in most warmwater habitats until the settlement period. Meek (1892), for example, described Iowa prairie streams in their original condition as being narrow, deep, clear, hard bottomed, and remarkably constant in flow throughout the year owing to the capacity of the dense prairie soil and numerous marshes of the region to retain meltwater and rain, filter it, and then slowly release it to the streams. Trautman (1957) described the native condition of streams in the Eastern Deciduous Forest Formation in similar terms, noting that turbid conditions occurred only briefly during freshets and floods and that stream bottoms were largely free of sediment. Given these highly favorable habitat conditions, the majority of the warmwater riverine fishes of eastern North America have focused their reproductive activities into brief intervals during the late spring to early summer rainy season (Table 1). In the native state, vernal rains were an essential component to the reproduction of many species, providing a stimulus for migrations, creating suitable spawning habitat through flooding and by clearing channel bottom areas, maintaining sufficient flow for egg development, etc. Because high levels of turbidity and sedimentation were relatively ephemeral and otherwise inconsequential, most species evolved only scant tolerance to these factors with respect to their reproductive activities. Subsequently, under present conditions of widespread habitat degeneration through siltation, this group has been the most severely decimated by reproductive failure. In many altered river systems today, reproductive success or failure among these fishes may be largely fortuitous, hinging upon the coincidence of spawning and flooding cycles. This was demonstrated by Starrett's (1951) observation of a consistent pattern of unsuccessful spawning among late spring - early summer spawning minnows in the Des Moines River, Iowa, a medium-sized prairie river. The river carries a heavy silt load throughout much of the year and particularly during the rapid rises in water level that accompany spring rains. Although the cause of the reproductive failure was not directly identified, it was suggested that smothering of eggs by silt, turbidity-reduced food supply for the young, and actual downstream displacement of eggs and fry all were contributing factors. It is noteworthy that in local tributaries of the river, several of the species enjoyed considerably greater reproductive success (Starrett 1950), perhaps as result of the more moderate and temporary impact of high waters in the smaller, relatively undisturbed streams.

Within erratically fluctuating environments, the potential for catastrophic reproductive loss is always present, demanding compensatory strategy on the part of resident populations. Among a variety of fishes living in the unstable streams of the Plains and Gulf Coastal regions, the problem is approached through extension of the reproductive period over much of the warm season. Within this lengthy period, spawning may occur more or less continuously, at relatively discrete intervals, or intermittently as environmental conditions allow. In some cases males are reproductively active for much or all of the period, and females may produce several egg clutches per season. Although this strategy is practiced by some relatively long-lived species, it is most appropriate and commonly employed among the small short-lived minnows, killifishes, and certain darters (Table 1). Examples among minnows are provided in Starrett (1951), Heins and Bresnick (1975), and Heins and Clemmer (1976). Cross (1967) gave additional examples from among a wide variety of Kansas fishes. Not uncommonly, such fishes also exhibit considerable tolerance to

turbidity and sediment in all life history stages. The reproductive superiority and ecological hardiness of these fishes have served them well in recent time, permitting many to expand their distributional ranges and assume greater community significance as general habitat deterioration has progressed. Larimore and Smith (1963) and Smith (1971) have documented this phenomenon in Illinois streams. Among the newly dominant species in that area are a number which have origins in turbid Plains streams to the west.

Owing perhaps to the slower seasonal rate of warming lentic environments, various pond and lake fishes also exhibit long spawning periods. Among the popular game species, sunfish (Lepomis spp.), crappies (Pomoxis spp.) and bullheads (Ictalurus spp.) are notable for this behavior. As a result of of their high reproductive potential and considerable tolerance to turbidity and sediment (see Section VI Table 8), populations in muddy ponds can become stunted because of turbidity reduced predation and food resources (Cross 1967).

Reproductive Movements

Numerous warmwater fishes engage in extensive reproductive migrations or at least local movements from deeper wintertime habitats to shallow spawning sites (Tables 1, 2). Any barrier to their free movement could detrimentally affect reproductive success. The concern that zones of high turbidity might present such a barrier was reviewed by the European Inland Fisheries Advisory Commission (EIFAC 1965). With reference to anadromous species, the Commission concluded that even quite high concentrations of suspended solids in rivers do not interfere with salmonid migrations although any available clear water routes may be preferentially utilized over muddier travelways. The report did not, however, comment on warmwater anadromous fishes, and neither is there such information in Morton's (1977) extensive review on the ecological effects of dredging in estuaries. At least several warmwater American anadromous fishes, e.g. American shad (Alosa sapidissima) and striped bass (Morone saxatilis), regularly traverse highly turbid tidal waters during their ascent into spawning streams.

There is scarcely more evidence to suggest that limited turbid zones act as a significant barrier to strictly freshwater reproductive movements of fishes. EIFAC (1965) cited Hofbauer (1963) as reporting that migration of the European barbel (Barbus fluviatilis) diminished with increasing turbidity at a fish ladder but that catadromous movements of the European eel (Anguilla anguilla) were aided by turbid water. Other direct observations indicating a barrier effect of turbidity upon reproductive movements of warmwater fishes have not been found during this review. Field observations made outside of the reproductive season or laboratory behavioral experiments should be addressed to this question only with great caution.

Spawning Habitat

Just as proper timing is often crucial to the reproductive fortunes of warmwater fishes, spawning activities must also be performed amidst habitat conditions conducive to mating and early development. Availability of proper spawning habitat thus represents the next critical element of the reproductive

TABLE 2. SPAWNING HABITATS AND PATTERNS OF PRE-SPAWNING BEHAVIOR AMONG WARMWATER FISHES.

Family	Spawning Habitat	Pre-spawning Associations	Territoriality and Site Preparation
Petromyzontidae	Riffles in streams	Both sexes aggregate on spawning site	No territoriality, pairs excavate depression nests
Acipenseridae	Turbulent, rocky channels of large rivers	Not known	Presumably none
Polyodontidae	Swift areas of large rivers	Not known	Presumably none
Lepisosteidae	Heavily vegetated quiet waters	Probably massing of entire population	None
Amiidae	Weedy sheltered shallows	Males probably arrive at site first	Males territorial, clear nest area among plants
Clupeidae	Open areas in lakes, shoals of larger rivers	Probably schooling of entire population	None
Hiodontidae	Open areas in lakes & larger rivers	Presumably schooling of entire population	None
Umbridae	Quiet weedy areas in marshes, ponds, streams	Not known	Probably not well developed
Esocidae	Weedy sloughs & flooded areas	Small aggregates of both sexes	None
Cyprinidae	Primarily in shallow streams, some in weedy areas of lakes	Males often arrive at site first, sexes may remain isolated until actual time of spawning	Territoriality & construction of depression or gravel mound nests by males common
Catostomidae	Similar to cyprinids	Close aggregation of entire population	No site preparation, limited male territoriality
Ictaluridae	Hard & soft bottoms of streams, swamps, lakes	None ?	Pairs or just males territorial, use cavity nests
Aphredoderidae	Streams	Not known	Not known
Percopsidae	Streams & lakes	Not known	Not known
Cyprinodontidae	Quiet weedy areas in streams, ponds	Small loose groups of both sexes	Limited male territoriality, some depression nest construction

TABLE 2. Continued --

Family	Spawning Habitat	Pre-spawning Associations	Territoriality and Site Preparation
Poeciliidae	Quiet weedy areas in streams, ponds, marshes	None apart from regular small social units	None
Atherinidae	Ponds, pools in streams	Males swarm, sexes segregated until spawning act	None
Gasterosteidae	Marshes, pools & back-waters of streams	Females may school	Males territorial, build nest of vegetation
Percichthyidae	Ponds, slower rivers	Schooling of entire population	None
Centrarchidae	Shallow lakes & streams	Males arrive at site first, colonial nest-ing in some	Males territorial, excavate & guard depression nests
Percidae			
Etheostomatinae	Shallows of streams	Some river species form separate male & female groups	Males territorial, many prepare cavity nests
Percinae	Shallow areas in lakes and rivers	Aggregations of both sexes or males alone	None
Sciaenidae	Lakes	Presumably schooling of entire population	None

process. For a given species, spawning habitat requirements are often stringent involving a complex combination of proper conditions of water (quality, flow, temperature, transparency), substrate, and special features, e.g. vegetation. A general survey shows, however, that among a preponderance of the regional warmwater species, spawning occurs primarily in shallow water habitats: riffle areas of streams, shoals of rivers and lakes, quiet sloughs, marshes and flooded areas, etc. (Tables 1, 2).

Balon's (1975) definition of reproductive guilds among fishes emphasizes the ecological significance of spawning substrate among oviparous species. Using the terminology of that system, several major ecological groups may be recognized among warmwater fishes on the basis of the site of egg deposition. Lithophilous species deposit their eggs on a rock or gravel bottom and utilize the substrate for concealment and early development of the young. As a group, lithophil embryos bear only moderately developed respiratory organs and, therefore, require well oxygenated water. Prominent regional warmwater lithophils are the lampreys, minnows, suckers, sunfishes, perches and many catfishes (Table 3). Some deposit eggs on the open substrate while others prepare a nest of some fashion. Phytophils, which attach their eggs to living or dead plants, are also well represented. Characteristically, phytophil embryos bear highly developed respiratory structures enabling them to survive conditions of low oxygen. The more open exposure of many, however, subjects them to greater predation than the concealed young of lithophils. Warmwater examples are the gars, mudminnows, and pikes especially, along with various minnows, suckers, killifishes, sunfishes, and darters (Table 3). An ecologically intermediate group, the phyto-lithophils, may also be recognized from among a variety of families. Speleophils deposit their spawn in natural holes and cavities or in specially constructed burrows. Some minnows, various catfishes and darters comprise this group. In virtually all cases, parents guard the nest and provide a flow of water over the eggs in some fashion. Several poorly represented groups and examples of each are: the psammophils, which spawn on sandy stream bottoms (some minnows, suckers and darters); the open water spawning pelagophils with bouyant eggs (freshwater drum); and the litho-pelagophils which deposit eggs on rocks but have bouyant embryos and larvae (some sturgeons, mooneye, herrings and temperate basses).

Although Balon's guild concept emphasizes two salient considerations of survival, predation and availability of oxygen, ecological complexities are such that the system may have broad inferential utility. Several observations may be made, for example, with reference to the tolerance of various substrate users to high levels of turbidity and sediment. Among the fishes which most benefit from such conditions are pelagophils and litho-pelagophils which are largely unaffected by bottom siltation and enjoy reduced susceptibility to predation in turbid waters. At the opposite extreme, the least tolerant species tend to be the open substrate spawning lithophils which are vulnerable to direct loss of spawning habitat and to suffocation of early developmental stages through siltation. Several regional ichthyofaunistic studies identify siltation of spawning habitat as a major contributor to recent decimation of warmwater fish populations in midwestern states (Cross 1967, Smith 1971, Smith et al. 1973, Trautman 1957). The same authors note that numerous phytophils have also suffered widespread loss of spawning habitat (aquatic vegetation) due to increasing turbidity. Speleophils may lose cavity nest sites to sediment as well (Gale and Gale 1976). At least moderate sediment deposits can be cleared

TABLE 3. PATTERNS OF MATING AND EGG DEPOSITION AMONG WARMWATER FISHES.

Family	Mating Groups	Courtship	Egg Deposition
Petromyzontidae	Pairing, both sexes polygamous	None	In sand-gravel nests
Acipenseridae	Not known	Not known	Over gravel-rock bottom
Polyodontidae	Small polyandrous groups	Not known	Over sand-gravel bars
Lepisosteidae	Pairing, or small polyandrous groups	Not known	On vegetation
Amiidae	Pairing, both sexes polygamous	Complex	On bottom of nest in vegetation
Clupeidae	Pairing, or polyandry within schools	Probably none	Pelagic or over variable bottom
Hiodontidae	Small polyandrous groups?	Not known	Pelagic
Umbridae	Pairing	Not known	In vegetation or scattered randomly
Esocidae	Pairing, or small polyandrous groups	Not known	On vegetation
Cyprinidae	Pairing, or small polyandrous groups	Simple to comolex, display often important	On vegetation or wide variety of bottom types, often buried
Catostomidae	Small polyandrous groups, some pairing	Relatively brief & simple	Over variety of bottom types, most often gravel
Ictaluridae	Pairing, lengthy pair bond in some cases	Complex, tactile & chemical stimuli important	Often in cavities, variable bottom type
Aphredoderidae	Presumably pairing	Not known	In nests
Percopsidae	Presumably pairing	Not known	On sand or hard bottoms
Cyprinodontidae	Pairing, polygamy common	Complex, display elements important	Primarily in vegetation, soft bottoms also used
Poeciliidae	Pairing, both sexes polygamous	Complex, display elements important	Internal in female
Atherinidae	Small polyandrous groups	Not known	In vegetation or on gravel shoals
Gasterosteidae	Pairing, both sexes may be polygamous	Complex, display elements important	In nest of plant materials
Percichthyidae	Small polyandrous groups	Probably simple	Over vegetation or variety of bottoms
Centrarchidae	Pairing, limited polygamy	Complex, display elements important	In depression nests, on vegetation in some
Percidae			
Etheostomatinae	Pairing, limited polyandry	Complex, display elements important	On plants, firm bottom, or in crevices
Percinae	Small polyandrous groups	Simple, mainly pursuit	On plants or firm bottom
Sciaenidae	Not known	Not known	Pelagic

away by many nest preparing species and some are extremely diligent in this effort. Breder and Rosen (1966) cited an example of attempted nest building by male redbreast sunfish (Lepomis auritus), pumpkinseeds, and smallmouth bass (Micropterus dolomieui) in a mud bottomed pond. Some of the fish excavated cavities nearly two feet deep but still failed to expose a hard substrate. No spawning occurred in the pond, perhaps because the males literally dug themselves out of sight. Even when nesting and spawning is possible in silted habitats, however, reproductive success may depend upon continuing parental effort to keep the eggs free of suffocating sediment.

Spawning and Parental Behavior

It is convenient to distinguish two main approaches to spawning among warmwater fishes based on the complexity of their reproductive behavioral patterns. The category of "simple" spawners consists of an ecologically diverse assemblage of fishes that are yet remarkably similar in reproductive behavior: sturgeons, paddlefish, gars, herrings, mooneyes, pikes, some minnows and suckers, silversides, temperate basses, perches (Percinae), freshwater drum, and perhaps some lesser known groups. In general, their reproductive movements and pre-spawning social organization involves aggregation of the entire local breeding population, i.e. free intermingling of both sexes (Table 2). This massing of the population on the spawning site is probably an important stimulus for the final phases of gonadal maturation, and mating units are established from within the aggregate. With few exceptions, simple spawners exhibit little sexual dimorphism beyond distinctions of body size and shape. Sex recognition and mate selection may, therefore, be based largely on behavioral interactions between the sexes. Simple spawners do not defend territories or in any way prepare the spawning substrate for egg deposition (Table 2), except for possible incidental effects of their general activity. A diversity of spawning substrates are utilized, however, with only the psammophilous and speleophilous categories of Balon (1975) not being commonly represented (Table 3). Recognizable courtship behavior is rare among simple spawners, if it exists at all (Table 3). The time of day at which spawning occurs is not known for many species but among sturgeons, herrings, mooneyes, pikes, temperate basses and perches, most spawning activity appears to occur at night. Most frequently, the mating unit consists of a female and a small number of males which briefly emerge from the spawning aggregate, rejoining it following completion of the spawning act (Table 3). None of the simple spawners provide any type of parental care to the developing generation (Table 4).

The behaviorally "complex" spawners may be regarded as the lampreys, bowfin, most minnows, some suckers, catfishes, pirate perch, trout-perches, killifishes, live-bearers, sticklebacks, sunfishes, and darters. Although there is much less behavioral uniformity among this group than among simple spawners, a number of common behavioral themes are apparent. Among many species, the sexes remain largely segregated until the formation of the individual mating units. Males commonly arrive at the spawning grounds first where they either swarm over the area or partition the available habitat into territories (Table 2). Territorial males actively defend against intruding conspecific males and often against other species as well. During the pre-spawning period, females may form loose aggregations in the general vicinity of the spawning site or may move about independently. As among the simple spawners,

TABLE 4. PATTERNS OF PARENTAL CARE AMONG WARMWATER FISHES.

Family	Behavior
Petromyzontidae	None, adults die after spawning
Acipenseridae	None
Polyodontidae	None
Lepisosteidae	None
Amiidae	Male guards nest and larvae
Clupeidae	None
Hiodontidae	None
Umbridae	Eggs guarded primarily by female
Esocidae	None
Cyprinidae	None in most, but in some male guards nest area for extended period
Catostomidae	None
Ictaluridae	One or both parents tend and protect eggs, juveniles guarded in some
Aphredoderidae	Guarding of eggs by both parents
Percopsidae	None
Cyprinodontidae	None in most, but in a few male tends eggs
Poeciliidae	Eggs develop within female, no care after birth
Atherinidae	None
Gasterosteidae	Male guards nest, tends eggs, guards young
Percichthyidae	None
Centrarchidae	Usually male only guards and tends eggs, sometimes guards young
Percidae	
Etheostomatinae	In some, male guards and tends eggs
Percinae	None
Sciaenidae	None

the period of pre-spawning aggregation may be an essential behavioral precursor to the actual mating act. The great majority of complex spawners exhibit some degree of sexual dimorphism, males most commonly assuming bright and distinctive patterns of nuptial coloration for the duration of the spawning period. Display of these color patterns figures significantly in sex recognition, agonistic behavior, and courtship activity.

Complex spawners are chiefly lithophilous in their choice of substrate but there are several prominent groups of phytophils (bowfin, killifishes, sticklebacks) and speleophils (catfishes, various minnows, and darters) (Table 3). Apart from the live-bearers, all major families of complex spawners include species which practice some form of nest construction (Table 2). Usually this is the responsibility of males alone although both sexes may participate among the lampreys and catfishes. The nests of lithophilous species range from areas simply cleared of silt and debris by vigorous swimming and fin fanning, to more complex structures involving extensive rock moving efforts. Various minnows and sunfishes construct depression nests by removing rocks with their mouths or by caudal vibrations. Others construct rock pile nests. The gravel nests of some species additionally provide spawning substrate for many non-nesting fishes. Open substrate lithophils are represented primarily by minnows, suckers, and darters. Speleophils typically utilize natural rock cavities and crevices, often establishing the nest area by fanning away sediment. Some catfishes can use burrows of aquatic mammals or excavate nests in soft bottoms. The phytophil sticklebacks and bowfin construct nests of plant material while most killifishes attach their eggs to the open surfaces of plants.

Distinct pair formation is the common mating unit among complex spawners, although small polyandrous mating groups may also form (Table 3). The pair bond is typically brief, females being chased from, or voluntarily leaving, the nest site immediately after egg deposition. Some catfishes, however, maintain rather long term mating associations. Pair formation is often preceded by elaborate courtship behavior in all families except the lampreys (Table 3). In many species courtship involves a prominent visual component, males displaying to females for purposes of sexual arousal and direction to the nest site. In general, species exhibiting pronounced sexual dimorphism and complex courtship behavior mate during the day (minnows, killifishes, live-bearers, sticklebacks, sunfishes, and some darters) while fishes relying more heavily on tactile and chemical communication between the sexes spawn more frequently at night (bowfin, suckers, catfishes, and other darters).

Several groups of complex spawners are notable for their guarding of the nest site after egg deposition and their direct care of the eggs and larvae. Guarding is directed against any potential predator that enters the vicinity of the nest and is often ferocious. Males alone usually provide this protection but among certain catfishes and the pirate perch both parents may participate, while among mudminnows the female guards the eggs (Table 4). Egg tending takes several forms. Various catfishes, killifishes, sticklebacks, sunfishes, and darters provide a flow of oxygenated water over the eggs through vigorous pectoral and caudal fin fanning. A few are known to clean eggs by nipping or mouthing and to remove dead or diseased eggs. Larvae of the bowfin, sticklebacks, catfishes, and sunfishes remain for some time in the vicinity of the nest under the protection of the guarding parent. Among bullhead catfishes especially, the young are guarded until well into the juvenile stage of

development. The survival value of parental care among these fishes can hardly be overemphasized. Numerous observations indicate that unguarded egg clutches and larvae are rapidly consumed by predators, and suffocation due to stagnant water or sedimentation is a common fate of neglected oxygen sensitive embryos.

Within both of these large categories of general spawning behavior, a spectrum of sensitivity to turbidity and sediment exists. Several trends are, nevertheless, apparent within each category. A number of simple spawners, in particular, are notable for their ability to reproduce successfully under highly turbid conditions: herrings, mooneyes, various minnows and suckers, temperate basses, and freshwater drum. Most are late spring spawning lithophils, pelagophils, and litho-pelagophils. The more intolerant forms (sturgeons, paddlefish, gars, pikes, and perches) are early to late spring spawning lithophils, phytophils, and phyto-lithophils. Reasons for the differential tolerances of these two groups of simple spawners have been discussed earlier. In general, complex spawners are rather sensitive to turbidity and sediment during the reproductive process. Within several of the larger families and subfamilies (minnows, catfishes, sunfishes, and darters), there are a number of tolerant and widespread species, however. They tend to be lithophils with long or late spawning seasons; this element of reproductive timing is a major factor in their present ecological success, as mentioned previously.

The remaining question, then, is why are many complex spawners so intolerant of turbid conditions? An explanation may lie in the role of the visual component of spawning behavior. In this regard, it is worth reiterating that the tolerant simple spawners are reproductively most active at night, do not show strong sexual dimorphism, and exhibit relatively simple courtship and mating behaviors that perhaps emphasize tactile communication. On the whole, they do not appear to have a strong visual orientation relative to spawning behavior. In contrast, most complex spawners carry on reproductive activities in daylight, exhibit pronounced sexual dimorphism, and perform courtship behaviors that are mediated primarily by visual stimuli.

The centrarchid sunfishes serve as typical examples of complex spawners and have been well studied because of their widespread distribution and value as game fishes. Breder and Rosen (1966) indicated that intense, direct solar radiation is important for spawning of all species, noting that breeding activity may be drastically reduced even under cloudy skies. Several of the black basses (genus Micropterus) are particularly sensitive to light levels. Miller (1975) expressed the opinion that fluctuations of largemouth bass populations in turbid waters may be due more to the inhibitory effects of turbidity on mating and egg survival than upon any direct effects on juveniles and adults. Chew (1969) observed that in turbid Lake Hollingsworth, Florida, largemouth bass spawning was very limited. Most females failed to shed their eggs and later gradually resorbed them. Other examples of reproductive failure among turbid water populations of this species are provided by Buck (1956), Cross (1967), and Robbins and MacCrimmon (1974). Trautman (1957) stated that smallmouth bass populations in Lake Erie shunned potential spawning areas that were highly turbid. Among Shenandoah River populations of the species, Surber (1969) noted that turbidities must decline to approximately 5-10 JTU before spawning activity will occur in otherwise suitable areas.

Reduced water transparency may, therefore, retard pre-spawning, courtship and mating behavior of visually oriented species. It may also be detrimental to territorial and nesting behavior. Trautman (1957), for example, observed that territorial males of the Tippecanoe darter (Etheostoma tippecanoe) will desert their holdings when stream silt loads increase after storms. Territories may be difficult to establish and defend when turbidity obscures structural features of the bottom. Turbidity may also promote nest desertion in some way. Coutant (1975) reported that wind-caused roiling drove male largemouth bass from their nests, resulting in siltation and suffocation of eggs. Disruption of parental care behavior may well be one of the most serious harmful impacts upon nesting species.

Unfortunately, the problem of assessing the influence of turbidity upon the reproductive behavior of complex spawners is complicated by the considerable degree of ecological diversity that often exists between even closely related species. For example, despite an overall strong similarity in spawning behavior among all species of sunfishes, there is a broad range of reproductive tolerance to turbidity within the family. Madtoms and a number of other catfishes are rather turbidity sensitive, yet some bullheads and channel catfish thrive under turbid conditions, apparently requiring reduced light levels for their reproductive activities (Cross 1967). A detailed behavioral analysis comparing tolerant and intolerant species within families might prove very enlightening.

In summary, it appears that turbidity reduced water transparency does have significant positive and negative impacts on the spawning behavior of warmwater fishes. Among the deleteriously affected species, reduced visual acuity and intraspecific communication is at least one possible explanation for the impact. Another plausible explanation is that species differences in general physiological sensitivity to suspended solids are reflected by their reproductive behavioral responses. As discussed in the previous chapter of this report, extremely high turbidity levels are required to cause direct mortality of warmwater species, but various sublethal effects may occur at much lower levels. Clearly, all aspects of reproductive behavior will be affected if the breeding population fails to attain gonadal maturation at the appropriate time or if serious health problems exist. Perhaps even temporary turbidity induced stresses are sufficient to disrupt reproductive behavior among sensitive species.

Conclusions

There is substantial evidence indicating that the reproductive behavior of warmwater fishes is variously affected by turbidity and sediment relative to the seasonal time of spawning, the place of spawning, and the nature of spawning behavior. Under conditions of increasing sediment loads in all forms of water bodies, the more adaptively successful species include those whose reproductive activities are carried on largely outside of times of highest turbidity. Species which protect their developing eggs from siltation by behavioral or other means have a reproductive advantage over those which afford no such protection. Reproductive failure among many species is also attributable to direct loss of spawning habitat through siltation of formerly clean bottoms and loss of vegetation due to reduction of the photic zone by turbidity. Fishes with complex patterns of reproductive behavior are vulnerable to interference by turbidity and sediment at

a number of critical behavioral phases in the spawning process. Species that have a strong visual component in their spawning behavior are particularly susceptible to such interference. Short term exposure to high levels of turbidity probably does not seriously impede reproductive movements of most warmwater fishes but chronic exposures could produce physiological effects that are disruptive to reproductive behavior.

EMBRYONIC DEVELOPMENT*

Introduction

The literature contains many statements concerning effects of suspended solids upon warmwater fish eggs, but few well-designed studies which document these effects are included. Most information in published reports is peripheral to other questions. Even less information is available on actual concentrations of suspended solids at which lethal or sublethal effects occur.

Resistance to suspended solids depends in part on the spawning habits of the species involved. Certain warmwater fish species are well adapted to turbid water conditions because even though eggs are tiny the location of egg deposition or parental care prevents smothering. In contrast to eggs of salmonids, eggs of most warmwater fish are shed either in the water column and are suspended during incubation, or are cast upon the bottom substrate and vegetation rather than being buried in gravel. Pelagic eggs that float tend to be resistant to suspended solids. For example, Mansueti (1961) contended that the striped bass spawns successfully in silt laden and turbid waters because its eggs and larvae are "pre-adapted" to this environment. Both eggs and larvae are normally suspended. Eggs of walleye (*Stizostedion vitreum*) and other species are adhesive so that the egg adheres to rocks or vegetation above the bottom silt where burying might occur. As mentioned in the previous section on reproductive behavior, certain species spawn successfully even though eggs are deposited on the bottom because the adult fans away settling sediment.

Sediment can harm the warmwater fish egg in various ways. Covering of the egg with sediment can cause physiological damage to the embryo either from anoxia or buildup of metabolic wastes. Abrasion and physical damage to the chorion is also possible. A result of exposure to sediment often not recognized is stress-induced disease (see section on gonad maturation). Rapidly spreading fungus, for example, is common among eggs of certain warmwater fishes exposed to silt turbidity in the hatchery environment. Physical damage of the chorion which allows the fungus spore to become established, and lowered resistance from the smothering effects of the sediment are probably the cause.

Mortality

Most information concerning sediment effects on eggs of different species of warmwater fish relates to direct mortality. Eggs of alewife (*Alosa pseudoharengus*), blueback herring (*Alosa aestivalis*) and American shad tolerated 1000 mg/l suspended solids under laboratory conditions with no increase in mortality (Auld and Schubel 1978).

Although the striped bass is an anadromous species, it has been successfully stocked in warmwater impoundments. Bayless (1967) tested hatching success of striped bass eggs on various substrates. An average of 35.7%

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hatched on coarse sand, 13.1% on silt sand, 3.2% on silt-clay-sand and 0.0% on muck-detritus substrate. He concluded that striped bass eggs need not be suspended for successful hatch, but that suffocation from silt, fungus infection from contact with a contaminated substrate, and perhaps undetected water quality factors around the egg increase mortality when eggs are deposited on unsuitable substrate. In nature, striped bass eggs are suspended in the water column so that sediment would have to be deposited on the egg for similar effects to occur. Evidently, suspended solids in excess of 2300 mg/l is necessary before much sediment adheres to striped bass eggs (Morgan et al. 1973). Hatch of striped bass eggs was not significantly affected by suspended solids from 20 to 2300 mg/l in laboratory studies by Morgan et al. (1973). In contrast, concentrations of 1000 mg/l of natural sediment (1-4 μm) caused significantly lower hatching success of striped bass eggs in experiments by Schubel et al. (1973) and Auld and Schubel (1978), who found no evidence of abnormal egg development in any suspension tested.

Eggs of white perch (Morone americana) which appear relatively tolerant of suspended solids, withstood concentrations of 50 to 5250 mg/l under laboratory conditions without any significant reduction in hatching success (Morgan et al. 1973). Auld and Schubel (1978) reported no effect on white perch eggs from 25 to 500 mg/l, but a statistically significant reduction occurred in percentage hatched when eggs were exposed to 1000 mg/l. The reason for the difference in results from the two studies is unknown because both groups used modifications of the same apparatus for maintaining suspended sediment concentrations.

Natural hatching success of yellow perch (Perca flavescens) was reduced in the Severn River, Maryland, as a result of an increase in soil particles in the water from highway construction and an increase in salinity (Muncy 1962). Hatching success was 65% in test boxes above the construction site where less than 7 mm per day of sediment was deposited 1 foot below the water surface; less than 1% survival occurred below the construction site where up to 30 mm of silt accumulated per day. Mortality was attributed partly to the abrasive effect of the sediment particles (Muncy, personal communication). Schubel et al. (1973) reported that concentrations of 1000 mg/l of natural fine-grained sediment caused a statistically significant increase in mortality of yellow perch eggs, but in a more detailed subsequent study (Auld and Schubel 1978), survival was unaffected at that concentration. Abnormal egg development was not observed in any concentration tested.

Butler (1936) reported serious loss of walleye eggs in the Gull Harbor, Manitoba Hatchery when wind increased the amount of suspended solids in the intake water. Similarly, I observed almost complete mortality of walleye eggs in incubation jars at the Clear Lake, Iowa Hatchery when strong winds resuspended sediment in the lake providing water for the hatchery. Shortly after silt began settling on the eggs, massive outbreaks of fungus occurred and caused high losses. Concentrations of suspended solids were not measured. Johnson (1961) found that incubation of walleye eggs on muck substrate also reduced survival under natural conditions. Survival ranged from 0.6 to 4.5% on mucky substrate vs. 17.5 to 35.7% on gravel bottom. Eggs on a gravel-rubble bottom were less enmeshed in debris and exposed to less scouring by wave action than were eggs resting on sediment.

Eggs of northern pike, Esox lucius, suffered 97% or higher mortality in two Missouri River reservoirs when sediment deposition exceeded 1.0 mm per day (Hassler 1970). At times, sediment deposition under natural conditions exceeded 15 mm during the normal incubation period and completely covered the eggs. Mortalities were lower if pike eggs were covered after the sixth day of incubation. Hatching success of pike eggs at culture stations has been greatly improved by filtering water from a reservoir (Peckham 1968) and a river (Hiner 1961).

Nonlethal Effects on Embryos

Less dramatic than immediate mortality, but equally important, are those responses by the embryo that reduce the chance of survival at later life stages. A review of sublethal effects of environmental stressors on marine fish eggs and larvae by Rosenthal and Alderdice (1976) is equally applicable to warmwater fish. They report potential biochemical, physiological morphological and behavioral effects (Table 5), many of which could result from excessive suspended sediment in the environment.

Although sediment can potentially have various sublethal effects on the developing warmwater fish embryo, few studies have documented specific changes. Morgan et al. (1973) reported that rate of development of striped bass and white perch embryos was reduced and incubation time lengthened when sediment concentrations exceeded 1500 mg/1. Wang and Tatham (1971) found no change in absolute hatching rate (percentage hatch) of eggs of yellow perch, walleye, alewife, striped bass and American shad from laboratory exposure to suspended sediment of 25 to 500 mg/1. Concentrations of 100 to 500 mg/1 delayed hatching of eggs of yellow perch by 6-12 h, white perch and striped bass 4-6 h, and American shad by 4 h. The delay was attributed to reduced light or oxygen from deposition of sediment on the eggs. In contrast, Reis (1969) reported early hatching of eggs of the zebra fish, Brachydanio rerio, from exposure to sedimented inorganic limestone and limestone in suspension.

Inasmuch as a major effect of blanketing of the fish egg with sediment is oxygen deprivation and hypoxic stress, the probable response to sediment for certain species may be determined by examining effects of low concentrations of dissolved oxygen. Reduction in concentration of available oxygen markedly affects many physiological, biochemical and behavioral processes in fish. Altered length of incubation period, reduced size at hatching, developmental deformities can result as well as mortality (Davis 1975).

Eggs of certain warmwater species including channel catfish (Carlson et al. 1974), largemouth bass (Carlson and Siefert 1974), northern pike (Siefert et al. 1973), and walleye (Siefert and Spoor 1974) experienced a delay in initial hatch and in time to 90% hatch from exposure to lowered oxygen saturation. In contrast, completion of hatch of smallmouth bass eggs was accelerated by low dissolved oxygen concentrations (Siefert et al. 1974). White sucker (Catostomus commersoni) embryos also hatched out slightly earlier at 25% saturation than at 50 and 100% (Siefert and Spoor 1974). Length of incubation of white bass eggs was unaffected down to 20% oxygen saturation where significant mortality occurred (Siefert et al. 1974). Although body

Table 5. Summary of some observed responses to environmental alteration considered as sublethal effects. (From Rosenthal and Alderdice, 1976)

Stage of organization where stress is imposed or recognized	Observed or deduced response to stress (altered structure or function)	Observed or suspected consequences of response to stress
Eggs (unfertilized and during fertilization)	Changes in properties of egg membranes, related to surface structure of capsule	Embryonic malformations reduced rates of gas diffusion, respiration changes in osmoregulatory capacity
	water uptake during and after fertilization	changes in buoyancy of pelagic eggs (changes in transport, distribution and location in water column) reproductive success
Embryonic development (early and advanced)	Biochemical effects changes in ATP levels	energy deficit retarded development necrotic tissue dedifferentiation organ malformation
	changes in enzyme activity	Interference with general metabolism and biosynthetic processes retarded development reduced yolk/energy conversion smaller larval size at hatching reduced hatching success
	Physiological effects respiration changes	changes in embryonic growth rates changes in incubation rate
	embryonic heart rate	retarded development
	Morphological effects unusual shape of blastodisc	embryonic malformations(?)
	deformation of blastomeres	embryonic malformations(?)
	irregular cleavage of blastomeres	embryonic malformations(?)
	amorphous embryonic tissue (no definite embryo formed)	no viable hatch
	yolk deformation	impaired yolk utilization, respiration (?)
	yolk-sac blood circulation not well developed	impaired yolk utilization (?) respiration (?)
	organ malformations bent body axis	impaired swimming, feeding, escape reactions
	elongated heart tube	impaired blood circulation (?)
	eye malformations	impaired vision, prey hunting, phototaxis
	malformed otoliths and/or otic capsules	impaired equilibrium, swimming, prey hunting
	Behavioral effects embryonic activity reduced	reduced mixing of perivitelline fluid affecting respiration, distribution of hatching enzyme; retarded development, abnormal hatching process
	pectoral fin movements reduced	as above (embryonic activity)
Larvae at hatching	Altered hatching parameters change in duration of hatching period	altered distribution, altered distribution, density of larvae in time and space
	increased or decreased incubation time	desynchronizing of food availability at time of first feeding
	reduced viable hatch	reduced survival potential at population level
	smaller larval size at hatching	reduced biomass, increased susceptibility to predation

length was not measured at hatching in these experiments, fry of all species except white bass were shorter in length 13-20 days after hatch than were fry held in 100% saturation at egg and fry stage.

Conclusions

Wilson (1960) suggested that sediment can coat the fish egg and interfere with gaseous exchange across membranes. Those species of fish producing adhesive eggs are perhaps not affected by sediment concentrations that merely coat the egg shell, as evidenced by the common practice in fish culture of treating adhesive eggs during water hardening with cornstarch, muck or clay to prevent eggs from sticking together. Embryo survival is not impaired by this practice. However, timing of exposure to sediment may be a factor. Even though embryos may suffer no effect from sediment at water hardening, during later stages of development when oxygen demand is greater, similar concentrations of sediment could be detrimental, as Wilson suggests.

Naturally occurring concentrations of suspended solids and sediment are sometimes sufficiently high to cause significant mortality to embryos of warmwater species, as reported for walleye, northern pike and yellow perch. Death is attributed to smothering when sediment deposition is sufficient for complete burial of the egg. The small size of many warmwater fish eggs makes smothering by settling sediment a real possibility in shallow wind-swept reservoirs, or lakes (Trautman 1957:489) and unstable streams where bank sloughing and soil erosion are common. Therefore, incubation -- that stage from fertilization to hatching -- is particularly susceptible to adverse effects from sediment, especially among those species where fanning of the nest does not occur. Additional documentation is needed for most species on lethal and sublethal effects of suspended solids and sediment on the incubation stage.

LARVAL DEVELOPMENT*

Introduction

It is evident from the literature that suspended solids affect larval fishes in a varied and complex manner. Exposure to high levels of suspended solids may be directly lethal, or influence larval survival indirectly by disrupting predator-prey relations, feeding success, and the ability to orient in the environment. Sedimentation of suspended particles can produce additional impacts as evidenced by extensive documentation of the adverse effects of sediment deposition on early life stages of salmonids (Cordone and Kelley 1961, EIFAC 1965, Iwamoto et al. 1978). Comparatively little is known, however, of the effects of suspended solids and sedimentation on larvae of warmwater fishes. Results of the few studies conducted are often inconclusive, reflecting in part the difficulties of establishing specific cause-effect relationships among the many potential influences of suspended solids in the aquatic environment. Furthermore, the utility of experimental evidence as a predictor of suspended solid impacts on larval fishes in nature is limited by the general lack of information on ecology and behavior of many warmwater species.

The larval period in most fishes is characterized by rapid changes in morphology which culminate in establishment of the adult form and mode of existence. Newly hatched individuals typically possess a large yolk sac, a conspicuous primordial finfold, and specialized cutaneous respiratory structures (Blaxter 1969, Balon 1975). Transference to an exogenous food source is accomplished as yolk reserves become depleted. Consequently, the eyes, jaws, fins, and other structures utilized in obtaining food must be functional at that time. The gills eventually assume a respiratory role and, in some fishes, inflation of the gas bladder provides additional mobility. Complete differentiation of fins and acquisition of scales and adult pigmentation generally marks the end of metamorphosis.

This series of developmental events is frequently associated with functional and behavioral modifications in larvae reflecting their continuously changing role in the ecosystem and varying degrees of sensitivity to environmental influences. Evolutionary processes have produced specialized adaptations and rather stringent habitat requirements in larvae of many species. As a result, survival to adulthood is largely dictated by the quality of the environment. Balon (1975) maintained that the oxygen regime and predation pressure were the most important environmental parameters governing survival of eggs and larvae in nature. Food availability may also have a significant influence on survival of feeding larvae as indicated by laboratory rearing experiments. Catastrophic mortalities have been known to occur among captive larvae immediately following final yolk absorption, implicating starvation as the major cause of death. Consequently, the period in development characterized by initiation of external feeding is often regarded as a "critical period" in the lives of fishes. Marr (1956), in reviewing the origin of the critical period concept, found little evidence of such catastrophic mortalities in nature. In a more recent review, May (1974) emphasized the multiplicity of factors other than food availability which may influence larval survival. Nevertheless, May (1974), along with other investigators (Hunter 1976), recognized the importance of starvation as a cause of mortality in larval fishes.

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A review of the effects of suspended solids on larval fishes is presented below. Because terminologies used in the literature to describe developmental intervals in larvae were variable and often vague, a standardized terminology could not be followed. An attempt was made to distinguish between yolk-sac larvae and more advanced stages when possible.

Direct Effects of Suspended Solids

Evidence of the direct lethal effect of suspended solids on larval fishes has been presented by several investigators. Morgan et al. (1973) utilized suspensions of naturally-occurring silt and clay sediments in conducting acute bioassays on striped bass and white perch larvae. Suspended solid concentrations ranging 1557-5210 ppm caused 20.0 to 27.3% mortality among striped bass larvae after a one-day exposure, and 38.7-66.0% mortality after two days of exposure. Similar results were obtained with white perch larvae: a one-day exposure to suspended solid levels varying from 1626 to 5380 ppm produced 27.3-29.3% mortality, while deaths resulting from two days of exposure ranged 22.6-62.0%. The authors observed increases in larval mortalities associated with increasing concentrations of suspended solids in these studies. However, no deaths occurred during short term (6 h) exposures to suspended solid levels up to 5200 ppm. Sherk et al. (1975) determined lethal limits of suspended solids for adult white perch and, in comparing their results with those of Morgan et al. (1973), concluded that larvae are likely to be killed at relatively lower concentrations.

Auld and Schubel (1978) subjected yolk-sac larvae of striped bass, American shad, and yellow perch to suspensions of natural fine-grained sediments obtained from Chesapeake Bay. Test concentrations were 50, 100, 500, and 1000 mg/1. All species were able to tolerate suspended solid levels of 50 mg/1. Survival of American shad larvae was significantly reduced at the higher concentrations, and mortalities among striped bass and yellow perch larvae were significant at the 500 and 1000 mg/1 levels. Although larvae were less tolerant of suspended solids than eggs of the same species, it was noted that naturally-occurring concentrations in the estuary rarely exceeded lethal limits.

Reis (1969) found extremely variable mortalities among yolk-sac larvae of the zebra danio hatched and maintained in solutions containing limestone particles. The author occasionally observed higher mortalities among test groups although the cause of death may have been attributable to more precocious hatching. Eggs incubated in the test solutions usually hatched earlier than controls and produced larvae in earlier stages of development. As a result, deleterious effects of exposure may have been more pronounced among these larvae. Other groups of eggs were incubated in clear water and the larvae subsequently transferred to limestone suspensions. All specimens died during 4 h of exposure to levels ranging 4.9-23.1 g/1, while no mortalities occurred among larvae held for 8 h in concentrations varying from 0 to 2.8 g/1.

The effects of intermittent additions of natural and artificial sediments on early life stages of brown trout were investigated by Stewart (1953). Newly hatched individuals prevented sediment deposition in the area immediately around their bodies through sustained sweeping motions of the pectoral fins. After the

mouth and gills began to function, solid particles accumulated in mucous-like secretions which passed out the gill cavities or were extruded by "coughing". The alevins were thus able to cope with limited amounts of sediment deposition in the test chambers. Continuous additions, however, eventually exceeding 1 mm in depth, caused inflation of the gill membranes which resulted in death.

Results of other studies suggested that exposure to suspended solids and sediment deposition was not harmful to larval fishes. Hassler (1970) conducted a field investigation of the effects of reservoir "silt" deposition on larvae of the northern pike. Yolk-sac larvae were placed in upright and inverted jars, representing test and control groups respectively. The jars were held in floating pens near natural spawning areas. Silt-related mortalities were not detected even though accumulations ranged to a depth of 13 mm. Survival in upright jars was substantial up to the 27th day after hatching, indicating larvae were successful in utilizing external sources of food during the study period.

The influence of "red-clay" turbidity on larval lake herring was studied by Swenson and Matson (1976). Yolk-sac larvae, hatched from eggs obtained in Lake Superior, were placed in suspensions of red clay particles varying in concentration from 0 to 28 ppm, levels which normally occur in the western part of the lake. Larvae were fed brine shrimp and provided with illumination simulating the natural diurnal light regime. Survival and growth was not adversely affected by turbidity during the 62-day bioassay. The authors did note a tendency of larvae to concentrate closer to the surface at high levels of turbidity.

Indirect Effects of Suspended Solids

Many reports alluded to the various indirect influences of suspended solids on larval fishes. The supporting evidence, however, was often subjective, highly speculative, and occasionally contradictory. This point is aptly illustrated by the controversy which arose over the decline of several commercially important species in Lake Erie. Langlois (1941) believed that high levels of turbidity and sedimentation were responsible for destroying spawning and nursery areas which eventually curtailed reproduction in the cisco, whitefish, and yellow perch populations. Several years later, Van Oosten (1948) refuted that contention in citing, along with other evidence, a lack of correlation between year class strength and levels of turbidity in the lake. In the interim, Doan (1941) published an account of the relationship between turbidity and Lake Erie sauger (*Stizostedion canadense*) dynamics. He maintained that turbid water enhanced sauger production in three ways: producing greater hatchability of eggs, promoting survival of the young by reducing predation, and facilitating feeding of the young by concentrating plankton near the surface. Others have observed the benefits of turbid water in reducing predation. Buck (1956) and Marzolf (1957) found production of channel catfish in turbid ponds was greater than that occurring in clear ponds. It was presumed that high levels of suspended solids provided concealment for the young but did not interfere with their feeding success. Predation on larvae of the Arkansas River shiner (*Notropis girardi*) and grass carp (*Ctenopharyngodon idella*) may be reduced by the prevailing high turbidities in areas selected by adults for spawning (Moore 1944, Stanley et al. 1978).

The ramifications of reduced light penetration in turbid water are not always beneficial. Soviet fish culturists reported that high turbidity increased mortality of grass carp in the hatchery. Also, the feeding efficiency of this species during the earliest stages of growth was found to be related to the amount of illumination. The minimum number of planktonic food organisms required to support a feeding larva in clear water was 1000 per liter, while 2000 - 2500 per liter were required in poorly illuminated water (Stanley et al. 1978). Cleary (1956) made a similar observation in noting that high turbidities may interfere with visual detection of prey by smallmouth bass fry. The laboratory studies of Vinyard and O'Brien (1976) generally support both the prey protection and predator inhibition hypotheses. They found high turbidities reduced the accessibility of Daphnia pulex as prey by decreasing the visual reactive distance of bluegill during feeding activities. Swenson (1978) attempted to elucidate the influence of natural red clay turbidity on predator-prey relations in the western Lake Superior fish community. He believed the reduced water clarity in this region may have promoted production of lake herring by concentrating zooplanktonic food organisms in near surface waters where the larvae congregated. Rainbow smelt, an introduced species, were also found to move into surface strata in response to turbidity, ostensibly increasing the potential for predation on larval lake herring. Consequently, the decline of the formerly abundant lake herring population in the western part of the lake was attributed to increased predation pressure on the larvae which resulted from turbidity-induced changes in distribution and feeding behavior of rainbow smelt. According to Irwin (Wilson 1960), the water clarity may also affect production of larval fish food organisms. High turbidities in Oklahoma reservoirs apparently caused a reduction in numbers of planktonic organisms by decreasing photosynthetic activity. The low density of prey was considered to be a critical factor limiting survival of newly hatched fishes in these habitats. Cairns (1968) postulated that any disruption of normal predator-prey relationships in nature would ultimately prove to be detrimental to the affected populations.

The phenomenon of larval fish drift among riverine fishes is not well understood. Loss of visual orientation, resulting in part from high turbidity, has been implicated as one of several possible causes. In that respect, high levels of suspended solids may influence the magnitude or periodicity of drifting movements. Larimore (1975) noted that conditions which simulate river flood stages i.e., rapid changes in velocity, turbulence, and turbidity, caused downstream displacement of smallmouth bass "black fry" as a result of disrupted visual and tactile orientation. Geen et al. (1966) found increases in numbers of drifting larvae associated with high water levels and high turbidity in a small stream in British Columbia. Gale and Mohr (1978) also suggested turbidity as a possible cause of increased larval drift in large rivers. Whether drifting movements are detrimental is largely speculative, however. Webster (1954) believed downstream dispersal of smallmouth bass fry during periods of high water and turbidity was beneficial in relieving overcrowding of stream sections used for spawning.

Fishes inhabiting highly turbid environments may possess special adaptations that promote their continued existence in these habitats. Spawning of striped bass in estuaries is known to occur in freshwater areas that frequently contain high levels of suspended solids. According to Mansueti (1961), water currents transport the pelagic eggs and larvae of this species to nursery areas of higher salinity. These locations were characterized as having lower turbidities than

other regions of the estuary and supported a correspondingly greater number of planktonic food organisms. By remaining suspended in the water column, the larvae were able to utilize this abundant food source and avoid the effects of high turbidity and sedimentation near the substrate. Other species, particularly those with demersal and semi-demersal larvae. were considered to be less well adapted for survival in the estuarine environment. Moore (1944) believed continual vertical swimming movements among larvae of the Arkansas River shiner represented a strategy for reducing losses to bottom predators and preventing destruction by shifting sand and silt. The validity of his contention is supported in principle by the frequent occurrence of pelagic larvae among warm-water fishes that inhabit permanently turbid environments or spawn in highly turbid areas.

Discussion

The wide range of early life history strategies in fishes precludes any definitive conclusions regarding the effects of suspended solids on larval fishes in nature. Documented evidence suggests that the mechanism and degree of suspended solid impact could vary interspecifically as well as temporally during the larval period. The vulnerability of newly hatched larvae to physical damage or smothering by solid particles apparently is a function of their habitat requirements, locomotive capabilities, and behavior, variables which may change appreciably as development progresses. An additional mode of impact is established once the larval gill begins to function. Everhart and Duchrow (1970) maintained that larval fishes are more susceptible to suffocation from exposure to suspended solids because they are unable to shed particles adhering to their body surfaces. But, as demonstrated by Stewart (1953), newly hatched brown trout were capable of sloughing solid particles from their gills in mucous-like secretions. Results of other studies with larvae are of little value in resolving this contradiction because the exact cause of sediment-induced mortality was not stated, or could not be determined. However, Sherk et al. (1975) speculated that the basis for age-specific differences in tolerance to suspended solids may be related to rate of metabolism and physical dimensions of the gill. Accordingly, mortalities incurred from a given concentration of suspended solids were believed to have been more pronounced among larval and juvenile stages as a result of a relatively higher oxygen demand per unit body weight and a greater tendency for the smaller-sized gill to sieve and entrap suspended particles, thus inhibiting gaseous exchange. Other investigators have noted that the respiratory capacity of the gill may be related to particle size, shape, concentration, and duration of exposure to suspended particles.

Most larval fishes are functionally and behaviorally adapted for survival within the environment selected by adults for spawning (Balon 1975). Consequently, a knowledge of species-specific reproductive strategies, including spawning time and location, fecundity, extent of parental care, and ecological characteristics of eggs and larvae is essential in assessing the potential impacts of suspended solids on early life stages of fishes. In that respect, Balon's (1975) ecological classification of fishes provides some insight into the degree of tolerance that may be exhibited by larvae of various species. The threat of smothering in larvae of the lithophils may be significant in view of their poor to moderately developed respiratory structures and habit of hiding within the interstices of rocky substrates.

Excess sediment deposition in the spawning area could also expose larvae to increased predation by reducing available bottom cover. Among the phytophilous groups, cutaneous respiratory structures are well developed and the larvae are able to remain above the substrate by continuous swimming or attachment to submerged vegetation. These forms presumably are less vulnerable to smothering by sediment deposition. Pelagic larvae of the pelagophils also appear to possess a considerable degree of resiliency to high levels of suspended solids and sedimentation.

Conclusions

Laboratory bioassays indicate that larval stages of selected species are less tolerant of suspended solids than either eggs or adults. Although the cause of larval mortality was not always apparent, available evidence suggests that lethal limits of suspended solids in nature may be determined by interactions between biotic and abiotic components of the ecosystem. These include age-specific and species-specific differences in tolerance among larvae and extent and duration of stress caused by the various particle sizes, shapes, concentrations, and amount of turbulence in the environment.

Indirect impacts of suspended solids on larval fishes are more difficult to evaluate. Many species rely upon visual detection of planktonic organisms during initial feeding stages. Rapid attenuation of light in turbid water may influence survival of these forms by reducing the biomass of plankton or providing protection for prey organisms. Larvae employing tactile senses for food detection are more suited to long term existence under low levels of illumination and possibly derive benefits from the concealing properties of suspended solids. Ascertaining the importance of turbidity as a cause of larval fish drift, and the influence of drift on larval survival, demands a more thorough understanding of the mechanics and ecological significance of drifting movements in riverine systems. Finally, there is evidence that larvae of several species have successfully circumvented the adverse effects of sustained high levels of suspended solids in their environment through acquisition of functional and behavioral adaptations that are conducive to survival in highly turbid habitats.

JUVENILE PERIOD*

Introduction

Abundance of a year-class has been defined as being established during the "critical phase" within the first few months of life (Gulland 1965). The "critical period" (May 1974, Hjort 1926) may occur at larval first-feeding stage and be related to proper food supply and environmental conditions. LeCren (1958:31) stated "Survival of larval and young fish varies very greatly and such variations can sometimes be correlated with climatic influences; rarely do they show clear signs of density-dependence." Fish mortality rates typically decrease with increasing age (Gulland 1965).

The juvenile period is defined as fish's stages between complete absorption of primordial fin-fold and acquisition of fin-rays and spines to the beginning of gonadal maturation. Since many references were not specific as to the exact stages of fishes life tested or sampled, fish sizes as total length or knowledge of sampling gear had to be evaluated to determine whether juvenile stages were included in the selected references.

This section attempts to focus on references reporting the impacts of suspended solids on juvenile stages of freshwater, warmwater fishes. To understand the significance, the mode of action should be identified and understood.

Direct Sediment Effects

Mechanical

Studies of the impact of suspended solids on larval and juvenile fishes have focused mainly on the direct impacts upon the soft portions of larval fishes and the gills of juvenile fishes. Since juvenile fishes have formed body covering similar to adults, the gills are the major exposed soft structures. Sediment clogging of warmwater juvenile fish's gills has been reported by Bulkley (1975) McKee and Wolf (1963:256), Heimstra et al. (1969), and Wallen (1951a). Wallen (1951a) found mortalities for 16 warmwater species to vary widely to montmorillonite clay turbidity. The lowest average lethal range was recorded at 69,000 ppm for pumpkinseed. Most fishes died at 175,000 to 225,000 ppm, which Wallen felt to be much above turbidity conditions encountered by juvenile and adult fishes in nature. Wallen (1951a) noted stress reactions, such as floating at surface and gulping air as well as reduced fin and opercular movements, when turbidities reached 20,000 ppm. Fish that succumbed had opercular cavities and gill filaments clogged with silt. Sparks et al. (1969) reported channel catfish fingerlings succumbed in 48 h to 24,200 to 30,400 mg/l $CaSO_4$ suspended solids. Wallen (1951a) found no evidence of gill injury and no unusual amounts of mucus were secreted by the gills. As size and hardness of particles increased, so did injury to gill structures (Ellis 1944).

Bulkley (1975:286) reported "coughing" of fish to expel accumulated detritus from the gills. Fish in turbid conditions showed high incidence of "coughing"

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(Heimstra et al. 1969). Neumann et al. (1975) found no effects of turbidity on respiratory or hematological responses of the (marine) oyster toadfish (Opsanus tau). Sherk et al. (1975) found increased hematocrit value, hemoglobin concentration and erythrocyte numbers in blood of three estuarine fishes exposed to sublethal concentrations of fuller's earth

Hubbs and Whitlock (1929:480) reported that young gizzard shad (Dorosoma cepedianum), with the alimentary canal jammed with inorganic materials (clay, mica, and silica), had enlarged heads and underdeveloped tail regions. "Abnormality of the Arkansas River specimens does not appear to be due to parasitization, but may be related to the excessive siltiness of the water in which they were living." However, Van Oosten (1948) speculated that fine silt may prove beneficial as substrate for microbiota used as fish food.

Morphological Changes

Moore (1950) indicated evolutionary changes which have helped species live in muddy North American rivers. Cross (1967:12) reported structural adaptations of fishes living in shallow, sandy, turbid rivers as (1) reduced size of scales especially on nape and embedding of those scales in thickened epidermis (2) reduced size of the eyes or partial shielding by surrounding tissue, and (3) increased development of other sensory structures such as taste-buds in the skin. Hubbs and Whitlock (1929) cautioned against failure to recognize differences caused by environmental factors rather than genetic differences.

Activity

Heimstra et al. (1969) reported that movement activity of juvenile largemouth bass was reduced in turbidity of 14-16 JTU for 30 days versus 4-6 JTU; whereas, juvenile green sunfish activity was not significantly altered. Turbidity disturbed normal social hierarchies in green sunfish. Fish in turbid conditions showed high incidence of "coughing" and more scraping behavior than controls. Horkel and Pearson (1976) found increased ventilation and oxygen consumption by green sunfish at turbid suspensions above 3,500 FTU. Vinyard and O'Brien (1976) demonstrated experimentally that reduced illumination and increased turbidity caused substantial reductions in reaction distance of bluegill for all prey sizes.

Orientation

Experimental data have shown increasing turbidity had similar effects on smallmouth bass "black fry" orientation in water currents as did decreasing light (Larimore 1975). Fewer fry were displaced in clear water (<10 JTU) than in turbid (250 and 2350 JTU). Losses of smallmouth bass fry during floods could be caused by rapid changes in velocity, turbulence, turbidity, and light exerting simultaneous influences. Larimore stated that loss of orientation may account for frequent disappearance of year classes from warmwater streams. Cleary (1956) and Surber (1939) mention the loss of smallmouth bass fry during the postnesting period, and Cleary suggested direct physical damage to eggs and fry or indirect losses by sweeping them out of nursery habitat.

Avoidance

Gammon (1968, 1970) indicated that standing crops of fishes decreased drastically when heavy (>120 mg/l) solids input from a limestone quarry occurred in the spring. After winter floods removed the sediments, small fishes repopulated the pools to approximately 50 to 75% of standing crop found above the quarry inlet. Gammon's studies suggested fish avoidance of silt impacted areas; however, he also found a 50% reduction in density of all macroinvertebrate populations in riffle areas impacted by the quarry sediment. Branson and Batch (1972) reported that the surface-feeding creek chub was able to remain over ensilted bottoms long after other species had been eliminated. Fishes were progressively eliminated from headwaters downstream or were forced to emigrate downgrade in low-level acid-mine water effluence containing high levels of siltation and turbidity from spoil banks. Forshage and Carter (1974) did not identify sizes of fish collected but their sampling with common 3/16 inch mesh seine and electrofishing gear should have collected juvenile fishes. Numbers of shiners (Notropis) decreased below a dredged area on the Brazos River, Texas; whereas, river carpsucker (Carpiodes carpio) populations increased. Changes in fish composition resulted from the disappearance of shelter and the reduction of food organisms. Cordone and Kelley (1961) cited references on reactions of salmonids to high turbidities in rivers and tributaries.

Langlois (1941) cited fishermen knowledge for pickerel avoidance of stirred up Lake Erie waters and sauger preference for roily waters. He also included freshwater drum, catfish, and carp as species which thrive in turbid waters. Swenson (1978) found that juvenile walleye (126-264 mm T.L.) prefer turbid waters (5-51 FTU); whereas, rainbow smelt, larval lake herring, and lake trout show avoidance. His laboratory findings agreed with larval and adult distribution in western Lake Superior sampling.

Impact on Feeding

Alimentary canals of young gizzard shad were found jammed with inorganic materials, containing limited plankton as the result of excessive siltation in the Arkansas River (Hubbs and Whitlock 1929). The impact was sufficient to cause abnormal body shapes. Cleary (1956:355) suggested that turbid conditions during postflood periods may inhibit sight-feeding activities of smallmouth bass fry. The magnitudes of change in reaction distance of bluegill to prey sizes under different conditions of light and turbidity could be of major importance in estimating fish feeding rates (Vinyard and O'Brien 1976).

Peters (1972) reported white suckers, mountain suckers (Catostomus platyrhynchus), and flathead chubs (Hybopsis gracilis) decreased in condition factor; whereas, longnose suckers (Catostomus catostomus) experienced increased growth increments but brown trout showed no growth changes following erosion control to reduce sediment on Montana trout stream. Reduction in sediment pollution influenced the ability of these species to compete for food.

Indirect Sediment Effects

Algae

Since plankton algae forms the food chain base for many zooplanktors and larval fishes, the reduction in primary production, as the direct result of increased turbidity and suspended solids (see Section III General Ecosystem Effects), would be expected to impact more on larval fishes. Orr (1958) reported paucity of phytoplankton after 1952 when turbidity increased in Oklahoma's Heyburn Reservoir following the third year of impoundment. The lower phytoplankton supply resulted in poor gizzard shad growth. Some juvenile and adult freshwater fishes continue to feed primarily on planktonic algae and many juvenile and adult stream fishes feed on attached algae and associated fauna. Jones (1964) stated that suspended coal dust cuts off the light from stream-bed, preventing photosynthesis by plants, thereby, eliminating invertebrates for fish foods. Van Oosten (1948:304-305) pointed out the possible natural breaks in the long chain of events in the phytoplankton - zooplankton - young fishes food chains as impacted by turbidity. He argued against Langlois' (1941) study of causal relationships based upon mere observations of fluctuations in fish abundance.

Buck (1956) found 161.5 lbs per acre of fish in clear (<25 ppm) ponds compared to 94 lbs per acre in intermediate turbidity (25-100 ppm) and 29.3 lbs per acre in muddy ponds (>100 ppm). Clear ponds yielded more larger fish and growth increased for bluegill and redear sunfish (*Lepomis microlophus*). First year growth was faster in clear ponds for bluegill, redear sunfish and largemouth bass. Volume of net plankton in surface tows was 8 times higher in clear ponds as in intermediate turbidities and 12.8 times greater than in muddy ponds. Fourteen hatchery ponds stocked with same numbers of largemouth bass, bluegill, and channel catfish revealed faster growth and greater total weights of bass and bluegill from clearer ponds. Channel catfish produced greater total weights in muddy ponds. Van Oosten (1948) cited a Schneberger and Jewell (1928) paper reporting largemouth bass, bluegill and crappie production decreasing in ponds when turbidity exceeded 100 ppm. Jenkins (1958) indicated a 10- to 30-lbs per acre increase in standing crop could be expected for Oklahoma ponds properly constructed to limit siltation and water exchange.

Aquatic Vascular Plants

Higher aquatic plants function in life of fishes for reproduction, shelter, food production, oxygen production, and soil stabilization (Beckman 1955). Beckman (1955) attributed an important fisheries role to higher aquatic plants for shelter from excessive sunlight, rest areas, and refuge from predation for fishes. Aggus and Elliott (1975) documented the importance of flooding of terrestrial vegetation for higher young largemouth bass survival during first summer of life, suggesting predation as primary cause of mortality. Strange et al. (1975) mostly pointed out the detrimental impacts of aquatic plants on fisheries by monopolizing light and nutrients, excessive sheltering of small prey species, and interfering with boat navigation and fishing. Strange et al.

(1975) cited three studies reporting increased predation and growth of predator fish following the reductions of aquatic plants.

Benthos

Flash floods may tear out portions of the smallmouth bass food chain by molar action of flood waters, and turbidity may inhibit sight-feeding activities of young fishes (Cleary 1956:355). Starrett (1951) stated the availability of food for young fishes is reduced by the increased turbidity, volume of water, and washing effect on bottom fauna and flora during high water stage in Des Moines River, Iowa. King and Ball (1964) found inorganic sediments from highway construction substantially reduced populations of herbivorous and carnivorous insects and tubificid worms. Smallmouth bass populations decreased in numbers with the decline in numbers of pools and when pools were filled by inorganic sediments.

Cordone and Kelley (1961:210) reported extensively on the impacts of sediments on bottom fauna of coldwater trout streams. They stated "There is no doubt that substantial quantities of inorganic sediment entering a flowing stream can seriously reduce the abundance of bottom-dwelling invertebrates, but what effect does this have on fish production?" Iwamoto et al. (1978:17), in an extensive review with emphasis on freshwater salmonid habitats, indicated inconclusive effects of various amounts of deposited sediments on benthic faunas.

Survival and Food Supply

McKee and Wolf (1963:290) cited five references supporting the increased protection of small fishes from predators in turbid waters. Ritchie (1972) suggested that turbidity reduces the ability of fish to find food but it also allows young fish to escape predators. Higher commercial gill net catches of sauger in Lake Erie were attributed to the protection of young sauger from sight feeding predators, concentrated microcrustacea closer to surface, and better coating of sauger eggs at higher turbidities (Doan 1941).

Cross (1967:208) indicated that reproduction and survival of channel catfish in clear ponds is limited because of bass predation; whereas excessive survival in turbid ponds results in "stunted" channel catfish populations. Buck (1956) reported higher survival of young channel catfish in turbid ponds containing carp. He also indicated young channel catfish were protected from predators, but could find food in turbid reservoir waters. Bullhead catfish reproduced successfully in muddy ponds; whereas, bass and bluegill were unable to reproduce (Swingle 1956). Forester and Lawrence (1978) reported the standing crop of bluegill decreased in ponds containing carp and suggested high turbidity had reduced overall standing crop. Cross (1967:199) characterized the habitat of black bullhead (*Ictalurus melas*) as soft bottoms and high turbidity in quiet backwaters and pools of intermittent streams. He stated that black bullhead are not abundant in larger rocky or sandy streams nor clear-water, small streams in Kansas.

Conclusions

Suspended sediments can directly impact juvenile freshwater, warmwater fishes at sublethal levels by reducing sight-feeding distances, disrupting activity and respiratory patterns, and changing migration and orientation responses. At levels above 20,000 ppm stress reactions have been observed; whereas, at levels between 69,000 to 200,000 ppm mortalities generally have been recorded for species experimentally challenged. Fishes reported to have adapted to turbid flowing waters appear to have evolved structures and sensory organs which reduce the impact of suspended solids on their bodies and improve food searching.

Beneficial effects upon fishes of increasing suspended sediment levels have been attributed to escapement from predation for species, such as catfishes with highly developed taste and smell organs. Growth rates of such fishes can be reduced because of more juveniles feeding upon the same or reduced food base in turbid waters.

Experimental data concerning the direct effects of suspended sediments on juvenile warmwater fishes have been limited mainly to high-level, short-term mortality investigations such as Wallen (1951a) and Sparks et al. (1969). Long-term studies by Buck (1956), Orr (1958), and Forester and Lawrence (1978) documented decreased standing crops and sometimes slower growth rates of fishes in ponds containing higher levels of suspended sediments; however, these results were confounded, in many instances, by presence of additional fishes such as carp. Also, the modes of action and exact stages of life were not experimentally demonstrated nor directly implicated. It would seem that well-designed laboratory or replicated long-term hatchery pond experiments could and should be designed to test the modes of action of suspended sediments on juvenile warmwater fishes.

SECTION V

REPRODUCTIVE STRATEGIES*

INTRODUCTION

It became clear early in the literature review process that either no information or very circumstantial evidence existed upon which to evaluate the impact of suspended solids or sediments on most fish species. Indeed, we rarely found data or statements based on explicit experimental designs aimed at testing sediment effects on fish reproductive processes. We, therefore, attempted to develop a methodology that would allow extrapolation from data gleaned from the literature to other species not specifically discussed in the literature. We felt that without such a mechanism, the little information found would have limited utility in evaluating the overall effects of suspended solids and sediment on diverse species in diverse warmwater ecosystems. If, through the literature, reproductive stages and strategies particularly susceptible to damage by sediment could be determined for some species, these findings could then be applied to other species, regardless of taxonomic status, with similar reproductive strategies.

To accomplish the objective of catagorizing species of warmwater fishes according to reproductive strategy, a format for collecting and analyzing reproductive data and information was developed (Table 6). Information was obtained from a number of books (Breder and Rosen 1966; Carlander 1969, 1977; Cross 1967; Mansueti and Hardy 1967; Moyle 1976; Scott and Crossman 1973; Trautman 1957) and many journal articles that will not be cited here. Each species was assigned a code number identifying family and species. Because of limitations of these references, the present analysis emphasizes reproductive behavior. Early life history elements, while important to overall reproductive strategies, were largely excluded owing to a dearth of available information. On the data form for each specific point, one of three potential scores was assigned along with those references that contributed to that determination. If that species displayed that particular trait or strategy, a 1 was assigned; if not, a 0 was assigned. When information was not available for a decision, 9 was assigned (see example, Table 6). With the form used and information available, many determinations are somewhat subjective. However, based on the quality of literature, it was difficult to avoid a certain amount of subjectivity.

The current study analyzed 110 species for which we have complete or nearly complete information on a number of aspects of reproductive behavior. A similarity matrix was first constructed for the species using a Jaccard similarity coefficient. Groups possessing similar patterns of reproductive behavior were then identified by cluster analysis employing the unweighted pair group method of McCannon and Wenniger (1970).

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Table 6. Example of spawning strategy form filled out for the bluegill (*Lepomis macrochirus*). Data thus collected for each of 110 species were used in the cluster analysis (Figure 1).

Species *Lepomis macrochirus* Code 23017

References: 1-Breder & Rosen 1966; 2-Cross 1967; 3-England 1968; 4-Priegel 1967; 5-Scott & Crossman 1973 (see Table 10 for specific citations)

			A. Spawning Season
	0	6.	Early spring
1,2	1	7.	Late spring
1,2	1	8.	Summer
	0	9.	Autumn
			B. Spawning period duration
	0	10.	Short, discrete
	0	11.	Long & uninterrupted
1,2	1	12.	Long; discrete spawning intervals
			C. Pre-spawning aggregations
	0	13.	Mass aggregates (close contact)
	0	14.	Loose aggregates
1,2	1	15.	None
			D. Mating complexes
	0	16.	Mass mating, large groups, sex ratio about equal
	0	17.	Small groups (<12), usually sex ratio strongly favoring males
	0	18.	Small groups, females>males
2,5	1	19.	Distinct pairing, with polygamy
	0	20.	Distinct pairing, no polygamy
			E. Sexual dimorphism
	0	21.	Little or none
5	1	22.	Moderate
	0	23.	Much
			F. Courtship
2,5	1	24.	Complex, with display
	0	25.	Simple, mainly chase
	0	26.	None
			G. Territoriality
	0	27.	None
1,2,5	1	28.	Males
	0	29.	Females
	0	30.	Both sexes
			H. Spawning habitat
1,5	1	31.	Lakes, reservoirs
	0	32.	Marshes, swamps
	0	33.	Large river
1	1	34.	Stream pool
	0	35.	Stream riffle-run
	0	36.	Estuarine
			I. Egg deposition
	0	37.	Internal
	0	38.	Pelagic
	0	39.	Rock
2,5	1	40.	Gravel
1,2,5	1	41.	Sand
1,2,5	1	42.	Silt
1,2,5	1	43.	Plant
	0	44.	Other
			J. Substrate preparation
	0	45.	Open surface - no preparation
1,2,5	1	46.	Open surface - fanning, minimal preparation
	0	47.	Open surface - excavation
	0	48.	Natural cavity users - minimal preparation
	0	49.	Cavity excavation
	0	50.	Nest constructed of organic materials
	0	51.	Other
			K. Egg buoyancy
	0	52.	Pelagic, semi-buoyant
2,5	1	53.	Demersal
			L. Egg adhesiveness
2,5	1	54.	Adhesive
	0	55.	Adhesiveness decreasing in time
	0	56.	Nonadhesive
			M. Fecundity
	0	57.	Low
1,5	1	58.	Medium
	0	59.	High
			N. Nest site guarding
	0	60.	None
2,5	1	61.	Males only
	0	62.	Females only
	0	63.	Both parents
			O. Duration of guarding
	0	64.	Eggs only
2,5	1	65.	Eggs & larvae on site
	0	66.	Eggs & off site larvae
	0	67.	Site guarding continuing after larvae leave
			P. Water circulation over eggs by parents
	9	68.	Present
	9	69.	Not present
			Q. Egg tending (cleaning, removal of dead eggs, embryos etc.)
	9	70.	Present
	9	71.	Not present
			R. Days to hatching
5	1	72.	< 4
5	1	73.	4-9
	0	74.	10-14
	0	75.	15 ≥
			S. Sensitivity to sediment
1,2,3	9	76.	Negative effect
4	9	77.	No effect
	0	78.	Positive effect

ANALYSIS

On the basis of reproductive behavior, the 110 species appear to be distinguishable into five major groups (I-V in Fig. 1). Group I consists of 35 species representing eight families, the most prominent forms being sunfishes (15 species), catfishes (7), and darters (4). The closest behavioral affinities are clearly within genera and families. Group I species (Fig. 2) are all complex spawners, most being nest builders that provide parental care. The few exceptions to this generalization are the livebearing mosquitofish (Gambusia affinis), and two killifish which may fashion crude nests in vegetation but do not provide parental care. Overall, the importance of parental care to this group appears to be the main factor separating it from the other four groups. Most of the species are lithophilous spawners but phytophils are also represented by two sticklebacks, two killifishes, and the bowfin. Although a few of the species are quite tolerant to turbidity and sediment (e.g. channel catfish), a greater number are rather intolerant or may at least be sensitive under certain conditions.

Group II (Fig. 3) is composed of 18 species of minnows, darters and the sea lamprey (Petromyzon marinus). All may be regarded as complex spawners. Several construct depression or gravel mound nests but most are open substrate, clean gravel spawners. None are known to practice any parental care beyond general male territoriality. At least half may be considered highly intolerant of turbidity and sediment, and several others appear to be only slightly more tolerant.

Among the 18 species comprising Group III (Fig. 4), 13 are minnows. The remainder are two shads (genus Dorosoma), the freshwater drum, the banded killifish (Fundulus diaphanus), and the Sacramento perch (Archoplites interruptus). The minnows include three exotic species (carp; goldfish; tench, Tinca tinca) which are very similar in reproductive behavior. Also included is the sole North American representative of the European shiner subfamily Abramidinae, the golden shiner (Notemigonus crysoleucas). The remaining native minnows are primarily eastern species but two western forms are also included. It is noteworthy that the Sacramento perch, the single native western centrarchid, is the only sunfish not occurring among Group I. All Group III fishes are simple spawners. They utilize a variety of substrates for egg deposition sites, and some may do limited nest area clearing but there is no true nest construction. Various species are noted for their prosperity in turbid waters: gizzard shad, freshwater drum, red shiner (Notropis lutrensis), goldfish, carp, and the Sacramento blackfish (Orthodon microlepidotus). Among the five groups, Group III can probably be regarded as the most tolerant of turbidity and sediment.

Group IV (Fig. 5) is recognized as a small assemblage (10 species) of simple spawning lithophils and phytophils. Several members of the coolwater phytophil community are represented: the pikes and the yellow perch. In some localities, these species have suffered declines through loss of aquatic vegetation due to turbidity or through egg suffocation from sediment. On the other hand, several other members of the group do well in turbid waters or over mud bottomed areas: goldeye, central mudminnow (Umbra limi), and bigmouth buffalo (Ictiobus cyprinellus).

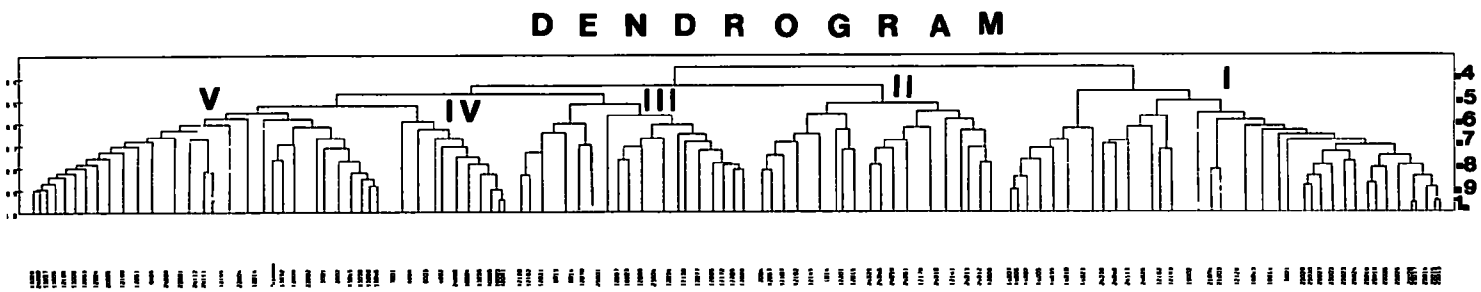

FIGURE 1
CLUSTER ANALYSIS-REPRODUCTIVE BEHAVIOR OF 110 FISH SPECIES

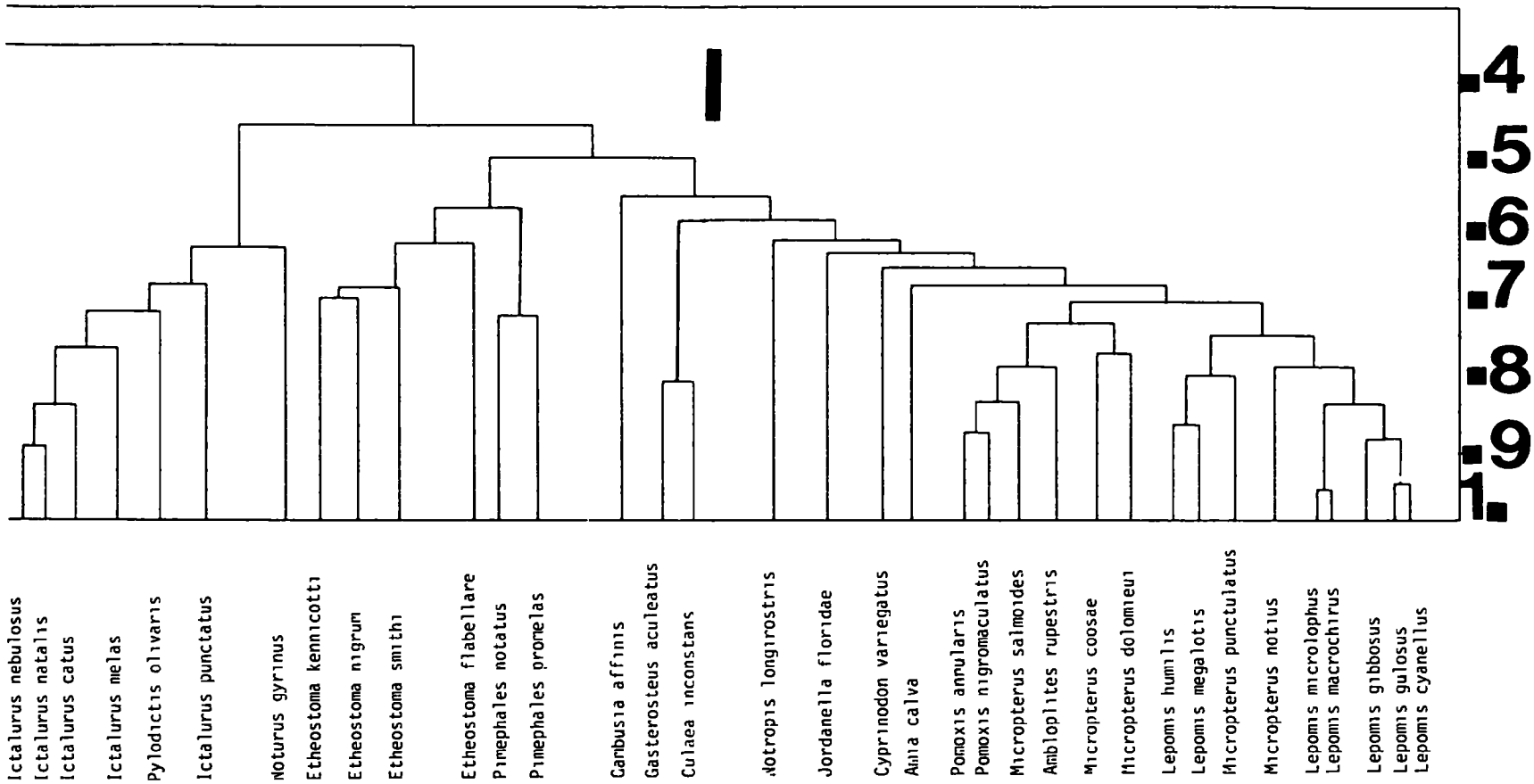

Figure 2. Cluster analysis dendrogram - Group 1 of Figure 1. Thirty-five species displaying complex spawning with parental care.

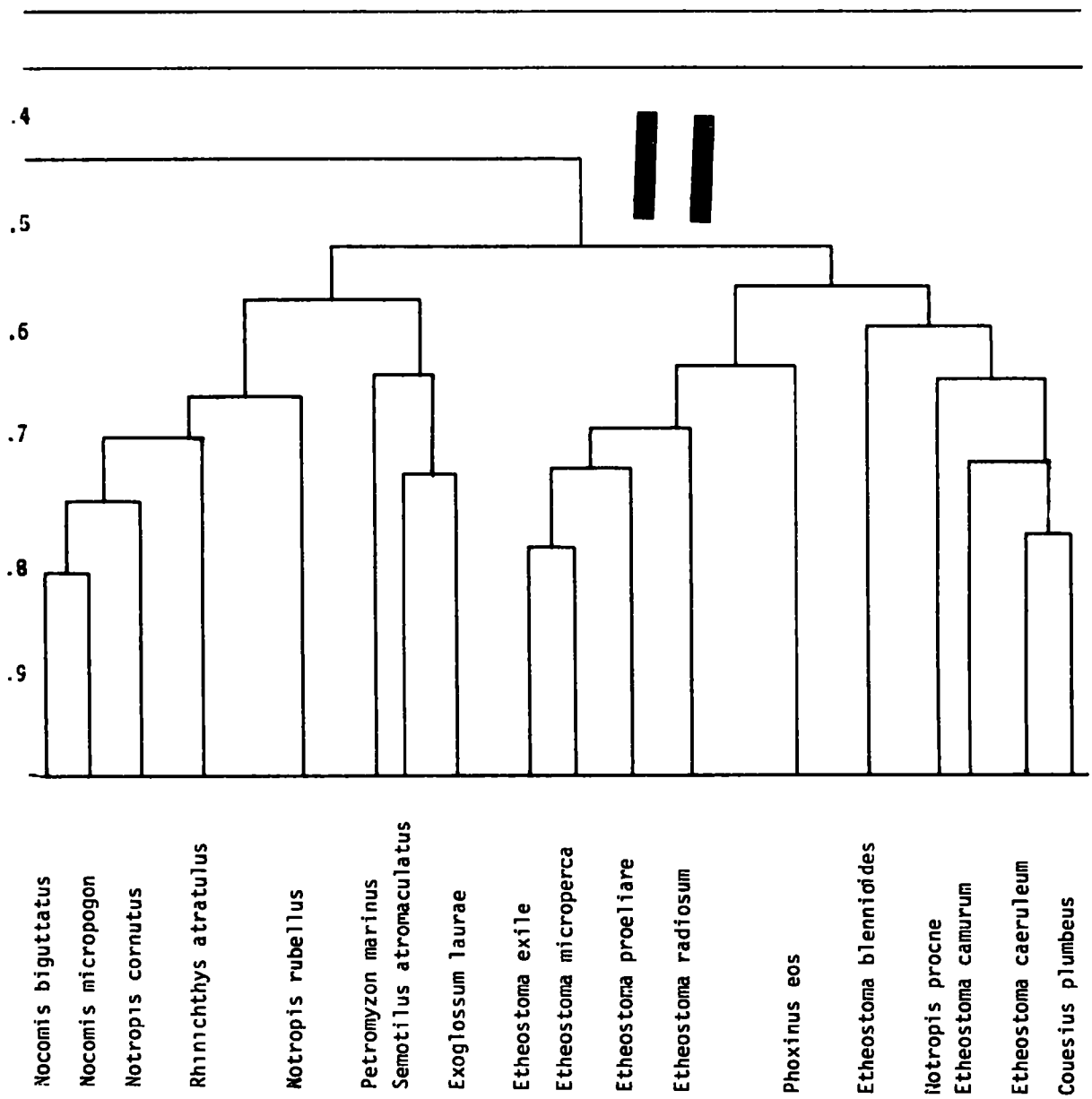

Figure 3. Cluster analysis dendrogram - Group II of Figure 1. Eighteen species displaying complex spawning without parental care.

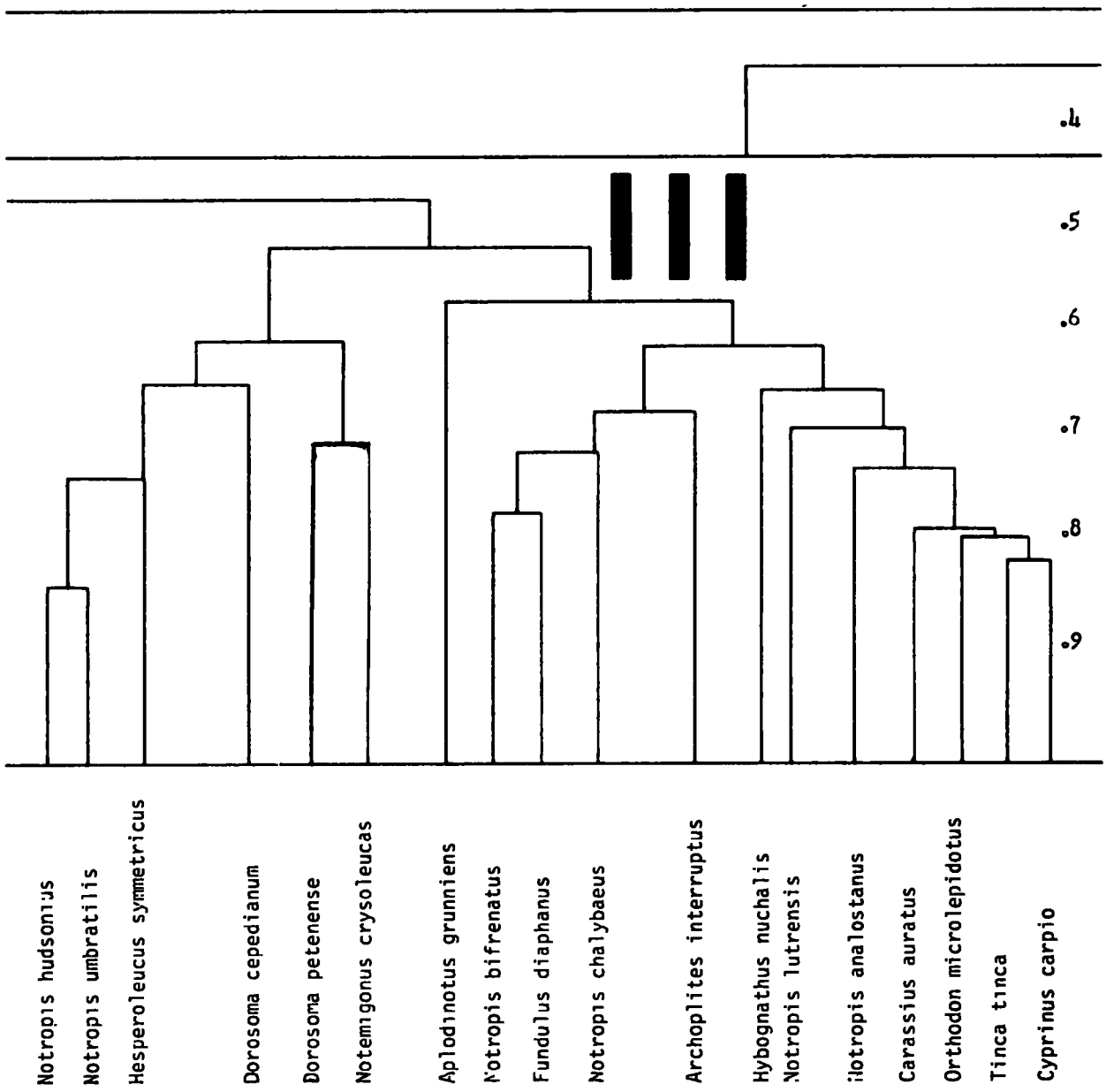

Figure 4. Cluster analysis dendrogram - Group III of Figure 1. Eighteen species of simple spawners using various substrate types.

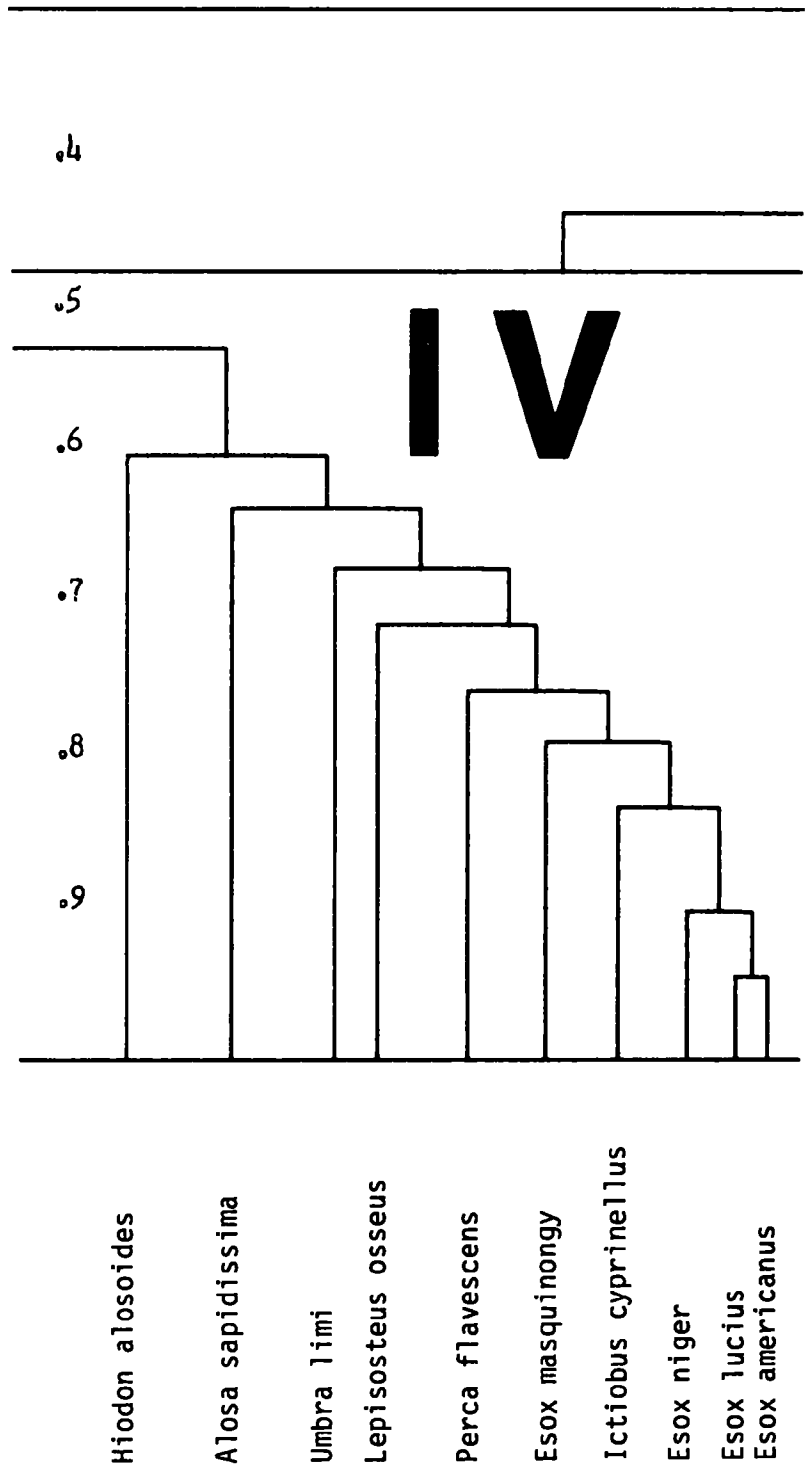

Figure 5. Cluster analysis dendrogram - Group IV of Figure 1. Ten species of simple spawning lithophils and phytophils.

Group V (Fig. 6) is large and taxonomically diverse, consisting of 29 species from 10 families. The prominent species groups include eight forms of western minnows and suckers, the walleye-sauger group (genus Stizostedion), three temperate basses (genus Morone), four redhorses (genus Moxostoma), plus the lake sturgeon (Acipenser fulvescens) and the paddlefish. It is perhaps not coincidental that most of the species are of large body size and relatively high fecundity. Although a number of the species are known to be quite sensitive to turbidity and sediment, e.g. redhorses, at least some are considered tolerant, e.g. striped bass. At present, we do not have enough information to adequately characterize the group according to this criterion, however.

Within each of the five major groups, there are one or more species which appear quite distinctive from other group members, i.e. they join subgroups only at rather low levels of similarity. It was of interest, therefore, to ask if these species might exhibit any ecological distinctiveness as well. To determine this, we first considered all species which joined a cluster at a Jaccard coefficient of 0.6 or less. This produced a list of eight species: Group I - mosquitofish; Group II - greenside darter (Etheostoma blenniodes) and northern redbelly dace (Phoxinus eos); Group III - freshwater drum; Group IV - goldeye; Group V - striped bass, spotfin shiner (Notropis spilopterus), and lanternjaw minnow (Ericymba buccata). Although the various species are ecologically diverse relative to general aspects of life history, it is interesting that at least six may be regarded as highly tolerant of turbidity and sediment. Of the remaining two, the spotfin shiner is at least moderately tolerant, but we have no knowledge of the sensitivity of the greenside darter. When we established a coefficient of 0.7 or less as our selection criterion, 23 more species were added to the list. These included a number of tolerant and sensitive forms but, overall, we have insufficient information to characterize the group at this time.

In summary, cluster analysis of this sample of reproductive behaviors of warmwater fishes produces relationships which are intuitively logical in virtually all cases. Refinements of the clustering technique are possible, and additional characteristics could be employed so as to reflect overall reproductive strategies rather than behavioral characteristics alone. To date, our literature survey has concentrated on a limited number of references. There is still a large body of literature that remains to be examined. It is reasonable to expect that the literature can provide sufficient information to compare the reproductive strategies of over 200 warmwater species and numerous coldwater fishes as well. It is possible that such an analysis will be useful in relating the question of reproductive success to factors of turbidity and sedimentation.

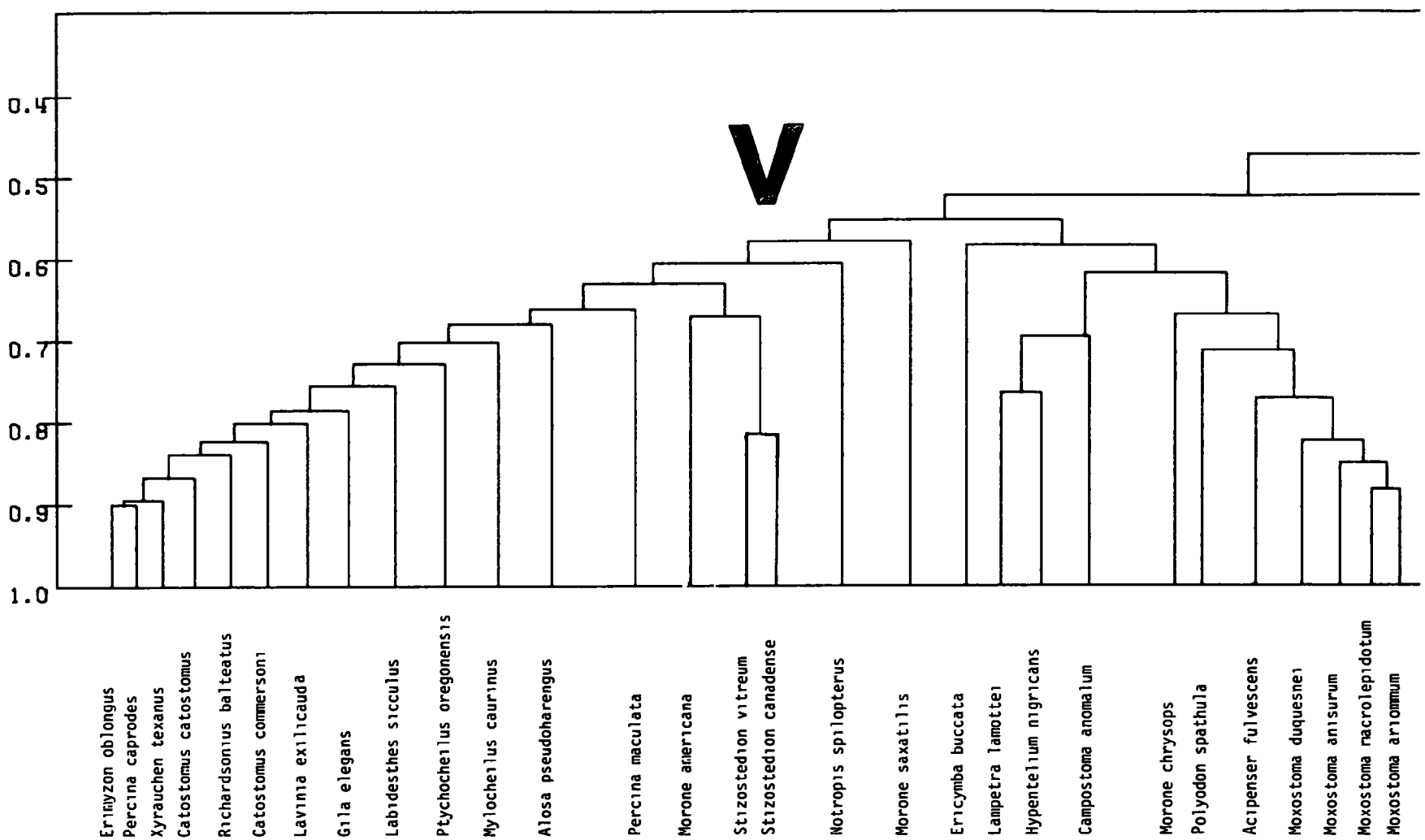

Figure 6. Cluster analysis dendrogram - Group V of Figure 1. Twenty-nine species of simple spawning lithophils.

SECTION VI

SENSITIVITY OF WARMWATER FISH POPULATIONS TO SUSPENDED SOLIDS AND SEDIMENT*

As discussed in previous sections, only limited direct information is available on the longterm effects of sediment and suspended solids on warmwater fish populations. Generally, the available reports provide circumstantial evidence based on ichthyofaunistic studies but implicate a variety of other environmental factors as well. In addition, the most susceptible life periods are rarely identified. Despite these shortcomings of the information base, it is clear, however, that warmwater fish species vary considerably in their population-level responses to suspended solids and sediments. To date, there have been no comprehensive accounts identifying the tolerances of individual species beyond some local faunal studies. In this section, therefore, we have summarized pertinent literature information known to us. This should be regarded as a preliminary effort since there are obvious gaps in our review. By and large, the cited references (Table 10) deal with fishes that range broadly throughout the agricultural regions of the northern and, especially the northcentral, United States. Endemic forms of the Far West and South and other species of relatively restricted distribution are only poorly represented.

In Tables 7 and 8, we have categorized species as either tolerant or intolerant of suspended and sedimented solids, primarily on the basis of their habitat preferences and recent range adjustments in areas which have been subject to increased sediment loads in historical time. In many cases. two or more independent literature sources provide similar or complementary information on a species' relative tolerance. The list of intolerant forms is considerably more extensive than that of tolerant fishes. Among the former, there are but a few examples where interference with reproductive activities has been specifically identified. Moreover, the literature is often vague as to whether the negative impact is through suspended materials, sediment, or both. In some cases, we were forced to interpret authors' intended meanings. Where this proved particularly difficult, we have indicated that both factors may be involved. As noted in the section on reproductive behavior, the intolerant assemblage is composed of a disproportionately large number of species with complex spawning behavior. On the other hand, the tolerant fishes include a larger percentage of simple spawners and forms with special early life adaptations for turbid waters.

Not all species treated in the literature could be categorized with confidence as either tolerant or intolerant. Examples are shown in Table 9. It is emphasized that these forms do not represent an intermediate category (even within the tolerant and intolerant groupings, a spectrum of species' sensitivities could be recognized), but rather they reflect the contradictory nature of some literature evidence. This result is not unexpected since the opinions of the various authors are mostly framed in the context of the local ichthyofauna with which they are most familiar.

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Table 9 is useful in demonstrating that there are different viewpoints on the susceptibility of individual species of fish and that for many forms the available information is incomplete. Clearly, in order to make meaningful judgments on the tolerance of individual species, more detailed information is required concerning sensitivities of various life periods and the mode of action of suspended solids and sediment.

This reemphasizes the need for a compilation and synthesis of reproductive strategies for warmwater species. The present study represents a beginning in that direction and it is our intention to continue development of the approach that has been outlined in Section V. There is undoubtedly much information on species sensitivity to suspended solids and sediment and fish reproductive strategies that is not available in a widely circulated format. We would appreciate receiving additional information that readers may be able to supply.

Table 7. Warmwater fishes which are intolerant of suspended solids (turbidity) and sediment. Numbers refer to references listed in Table 10.

Species	Effect		Impact through	
	Spawning	General	Suspended solids	Sediment
Ichthyomyzon castaneus	7			7
Acipenser fulvescens	7	27,29		7,27,29
Polyodon spathula	21	29		21,29
Lepisosteus platostomus		27		27
Amia calva	25,30		25, 30	
Hiodon tergisus		27,29	27, 29	
Esox lucius	24,28,30		30	24,28,30
Esox masquinongy		27,30	27, 30	
Clinostomus elongatus		8,30		8,30
Dionda nubila		29		29
Exoglossum laurae		27,30		27,30
Exoglossum maxillingua		25		25
Hybopsis amblops		29,30	29	29,30
Hybopsis dissimilis		27,30		27,30
Hybopsis x-punctata		8,27,30		8,27,30
Nocomis biguttatus	7			7
Nocomis micropogon		27,30	27, 30	27,30
Notropis amnis		5	5	
Notropis boops		29,30	29, 30	29,30
Notropis cornutus		7		7
Notropis emiliae		27,29,30	27, 29, 30	27,29,30
Notropis heterodon		8,13,30	8, 13, 30	8,13,30
Notropis heterolepis		7,30	7, 30	
Notropis hudsonius		8,30	30	8
Notropis rubellus		2,30	2, 30	30
Notropis stramineus		7,8,30	7, 30	7,8
Notropis texanus		29		29
Notropis topeka		8		8

Table 7. Continued --

Species	Effect		Impact through	
	Spawning	General	Suspended solids	Sediment
Notropis volucellus		30	30	
Carpiodes velifer		29	29	
Cycleptus elongatus		7,29		7,29
Erimyzon oblongus		30	30	
Erimyzon sucetta		27,30	27, 30	27,30
Hypentelium nigricans		7,8,25,30	25, 30	7,25,30
Lagochila lacera		30	30	30
Minytrema melanops		7,30	7, 30	
Moxostoma carinatum		30	30	30
Moxostoma duquesnei		8,25,30	8, 30	8,25
Moxostoma valenciennesi		8,27,30	8, 27, 30	27,30
Ictalurus furcatus		5,7,30	5, 30	7,30
Noturus flavus		8		8
Noturus furiosus		30	30	
Noturus gyrinus		25,30	30	25,30
Noturus miurus		7,25	7, 25	
Noturus trautmani		27	27	27
Pylodictis olivaris		30	30	30
Percopsis omiscomaycus		30		30
Fundulus notatus		30	30	
Labidesthes sicculus		30	30	
Culaea inconstans		30	30	
Ambloplites rupestris		29	29	
Lepomis gibbosus		9,25,30	9, 25, 30	9
Lepomis megalotis		29,30	29, 30	
Micropterus dolomieui	23,30	23,30	23, 30	23,30
Micropterus salmoides		23,30	23, 30	23,30
Ammocrypta asprella		29,30		29,30
Ammocrypta clara		29		29
Ammocrypta pellucida		27,30		27,30

Table 7. Continued --

Species	Effect		Impact through	
	Spawning	General	Suspended solids	Sediment
Etheostoma blennioides		30		30
Etheostoma exile		27, 30	27,30	
Etheostoma tippecanoe		27		27
Etheostoma zonale		29		29
Perca flavescens	25,30	25,30	25,30	25,30
Percina caprodes		7,30	7	30
Percina copelandi		27,30	27, 30	27,30
Percina evides		29,30	30	29
Percina maculata		30	30	
Percina phoxocephala		27,30	27, 30	27,30

Table 8. Warmwater fishes which are tolerant of suspended solids and sediment. Numbers refer to references listed in Table 10.

Species	General tolerance	Preference for turbid systems
Scaphirhynchus albus	7	
Dorosoma cepedianum		30
Hiodon alosoides	25, 30	
Carassius auratus	30	
Couesius plumbeus	3	
Cyprinus carpio		19, 25, 30
Ericymba buccata	5, 14, 30	27
Hybopsis gelida	5	
Hybopsis gracilis	5	
Notropis dorsalis		27
Notropis lutrensis		7, 27
Orthodon microlepidotus	19	
Phenacobius mirabilis	7, 30	
Phoxinus oreas	9	
Pimephales promelas	7, 30	29
Pimephales vigilax	7, 30	
Plagopterus argentissimus	5	
Semotilus atromaculatus	7, 22	29
Catostomus commersoni	9, 30	
Ictiobus cyprinellus	7, 25, 30	
Moxostoma erythrurum	30	
Ictalurus catus	30	
Ictalurus melas	7	25, 30
Aphredoderus sayanus	30	
Lepomis cyanellus	7, 30	
Lepomis humilis	7, 27, 30	
Lepomis microlophus	29	
Micropterus punctulatus	11, 23, 30	
Micropterus treculi	18, 23	
Pomoxis annularis	12, 26, 30, 31	
Pomoxis nigromaculatus	7, 12, 20, 25	
Etheostoma gracile	7	
Etheostoma microperca	30	
Etheostoma nigrum	30	
Etheostoma spectabile	7, 30	
Stizostedion canadense	6, 25, 30	
Aplodinotus grunniens	30	

Table 9. Warmwater fishes for which contradictory information was found on their tolerance or intolerance to suspended solids and sediment. Numbers refer to references listed in Table 10.

Species	Tolerant	Intolerant
Campostoma anomalum	7	30
Clinostomus funduloides	9	27
Hybognathus nuchalis	2, 7	30
Notropis buchanani	7	30
Notropis spilopterus	30	7, 10
Notropis umbratilis	5, 29	7, 30
Pimephales notatus	30	7
Rhinichthys atratulus	9	30
Carpiodes carpio	7, 30	5
Ictalurus nebulosus	20	30
Ictalurus punctatus	7, 16, 17	4, 25, 30
Morone chrysops	20	25, 30
Lepomis gulosus	15	30
Lepomis macrochirus	20	9, 30
Etheostoma flabellare	25, 30	9
Stizostedion vitreum	1, 20, 25	27, 30

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SECTION VII

RESEARCH NEEDS

One conclusion that we drew from this literature review was that many of our long held beliefs as to the impacts of suspended solids and sediment on fish reproduction are based on very circumstantial evidence. Much of our current knowledge eminates from ichthyofaunistic studies reporting changes in community structure or species distribution over time. Increased sediment load may well contribute greatly to these observed changes, but is one of many environmental conditions that changed over these time spans. Very little experimental evidence, based either on controlled laboratory studies or well designed field studies, exists upon which to judge the widespread impacts of suspended solids and sediment on warmwater fish reproductive success. We, therefore, strongly disagree with the following statement by Sorensen et al. (1977:47): "Considerable amounts of research have been published on the effects of dissolved and suspended solids on fishes, consequently additional research should have a lower priority."

We feel that the following experimental approaches hold promise for contributing needed information on the effects of suspended solids and sediment on warmwater fish reproductive success:

1) Research is needed for most species to experimentally determine the lethal and sublethal effects on all life stages of fish chronically exposed to elevated levels of suspended solids and sediment. Acute studies are of use primarily for effects on embryonic development of species with relatively short incubation periods. Although few laboratory experiments have been conducted seeking to determine the effects on fish of chronic exposure to suspended solids, these should be designed and carried out.

2) On a larger scale, well-designed, long-term, studies carried out in replicated ponds or experimental streams should be devised to test modes of action of suspended solids and sediments on fish reproductive success.

3) Ultimately, realistic experiments could be undertaken in well-monitored watersheds to relate quantity and quality of sediment variables to ecological conditions and faunal variables. Fish reproductive success should be related to runoff situations under conditions in which both runoff and reproduction are studied simultaneously. Experiments should be duplicated on enough watersheds to obtain a subclassification of pollutant-related effects to soil groups, pesticide residue, and cropping system.

4) It is reasonable to expect that further evaluation of the literature could provide sufficient information to compare the reproductive strategies of over 200 warmwater species and numerous coldwater fishes as well. Cluster analysis is an effective tool in making such comparisons. Such an analysis should prove quite useful in further evaluating the impact of suspended solids and sediment on fish reproductive success.

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SECTION IX

APPENDIX

Alphabetical listing of scientific and common names of fishes (Bailey et al. 1970) cited in text, figures and tables. Six species* starred are not listed in Bailey et al. 1970.

Scientific name		
Genus	Species	Common name
Acipenser	fulvescens	lake sturgeon
Alosa	aestivalis	blueback herring
Alosa	pseudoharengus	alewife
Alosa	sapidissima	American shad
Ambloplites	rupestris	rock bass
Amia	calva	bowfin
Ammocrypta	asprella	crystal darter
Ammocrypta	clara	western sand darter
Ammocrypta	pellucida	eastern sand darter
*Anguilla	anguilla	European eel
Aphredoderus	sayanus	pirate perch
Aplodinotus	grunniens	freshwater drum
Archoplites	interruptus	Sacramento perch
*Barbus	fluviatalis	European barbel
*Brachydanio	rerio	zebra danio (fish)
Campostoma	anomalum	stoneroller
Carassius	auratus	goldfish
Carpiodes	carpio	river carpsucker
Carpiodes	velifer	highfin carpsucker
Catostomus	catostomus	longnose sucker
Catostomus	commersoni	white sucker
Clinostomus	elongatus	redsided dace
Clinostomus	funduloides	rosy dace
Clupea	harengus	Atlantic herring
Coregonus	artedii	lake herring
Couesius	plumbeus	lake chub
*Ctenopharyngodon	idella	grass carp
Culaea	inconstans	brook stickleback
Cycleptus	elongatus	blue sucker
Cyprinodon	variegatus	sheepshead minnow
Cyprinus	carpio	carp
Dionda	nubila	Ozark minnow
Dorosoma	cepedianum	gizzard shad
Dorosoma	petenense	threadfin shad

Appendix continued --

Scientific name		
Genus	Species	Common name
Ericymba	buccata	silverjaw minnow
Erimyzon	oblongus	creek chubsucker
Erimyzon	sucetta	lake chubsucker
Esox	a. americanus	redfin pickerel
Esox	lucius	northern pike
Esox	masquinongy	muskellunge
Esox	niger	chain pickerel
Etheostoma	blennioides	greensided darter
Etheostoma	caeruleum	rainbow darter
Etheostoma	camurum	bluebreast darter
Etheostoma	exile	Iowa darter
Etheostoma	flabellare	fantail darter
Etheostoma	gracile	slough darter
Etheostoma	kennicotti	stripetail darter
Etheostoma	microperca	least darter
Etheostoma	nigrum	johnny darter
Etheostoma	proeliare	cypress darter
Etheostoma	radiosum	orangebelly darter
*Etheostoma	smithi	slabrock darter
Etheostoma	spectabile	orangethroat darter
Etheostoma	tippecanoe	tippecanoe darter
Etheostoma	zonale	banded darter
Exoglossum	laurae	tonguetied minnow
Exoglossum	maxillingua	cutlips minnow
Fundulus	notatus	blackstripe topminnow
Gambusia	affinis	mosquitofish
Gasterosteus	aculeatus	threespine stickleback
Gila	elegans	bonytail
Gillichthys	mirabilis	longjaw mudsucker
Hesperoleucus	symmetricus	California roach
Hiodon	alosoides	goldeye
Hiodon	tergisus	mooneye
Hybognathus	nuchalis	silvery minnow
Hybopsis	amblops	bigeye chub
Hybopsis	dissimilis	streamline chub
Hybopsis	gelida	sturgeon chub
Hybopsis	gracilis	flathead chub
Hybopsis	x-punctata	gravel chub
Hypentelium	nigricans	northern hog sucker
Ichthyomyzon	castaneus	chestnut lamprey
Ictalurus	catus	white catfish
Ictalurus	furcatus	blue catfish
Ictalutus	melas	black bullhead
Ictalurus	natalis	yellow bullhead

Appendix continued --

Scientific name		
Genus	Species	Common name
Ictalurus	nebulosus	brown bullhead
Ictalurus	punctatus	channel catfish
Ictiobus	cyprinellus	bigmouth buffalo
Jordanella	floridae	flagfish
Labidesthes	sicculus	brook silverside
Lagochila	lacera	harelip sucker
Lampetra	lamottei	American brook lamprey
Lavinia	exilicauda	hitch
Lepisosteus	osseus	longnose gar
Lepisosteus	platostomus	shortnose gar
Lepomis	auritus	redbreast sunfish
Lepomis	cyanellus	green sunfish
Lepomis	gibbosus	pumpkinseed
Lepomis	gulosus	warmouth
Lepomis	humilis	orangespotted sunfish
Lepomis	macrochirus	bluegill
Lepomis	megalotis	longear sunfish
Lepomis	microlophus	redear sunfish
Micropterus	coosae	redeye bass
Micropterus	dolomieui	smallmouth bass
Micropterus	notius	Suwannee bass
Micropterus	punctulatus	spotted bass
Micropterus	salmoides	largemouth bass
Micropterus	treculi	Guadalupe bass
Minytrema	melanops	spotted sucker
Morone	americana	white perch
Morone	chrysops	white bass
Morone	saxatilis	stiped bass
Moxostoma	anisurum	silver redhorse
Moxostoma	ariommum	bigeye jumprock
Moxostoma	carinatum	river redhorse
Moxostoma	duquesnei	black redhorse
Moxostoma	erythrurum	golden redhorse
Moxostoma	macrolepidotum	shorthead redhorse
Moxostoma	valenciennesi	greater redhorse
Mylocheilus	caurinus	peamouth
Nocomis	biguttatus	hornyhead chub
Nocomis	micropogon	river chub
Notemigonus	crysoleucas	golden shiner
Notropis	amnis	pallid shiner
Notropis	analostanus	satinfin shiner
Notropis	bifrenatus	bridle shiner
Notropis	boops	bigeyed shiner

Appendix continued --

Scientific name		
Genus	Species	Common name
Notropis	buchanani	ghost shiner
Notropis	chalybaeus	ironcolor shiner
Notropis	cornutus	common shiner
Notropis	dorsalis	bigmouth shiner
Notropis	emiliae	pugnose shiner
Notropis	girardi	Arkansas River shiner
Notropis	heterodon	blackchin shiner
Notropis	heterolepis	blacknose shiner
Notropis	hudsonius	spottail shiner
Notropis	longirostris	longnose shiner
Notropis	lutrensis	red shiner
Notropis	procne	swallowtail shiner
Notropis	rubellus	rosyface shiner
Notropis	spilopterus	spotfin shiner
Notropis	stramineus	sand shiner
Notropis	texanus	weed shiner
Notropis	topeka	Topeka shiner
Notropis	umbratilis	redfin shiner
Notropis	volucellus	mimic shiner
Noturus	flavus	stonecat
Noturus	furiosus	Carolina madtom
Noturus	gyrinus	tadpole madtom
Noturus	miurus	brindle madtom
Noturus	trautmani	Scioto madtom
Opsanus	tau	oyster toadfish
Orthodon	microlepidotus	Sacramento blackfish
Osmerus	mordax	rainbow smelt
Perca	flavescens	yellow perch
*Perca	fluviatilus	perch
Percina	caprodes	logperch
Percina	copelandi	channel darter
Percina	evides	gilt darter
Percina	maculata	blackside darter
Percina	phoxocephala	slenderhead darter
Percopsis	omiscomaycus	trout-perch
Petromyzon	marinus	sea lamprey
Phenacobius	mirabilis	suckermouth minnow
Phoxinus	eos	northern redbelly dace
Phoxinus	oreas	mountain redbelly dace
Pimephales	notatus	bluntnose minnow
Pimephales	promelas	fathead minnow
Pimephales	vigilax	bullhead minnow
Plagopterus	argentissimus	woundfin
Polyodon	spathula	paddlefish
Pomoxis	annularis	white crappie

Appendix continued --

Scientific name		
Genus	Species	Common name
Pomoxis	nigromaculatus	black crappie
Ptychocheilus	oregonensis	northern squawfish
Pylodictis	olivaris	flathead catfish
Rhinichthys	atratulus	blacknose dace
Richardsonius	balteatus	redside shiner
Salmo	gairdneri	rainbow trout
Salmo	trutta	brown trout
Scaphirhynchus	albus	pallid sturgeon
Semotilus	atromaculatus	creek chub
Stizostedion	canadense	sauger
Stizostedion	v. vitreum	walleye
Tinca	tinca	tench
Umbra	limi	central mudminnow
Xyrauchen	texanus	humpback sucker

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16 ABSTRACT

Review of published literature and research reports revealed limited data for a few warmwater fish species concerning the impacts of suspended solids and sediments on reproductive success. Laboratory and field studies during the 1930-50s examined direct mortality as the result of extremely high levels of suspended solids. Controversy ensued in the 1940-60s over the impacts of turbidity on fish populations in the Great Lakes and midwestern rivers. Variations in year-class strength of important fishes have not been correlated with sediment loading, concentrations of suspended solids, nor sedimentation rates. Renewed interest in suspended solid impacts on aquatic ecosystems was evident in 1970s as indicated by published literature and symposia reporting laboratory bioassays and ecological field studies. Species and stages of warmwater fishes are not equally susceptible to suspended solids. Only limited circumstantial evidence was found on the potential effects on gonad development in fish. There was substantial evidence that reproductive behavior was variously affected by suspended solids and sediment relative to spawning time, place of spawning, and spawning behavior. The more adaptively successful species reproductive activities were not carried on at times of highest turbidity. Fishes with complex patterns of reproductive behavior are more vulnerable to interference by suspended solids at a number of critical behavioral phases during the pawning process. Incubation stage is particularly susceptible to adverse effects from sediment.

17 KEY WORDS AND DOCUMENT ANALYSIS

a DESCRIPTORS	b IDENTIFIERS/OPEN ENDED TERMS	c COSATI Field/Group

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