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Oligotrophication and Its Discontents: Effects of Reduced Nutrient Loading on Reservoir Fisheries

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Abstract.—Oligotrophication is the reversal of the eutrophication process and can occur in reservoirs as the result of nutrient trapping in upstream impoundments or of operation of advanced waste treatment (AWT) facilities on inflowing rivers. I examined the response of reservoir fisheries to oligotrophication using case studies and regression analysis of the relationship between concentration of phosphorus, the principal limiting nutrient, and fishery productivity. In Smith Mountain Lake, Virginia, and Beaver Lake, Arkansas (upstream AWTs), and in Lake Mead, Nevada (upstream impoundment), oligotrophication was accompanied by declines of more than 50% of standing stock of planktivorous forage fishes and reductions in growth, standing stock, or harvest of piscivorous sport fishes. Both phytoplankton and total fish productivity were highly correlated (r = 0.7–0.9) with total phosphorus concentration in lakes and reservoirs, increasing linearly over a wide range of concentrations. Eutrophication status, in terms of cholorophyll *a* and water transparency, is achieved in temperate storage reservoirs when total phosphorus concentration exceeds 40 μg/L, but sport fish biomass probably does not peak at less than 100 μg/L, providing the basis for conflicts among reservoir user groups. Remedial measures to restore reservoir sport fisheries following oligotrophication include species introductions and in-lake fertilization, both of which are unlikely to be successful. Prevention of oligotrophication through top-down manipulation of the food web has the potential to promote both "clean" lakes and good fishing, but will probably not be effective in large eutrophic impoundments. A more promising approach is to prevent undesirable oligotrophication through informed decision making. Fisheries scientists first must collaborate with limnologists to predict the impacts of proposed nutrient loading reductions on reservoir fisheries, then act as educators and advocates for their resource.

The limnological term "eutrophication" has become synonymous in the public consciousness with water quality degradation. Eutrophication is the process through which aquatic plant and other biomass of a waterbody increases (Lee and Jones 1991), most often as the result of nutrient additions. Because the buildup of plant (algae and macrophyte) biomass is considered undesirable for aesthetic and recreational uses (Heiskary and Walker 1988; Harper 1992), the United States and many other countries have undertaken large programs to reduce nutrient concentrations in surface waters (Moore and Thornton 1988). These well-intentioned efforts generally ignore nonplant biomass, under the perception that "cleaner" water will benefit all aquatic life forms, including fish. However, community energetics dictates otherwise: the biomass of fish at or near the top of the trophic pyramid is highly dependent on the amount of primary production at the base (Lindemann 1942). Consequently, expected outcomes of reduced nutrient loading should include not only less algae and clearer water, but also lower total fish biomass and, to the degree that sport fishes are affected, poorer fishing and lower angler satisfaction (Yurk and Ney 1989).

Phosphorus is usually the limiting nutrient for primary production in surface waters and the focus of nutrient reduction programs. Decreases in water column phosphorus concentrations may reduce biological productivity at all trophic levels; this reversal of the eutrophication process is oligotrophication. Where the process is induced by human actions, the term "cultural oligotrophication" properly may be applied.

Reservoirs are particularly susceptible to experiencing large and rapid reductions in phosphorus and other nutrient concentrations because of their dependence on upstream water quality. The two principal causes of oligotrophication of reservoirs are point-source nutrient abatement programs on tributary rivers and construction of upstream impoundments. Both actions have been widely implemented, but the consequences to the fisheries of downstream reservoirs have seldom been considered in advance or documented afterwards.

I reviewed case histories of reservoir fisheries responses to phosphorus reductions from both nutrient abatement programs and upstream dams, examined the relation of phosphorus to water quality and fisheries productivity, and critiqued alternatives

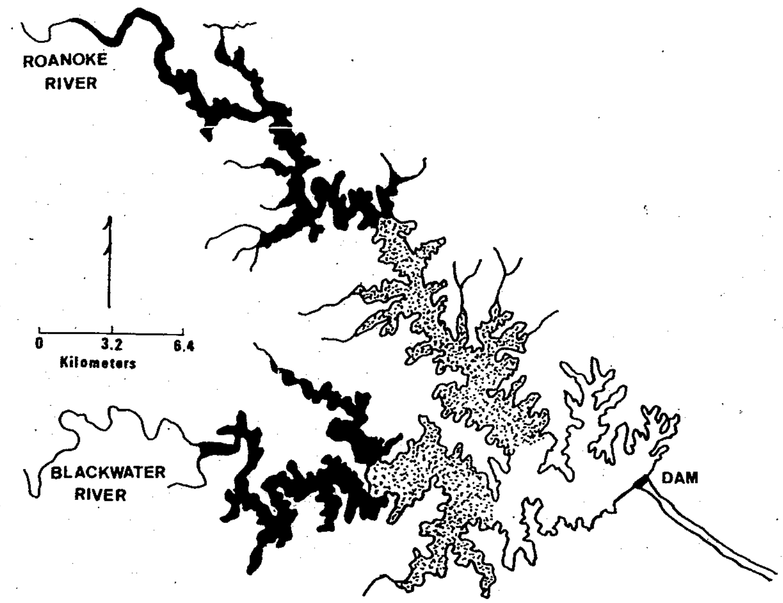

FIGURE 1.—Smith Mountain Lake, Virginia. Stippled and darkened areas experienced summer hypolimnetic oxygen deficits in 1974, before nutrient abatement. Only darkened portions had such deficits during 1984–1994.

for prevention as well as remediation of the consequences of oligotrophication.

Case Studies

Response to Nutrient Abatement Programs

Smith Mountain Lake, Virginia, is an 8,300-ha hydroelectric impoundment on the Roanoke River (Figure 1). This highly dendritic reservoir was impounded in 1963 and soon developed a premier fishery for black bass *Micropterus* spp. and stocked striped bass *Morone saxatilis*. The forage fish resource was dominated by alewife *Alosa pseudoharengus* and gizzard shad *Dorosoma cepedianum*. In response to complaints about algal blooms in the upper section of the reservoir, an advanced waste treatment plant (AWT) began operation in the city of Roanoke, 40 km upstream, in 1975. Yurk and Ney (1989) compared mean annual epilimnetic total phosphorus concentrations with estimates of fish standing stock (kg/ha) obtained from cove rotenone samples over the 12-year period 1973–1984. Total phosphorus concentration declined 79% while total fish standing stock dropped 76%. Standing stock of planktivorous fishes (primarily gizzard shad) was highly correlated (r = 0.81) with total phosphorus, but biomass of piscivorous sport fish was not (r = 0.01). However, the annual growth rate (in total length) of black bass and striped bass declined about 12% between 1973 and 1984 (Ney et al. 1988).

The apparent lack of relationship between phosphorus concentration and piscivore standing stock may be spurious. Standing stock of piscivores, particularly pelagic fishes such as striped bass, is poorly estimated by cove rotenone sampling (Davies and Shelton 1983); creel survey data indicate that striped bass harvest in Smith Mountain Lake was 65% lower in 1984 than in 1977 (Hart 1978; Whitehurst 1987). However, oligotrophication did expand potential summer habitat for striped bass. By 1984, the percentage of Smith Mountain Lake (by surface area) experiencing summer hypolimnetic oxygen deficits contracted by 60%, doubling the suitable habitat (≤24°C, ≥5 mg/L dissolved oxygen) for this coolwater species (Figure 1). The trade-off between less food and more habitat might have partially mitigated nutrient abatement impacts on the sportfish resource in this case. Between 1984 and 1994, the phosphorus–fishery relationship stabilized in Smith Mountain Lake; total phosphorus concentration averaged about 20 μg/L and total fish standing stock fluctuated around 370 kg/ha. Summer habitat for coolwater fish also stabilized (Figure 1).

Beaver Lake, Arkansas, has experienced a more recent, but similar, response to an upstream nutri-

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ent abatement program. Beaver Lake is an 11,000-ha flood control hydroelectric impoundment on the White River, which historically provided about 60% of the phosphorus load to the lake (Aggus 1985). In 1987, an AWT went into service in the upstream city of Fayetteville, reducing phosphorus load to Beaver Lake by about 50%. Before-and-after comparisons of mean annual standing stock, as described by cove rotenone sampling for the 6-year periods 1982–1987 and 1988–1993 showed reductions of 55% in planktivorous clupeids and 9% in piscivorous sport fishes (primarily black bass and ictalurids). Possible changes in sportfish growth rate and condition as consequences of the shad decline have not been investigated, and long-term effects of the phosphorus loading reduction on the fishery have not been extrapolated. Further, there is some indication that the AWT-induced reduction may eventually be replaced with phosphorus from other sources (M. Bivin, Arkansas Game and Fish Commission, personal communication).

The phosphorus–fish biomass relationship has been poorly documented for most other reservoir systems with upstream AWTs. However, anecdotal evidence of fisheries responses is abundant and usually negative in terms of post-AWT changes in biomass, growth, or harvest. Further substantiation of the impact of phosphorus abatement programs on fishery productivity is provided by the ongoing saga in Lake Ontario (Great Lakes Fishery Commission 1992). A basinwide nutrient abatement program has resulted in a 25% reduction in the total phosphorus concentration in offshore Lake Ontario since the early 1980s. Although water transparency has increased 20%, zooplankton production has dropped 50%, as has the forage fish biomass (rainbow smelt *Osmerus mordax* and alewife). Weight and condition of stocked salmonids has begun to decrease, and dead and dying salmon are collected in trawl catches. State and provincial fisheries agencies reduced annual salmonid stockings by 50% in 1993 to adjust predator abundance to the lower prey supply (Jude and Leach 1993). Despite a potentially large economic impact on the sport fishery, the Lake Ontario nutrient abatement program will continue due to a "strong international commitment to water quality enhancement" (Great Lakes Fishery Commission 1992).

Effects of Upstream Impoundments

Most large river systems in the United States host series of impoundments, including those built primarily for navigation. In the Southeast, about 75% of major (>500 ha) impoundments are arranged in series (Soballe et al. 1992). Because it functions as a nutrient and sediment trap, each new upstream reservoir has the potential to diminish the fertility of existing downstream impoundments. The degree of oligotrophication will be situation specific, depending on watershed nutrient load, water retention time, reservoir morphometry, and depth of the discharge port (epilimnetic or hypolimnetic).

Lake Mead, Nevada–Arizona, is perhaps the best documented example of fisheries response to nutrient deprivation following upstream dam construction. Lake Mead is a 66,000-ha storage reservoir on the Colorado River impounded in 1935. A highly successful fishery for largemouth bass *Micropterus salmoides* soon developed. Threadfin shad *Dorosoma petenense* was introduced as forage in the mid 1950s. Glen Canyon Dam, 450 km upstream of Lake Mead, was closed in 1963, creating Lake Powell. The new reservoir retained up to 90% of the phosphorus load in the Colorado River (Gloss et al. 1981), and much of the remainder entered Lake Mead as a density current deeper than the photic zone (Prentki and Paulson 1983). The new dam also substantially altered the annual flow regime of the Colorado River: spring floods were replaced with 2–3-m drawdowns in Lake Mead (Evans and Paulson 1983). Annual harvest of largemouth bass declined 50% by 1969, apparently due to poor reproduction resulting from the spring drawdowns (Romero and Allan 1975). Striped bass and rainbow trout *Oncorhynchus mykiss* were introduced in 1969 as limnetic predators of threadfin shad. The trout fishery soon collapsed under predation by striped bass, which established a large reproducing population (Baker and Paulson 1983). Between 1975 and 1980, the threadfin shad population also crashed, in response to both intense predation by striped bass and declining primary productivity (Paulson 1994). Adult striped bass soon became emaciated and experienced die-offs, but managed to reproduce successfully. Lake Mead has shifted from mesotrophic to oligotrophic status (<10 μg/L total phosphorus), and the fishery is now dominated by small striped bass in poor condition (Paulson 1994). Although it is not possible to precisely partition the effects of species introductions and reduced lake fertility, it is evident that the fishery of Lake Mead has suffered from oligotrophication (Kimmel et al. 1990).

In particular situations, upstream impoundments may enhance primary production (and perhaps fishery productivity) of downstream reservoirs by increasing the availability of nutrients during the growing season. Elser and Kimmel (1985) theorized

TABLE 1.—Predictive relationships between measures of plant and fish productivity in lakes and reservoirs, as determined from single-variable regression models.

Independent variable	Dependent variable	Data set (N)	Percent of variation explained (r^2)	Source
Gross photosynthesis	Total fish yield	Indian lakes (15)	82	Melack (1976)
Phytoplankton standing stock	Total fish yield	Natural lakes, northern hemisphere (19)	84	Oglesby (1977)
Gross photosynthesis	Total fish yield	Chinese lakes and ponds (18)	76	Liang et al. (1981)
Chlorophyll *a*	Sport fish yield	Midwestern U.S. lakes and reservoirs (25)	83	Jones and Hoyer (1982)
Primary production	Total fish production	Cosmopolitan lakes (19)	67	Downing et al. (1990)

that deep-discharge storage reservoirs, which release nutrients downstream in late summer, stimulate algal production more than unregulated river discharge, which carries peak nutrient loads in the winter–spring periods.

Phosphorus, Fisheries, and Water Quality

Enhancement of water quality is the principal goal of nutrient abatement programs and may also be considered a benefit of upstream impoundment. As applied to lakes and reservoirs, water quality and lake trophic status are usually defined in terms of phytoplankton production and water transparency, most often measured as chlorophyll *a* (mg/m^3) and Secchi disk disappearance depth (Carlson 1977; Moore and Thornton 1988). Dense growths of aquatic macrophytes are sometimes perceived as a water quality problem in shallow, relatively stable reservoirs, but excessive algae and resultant low transparency are considered a more ubiquitous threat to aesthetic and recreational uses (Heiskary and Walker 1988; Klessig et al. 1988).

Primary production in most lentic waters is limited by phosphorus (Jones and Bachmann 1976; USEPA 1993), and the correlation between total phosphorus concentration and chlorophyll *a* is strongly positive (Canfield and Bachmann 1981; Maceina et al. 1996, this volume). Regressions of data from several sets of lakes and reservoirs show that the relationship between primary production and various measures of fishery productivity is also strongly positive; differences in the former explain most of the variation in the latter (Table 1). Consequently, it is not surprising that total phosphorus concentration has been an excellent predictor of the standing stock, yield, and production of fish in lakes and reservoirs (Table 2). Because phosphorus promotes both algal and fish production, it would seem that target concentrations for phosphorus management might differ substantially between anglers and other users. A logical first step in optimal phosphorus management in multiple-use waters is to answer two questions: (1) how low must the concentration be to avoid undesirable algal production?; and (2) how high must the concentration be to sustain good fishing? Some effort has been directed to answer the first question, but the phosphorus–fishery issue has received little quantitative attention. What follows is an interpretative synthesis of the state of knowledge regarding desirable phosphorus concentrations in reservoirs.

Phosphorus Concentration and Water Quality

There is general agreement among limnologists that total phosphorus concentrations of 20–30 μg/L are associated with eutrophic conditions in natural lakes (Carlson 1977; Rast and Lee 1978; Wetzel 1983). Eutrophic lakes are characterized by high photosynthetic activity, low (<2.0 m) transparency, and development of anoxic conditions in the hy-

TABLE 2.—Relationship between total phosphorus concentration (μg/L) as the independent variable and various measures of fish production in lakes and reservoirs.

Dependent variable	Data set (N)	Percent of variation explained (r^2)	Source
Total yield	North American lakes (21)	84	Hanson and Leggett (1982)
Sport fish yield	Midwestern U.S. lakes and reservoirs (21)	52	Jones and Hoyer (1982)
Total standing stock	Southern Appalachian (U.S.) reservoirs (21)	84	Ney et al. (1990)
Piscivore standing stock	Southern Appalachian (U.S.) reservoirs (11)	51	Ney et al. (1990)
Total fish production	Cosmopolitan lakes (14)	67	Downing et al. (1990)

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polimnion (USEPA 1993). However, there is a great deal of variability among lakes in the phosphorus–phytoplankton relationship. In the National Eutrophication Survey (NES) of 894 U.S. lakes and reservoirs, only 40% of lakes with total phosphorus of 40 μg/L were considered eutrophic; at 60 μg/L, the eutrophic percentage climbed to sixty (Walker 1988).

User perceptions ultimately determine whether the phosphorus concentration of a water body is acceptable. Heiskary and Walker (1988) surveyed users of 99 Minnesota natural lakes, finding that impairment of physical appearance and swimming use occurred in only 25% at 40 μg/L total phosphorus and 50% at 60 μg/L.

Chlorophyll-*a* concentrations tend to be lower in reservoirs than in natural lakes (Soballe et al. 1992) because higher turbidity and flushing rates may limit the ability of phosphorus to stimulate phytoplankton production (Maceina et al. 1996). In the southeastern United States, storage reservoirs on tributary streams have higher chlorophyll-*a* levels at particular phosphorus concentrations than do mainstem, run-of-the-river impoundments (Soballe et al. 1992). Algal production is particularly low in reservoirs with retention times less than 7 d, the approximate phytoplankton doubling rate (Kimmel et al. 1990). In a comparative analysis of the NES data set, Canfield and Bachmann (1981) found that reservoirs tended to have substantially lower chlorophyll-*a* levels than natural lakes at the same phosphorus concentrations. Interpretation of their scatter diagram indicates that to produce 10.0 mg/m^3 of chlorophyll *a*, indicative of eutrophic status, the average natural lake would require 30 μg/L total phosphorus, whereas the average reservoir would need 40 μg/L.

In summary, excessive algal production is defined by user perception, and the phosphorus concentrations causing it vary with the characteristics of the water body (morphometry, chemistry, and hydrology). A conservative, "not to exceed" target for storage reservoirs appears to be 40 μg/L total phosphorus. Because this concentration is a whole-lake average, localized nuisance algae problems still may occur, particularly near nutrient point sources. For highly turbid or rapidly flushing systems, higher phosphorus concentrations may produce no objectionable results.

The concentration of total phosphorus in U.S. reservoirs ranges from less than 10 to more than 100 μg/L (Dodd et al. 1988; Yurk and Ney 1989; Soballe et al. 1992). Because of their higher ratios of drainage to surface areas and their dependence on river nutrient load, reservoirs are more frequently eutrophic than are natural lakes. Nutrient abatement programs can be expected to affect the biological productivity of more reservoirs in the future.

Phosphorus Concentration and Fishery Productivity

Regression analysis has also been used to determine how fish standing stock and production vary with total phosphorus concentration (Table 2). The strength of these relations (r^2) and their shape (i.e., linear, asymptotic, or parabolic) can be examined to develop a first-order estimate of how much phosphorus is required to maximize fishery productivity.

Only one of these empirical analyses has focused exclusively on reservoirs. Ney et al. (1990) examined the relationship between fish standing stock and a variety of potential predictors in a set of 21 southern Appalachian reservoirs for which fishery and water chemistry information was available for similar lengths of time ($\pm$2 years). These reservoirs varied greatly in surface area (1,700–132,000 ha), retention time (4–438 d), and total standing stock (77–2,321 kg/ha). Total phosphorus was the best predictor of fish standing stock ($r^2 = 0.84$; Figure 2), followed by Secchi disk depth (negative slope; $r^2 = 0.42$) and $\log_{10}$chlorophyll *a* ($r^2 = 0.31$). Retention time and the morphoedaphic index (MEI, total dissolved solids/mean depth) had no predictive power ($P > 0.3$ for each variable) in this data set ($r^2 = 0.01$ and 0.14, respectively). Fish standing stock increased linearly over the range of total phosphorus concentrations (8–81 μg/L) in the southern Appalachian reservoirs, suggesting that maximum fish biomass would occur at higher phosphorus concentrations.

Downing et al. (1990) reported a linear increase in total annual fish production (kg/ha) through 100 μg/L total phosphorus for a data set of 13 natural, northern hemisphere lakes. However, inclusion of fish production in a hypereutrophic African lake (9,850 μg/L total phosphorus) produced a curvilinear regression, suggesting that fish production will peak somewhere between 100 and 1,000 μg/L total phosphorus in temperate waters.

Total fish standing stock or total fish production may not be indicative of sportfishing potential of reservoirs because sport and food fishes usually account for less than half of that total (USEPA 1993). Three studies have examined the relationship between total phosphorus and sport or food fish productivity. For the southern Appalachian reservoirs data set, Yurk and Ney (1989) found that

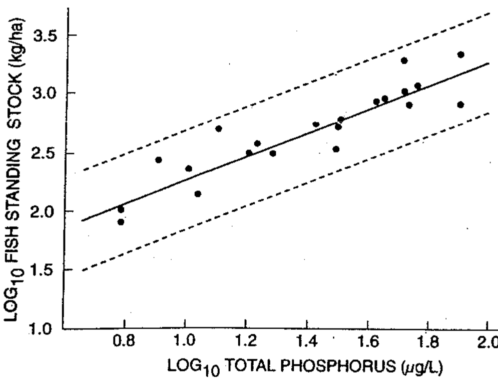


FIGURE 2.—Regression of $\log_{10}$ total fish standing stock (FSS) versus $\log_{10}$ total phosphorus (TP) concentration for 21 southern Appalachian reservoirs. $\text{Log}_{10}\text{FSS} = 1.24 + 1.02\log_{10}\text{TP}$; $r^2 = 0.84$. Dashed lines are 90% predictive limits (from Ney et al. 1990).

piscivore (largely sport fish) standing stock increased linearly over the range of total phosphorus concentrations, however, the relationship was not as strong ($r^2 = 0.51$) as for planktivores ($r^2 = 0.84$).

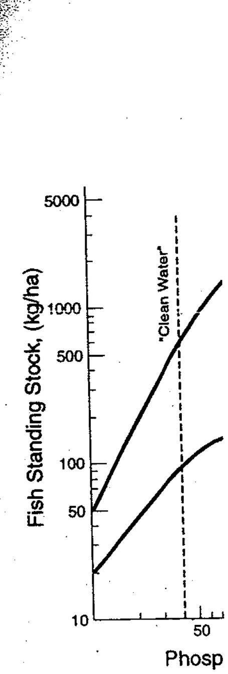
Jones and Hoyer (1982) reported that annual sportfish harvest increased linearly with total phosphorus concentration over the range of 15–90 μg/L in 25 midwestern U.S. lakes and reservoirs ($r^2 = 0.52$). In a study of 21 north temperate natural lakes, Hanson and Leggett (1982) found that long-term sport and commercial annual harvests increased with total phosphorus concentrations up to 500 μg/L ($r^2 = 0.84$). However, only five of the 21 lakes had phosphorus concentrations greater than 100 μg/L.

Within the sport fish complex, individual species are likely to respond differently to varying levels of lake fertility. Schupp and Wilson (1993) compared their knowledge of the relative abundance of several sport fish species in northern U.S. natural lakes to trophic status indicators. Extrapolation of their data indicates that relative abundance of lake trout *Salvelinus namaycush* and walleye *Stizostedion vitreum* peaks at less than 10 μg/L and at 25 μg/L total phosphorus, respectively. Black crappies *Pomoxis nigromaculatus* are most abundant at 70 μg/L total phosphorus, but white crappie *P. annularis* populations do best at more than 100 μg/L total phosphorus. In a study of four large Alabama reservoirs, Bayne et al. (1994) found that largemouth bass growth and harvest were substantially greater in eutrophic systems (50–100 μg/L total phosphorus) than in a mesotrophic (10 μg/L total phosphorus) counterpart. Using an expanded data base of 32 Alabama impoundments, Maceina et al. (1996) confirmed that growth rates and condition of both largemouth bass and crappies were higher in eutrophic than in oligo-mesotrophic reservoirs, but that angler catch rates did not differ significantly with trophic status. They suggested that good fishing and publicly acceptable water clarity (120 cm Secchi disk transparency) might be compatible in Alabama impoundments, although the catch of trophy black bass and crappies would decline. Maceina et al. (1996) developed linear regressions to predict chlorophyll-*a* concentration from total phosphorus level and water clarity from chlorophyll-*a* concentration. In combination, these regressions predict transparency of 120 cm at 13 μg/L chlorophyll *a* and 46 μg/L total phosphorus.

The phosphorus–fishery regressions in the multilake data set (Table 2) failed to clearly identify those total phosphorus concentrations that promote maximum productivity of either the total fish assemblage or the sport fish component, in part because few data points with total phosphorus exceeding 100 μg/L were included. The species-specific analyses above did not consider standing stock or yield as the dependent variable. Clearly, more detailed examinations of the phosphorus–sport fish relationship are warranted (Carline 1986; Lee and Jones 1991).

It is intuitive that both total fish and sport fish productivity in reservoirs will peak at some specific phosphorus concentration as the trade-off between more food and less habitat (through hypolimnetic oxygen depletion or excessive vegetative cover) becomes acute. The sport fish maximum will likely occur at a substantially lower total phosphorus concentration than the total fish maximum. Sport fishes, especially coolwater and coldwater species, are relatively demanding in habitat and reproductive requirements, as the Smith Mountain Lake case study illustrates. Opportunistic, eurytolerant, nonsport species are likely to replace stenotolerant fishes, maintaining or increasing total fish biomass over a range of increasing fertility.

Considered collectively, the available evidence indicates that maximum biomass of sport fish will occur at phosphorus concentrations above 100 μg/L, which will stimulate eutrophic conditions in many reservoirs (Figure 3). Potential for user conflicts over lake trophic status will remain high, and fisheries managers will need to seek innovative means to cope with the threat as well as the realities of induced oligotrophication.



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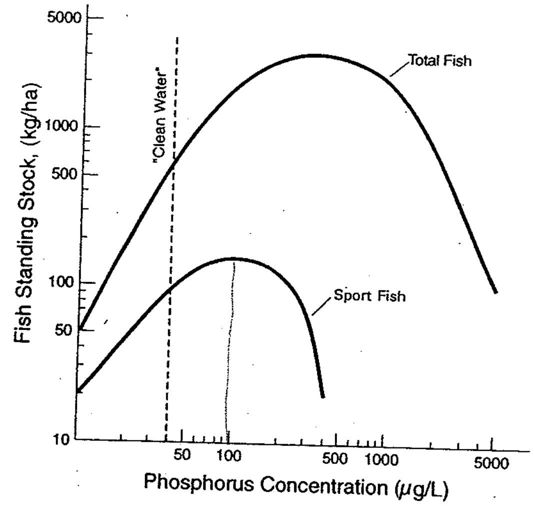

FIGURE 3.—Generalized relation of total and sport fish standing stock to total phosphorus concentration and trophic status in temperate-latitude reservoirs. Standing stock values are representative of southeastern U.S. reservoirs to 100 μg/L total phosphorus. Standing stocks at higher phosphorus concentrations are hypothetical.

Meeting the Challenge of Oligotrophication

Declines in fishery productivity following construction of upstream impoundments or AWTs have usually come as a surprise to both anglers and the general public; reservoir fisheries managers have not been vocal prophets or advocates for their resource. If the challenge of oligotrophication is to be met, fisheries scientists need to be involved at the education and decision-making stages long before construction begins; remedial measures to restore fishery productivity (species manipulations; in-lake fertilization) are likely to achieve limited success at best.

Remedial Measures

Stocking salmonids or coolwater sport fishes to use newly created pelagic habitat may succeed in diversifying a reservoir fishery, but stocking will not restore its productive capacity. There are no precedents by which to evaluate the success of post-oligotrophication species manipulations on angler satisfaction. Fertilizing a large reservoir is a massive undertaking and could arouse the ire of those responsible for nutrient abatement. The only large-scale fertilization experiment reported to date, the Lake Mead Nutrient Enhancement Project, was expensive, ineffective, and controversial (Vaux and Paulson 1990). In May and June 1987, 1,000 volunteers in 300 boats added 76,000 L of ammoniu polyphospate to an 8,000-ha arm of Lake Mead raise the phosphorus concentration and stimula plankton production, thereby increasing reprodu tive success and abundance of threadfin shad. Sin ilar phosphorus additions were made in 1988 ar 1989, but the effects on plankton abundance wei small and transitory; threadfin shad abundance di not increase perceptibly. The Colorado River is major drinking water supply for 20 million peopl and opposition from downstream users caused th experiment to be terminated, despite negligible ir pacts on downstream drinking water quality (Vau et al. 1995).

Preventive Measures

Fisheries managers must be proactive, becomin involved when the first consideration of an up stream impoundment is announced or the first com plaints are made about deteriorating water quality In the latter situation, it may be possible to treat the symptom of eutrophication, excessive algae, through food web management without resorting to nutrien abatement. For either situation, the potential change in nutrient loading and its impact on fishery productivity can be predicted. An informed dialogue among reservoir user groups can then develop before the decision-making stage.

Food web management.—Also known as biomanipulation or the trophic cascade, top-down food web management has great appeal to lake and reservoir managers because it promises both good fishing and clear water (Ney 1993). The central premise of top-down management is that planktivorous fishes affect algal abundance through intense predation on zooplankton. Predation pressure on zooplankton can be relieved by the addition of piscivorous sport fishes to prey on the planktivores. Large, efficiently grazing zooplankton then reappear to crop phytoplankton, improving water clarity (Carpenter et al. 1985). A number of case studies in natural lakes, ranging from small New England ponds to Lake Michigan, provide evidence that top-down food web manipulations do sometimes succeed in improving water clarity (Hayes et al. 1993). However, it appears unlikely that increasing the abundance of piscivorous sport fishes will in itself overcome the effects of bottom-up algal productivity due to high nutrient loading. An ambitious experiment in 4,000-ha, eutrophic Lake Mendota, Wisconsin, demonstrated the limitations of top-down management (Kitchell 1992). Between 1987 and 1989, fingerling walleye and northern pike *Esox*

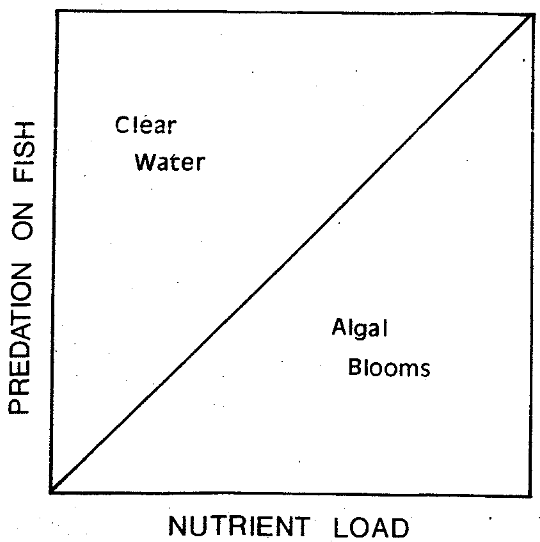

FIGURE 4.—Opposing effects of predation on zooplankton-feeding fish and nutrient loading on the potential for algal blooms in reservoirs and lakes. (Adapted from Kitchell and Carpenter 1992.)

lucius were stocked at an annual combined rate of 140/ha to reduce the abundance of planktivorous cisco *Coregonus artedi* and yellow perch *Perca flavescens*. In succeeding years, yellow perch and cisco year-class strength declined, but summer algal blooms still occurred in wet, high-runoff years. In reviewing the Lake Mendota experiment, Kitchell and Carpenter (1992) concluded that top-down and bottom-up processes interact to affect algal production and water clarity over years and among water bodies (Figure 4).

The potential for top-down control of algal blooms in reservoirs will be limited also by the characteristics of the forage fish resource and the ability to manipulate piscivore abundance (USEPA 1993). Gizzard shad are the dominant forage species in many U.S. reservoirs and rapidly grow too large to be vulnerable to predators (Noble 1981). Gizzard shad also feed on both phytoplankton and zooplankton, complicating the food web and energy flow pathways. In most situations, economic constraints will dictate that an effective increase in predation by piscivores can happen only through the establishment of self-sustaining populations, which may not be easily manipulated. The explosion of the striped bass population and subsequent crash of rainbow trout and threadfin shad in Lake Mead provides a cautionary example (Paulson 1994). In summary, predator–prey manipulations must still be considered as a highly experimental option for preventing reservoir oligotrophication.

Informed decision-making.—The consequences of proposed nutrient abatement programs for reservoir fisheries can be predicted and used in the decision-making process to determine how much, if any, reduction in point source nutrient loading to impose. Limnologists have developed accurate models for projecting water column phosphorus concentration from annual phosphorus load (reviewed by Walker 1988). Prediction of sport fish standing stock from water column phosphorus concentration is less certain, but first-order approximations are clearly possible (see preceding section).

Prediction of impacts of a potential upstream impoundment on the fishery of a downstream reservoir is more complicated but may offer an opportunity to recommend beneficial alterations in dam design and operation. Downstream changes in nutrient loading will depend on outlet depth, annual discharge regime, retention time, reservoir morphometry, and sediment transport as well as incoming nutrient load. Limnologists must be consulted to estimate how much of the nutrient load will reach the dam and at what depth. A deep discharge will not effectively transport nutrients downstream during the growing season unless nutrients accumulate in an anoxic hypolimnion adjacent to the dam and summer releases are substantial and consistent (Soballe et al. 1992). If the temperature of the upstream discharge is lower than that of the surface water in the downstream impoundment, it may travel through the impoundment as a deep density current, inaccessible to phytoplankton (Kimmel et al. 1990). Limnological projections, coupled with phosphorus loading models and phosphorus concentration–fish standing stock regressions, should permit the development of realistic fishery response scenarios under different operation and design alternatives.

Prediction of impacts on fisheries associated with reduced nutrient loading must be made known early in the planning process to receive thorough consideration. Public education and involvement, not only of anglers but of other user groups, is also essential; most people will be surprised that clearer water may not be an unmitigated blessing. Fisheries managers also have an obligation to argue for their resource. Conflicts among reservoir user groups can be expected, and mediation techniques are increasingly used for their resolution (McMullin and Nielsen 1991). The end result may not be an outright victory, but rather a compromise between water clarity and fish production (see Maceina et al. 1996). In the

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Conclusions

The reversal of the eutrophication process can have deleterious effects on reservoir fisheries, as the case histories and strength of the phosphorus–fishery relation indicate. However, the nature and magnitude of the response of the sport fish component of the reservoir fish assemblage to oligotrophication cannot be precisely predicted in any particular reservoir until the database is greatly expanded. Concurrent nutrient, water quality, and fishery productivity (standing stock, harvest, or production) measurements must be made and compared over many years for before-and-after assessment of the response to reduced fertility. These data also must be developed on a same-year basis for a large number of impoundments to facilitate empirical prediction of how reservoir characteristics (biology, morphometry, hydrology, and chemistry) influence the oligotrophication response.

Uncertainties in predictive precision do not absolve reservoir fisheries managers from treating potential reductions in nutrient loading as they would any other environmental impact. First, they must assess the present status of their fisheries: are growth and abundance high or limited by habitat or food deficiencies? Next, they must consult with limnologists to determine how reduced nutrient load will affect water column nutrient concentration. Finally, reservoir managers should compare their fisheries to those in other impoundments in the region which have similar as well as lower nutrient levels. From this analysis, a first-order assessment of the impact of pending oligotrophication can be developed, an assessment which is probably as accurate as those now possible for a host of other perturbations.

Reservoir fisheries managers have not collected nutrient and water quality data routinely, nor have they coordinated sampling with limnologists who do. This oversight is due, in part, to a lack of appreciation of the importance of nutrients to fisheries productivity, an ignorance shared with the general public and policy makers. In the United States, the Clean Lakes Program initiated pursuant to Public Law 92–500 has provided a major impetus for nutrient abatement. Although this program has been beneficial in the treatment of hypereutrophic waters, its objectives are often narrowly focused on enhancement of aesthetic and recreational uses of lakes with little consideration of fisheries (Lee and Jones 1991). Fisheries scientists have been conspicuously absent in the formulation of nutrient abatement policy, relinquishing their advisory role to limnologists. A collaborative effort must be initiated between fisheries scientists and limnologists to first educate themselves and then the public and policy makers regarding all the consequences of nutrient control programs. Only then can the issue of eutrophication versus oligotrophication be resolved satisfactorily on a case-by-case basis.

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References

Aggus, L. R. 1985. A strategy for managing water quality in Beaver Lake. Report to the Arkansas Water Resources Research Center, Fayetteville.

Baker, J. R., and L. J. Paulson. 1983. The effects of limited food availability on the striped bass fishery in Lake Mead. Pages 551–561 *in* V. D. Adams and V. A. Lamarra, editors. Aquatic resources management of the Colorado River ecosystem. Ann Arbor Science Publishers, Ann Arbor, Michigan.

Bayne, D. R., M. J. Maceina, and W. C. Reeves. 1994. Zooplankton, fish, and sport fishing quality among four Alabama and Georgia reservoirs of varying trophic status. Lake and Reservoir Management 8:153–163.

Canfield, D. E., and R. W. Bachmann. 1981. Prediction of total phosphorus concentrations, chlorophyll *a* and Secchi disk depths in natural and artificial lakes. Canadian Journal of Fisheries and Aquatic Sciences 38:414–423.

Carline, R. F. 1986. Indices as predictors of fish community traits. Pages 45–56 *in* G. E. Hall and M. J. Van Den Avyle, editors. Reservoir fisheries management: strategies for the 80's. American Fisheries Society, Southern Division, Reservoir Committee, Bethesda, Maryland.

Carlson, R. E. 1977. A trophic status index for lakes. Limnology and Oceanography 22:361–369.

Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985.

Cascading trophic interactions and lake productivity. BioScience 35:634–639.

Davies, W. D., and W. L. Shelton. 1983. Sampling with toxicants. Pages 191–213 *in* L. A. Nielsen and D. L. Johnson, editors. Fisheries techniques. American Fisheries Society, Bethesda, Maryland.

Dodd, R. C., J. F. Smith, and J. D. Vogt. 1988. The development of a phosphorus management strategy for two Piedmont reservoirs. Lake and Reservoir Management 4:243–252.

Downing, J. A., C. Plante, and S. Lalonde. 1990. Fish production correlated with primary productivity, not the morphoedaphic index. Canadian Journal of Fisheries and Aquatic Sciences 47:1929–1936.

Elser, J. J., and B. L. Kimmel. 1985. Nutrient availability for phytoplankton production in multiple-impoundment series. Canadian Journal of Fisheries and Aquatic Sciences 42:1359–1370.

Evans, T. D., and L. J. Paulson. 1983. The influence of Lake Powell on the suspended sediment-phosphorus dynamics of the Colorado inflow to Lake Mead. Pages 57–68 *in* V. D. Adams and V. A. Lamarra, editors. Aquatic resources management of the Colorado River ecosystem. Ann Arbor Science Publishers, Ann Arbor, Michigan.

Gloss, S. P., R. C. Reynolds, Jr., L. M. Mayer, and D. E. Kidd. 1981. Reservoir influences on salinity and nutrient flux in the arid Colorado River basin. Pages 1618–1629 *in* H. G. Stefan, editor. Symposium on surface water impoundments. American Society of Civil Engineering, Minneapolis, Minnesota.

Great Lakes Fishery Commission. 1992. Status of the Lake Ontario pelagic fish community and related ecosystem in 1992. Great Lakes Fishery Commission, Kingston, Ontario.

Hanson, J. M., and W. C. Leggett. 1982. Empirical prediction of fish biomass and yield. Canadian Journal of Fisheries and Aquatic Sciences 39:257–263.

Harper, D. 1992. Eutrophication of freshwaters: principles, problems, and restoration. Chapman and Hall, London.

Hart, L. G. 1978. Smith Mountain Reservoir research study, 1973–1976. Completion report to the Virginia Commission of Game and Inland Fisheries, Richmond.

Hayes, D. B., W. W. Taylor, and E. E. Mills. 1993. Natural lakes and impoundments. Pages 493–515 *in* C. C. Kohler and W. A. Hubert, editors. Inland fisheries management in North America. American Fisheries Society, Bethesda, Maryland.

Heiskary, S. A., and W. W. Walker. 1988. Developing phosphorus criteria for Minnesota Lakes. Lake and Reservoir Management 4:1–9.

Jones, J. R., and R. W. Bachmann. 1976. Prediction of phosphorus and chlorophyll levels in lakes. Journal of the Water Pollution Control Federation 48:2176–2182.

Jones, J. R., and M. V. Hoyer. 1982. Sportfish harvest predicted by summer chlorophyll-a concentrations in midwestern lakes and reservoirs. Transactions of the American Fisheries Society 111:176–179.

Jude, D. J., and J. Leach. 1993. The Great Lakes fisheries. Pages 517–551 *in* C. C. Kohler and W. A. Hubert, editors. Inland fisheries management in North America. American Fisheries Society, Bethesda, Maryland.

Kimmel, B. L., O. T. Lind, and L. J. Paulson. 1990. Reservoir primary production. Pages 133–194 *in* K. W. Thornton, B. L. Kimmel, and F. E. Payne, editors. Reservoir limnology: ecological perspectives. Wiley, New York.

Kitchell, J. F., editor. 1992. Food web management: a case study of Lake Mendota. Springer-Verlag, New York.

Kitchell, J. F., and S. R. Carpenter. 1992. Summary: accomplishments and new directions for food web management in Lake Mendota. Pages 539–543 *in* J. F. Kitchell, editor. Food web management: a case study of Lake Mendota. Springer-Verlag, New York.

Klessig, L., R. Wedepohl, and D. Knauer. 1988. Problem identification. Pages 3-1–3-29 *in* L. Moore and K. Thornton, editors. Lake and reservoir restoration guidance manual. U.S. Environmental Protection Agency Publication (EPA 44015-88-002), Washington, DC.

Lee, G. F., and R. A. Jones. 1991. Effects of eutrophication on fisheries. Reviews in Aquatic Sciences 5:287–305.

Liang, Y., J. M. Melack, and J. Wang. 1981. Primary production and fish yields in Chinese ponds and lakes. Transactions of the American Fisheries Society 110:346–350.

Lindemann, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology 23:399–418.

Maceina, M. J., and five coauthors. 1996. Compatibility between water clarity and quality black bass and crappie fisheries in Alabama. Pages 296–305 *in* L. E. Miranda and D. R. DeVries, editors. Multidimensional approaches to reservoir fisheries management. American Fisheries Society Symposium 16.

McMullin, S. L., and L. A. Nielsen. 1991. Resolution of natural resource allocation conflicts through effective public involvement. Policy Studies Journal 19:553–559.

Melack, J. M. 1976. Primary productivity and fish yield in tropical lakes. Transactions of the American Fisheries Society 105:575–580.

Moore, L., and K. Thornton, editors. 1988. Lake and reservoir restoration guidance manual. U.S. Environmental Protection Agency Publication (EPA 440/5-88-002), Washington, DC.

Ney, J. J. 1993. Top-down management of water quality: clear lakes plus better fishing? Lake Line 13(4):16–17.

Ney, J. J., C. M. Moore, M. S. Tisa, J. J. Yurk, and R. J. Neves. 1988. The Smith Mountain Lake fishery: factors affecting major sport and forage fish populations. Report to the Virginia Department of Game and Inland Fisheries, Richmond.

Ney, J. J., C. M. Moore, M. S. Tisa, J. J. Yurk, and R. J. Neves. 1990. Factors affecting the sport fishery in a multiple-use Virginia reservoir. Lake and Reservoir Management 6:21–32.

Noble, R. L. 1981. Management of forage fishes in im-

poundments of tl
tions of the Ame
Oglesby, R. T. 1977.
phytoplankton st
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Paulson, L. J. 1994. I
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Prentki, R. T., and I
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Pages 105–123 *in*
editors. Aquatic
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Soballe, D. M., B. L.

: Kohler and W. A. Hubert,
ianagement in North Amer-
ociety, Bethesda, Maryland.
d L. J. Paulson. 1990. Res-
n. Pages 133–194 *in* K. W.
, and F. E. Payne, editors.
ılogical perspectives. Wiley,

Food web management: a
Iota. Springer-Verlag, New

ıenter. 1992. Summary: ac-
lirections for food web man-
ıta. Pages 539–543 *in* J. F.
b management: a case study
ger-Verlag, New York.
D. Knauer. 1988. Problem
-3-29 *in* L. Moore and K.
and reservoir restoration
Environmental Protection
A 44015-88-002), Washing-

1991. Effects of eutrophica-
; in Aquatic Sciences 5:287–

ıd J. Wang. 1981. Primary
lds in Chinese ponds and
American Fisheries Society

: trophic-dynamic aspect of
418.
uthors. 1996. Compatibility
quality black bass and crap-
a. Pages 296–305 *in* L. E.
Vries, editors. Multidimen-
ervoir fisheries management.
ety Symposium 16.
ielsen. 1991. Resolution of
ın conflicts through effective
cy Studies Journal 19:553–

productivity and fish yield in
ıns of the American Fisher-

n, editors. 1988. Lake and
lance manual. U.S. Environ-
cy Publication (EPA 440/5-

anagement of water quality
shing? Lake Line 13(4):16–

3. Tisa, J. J. Yurk, and R. J.
Mountain Lake fishery: fac
and forage fish populations
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ınd.
3. Tisa, J. J. Yurk, and R. J.
ecting the sport fishery in a
servoir. Lake and Reservoir

nent of forage fishes in im-

poundments of the southern United States. Transactions of the American Fisheries Society 110:738–750.

Oglesby, R. T. 1977. Relationships of fish yield to lake phytoplankton standing crop, production and morphoedaphic factor. Journal of the Fisheries Research Board of Canada 34:2271–2279.

Paulson, L. J. 1994. Effect of water diversions in the Virgin River on the sport fisheries in the Overton arm of Lake Mead. Report to the U.S. National Park Service, Boulder City, Nevada.

Prentki, R. T., and L. J. Paulson. 1983. Historical patterns of phytoplankton productivity in Lake Mead. Pages 105–123 *in* V. D. Adams and V. A. Lamarra, editors. Aquatic resources management of the Colorado River ecosystem. Ann Arbor Science Publishers, Ann Arbor, Michigan.

Rast, W., and G. F. Lee. 1978. Summary analysis of the North American (U.S. portion) OECD eutrophication project: nutrient loading-lake response relationships and trophic state indices. U.S. Environmental Protection Agency Publication (EPA-60013-78-008), Corvallis, Oregon.

Romero, J., and R. C. Allan. 1975. Underwater observation of largemouth bass spawning and survival in Lake Mead. Pages 104–112 *in* R. H. Stroud and H. Clepper, editors. Black bass biology and management. Sport Fishing Institute, Washington, DC.

Schupp, D., and B. Wilson. 1993. Developing lake goals for water quality and fisheries. Lake Line 13(4):18–21.

Soballe, D. M., B. L. Kimmel, R. H. Kennedy, and R. F. Gaugush. 1992. Reservoirs. Pages 421–474 *in* C. T. Hackney, S. M. Adams, and W. H. Martin, editors. Biodiversity of the southeastern United States: aquatic communities. Wiley, New York.

Vaux, P. D., and L. J. Paulson. 1990. Lake Mead nutrient enhancement project. Final report to the Nevada Department of Wildlife, Las Vegas.

Vaux, P. D., L. J. Paulson, R. P. Axler, and S. Leavitt. 1995. The water quality implications of artificially fertilizing a large desert reservoir for fisheries enhancement. Water Environmental Research 67:189–200.

USEPA (U.S. Environmental Protection Agency). 1993. Fish and fisheries management in lakes and reservoirs. U.S. Environmental Protection Agency Publication (EPA-841-R-93-002), Washington, DC.

Walker, W. W. 1988. Predicting lake water quality. Pages 4-1–4-23 *in* L. Moore and K. Thornton, editors. The lake and reservoir restoration guidance manual. U.S. Environmental Protection Agency Publication (EPA 440/5-88-002), Washington, DC.

Wetzel, R. G. 1983. Limnology. Saunders, Philadelphia.

Whitehurst, D. K. 1987. Reservoir investigations: Smith Mountain Lake, 1986–1987. Report to the Virginia Commission of Game and Inland Fisheries, Richmond.

Yurk, J. J., and J. J. Ney. 1989. Phosphorus–fish community biomass relationships in southern Appalachian reservoirs: can lakes be too clean for fish? Lake and Reservoir Management 5:83–90.