

LONGITUDINAL SPATIAL DYNAMICS OF
PELAGIAL FISH AND PLANKTONIC
ASSEMBLAGES IN TENKILLER
FERRY LAKE

By


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Stillwater, Oklahoma

1992

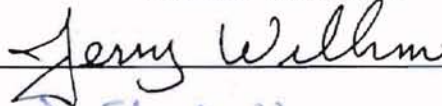
Submitted to the Faculty of the
Graduate College of the
Oklahoma State University
in partial fulfillment of
the requirements for
the Degree of
MASTER OF SCIENCE
July, 1996

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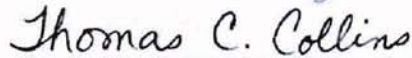
Thesis Approved:



Thesis Adviser







Dean of the Graduate College

ACKNOWLEDGEMENTS

I wish to express utmost appreciation to my major advisor, Dr. S. L. "Bud" Burks. His personability, charisma, and intelligent guidance throughout my graduate experience were both supportive and refreshing. I am grateful for the space, equipment, and financial support he provided throughout the duration of my studies.

I thank Drs. J. L. Wilhm and W. H. Henley for serving on my graduate committee. I am grateful to Dr. Wilhm for the challenging but rewarding teaching assistantships provided from the beginning of my graduate program. To Dr. Henley, I extend many thanks for agreeing to serve on my committee on such short notice.

I wish to express sincere gratitude to my fellow compatriots Noble Jobe III and Shanon Haraughty for their friendship and countless contributions to this study. I thank my parents, Gary and Candy Kloxin, for their endless encouragement and support. Finally, I acknowledge my wife, Melody, whose unselfishness, devotion, and love were a foundational inspiration during this period.

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CHAPTER I

INTRODUCTION

Demand for lentic resources has led to the construction of many reservoirs over the past 50 years. Development primarily has been for (1) municipal demands (i.e., water, hydroelectric power, navigable waterways), (2) flood control, (3) sedimentation in intensely disturbed watersheds, and (4) recreation. In 1985, about 1,650 impoundments greater than 200 hectares existed comprising nearly four million hectares (Hall 1985). Excluding the Great Lakes, reservoirs cover a significantly greater area of the United States than natural lakes. The distribution of reservoirs is greatest in the southeastern, central, southwestern, and western regions of the country (Marzolf 1984, Thornton et al. 1990). Such pervasiveness suggests the importance of these systems and, if they are to be managed, predicates the need for an understanding of their functioning.

Reservoirs possess extreme spatial heterogeneity in physical and chemical properties. As with most lentic bodies, reservoirs undergo thermal stratification. This condition, complexed with excessive organic loading due to cultural eutrophication, frequently produces anoxic conditions in the hypolimnion. Hypolimnetic anoxia, in

turn, contributes to stratification in water chemistry as chemical species are converted to their reduced forms.

Reservoirs also exhibit longitudinal gradients persistent with their lotic derivation. Changes in basin morphology and linear distance result in lengthwise changes in current. As a result, suspended loads from the mainstream differentially settle resulting in a longitudinal gradient in water clarity and adsorbed nutrient loads. Dilution of riverine water with lentic reaches result in lengthwise gradients in other physicochemical parameters (e.g., conductivity, alkalinity). Recent examination of these longitudinal processes among reservoirs by Thornton et al. (1990) lead to the elucidation of the riverine-transition-lacustrine (R-T-L) paradigm.

Insights into the limnological functioning of reservoirs have fostered appreciation of their uniqueness as habitat. Of particular significance are the longitudinal processing and associated gradients in water quality variables previously mentioned. Intuitively, reservoir biota should respond to this abiotic phenomenon and, *a priori*, exhibit analogous gradients in distributional dynamics.

Until recently, most investigations of biotic spatiality in reservoirs dealt with plankton. Related fisheries investigations have been rare, mostly addressing vertical distribution in relation to water quality. Several knowledge gaps in reservoir fishery research were identified by Hall (1985). Preeminent among those listed were an

adequate understanding of predator/prey interactions and firmer information on water quality/fish interactions. In light of heightened understanding of reservoir processes (i.e., the R-T-L paradigm), studies concerned with such biological phenomena are warranted and should result in better understanding.

Since its construction, Tenkiller Ferry Lake (hereafter referred to as Lake Tenkiller) has been noted as one of the clearest waterbodies in Oklahoma and is exemplary of multi-use reservoirs. However, in recent years, accelerated eutrophication (primarily attributed to impinging nutrient inputs of intense poultry and municipal discharges) has markedly affected water quality lake-wide with greatest influence exhibited in the headwaters. Primary deleterious results have included magnified algal blooms and, as a consequence, exacerbated hypolimnetic anoxia.

As a result, Oklahoma State University Water Quality Research Lab with the U.S. Army Corps of Engineers and the Oklahoma Water Resources Board was granted E.P.A. "Clean Lakes" funding, and a basin-wide water quality assessment of Lake Tenkiller was begun in 1992. Ensuing field studies resulted in determination of longitudinal gradients in the reservoir (e.g., nutrient, chlorophyll a, suspended solids). These gradients were suggested to reflect a trophic continuum in the reservoir ranging from hypereutrophic in the upper reaches to oligotrophic near the dam.

In further fulfillment of the biotic requirements of the study, this investigation was begun to examine response

of biota to habitat gradients in the reservoir. The primary objective was to determine exact longitudinal trends in selected pelagic fish and planktonic parameters in Lake Tenkiller. The following null hypothesis was the foundation of the study:

H₀: longitudinal gradients in pelagic fish and planktonic assemblages with respect to physical-chemical parameters do not exist in Tenkiller Ferry Lake.

CHAPTER II

LITERATURE REVIEW

Physicochemical Trends

General Zonation

Lentic systems have been divided into vertical and horizontal zones. Water column divisions include those due to photosynthetically-effective light penetration (euphotic and aphotic zones), and those due to stratification (epilimnion, metalimnion, and hypolimnion). Areal zonation of lentic bodies entails distinction of vegetated shoreline (littoral) from open water zones (pelagial) (Reid and Wood 1976; Wetzel 1983). Although these zones are conserved among all lentic systems, reservoirs are not static water bodies and require additional zones to account for their unique limnological functioning.

Longitudinal Processing

Reservoirs in broad definition are "hybrid" systems, blending characteristics of both lentic (lake) and lotic (river) environments. Dependent on basin morphology and hydraulic budgets, the river-like flow regimes in reservoirs and resultant longitudinal processes dictate the degree of lake-like character. Focus on longitudinal processing in

reservoirs by Thornton et al. (1981) led to the characterization of three zones, each possessing distinct abiotic and biotic attributes. The three zones are the riverine (river-like) zone, the transition zone, and the lacustrine (lake-like) zone. These three arbitrary zones partition a reservoir's continuous gradient of processes and characters from headwaters to dam (Thornton et al. 1990).

In general, the riverine zone reflects many characteristics of the in-flowing river. Although decrease in water velocity results in deposition of larger suspensoids, this zone maintains and transports significant loads of finer particulates. Therefore, the riverine zone is lowest in transparency and thus light-limited in primary productivity. This results in a high net transfer of nutrient loads to the transition zone. The riverine zone is well mixed and dominated by allochthonous (external) organic input (Thornton et al. 1990).

In the transition zone, water velocity decreases substantially resulting in deposition of most of the suspended load. Primary productivity normally increases (and usually peaks) in response to increased water transparency and abundant nutrients. As a result, a shift is made from allochthonous to autochthonous (internal) organic production. The location and extensiveness of the transition zone is flow-dependent and highly variable throughout the year (Thornton et al. 1990).

Characteristics of the lacustrine zone are most consistent with lentic systems. The larger size and slower

flow of the zone buffer against rapid fluctuations in environmental characters (e.g., ionic composition, thermal regime). This affords a certain degree of stability relative to the other zones (Thornton et al. 1990). Light penetration is maximal and producers often deplete essential nutrients. As productivity generally exceeds consumption, autochthonous nutrient pathways dominate this zone.

Biological Dynamics

Spatial Trends

Spatial gradients characterize both lotic and lentic systems. In riverine systems, longitudinal gradients in physical conditions dominate, giving rise to a continuum of biotic responses (Cummins 1974, Vannote et al. 1980, Minshall et al. 1983). Vertical gradients (e.g., light, temperature, photosynthetic productivity) characterize lacustrine environments. Being "hybrids" of lotic and lentic systems, reservoirs exhibit both horizontal and vertical abiotic gradients (Thornton et al. 1990). As with the parent systems, these gradients should and do manifest in analogous biological trends.

Plankton

Whether in lakes or reservoirs, primary production is constrained by like factors: temperature, light availability, macro- and micro-nutrient availability, and biological factors (e.g., competition, predation) (Kimmel

and Groeger 1984). Thus, gradients in these factors as seen in reservoirs should result in response gradients by endemic producers. Indeed, spatial heterogeneity in phytoplankton biomass, productivity, and relative abundance has been shown to exist (Thornton et al. 1981, Kennedy et al. 1982, Kennedy 1984, Kimmel and Groeger 1986, Thornton et al. 1990).

Algal community structure commonly follows changes in nitrogen and phosphorus, particularly their ratio (N:P). In most southern reservoirs, phosphorus is the limiting nutrient. The N:P ratio is lowest in the riverine zone and increases downstream. Reservoir algal assemblages commonly exhibit a preponderance of nitrogen fixing blue-green algae in the headwaters grading to a dominant green algae and diatom assemblage near the dam.

The longitudinal (from headwaters to dam) trend in chlorophyll a (an index of phytoplankton standing crop) in reservoirs resembles a maxima function with the peak occurring in the transition zone. Frequently, hydraulic budget and nutrient loads (including autochthonous cycling) determine the width and magnitude of the peak, respectively. Inflow and outflow dynamics may skew the trend toward or away from the dam (Thornton et al. 1990, Jobe 1995). Areal photosynthetic production in a Great Plains reservoir was found to be lowest near the headwaters and dam and maximal near mid-reservoir (Marzolf and Osborne 1971).

Protista, Rotifera, and Crustacea comprise the majority of fresh water zooplankters. Coelenterates, flatworms, gastrotrichs, mites, and larval insects may also occur

(Hutchinson 1967). Some zooplankters (particularly cladocerans and copepods) are relatively mobile and move semi-autonomously of their environment. Diel, vertical migrations and distributions of many species are well known and documented (Worthington 1931, Cushing 1951, Wells 1960, McNaught and Hasler 1961, Adeniji 1978).

Variation in horizontal distribution of zooplankton in natural lakes has been investigated. Berzins (from discussion in Hutchinson 1967) examined the cross-sectional distribution of zooplankton in a Swedish lake. Epilimnetic rotifer (e.g., *Polyarthra vulgaris*, *P. euryptera*, *Kellicottia longispina*) concentrations were found on either side of the lake's longitudinal axis. Crustacean zooplankters were found deeper and more concentrated on one side of the lake, which possessed an extensive littoral reach. Pelagic species were non-randomly dispersed across the zone.

In a similar investigation, Tonolli (from discussion in Hutchinson 1967) analyzed samples collected along longitudinal transects in a natural lake. Populations of several taxa were, again, found to be "super-dispersed" (individuals less regularly spaced than at random). Changes in inter- and intra-taxon densities occurred over distances of 100 m.

Hutchinson (1967) suggests such heterogeneity in zooplankton distribution can be expected in large lakes. A function of size, the diversity of such systems creates "independent water masses," each possessing minutely

different physicochemical characters to which biota respond. Reservoirs, given their marked longitudinal gradients, epitomize this condition. Thus, investigation of biological spatial trends in reservoirs appears especially appropriate.

Spatial dynamics in reservoir zooplankton are elucidated from a complex of abiotic and biotic factors. The longitudinal distribution of zooplankton should, *a priori*, parallel trends in primary productivity as most are primary consumers. Thus, the peak in zooplankton biomass should coincide with the peak in phytoplankton biomass, which normally occurs at the transition zone (a trophic upsurge). However, an exclusive "bottom-up" regulation does not exist. Specific physicochemical (e.g., current, conductivity, turbidity,) and biological (e.g., predation, competition) factors also contribute to spatial dynamics.

Several investigations have shown a non-random spatial distribution of zooplankton in reservoirs. Taylor (1971) showed that zooplankton densities peaked at mid-reservoir stations in a Kansas reservoir. In an investigation of Tuttle Creek Reservoir, shifts in population densities and composition also occurred with longitudinal distance. Dominance of two particular species (*Daphnia parvula* and *D. schodleri*) was found to depend on location, whether upstream or downstream. Abundance maxima for both species occurred approximately one-third the thalweg distance from the headwaters (Marzolf 1984). Bowels and Wilhm (1977) found that concentration estimates (both inter/intra-specific and total) varied greatly within and among stations, while

diversity was determined to be more stable.

Spatial variation in zooplankton community structure in reservoirs has been suggested to be a function of physicochemical conditions. Kochsiek et al. (1971) investigated net zooplankton dynamics and physicochemical variables in Keystone Reservoir, Oklahoma. Rotifers were found to dominate mean annual frequencies in the riverine stations, while cladocerans and copepods exhibited their greatest abundance at stations near or at the dam. Mean annual zooplankton density was reported highest at middle (presumably transitional) stations. Diversity was positively correlated with turbidity and temperature and negatively correlated with conductivity and alkalinity.

Yacobi et al. (1993) determined simultaneous distribution of plankton, fish, temperature, and dissolved oxygen in Lake Kinneret, Israel. Rotifer and copepod assemblages were significantly correlated with dissolved oxygen concentration. Results suggested that during low water temperatures, physical conditions regulated zooplankton distribution more than biotic interactions. Ectotherms (both predators and competitors) must meet less metabolic demand in colder environments and are thus less active.

Plankton dynamics and distribution are also affected by turbidity. Direct and indirect effects include the following: (1) suspended sediments may decrease (by mechanical interference) ingestion rate of algal cells; (2) ingested suspended clay/adsorbed nutrient complexes may

relieve temporal and/or spatial deficiencies in natural food abundance; (3) concentrated suspended clays scatter light which limits primary production and reduces food availability; and (4) turbidity decreases sight-dependent planktivory and thus the predation rate (Arruda et al. 1983, Kirk and Gilbert 1990).

The general effect of turbidity is taxon-specific and can affect competitive outcomes and subsequent community structure. Laboratory experiments involving rotifers and cladocerans indicate rotifer dominance in highly turbid environments and cladoceran dominance otherwise. Rotifers are more selective feeders and outcompete cladocerans (which ingest both clay and algae) for available food. In low suspended clay, cladocerans were found to consistently suppress and often supplant rotifers (Kirk and Gilbert 1990). Arruda et al. (1983) also suggested inefficient filtration by cladocerans in turbid water. However, results demonstrated that when algal biomass was low, adsorbed nutrients on the clay supplemented the diet and afforded advantage to cladocerans.

Biotic interactions, especially predation, can alter population dynamics and structure zooplankton assemblages. In a classic study, Brooks and Dodson (1965) determined the influence by a planktivore (alewife) on zooplankton populations in southern New England lakes. Zooplankton communities in similar lakes were found to differ in dominant species and size composition dependent upon presence/absence of alewives. "Non-alewife lakes" exhibited

an expected spectrum of body size within and among species. Lakes containing alewives were found to possess greater abundance of smaller zooplankters. Differential (size selective) predation by alewives was suggested to account for these observations.

The effects of planktivorous fish on zooplankton are decided in large part by feeding mode. Fish planktivory occurs by particulate or filter modes of action. Particulate planktivores are highly selective and thus sight-dependent feeders. Thus, predation rates are higher on large-bodied species resulting in proliferation of smaller forms. Selection of *D. longispina* by three-spine sticklebacks (an extreme littoral species) was suggested to favor littoral abundance of its smaller competitor *B. longispina* in Lake Kvernavatn, Norway (Jakobsen and Johnsen 1987).

Filter planktivores are passive feeders. These fish filter volumes of water over fine gill-rakers through pump or ram methods. Zooplankton incurring rampant filter planktivory should exhibit abundance of evasive species (Drenner et al. 1982).

Spatial heterogeneity in zooplankton assemblages may be ephemeral or stable. Ephemeral variation results from collective response to temporal phenomenon. Wind-induced patchiness (e.g., abundance maxima on leeward sides, "windrowing" due to langmuir circulation) and reproductive swarms are examples. However, horizontal variation in assemblages may remain in response to persistent

environmental conditions (McNaught and Hasler 1961, Urabe 1990). Reservoirs possess persistent conditions (e.g., flow, turbidity gradients, productivity gradients) which should maintain general patterns in zooplankton and other organisms' distributions.

Urabe (1990) concluded biotic interactions (predation and competition) could maintain variation in pelagic zooplankton. *In situ* competition experiments revealed dominance by *Daphnia galeata* in enclosures throughout the study reservoir, especially in the upper end. However, field samples revealed highest abundance near the dam, and dominance of upper end assemblages by *Bosmina longirostris* (a smaller species). Concurrent gillnet samples revealed an abundance of planktivorous fish in the upper end. Differential predation on *D. galeata* in the upper end and exploitative dominance by such near the dam were suggested to cause and maintain the distribution.

Fish

Due to location of most reservoirs in the lower continental U. S., reservoir fisheries are comprised mostly of warm water species (Thornton et al. 1990). Many of the riverine species initially present are unable to expand into pelagic areas post inundation and are either limited to shallow, upper reaches and littoral areas or extirpated (Kohler et al. 1986). Beyond persistent riverine endemics, most reservoir fisheries are subsidized by stocking.

Sportfish species commonly stocked include largemouth

bass, white bass, walleye, channel catfish, blue catfish, flathead catfish, crappie, and recently striped bass, saugeye (walleye X sauger hybrid), and wipers (striped bass X white bass hybrid). Such unnatural predator abundance necessitates concurrent stocking of supplemental forage species. Forage fishes commonly stocked include bluegill sunfish, gizzard shad, threadfin shad, and inland silverside (Thornton et al. 1990). Of the reservoir fishes, gizzard shad, threadfin shad, white bass, striped bass, wipers, and larval crappies are predominantly pelagic.

Although fish are mobile, they should exhibit stable longitudinal patterns in abundance, production, etc. given relatively static environmental conditions (e.g., while stratified). Due to proportionality of trophic levels, zooplankton afford the greatest potential biomass available to fish in the pelagic zone (Thornton et al. 1990). As discussed, zooplankton abundance maxima generally occur near transition zones. Thus, a trophic upsurge would place the peak in planktivorous fish abundance, production, etc. near that of zooplankton (Marzolf 1984). In reservoirs, most planktivorous fish are principal forage species and include gizzard shad, threadfin shad, and atherinid species such as the inland silverside. Thus, relevant piscivorous fishes should exhibit similar distributions.

Reservoir fish diversity should also be spatially variable. Diversity should be highest at the headwaters and decrease to the dam due to limited expansion of riverine species into the reservoir proper (Kohler et al. 1986).

Wilhm (1976) determined that reservoirs indeed possessed spatial variation in fish diversity, but a dominate trend was not evident.

Wilde and Paulson (1989) found pelagic threadfin shad in Lake Mead to vary temporally and spatially. Although no difference was found in inter-annual abundance, seasonal variation in fish abundance was highly significant. Spatial variation was also highly significant with greatest abundances exhibited near riverine stations (inflows) and declining downstream. Analysis of chlorophyll a samples revealed a similar trend that was positively correlated with that in fish abundance.

Rinne et al. (1981) reported similar results. Gillnet catches for largemouth bass, black crappie, threadfin shad, and carp were consistently higher at upstream stations. Mean chlorophyll a concentration also exhibited a declining trend that was highly and positively correlated with fish abundance.

Siler et al. (1986) reported spatial heterogeneity in additional fish parameters. Fishing pressure and harvest of predominant sport fish exhibited increasing trends from downlake to uplake areas. Standing crop estimates for all species reported (gizzard shad, threadfin shad, carp, ictalurids, largemouth bass, crappie, sunfish, and yellow perch) were highest in uplake areas, particularly near transitional stations. Concurrent monitoring of total phosphorus (the limiting nutrient) revealed a longitudinal gradient with values twice higher uplake than near the dam.

Chlorophyll a increased from the headwaters, peaked at the transition zone, then decreased to the dam. Total fish harvest, largemouth bass harvest and abundance, crappie harvest, ictalurid harvest and standing stock were significantly correlated with total phosphorous, chlorophyll a, and selected morphometric features.

Spatial heterogeneity in fish distribution may be attributed to both intrinsic and extrinsic factors (Rinne 1981). Intrinsic factors include genetic predispositions such as habitat, behavioral or physical preferences (Siler 1986). Extrinsic factors entail all environmental (physical, chemical, etc.) and most biotic interactions.

Of the intrinsic factors, physiological tolerances may solely dictate distribution. During stratification, fish have been shown to selectively occupy the thermocline to optimize coolest temperature with highest dissolved oxygen. This thermal-d.o. "squeeze" and its effects on distribution have been investigated particularly for striped bass, which must seek temperatures less than 25 °C to avoid stress (Cheek et al. 1985, Matthews 1985). Large striped bass have been shown to congregate in the coolest layer available while isolating themselves from their preferred forage (threadfin shad) which occur in the epilimnion (Siler 1986). Cheek et al. (1985) reported uniform distribution of striped bass during winter and early spring and patchy assemblages in summer as fish selected for the cooler tributary arms (due to upstream hypolimnetic discharges).

Distribution of fish can be expected to be a function

of spatial variability of preferred habitat. Summerfelt (1973) determined that variability in catch of a species was often a function of only a few variables (e.g., food, temperature, depth). In most cases, these variables were confirmations of known habitat preferences. For example, 54.8% of the spatial variability in catch rate of the carpsucker was due to water depth, sediment organic content, and biomass of Tubificidae. Assuming these variables constituted habitat preferences, their heterogeneity in the system manifested in heterogeneity in carpsucker distribution.

Trophic interaction, existing both as an intrinsic and extrinsic factor, exerts a significant influence on spatial dynamics. Food availability and/or predator abundance often dictate residence zones, which constitute patchiness or heterogeneity in distribution. Variation in flathead catfish abundance was highly correlated with occurrence of its preferred food (drum and gizzard shad) (Summerfelt 1973). Threadfin shad, which are predominantly phytoplanktivorous as adults, followed closely trends in phytoplankton standing crop (Rinne 1981, Siler 1986). Spatial variation in white bass distribution was suggested to result from patchiness of larger *Daphnia* (caused by Langmuir cells and prevailing winds) upon which they were feeding (McNaught and Hasler 1961).

Threat of predation often serves to restrict distribution in spite of other factors. Jakobsen and Johnsen (1987) reported confinement of three-spined

sticklebacks to littoral areas by introduced pelagic piscivores (Atlantic salmon). Although the larger, most preferred zooplankter (*Daphnia longispina*) was pelagic, sticklebacks were more governed by predation threat than forage abundance.

The morphoedaphic index (MEI), initially developed by Ryder (1965) for estimating potential fish yield in Canadian lakes, has been applied to many aquatic systems including U. S. reservoirs (Jenkins 1967, Jenkins and Morais 1971, Jenkins 1982). In concept, the MEI is an association of environmental variables most critical in governing productivity in aquatic systems. For lentic systems, crucial variables include climate, watershed geology, and basin morphology (Ryder et al. 1974). On a regional scale, climate is essentially equivalent and only geologic and morphological characters are considered. Total dissolved solids (TDS) and mean depth (Z_{mean}) are the most influential edaphic (from soil or geology) and morphological (basin shape) variables on lacustrine production, respectively. Hence, their ratio, $\text{TDS}:Z_{\text{mean}}$, constitutes the predominant MEI equation (Ryder 1982).

A high MEI value indicates adequate dissolved solids (an index of required nutrients) and shallow mean depth (proportionally greater volume of water in the trophogenic zone) and is assumed to pose the greatest productive potential. The use of the MEI lies in a mathematical relationship to fish yield, biomass, etc. which is usually significant and positive. Once established for a

characteristic set of lakes, it may then be used to estimate fish production in similar systems.

Fish standing crops, yields, etc. in reservoirs have been shown to be a function of several environmental variables including the MEI. Of 11 variables examined by Aggus and Lewis (1978), storage ratio, outflow volume, and dissolved solids were consistently related to fish standing crop. Hydropower mainstream impoundments (such as Lake Tenkiller) with low storage ratios (high water exchange rates) exhibited higher total, clupeid, and small fish standing crops than hydropower storage reservoirs. Jenkins (1967) supports this as total standing crops were again negatively correlated with storage ratio and in addition positively correlated with shore development and the MEI. The MEI has been positively correlated with reservoir fish production in several studies (Jenkins 1967, Jenkins 1971, Jenkins 1982, Adams et al. 1983).

Trophic Interactions

As discussed, the productive potential of aquatic fauna is dictated mostly by edaphic and morphologic parameters (Ryder et al. 1974, Carpenter et al. 1985). The temporal and/or spatial translation of these variables into biological phenomenon is, at the outset, intuitive; increased nutrients result in increased producers which in turn result in increased consumers. Research highly supports the nutrient-producer paradigm with phosphorus (most often the limiting nutrient) explaining up to 95 % of

the variability in chlorophyll (Dillon and Rigler 1974, Oglesby 1977). Subsequent consumer responses such as yield, standing crop, and biomass have been highly and positively correlated with morphoedaphic factors and phytoplankton standing crop (Oglesby 1977, Mills and Schiavone 1982).

Such "bottom-up" processes, however, do not exclusively regulate ecosystem functioning. After establishment of higher trophic components in new systems, "top down" influences feedback through the structure affecting lower trophic levels. These "cascading trophic interactions" are purported to account for differences in productivity among similar lakes (Carpenter et al. 1985).

Consumer control of system dynamics is best exemplified in introductions of piscivorous fish species to affect changes in water quality. As piscivores increase, planktivorous fishes decrease resulting in proliferation of planktivorous invertebrates which select for smaller zooplankters. Zooplankton assemblages shift in size structure to a dominance of larger species which, in turn, crop greater quantities of phytoplankton and increase water clarity (Carpenter et al. 1985).

Several studies have investigated top-level manipulations and subsequent trophic cascades. Most of the investigations concluded (1) planktivore removal or absence results in increased larger zooplankters; (2) resultant increases in herbivory shift algal community structure to larger species, which are proportionately less productive and lower in chlorophyll concentration; increased water

clarity often results; (3) infrequent and inefficient nutrient turnover by macro-zooplankters results in decreased epilimnetic nutrient concentrations in oligotrophic systems; and (4) trophic cascades usually break down at the zooplankton-phytoplankton interface; extensiveness is mostly determined by system trophic state (Henrikson 1980, Mills and Schiavone 1982, Carpenter et al. 1985, Post and McQueen 1987, Vanni 1987, Carpenter and Kitchell 1988, Christoffersen 1993).

The bottom-up:top-down theory (McQueen et al. 1989) reconciles discrepancies in the trophic cascade theory. Simply stated, strength of top-down (bottom-up) control weakens with descent (progression) through the food web. Considering top-down control, the strongest influence would be expected at the piscivore-planktivore interface; the planktivore-zooplankton interface would be expected to exhibit less of an effect, and so on.

McQueen et al. (1986) found interannual correlations between piscivores and planktivores strongest followed by that of planktivore-zooplankton. The zooplankton-chlorophyll correlation was positive but not significant. However, there was a highly significant correlation between chlorophyll and total phosphorous. The zooplankton-chlorophyll interface was suggested to be a convergence between top-down and bottom-up controls that confounded interaction predictability. The trophic position of such a convergence point was thought to depend on the relative strength of top and bottom controls. Thus, top-down effects

would be expected to carry further through the food chain (i.e., to zooplankton-phytoplankton or phytoplankton-nutrient levels) in oligotrophic than eutrophic systems. Results of several investigations support this premise (see Elser et al. 1990 and Post and McQueen 1987).

CHAPTER III

MATERIALS AND METHODS

Description of Area

Lake Tenkiller extends through Cherokee and Sequoyah counties, Oklahoma. The hydrologic flow through Lake Tenkiller is dictated by its mainstream, the Illinois River, with nominal inflows from 12 creeks (Figure 1). Drainage into Lake Tenkiller incorporates approximately 4,170 km² (Table I).

Sampling Regimen

Sampling stations were established along the thalweg (approximately 40 river km) and one at the tailrace. Water quality monitoring for the overall project began 25 APR 1992

Table I. Lake Tenkiller Morphometry at Normal Pool Elevation (OWRB 1990).

Parameter	Value
Elevation (NGVD)	632
Area (ha)	5221
Drainage area/surface area	80
Capacity (m ³)	8.07 X 10 ⁸
Mean depth (m)	15.5
Max. depth (m)	46
Shoreline (km)	209
Shoreline Development	8.17

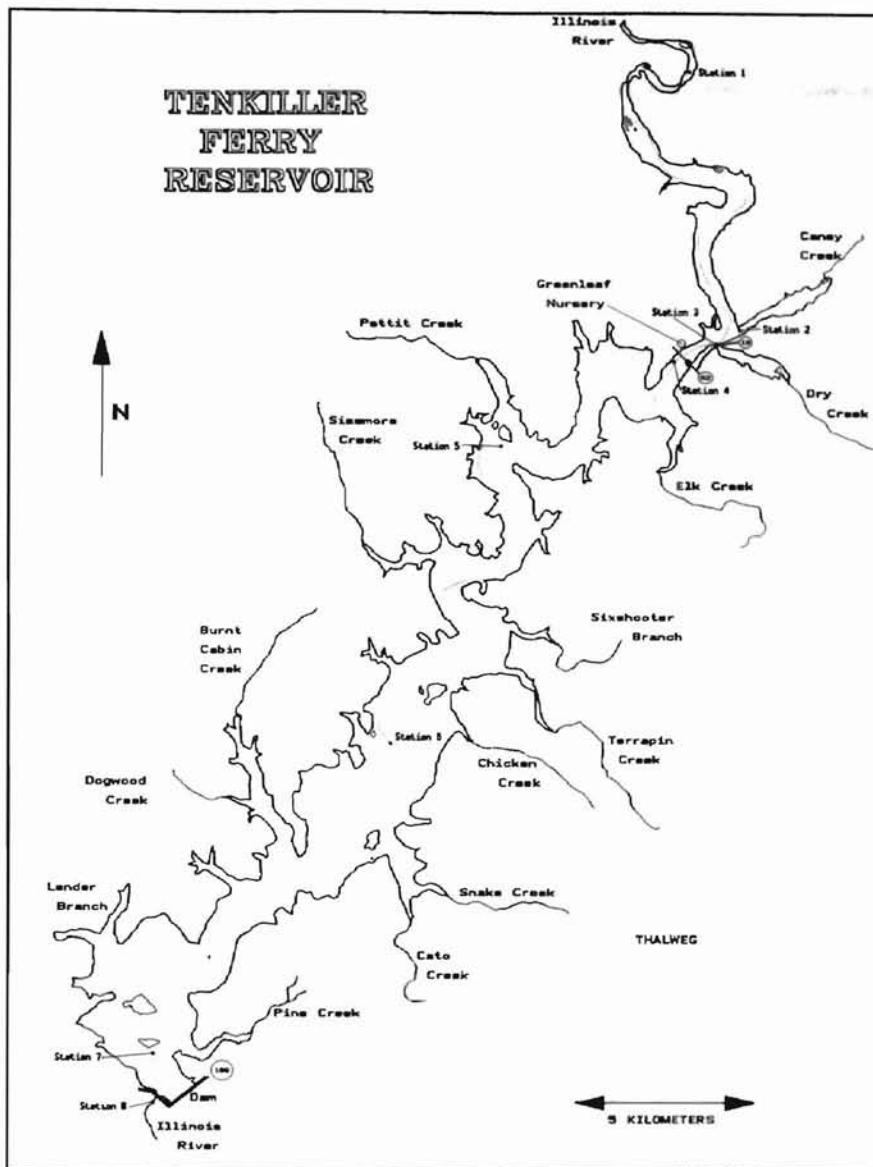


Figure 1. Tenkiller Ferry Lake

and continued through 22 OCT 1993. For relevant dates, water quality data from TK2, TK5, and TK6, (chosen to represent the reservoir's zones) were used for this study.

Transects across the three stations were established (Table II). The data collected for this study incorporated six, two-day sampling events occurring on the following dates: 18-19 AUG 93, 2-3 SEP 93, 16-17 SEP 93, 30 SEP-1 OCT

Table II. Global Position System Coordinates of Transect Endpoints.

Transect	Start	End
1 (Station 2)	35°45.53 N LAT., 94°53.05 W LONG. (S side)	35°45.57 N LAT., 94°53.09 W LONG. (N side)
2 (Station 5)	35°44.03 N LAT., 94°56.56 W LONG. (East side)	35°43.52 N LAT., 94°57.20 W LONG. (West side)
3 (Station 6)	35°40.04 N LAT., 94°58.14 W LONG. (East side)	35°41.01 N LAT., 94°59.05 W LONG. (West side)

93, 18-19 OCT 93, and 21-22 OCT 93. This period was chosen to avoid seasonal bias in longitudinal fish distributions due to reproductive migrations which occur in spring (Howell 1945, Eley et al. 1967, Walburg et al. 1971, Adornato 1990). Each sampling event entailed two replicate days of biological sampling and one water quality (except 18-19 OCT 93) sampling.

Water Quality

Field data collected included standard water quality profiles (temperature, D.O., and conductivity), pH, and Secchi depth. Samples were collected 0.5 m from surface and bottom via 2 L van Dorn for analysis of the following parameters: alkalinity, total hardness, turbidity, total phosphate (as P), and orthophosphate (as P) by conventional methods (Lind 1985); chloride, nitrate-nitrogen, and sulfate by ion-chromatography; and total nitrogen by a

spectrophotometric procedure (Bachman and Canfield 1991).

Biological Parameters

Plankton

Phytoplankton standing crop was monitored via chlorophyll a analysis. Surface samples were placed in opaque, non-acid-washed, polyethylene bottles and retained in cold storage until analysis. Samples were analyzed as per Lind (1985) including phaeophytin correction.

Four net-zooplankton samples were collected randomly along each of the three station transects within the pelagic zone. A 12.0 cm (mouth diameter) Wisconsin Plankton Net with number 20 nylon bolting cloth was used to make a bottom to surface vertical tow at an anchored position. Samples were fixed in neutral formalin (Lind 1985) and placed in cold storage until analysis.

Three of the four zooplankton samples collected for each transect were analyzed. Samples were identified (Edmondson 1958, Pennak 1978) and enumerated via random strip counts made on sample aliquots in a Sedgewick-Rafter cell. A compound, binocular microscope at 100X magnification was used for the counts (Lind 1985). Counts were made for each aliquot until changes in moving averages were insignificant or until approximately 300 individuals were counted. Longitudinal trends in density and relative frequency of major net zooplankton were determined from replicate averages for all stations and dates. Generic

trends were derived using dates only for which a capture was recorded to alleviate effects of temporal variation.

Fish

To assess semi-instantaneous pelagic fish abundance, sonar transects (Thorne 1983, O'Brien et al. 1984, Wilde and Paulson 1989) were conducted using a Lowrance X-15 recording sonar device. The sonar was operated at the factory set frequency of 192 KHz with a beam angle of 20°. Care was taken to ensure that operation of the sonar (i.e., control settings, transducer position) and boat speed (app. 7 km/h) was standardized throughout the study. Station transects were echosounded once within 1.5 hr of each other for each sampling date between 1500 and 1900 hr. Echograms were analyzed by counting all discernable targets and expressing this as a function of linear distance across the respective transect.

Gillnetting was conducted to directly assess the pelagic fish assemblage. Efficient experimental design necessitated the development of a portable gillnet system. The system had to be deployable along station transects and afford standardized, inter-transect comparisons of catch/effort (C/f) irrespective of vertical distribution. The resulting design emulated the traditional horizontal, experimental gillnet stretched in a vertical plane. Use of multiple nets allowed investigation of vertical and horizontal trends in fish distribution.

The vertical "diving" gillnet (Figure 2) consisted of a

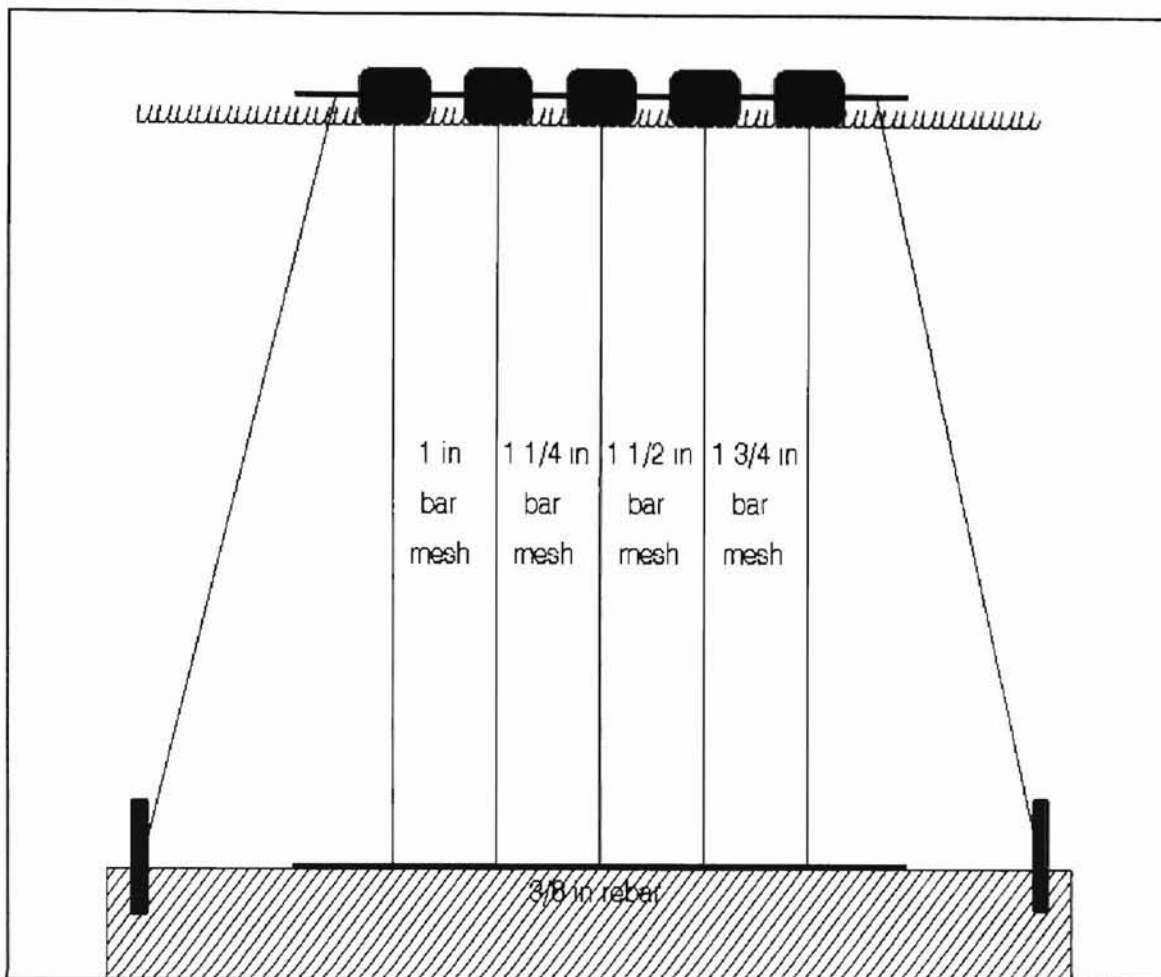


Figure 2. Vertical "Diving" Gillnet.

series of four, adjacent, vertical panels of 1, 1.25, 1.5, and 1.75 inch bar mesh monofilament netting (size #69). All netting was depth stretched to accommodate maximum dorso-ventral extension and was bordered with 0.375 inch polypropylene line. The floatation was constructed of 1 inch schedule 40 pvc pipe equipped with five, six inch pvc sponge floats. Re-bar (0.375 inch) was used for the leadline. Additional lateral anchors of variable lengths were attached to the floatation.

One vertical net was randomly used (accommodating

damaging structure) along each of three study transects between 1200 to 1800 hrs. All nets were set within one hour and allowed a minimum 4-hr soak-time before retrieval. Upon retrieval, fish were identified and length, weight, and vertical position recorded. Net captures (both as number and wet weight) were converted to standardized C/f's for inter-transect comparison. Total and species-specific gillnet yields were analyzed for longitudinal trends.

Statistical Analyses

Differences among sample stations for all data were assessed using the nonparametric Kruskal-Wallis one-way analysis of variance (Zar 1974). This test is distribution-free and often applicable in situations where assumptions for the parametric ANOVA are violated or unknown. However, if data meet assumptions for parametric analysis, the test is only 95.5 % as powerful (i.e., more conservative) and will be less likely to show significance (Sokal and Rohlf 1973, Zar 1974).

All water quality parameters were analyzed for spatial differences replicated over at least five equivalent dates (i.e., n=5 for each station). Exceptions included chlorophyll, Secchi disk, and surface pH which included additional replications. Surface and bottom samples were analyzed categorically for each parameter. Profile data (i.e., temperature, D.O., and conductivity) were represented using values at 1 meter from surface and bottom.

Echogram, gillnet, and select net zooplankton data

(total and general taxonomic groups) were analyzed for all sample dates (i.e., n=12 for each station except n=11 for TK2 for both zooplankton and echogram data). Gillnet captures often did not occur for particular fishes at certain stations and/or dates. A value of "0" was recorded for each of these instances to equalize replication preceding analysis. Significant temporal (i.e., monthly) fluctuations in zooplankton parameters have been demonstrated and were expected (Wetzel 1983). Thus, replication was not equalized preempting analysis for zooplankton genera and species-specific trends. All ANOVA's and plots (except profiles) were performed with the computer statistical program SYSTAT™ (Wilkinson 1991).

Upon determination of significant trends, stations were analyzed for pairwise differences at an imposed alpha of 0.05. In instances of equal replication, a nonparametric analogue of the Newman-Keuls multiple range test (Zar 1974) was employed. For unequally replicated data, the Newman-Keuls test with modified standard error calculation (Zar 1974) was implemented.

CHAPTER IV

RESULTS AND DISCUSSION

Longitudinal Trends

Water Quality

Profile Parameters

Longitudinal trends in temperature and dissolved oxygen were apparent but not statistically significant. Surface temperatures increased from TK2 and stabilized at TK5, while bottom temperatures decreased downlake (Figure 3). Dissolved oxygen exhibited a slight decline downlake in the upper layer but decreased markedly in the lower stratum (Figure 4). Increase in hypolimnetic proportion (and thus influence) with downlake distance directed bottom trends for both parameters (Thornton et al. 1990). Vertical profiles of these parameters (Appendix A) show stratification at one or more stations from 16 AUG 93 through 30 SEP 93.

Surface conductivities showed an expected decrease from upper to lower end (Figure 5). Many reservoirs have been shown to exhibit similar decrease in dissolved solids concentration due to biotic assimilation, hypolimnetic entrainment, etc. (Thornton et al. 1990). Due to hypolimnetic anoxia, bottom conductivities were different

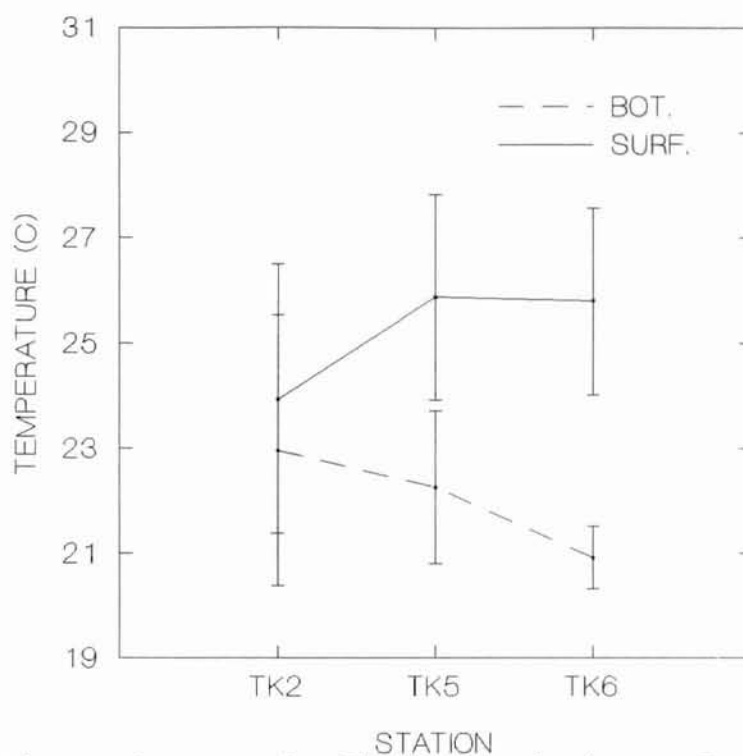


Figure 3. Longitudinal Trends in Surface and Bottom Temperatures (average \pm SEM).

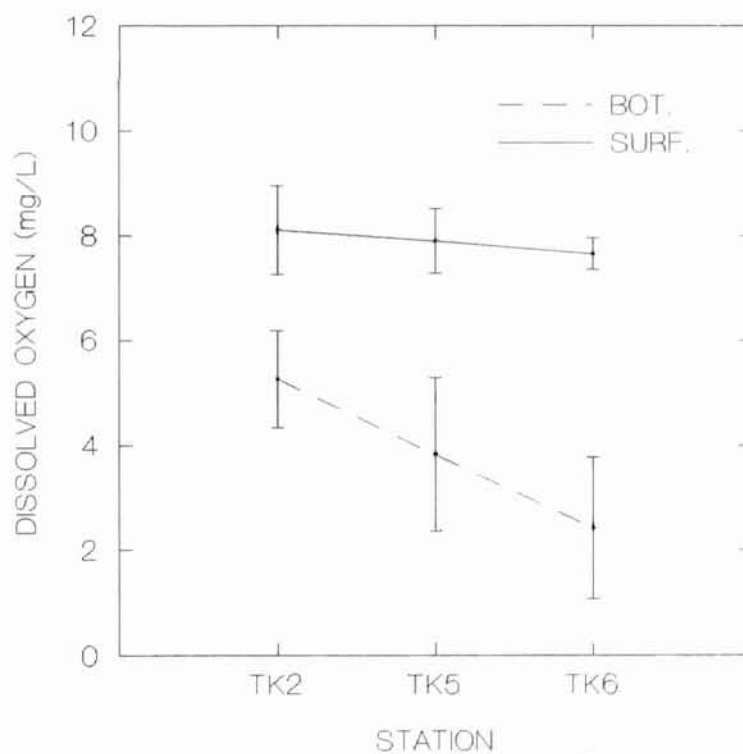


Figure 4. Longitudinal Trends in Surface and Bottom Dissolved Oxygen (average \pm SEM).

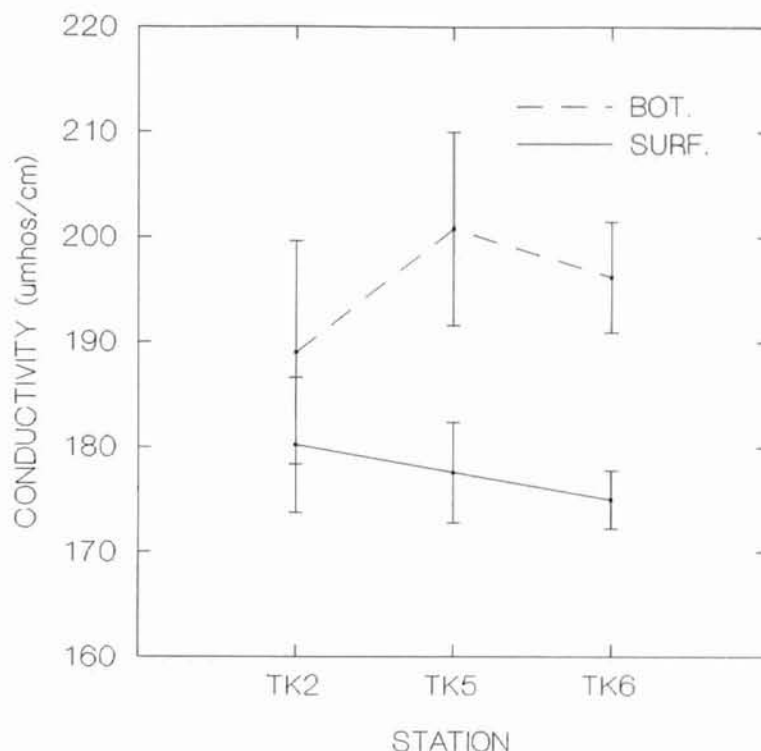


Figure 5. Longitudinal Trends in Surface and Bottom Conductivities (average \pm SEM).

and exhibited a peak at TK5 (Figure 5). Neither trend was significant.

Total Alkalinity, Hardness, $[H^+]$

Longitudinal trends in total alkalinity, hardness, and $[H^+]$ were also evident and were not significant. Surface values for all three parameters were lower than bottom measurements. Surface alkalinities peaked at TK5, while bottom values increased downlake (Figure 6). Surface total hardness declined slightly from TK2 down the thalweg, while values in the lower layer bottomed at TK5 (Figure 7). Surface hydrogen ion concentration was lowest at TK5, and bottom concentrations increased downlake (Figure 8).

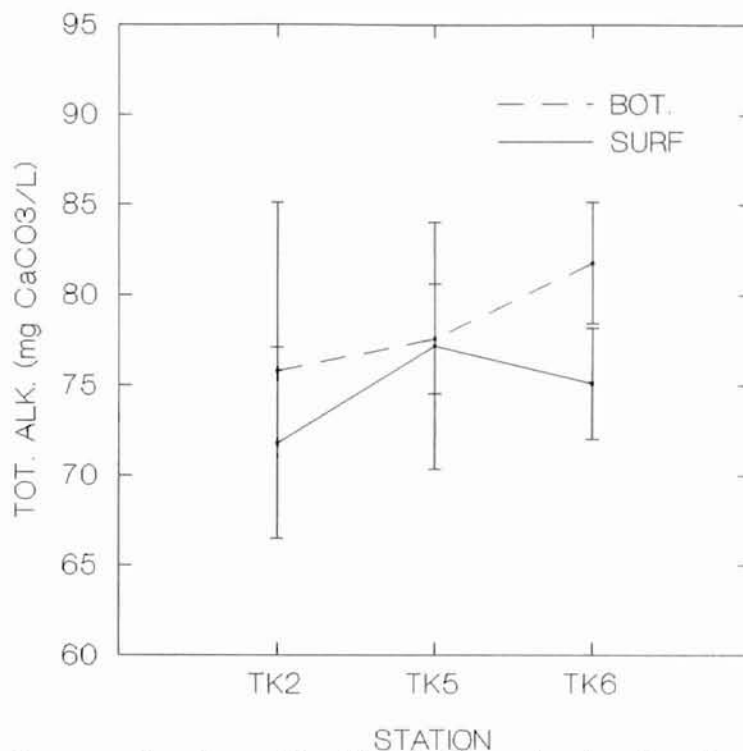


Figure 6. Longitudinal Trends in Surface and Bottom Total Alkalinities (average \pm SEM).

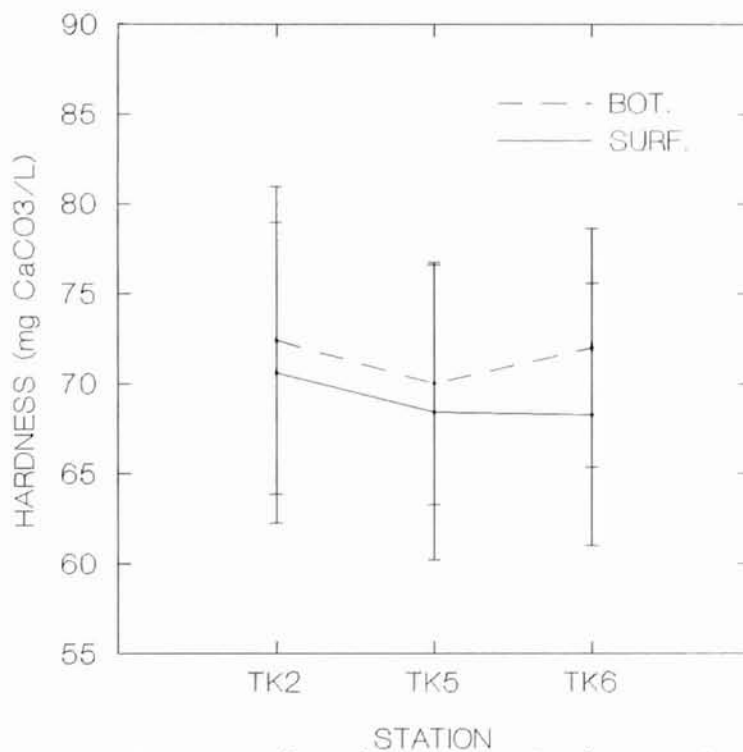


Figure 7. Longitudinal Trends in Surface and Bottom Hardness (average \pm SEM).

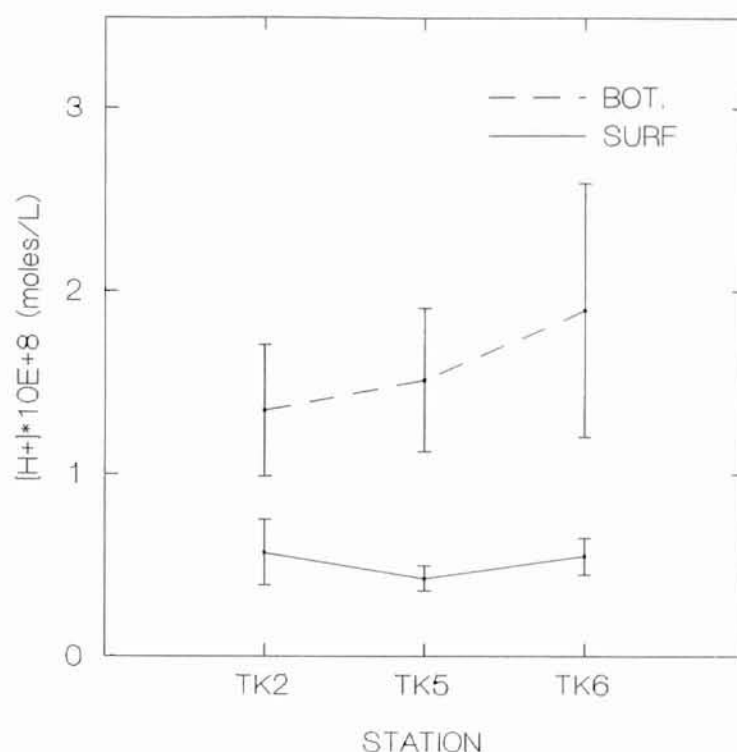


Figure 8. Longitudinal Trends in Surface and Bottom $[H^+]$ (average \pm SEM).

Chloride, Sulfate

Trends in surface and bottom chloride were similar and peaked at TK5 (Figure 9). Surface sulfate increased slightly downlake, while bottom concentration varied little to TK5 and decreased markedly to TK6 (Figure 10). Such a decrease in bottom sulfate is expected due to reduction to sulfides in anoxic, hypolimnetic waters (Wetzel 1983). None of the trends were significant.

Nitrate, o-Phosphate-P

Longitudinal trends in the soluble nutrient fractions of Lake Tenkiller were apparent. Surface nitrate-N declined from TK2 and stabilized at TK5, while hypolimnetic

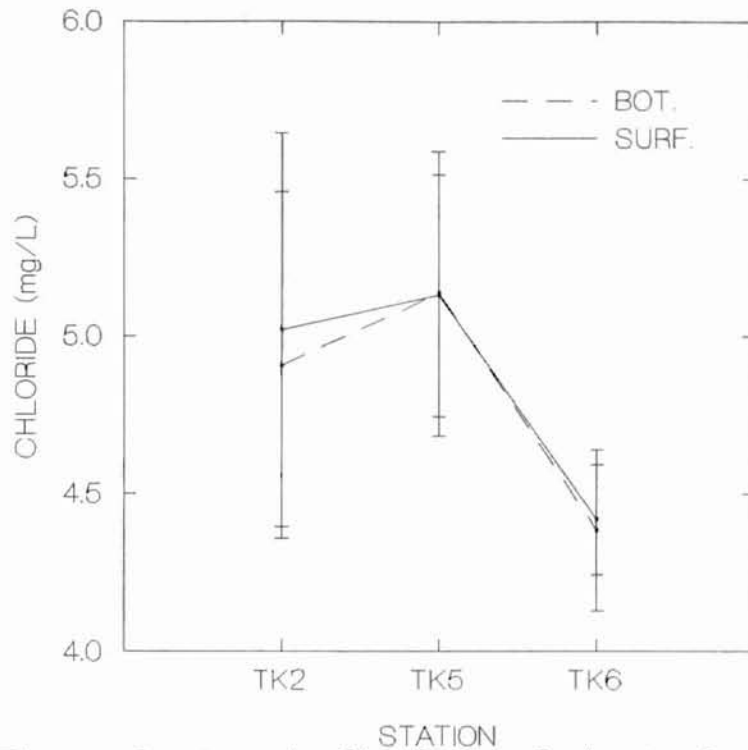


Figure 9. Longitudinal Trends in Surface and Bottom [Cl⁻] (average +/- SEM).

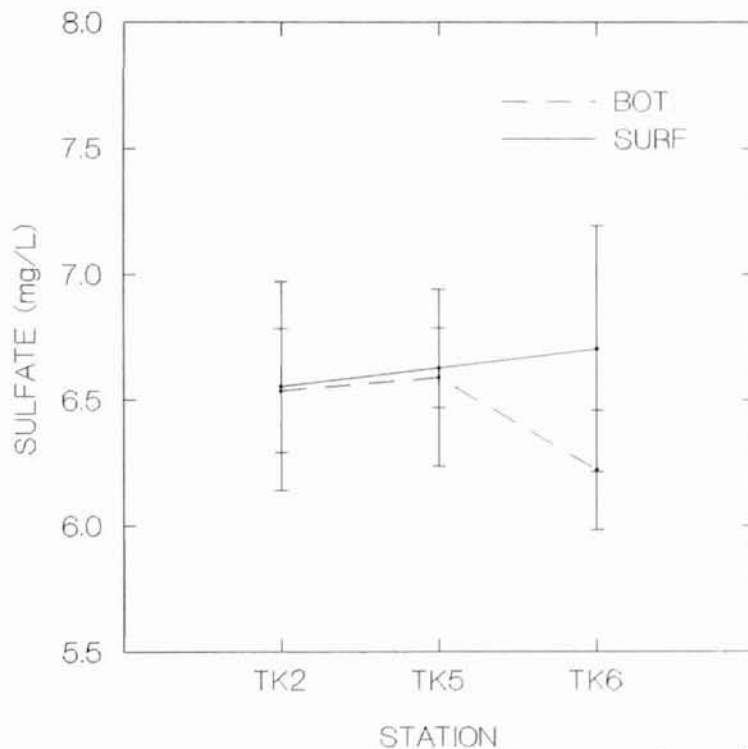


Figure 10. Longitudinal Trends in Surface and Bottom [SO₄⁻²] (average +/- SEM).

concentration decreased down the lake; neither trend was significant (Figure 11). Surface o-phosphate-P showed a significant ($P < 0.01$) decrease from upper to lower stations (Figure 12). This has been shown to be a persistent trend among reservoirs (Kennedy et al 1982, 1984, Siler 1986, Thornton 1990). A steady decline in bottom o-phosphate-P was also evident but not significant ($P = 0.09$).

Reservoirs are often phosphorus-limited at their lacustrine zone (Thornton et al. 1990). The decrease in soluble phosphorus to nitrogen after TK5 suggests possible phosphorus limitation with downlake distance. In nutrient (non-nitrogen) limited scenarios, smaller celled algae generally outcompete larger forms due to better absorption (greater surface area to volume ratios) (Harris 1986). Thus, response to nutrient gradients by algae should result in heterogeneous distributions. As these smaller algae are more available to and preferred by most herbivorous zooplankton, a parallel response in zooplankton would be expected (Watson and Kalff 1981, Kirk and Gilbert 1990).

Total Nitrogen, Total Phosphorus

Total nitrogen (TN) (Figure 13) and total phosphorus (TP) (Figure 14) decreased downlake. As nutrients (particularly phosphorus) are associated with suspended particles, a decreasing trend is expected due to sedimentation along the lake's axis (Canfield and Bachmann 1981, Thornton et al. 1990). Surface decreases down the thalweg for TN and TP were significant ($P = 0.05$ and $P =$

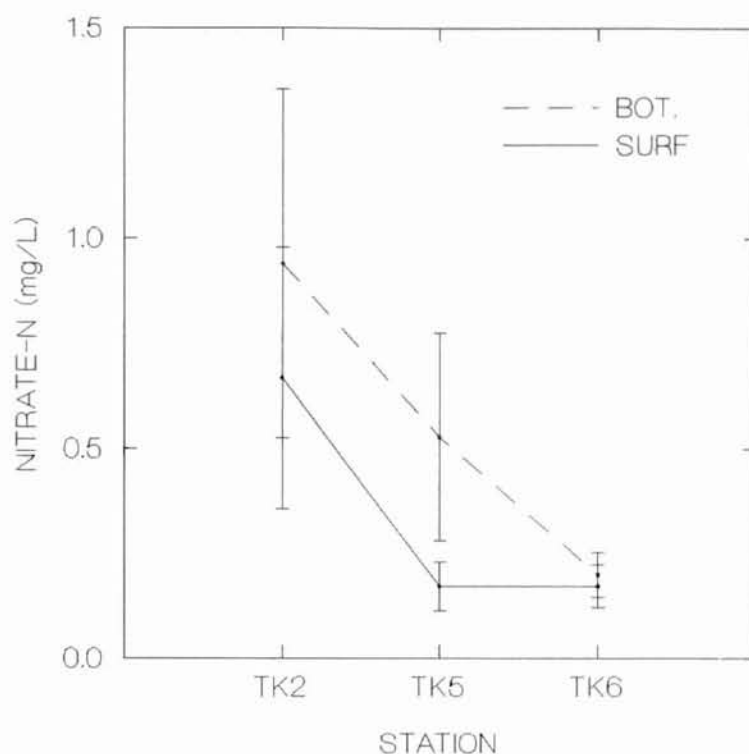


Figure 11. Longitudinal Trends in Surface and Bottom Nitrate-N (average \pm SEM).

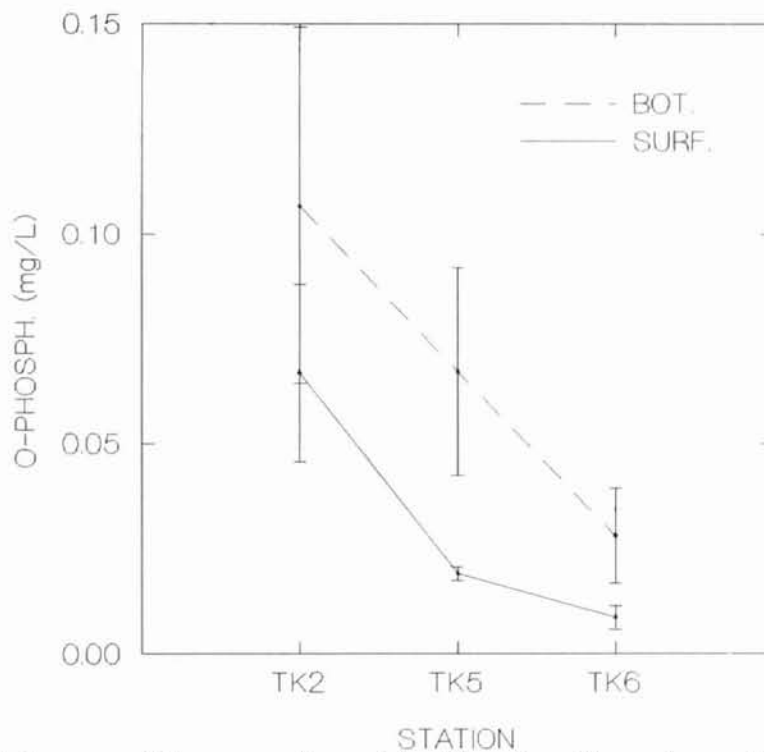


Figure 12. Longitudinal Trends in Surface and Bottom o-phosphate-P (average \pm SEM).

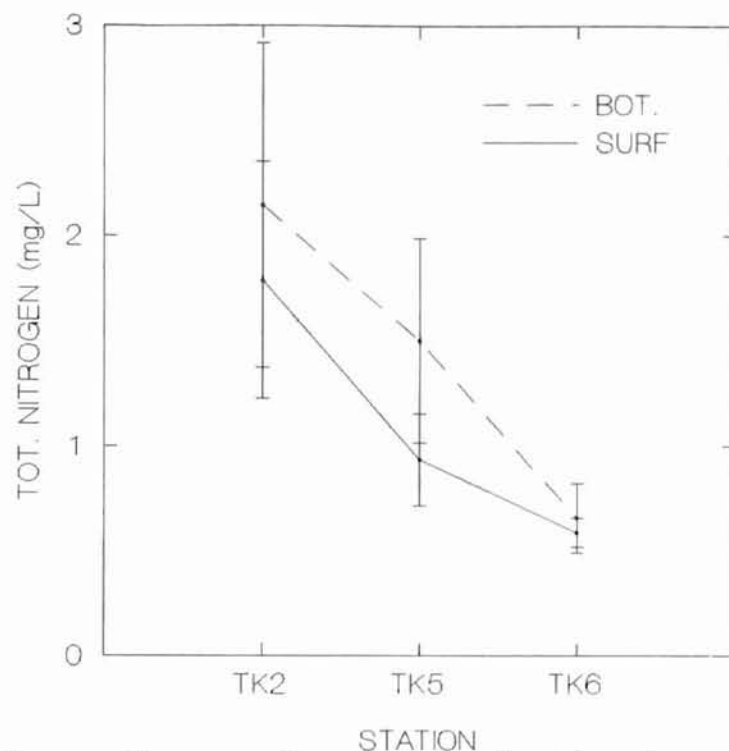


Figure 13. Longitudinal Trends in Surface and Bottom Total Nitrogen (average \pm SEM).

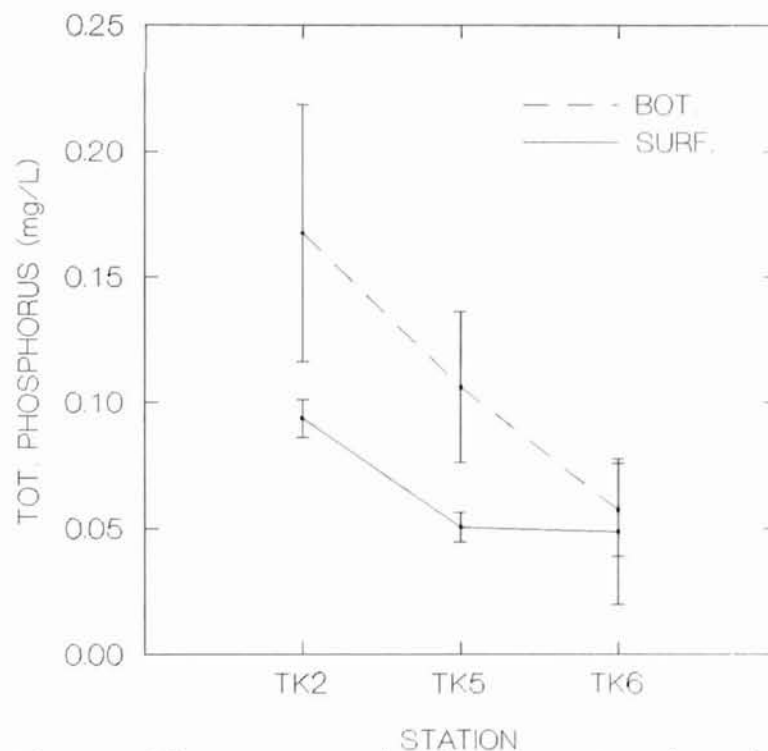


Figure 14. Longitudinal Trends in Surface and Bottom Total Phosphorus (average \pm SEM).

0.04, respectively), while bottom trends were not significant ($P = 0.12$ and $P = 0.08$, respectively). Surface concentrations at TK2 were significantly different than remaining stations for both nutrients.

Secchi Disk Transparency, Turbidity

Downlake increase in Secchi depth was highly significant ($P < 0.01$), and all stations were statistically different (Figure 15). Although results support distinction of stations, Secchi depth may not always afford zone delineation. Water transparency is a function of both light absorption (by dissolved organic matter, chlorophyll, etc.) and scattering by particulates. Increased algae in the transition zone may compensate for sedimentation of particulates from the riverine zone and obscure differentiation by Secchi depth.

When apportioned into its abiotic and biotic components, turbidity is a more definitive parameter for zone determination. As sedimentation of abiotic particulates precedes algal response, focus on this fraction seems most appropriate. Overall, turbidity decreased downlake (Figure 16). The surface turbidity trend was significant ($P = 0.02$), and values at TK2 were significantly different from remaining stations. The trend in bottom turbidity was not significant ($P = 0.08$). Higher turbidity in the bottom stratum suggests underflow throughout the study period (Thornton et al. 1990).

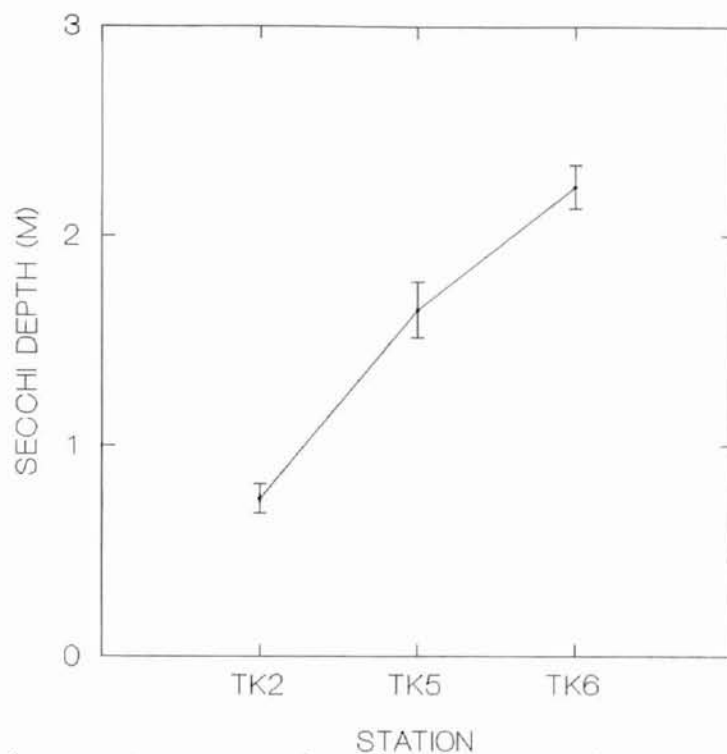


Figure 15. Longitudinal Trend in Secchi Depth (average \pm SEM).

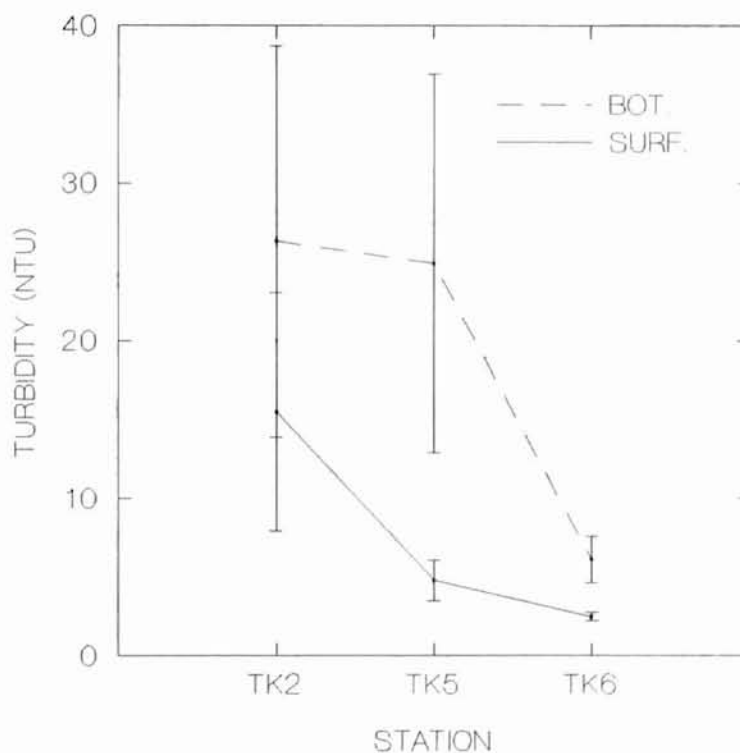


Figure 16. Longitudinal Trends in Surface and Bottom Turbidities (average \pm SEM).

Biological Parameters

Plankton

Chlorophyll a decreased downlake, but the trend was not significant ($P = 0.13$) (Figure 17). In theory, the chlorophyll peak should occur at the transition zone (represented by TK5). However, several studies have reported a similar decline from headwaters to dam (Marzolf and Osborne 1971, Rinne et al. 1981, Marzolf 1984, Wilde and Paulson 1989).

Considering temporal volatility of plankton, I compared chlorophyll data during and after stratification, a more stable period (Figure 18). During stratification, chlorophyll concentration showed a similar but significant ($P = 0.05$) decreasing trend. After stratification, the trend exhibited a slight but insignificant ($P = 0.17$) peak at TK5.

Regarding TK5 as a transitional station, the latter trend is more consistent with the zonation model. Difference between the trends is suggested to result from the spatial and temporal variability of the transition zone (Thornton et al. 1990). Greater inflows due to seasonal increase in rainfall pushed the transition zone down the thalweg. Decreased algal abundance at TK2 (due to turbidity) and incorporation of TK5 at an earlier location in the transition is suggested to account for the latter trend.

In retrospect, TK5 should be considered a late-

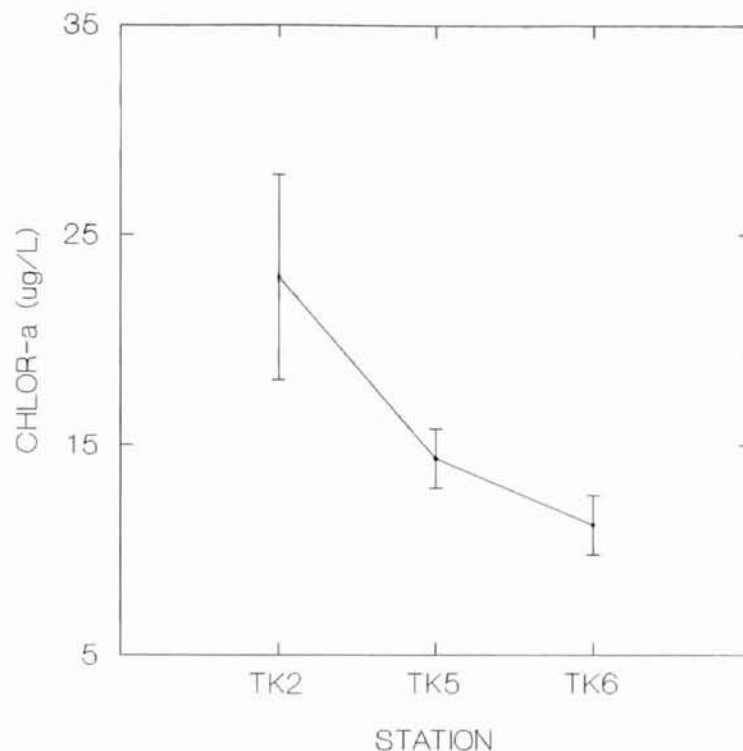


Figure 17. Longitudinal Trend in Chlorophyll a (average +/- SEM).

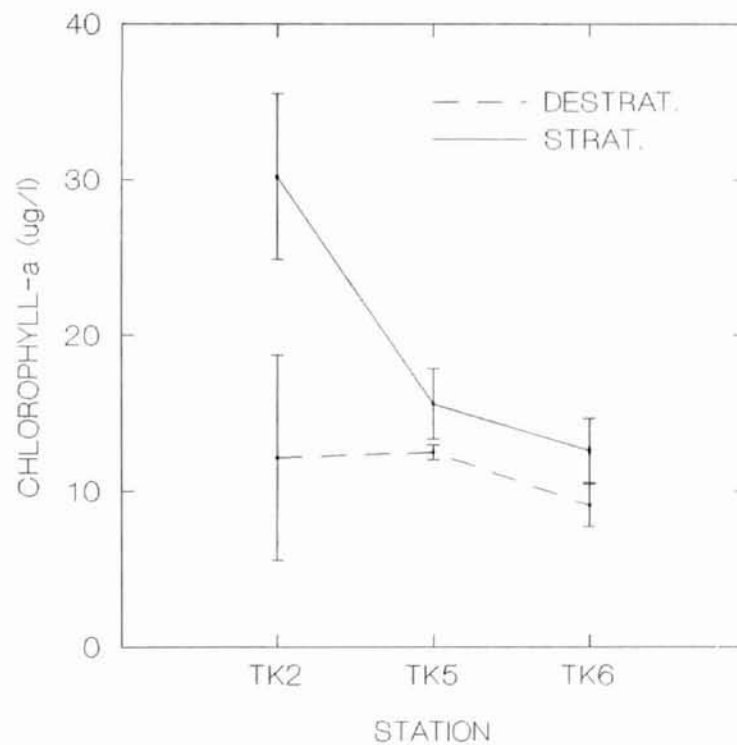


Figure 18. Longitudinal Trend in Chlorophyll a (average +/- SEM) During and After Stratification.

transitional station and thus likely to exhibit similarity in variables with lacustrine stations. Although a late-transitional station would exhibit a greater average chlorophyll than lacustrine stations, it would not exhibit the peak for the reservoir. This explains the continued decline in chlorophyll seen for the study. For further information on phytoplankton dynamics in Lake Tenkiller, see Haraughty (1995).

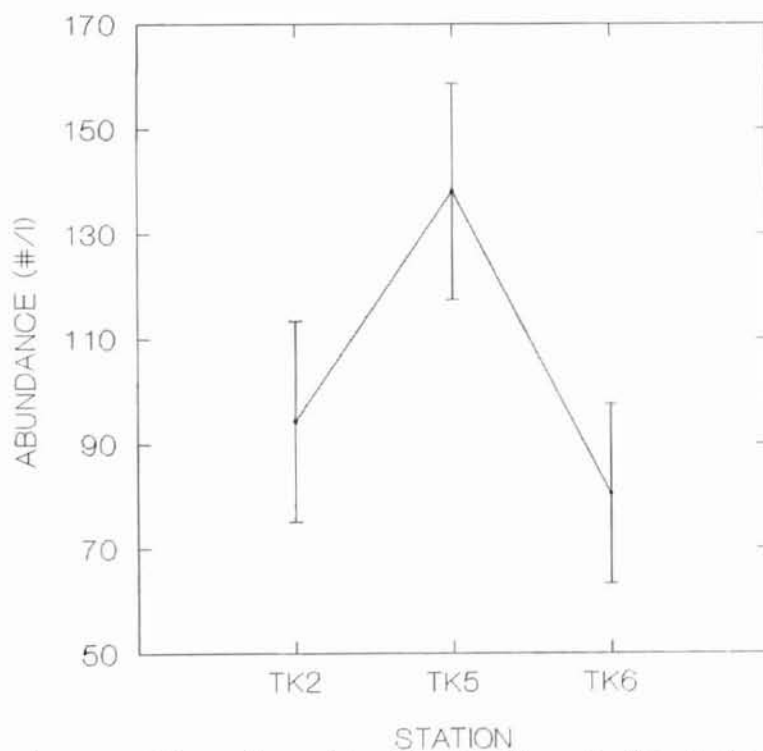
A longitudinal trend in total net zooplankton was evident, although not significant ($P = 0.11$). A total of 38 net zooplankton taxa were collected over the study period (Table III). Zooplankton density peaked at TK5 and exhibited similar variability among stations (Figure 19). This trend supports the hypothesized peak in density at transitional localities and may, in part, account for low chlorophyll at this station. Taylor (1971) determined that zooplankton density in a Kansas reservoir generally peaked at mid-reservoir stations. This trend has been reported in other reservoirs (Kochsiek et al. 1971, Marzolf 1984, Thornton et al. 1990).

Densities of general net zooplankton groups were variable among stations (Figure 20). Rotifers were the most abundant and peaked at TK5. However, the trend was not significant ($P = 0.07$). Copepoda and other net zooplankters also peaked at TK5, while cladocerans increased downlake; trends were not significant ($P = 0.36$, $P = 0.49$, and $P = 0.09$, respectively).

As total density inadequately reflects changes in

Table III. Net Zooplankton Taxa Collected in Lake Tenkiller.

ROTIFERA	CLADOCERA	COPEPODA	OTHER
<i>Ascomorpha</i>	<i>Bosmina</i>	Calanoida	Chaoborus
<i>Asplachna</i>	<i>Ceriodaphnia</i>	Cyclopoida	Ciliata
<i>Brachionus</i>	<i>Daphnia</i>	<i>Ergasilus</i>	Diffflugia
<i>Colurella</i>	<i>Diaphanosoma</i>	juveniles	Gyrinidae
<i>Filinia</i>	<i>Latona</i>		Nematoda
<i>Gastropus</i>	<i>Moina</i>		Ostracoda
<i>Hexarthra</i>	<i>Pleuroxus</i>		<i>Tanypus</i>
<i>Kellicotia</i>	<i>Polyphemus</i>		
<i>Keratella</i>			
<i>Lecane</i>			
<i>Monostyla</i>			
<i>Platyias</i>			
<i>Ploesoma</i>			
<i>Polyarthra</i>			
<i>Syncheata</i>			
<i>Testudinella</i>			
<i>Trichocerca</i>			
Rotifer sp. 1			
Rotifer sp. 2			

**Figure 19.** Longitudinal Trend in Total Net Zooplankton Density (average +/- SEM).

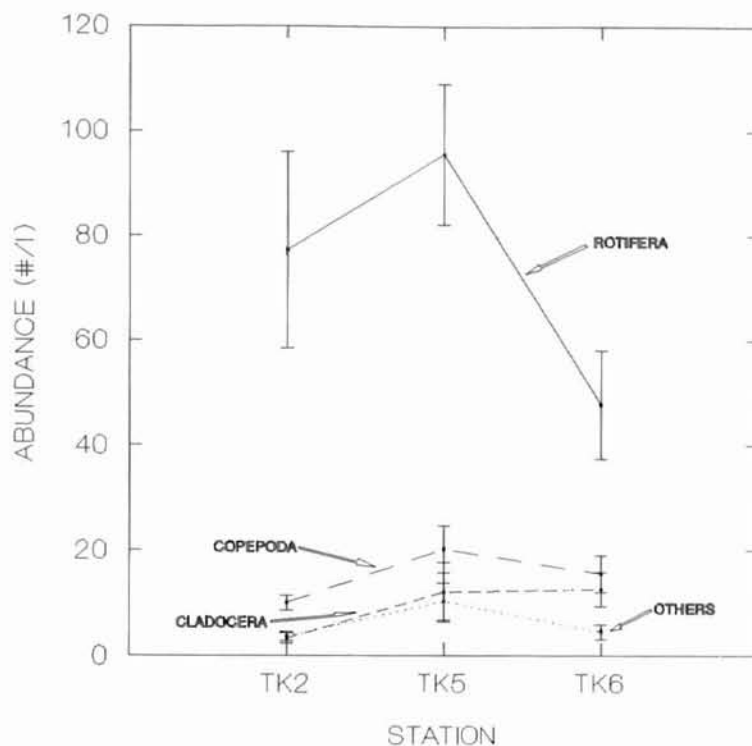


Figure 20. Longitudinal Trends in Densities of Major Net Zooplankton Groups (average \pm SEM).

community structure, relative frequencies of taxonomic groups were computed (Figure 21). Rotifers were most frequent and exhibited a significant ($P = 0.02$) declining trend; TK6 was statistically different from remaining stations. Copepod frequencies increased from TK5, but the trend was not significant ($P = 0.18$). The increasing trend in cladoceran frequency with downlake distance was highly significant ($P < 0.01$), and TK6 was statistically separate from remaining stations. Remaining taxa showed no appreciable longitudinal tendency in percent occurrence.

Similar results have been reported. Kochsiek et al. (1971) noted dominance of mean annual frequency by rotifers at upstream stations, and increase in copepods and

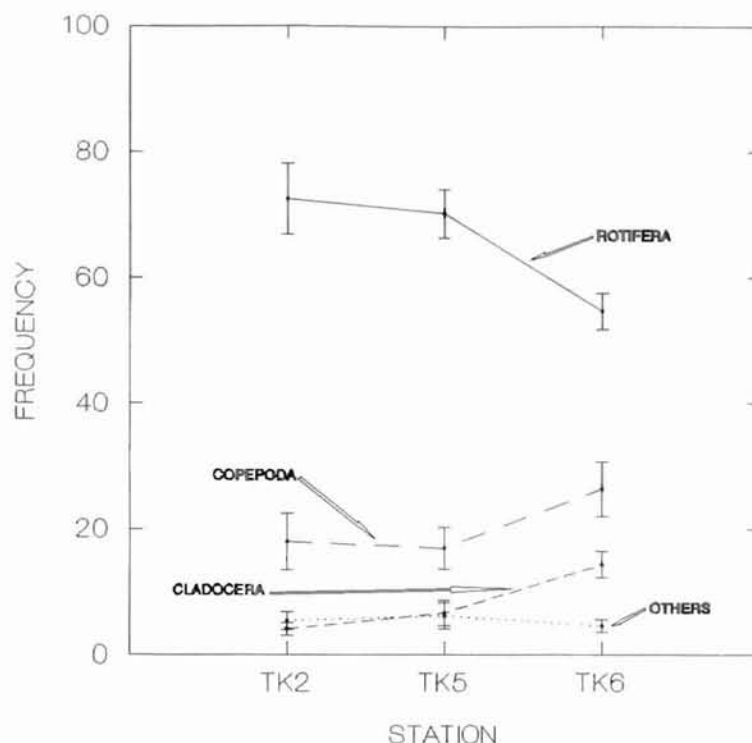


Figure 21. Longitudinal Trends in Relative Frequency of Major Zooplankton Taxa (average \pm SEM).

cladocerans downlake in Keystone Reservoir, Oklahoma.

Benson and Cowell (1967) found lowest densities of copepods and cladocerans near the headwaters, and highest densities downstream. Marzolf (1984) reported similar longitudinal variability in species composition and density of *Daphnia*.

The longitudinal trends observed in Lake Tenkiller zooplankton may be explained by the turbidity gradient. As discussed, filter feeding cladocerans are hampered by turbidity and are outcompeted by particulate feeding rotifers (Kirk and Gilbert 1990). Greater turbidity in the riverine zone (TK2) should predispose assemblage dominance by rotifers. As sedimentation of abiotic particulates occurs along the thalweg, cladocerans should increase in

abundance.

Longitudinal trends in rotifer densities were variable (Figure 22 and Figure 23). Most taxa exhibited trends which decreased downlake or peaked at TK5. Statistically significant trends included those for *Hexarthra* ($P = 0.02$; TK2 TK5 TK6), *Syncheata* ($P = 0.02$; TK2 TK5 TK6), *Filinia* ($P = 0.02$; erroneous comparison results) *Asplanchna* ($P = 0.02$; erroneous comparison results), and *Kellicottia* ($P < 0.01$; TK2 TK5 TK6).

Copepoda densities also varied among stations (Figure 24). Juveniles were most abundant and peaked at TK5 ($P = 0.75$). The trend for Cyclopoida was highly significant ($P = 0.01$) and showed an increase to TK5, then slight decrease; TK2 was distinct from remaining stations. The parasitic cyclopoid *Ergasilus* peaked slightly at TK5, but the trend was not significant ($P = 0.23$). Calanoida were invariable among stations ($P = 0.73$).

Strong horizontal tendencies in cladocerans were apparent (Figure 25). Most abundant, *Bosmina* increased significantly ($P < 0.01$) and was statistically different among stations. *Diaphanosoma* and *Daphnia* both exhibited non-significant ($P = 0.11$ and $P = 0.88$, respectively) peaks in density at TK5. *Moina* density exhibited a declining downlake trend ($P = 0.33$). *Ceriodaphnia* showed a slight increase from TK2 to TK6 ($P = 0.22$).

Remaining net zooplankters also exhibited appreciable longitudinal trends in density (Figure 26). *Diffflugia* and ciliate densities peaked at TK5, but neither trend was

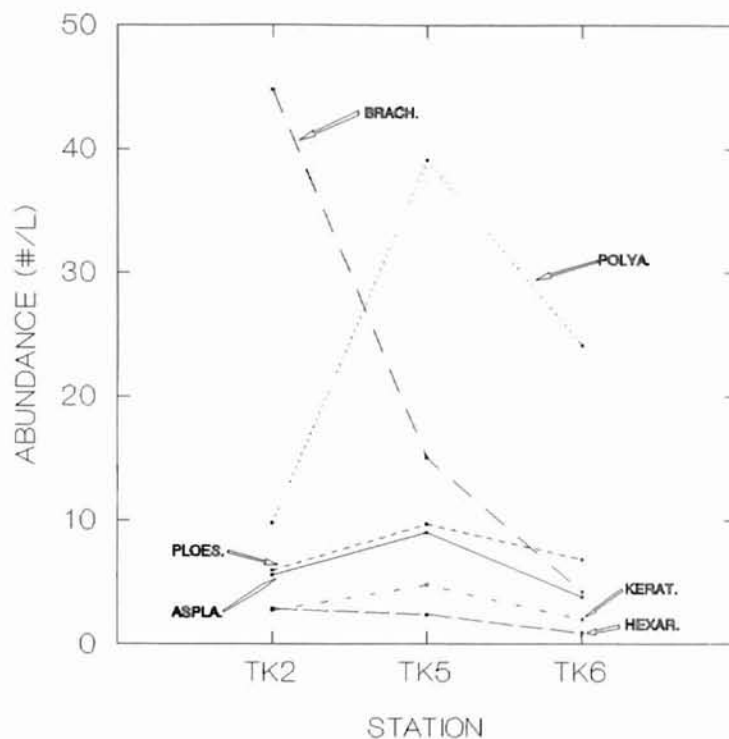


Figure 22. Longitudinal Trends in Rotifer Densities.

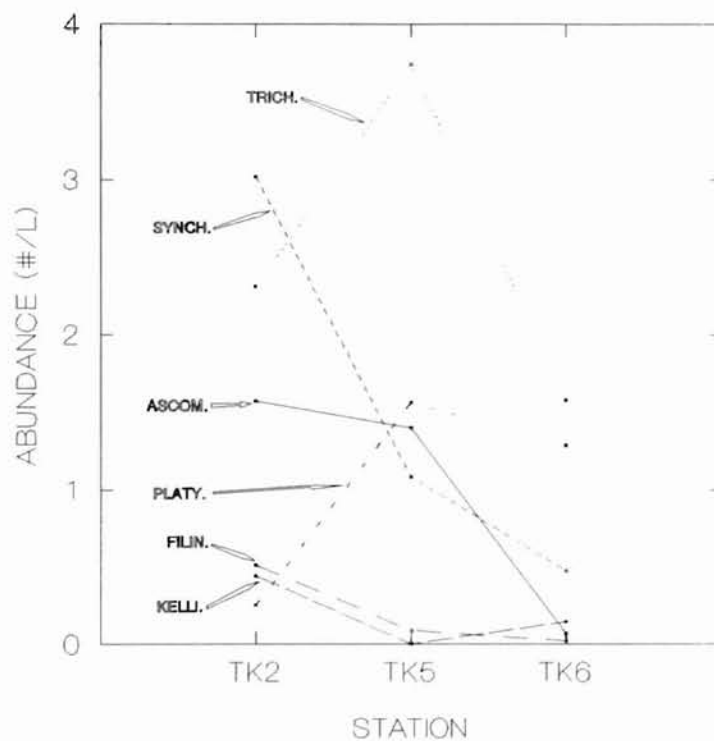


Figure 23. Longitudinal Trends in Rotifer Densities, continued.

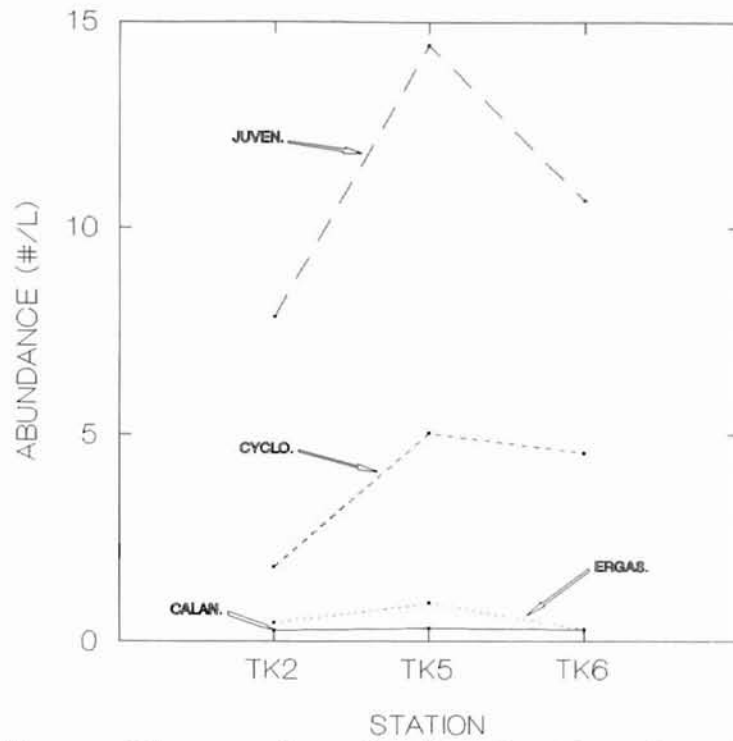


Figure 24. Longitudinal Trends in Copepod Densities.

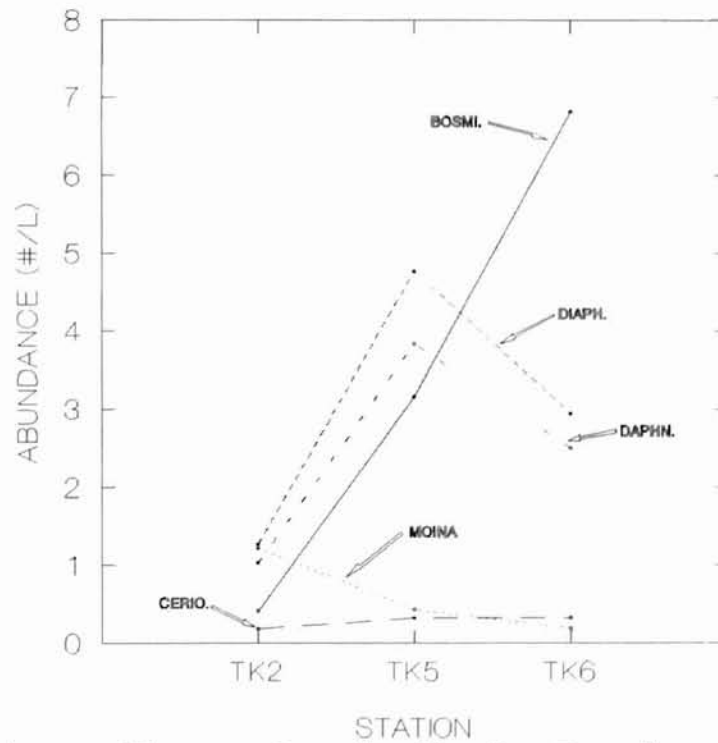


Figure 25. Longitudinal Trends in Cladoceran Densities.

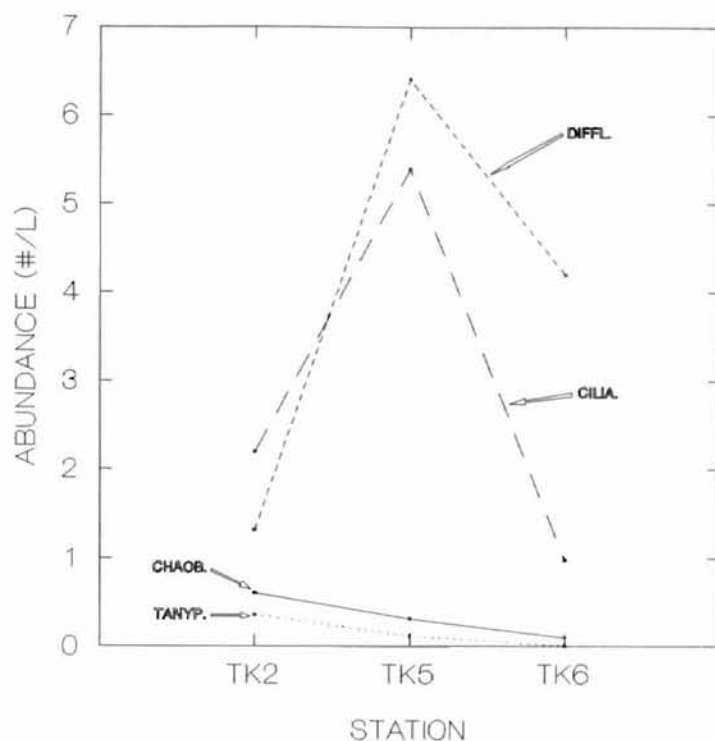


Figure 26. Longitudinal Trends in Remaining Net Zooplankton Densities (average \pm SEM).

significant ($P = 0.25$ and $P = 0.12$, respectively). The downlake decline in *Chaoborus* density was significant ($P = 0.02$); stational comparisons were erroneous. As *Chaoborus* are known predators of larger crustacean zooplankters, their distribution may be a component of the longitudinal distribution of their prey (Dodson 1988). *Tanytus* showed a steady and significant ($P = 0.03$) decrease downlake; TK2 was statistically different from remaining stations.

Fish

Total pelagic target density (TPTD) declined to TK5 and increased slightly to TK6 (Figure 27). This trend was highly significant ($P = 0.01$), and TK2 was significantly

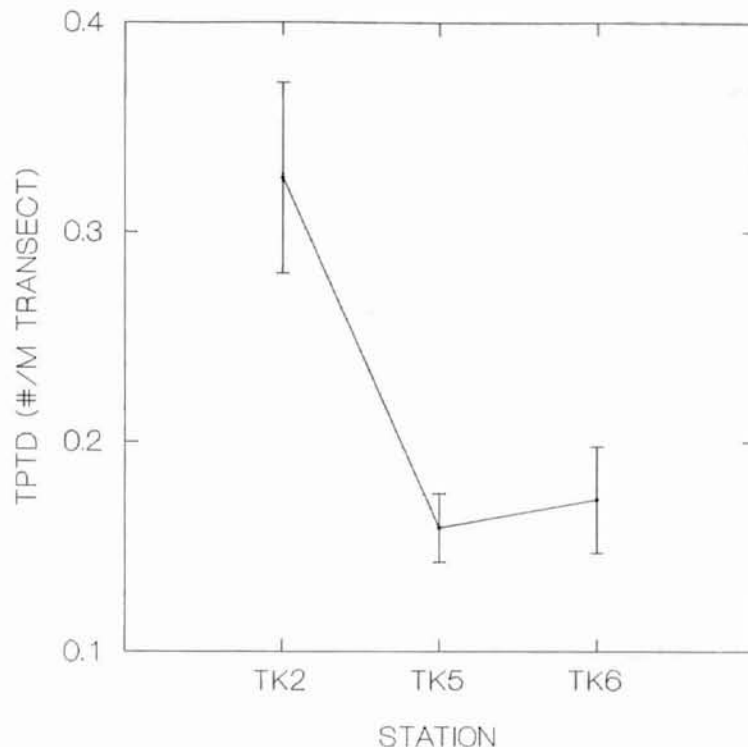


Figure 27. Longitudinal Trend in Total Pelagic Target Density (TPTD) (average \pm SEM).

different from remaining stations. Wilde and Paulson (1989) found fish abundance (as per echograms) to decrease from inflows into Lake Mead. Siler et al. (1986) reported similar downlake decreases for other fish parameters as well as abundance.

As echograms are more holistic than discreet net samples, their results should more reliably reflect the trend in fish density. However, target strength (and thus discernability) is dependent on target size. Therefore, results reflect only trends in targetable individuals and would exclude small species and juvenile stages.

A total of 10 species and 527 individuals were captured in the vertical nets (Table IV). Total yield as number

Table IV. Fish Species and Abundance Collected in Lake Tenkiller.

Species	Total	
	Number	%
White bass (<i>Morone chrysops</i>)	371	70.4
Gizzard shad (<i>Dorosoma cepedianum</i>)	98	18.6
Channel catfish (<i>Ictalurus punctatus</i>)	21	3.98
Freshwater drum (<i>Aplodinotus grunniens</i>)	16	3.03
Largemouth bass (<i>M. salmoides</i>)	9	1.71
Bluegill (<i>Lepomis macrochirus</i>)	5	0.95
Spotted bass (<i>Micropterus punctulatus</i>)	3	0.57
White crappie (<i>Pomoxis annularis</i>)	2	0.38
River carpsucker (<i>Carpionodes carpio</i>)	1	0.19
Smallmouth buffalo (<i>Ictiobus bubalus</i>)	1	0.19
TOTALS	527	100.00

(Figure 28) steadily declined downlake. Catch as wet weight (Figure 29) bottomed at TK5. Neither trend was significant ($P = 0.47$ and $P = 0.58$, respectively).

Vertical trends in fish distribution were evident but not statistically evaluated. Echograms revealed restricted distribution of targets near the thermocline. Upon destratification, fish were more variable in depth of capture (Appendix A). Matthews et al. (1985) reported similar concentration of fish above a chemocline, while thermally stratified. This zone was found to optimize lowest temperature and highest dissolved oxygen.

Species-specific longitudinal trends were evident (Figure 30). White bass dominated catch in numbers and varied little among stations. Gizzard shad showed a significant ($P = 0.02$) downlake decrease in numbers; TK2 was

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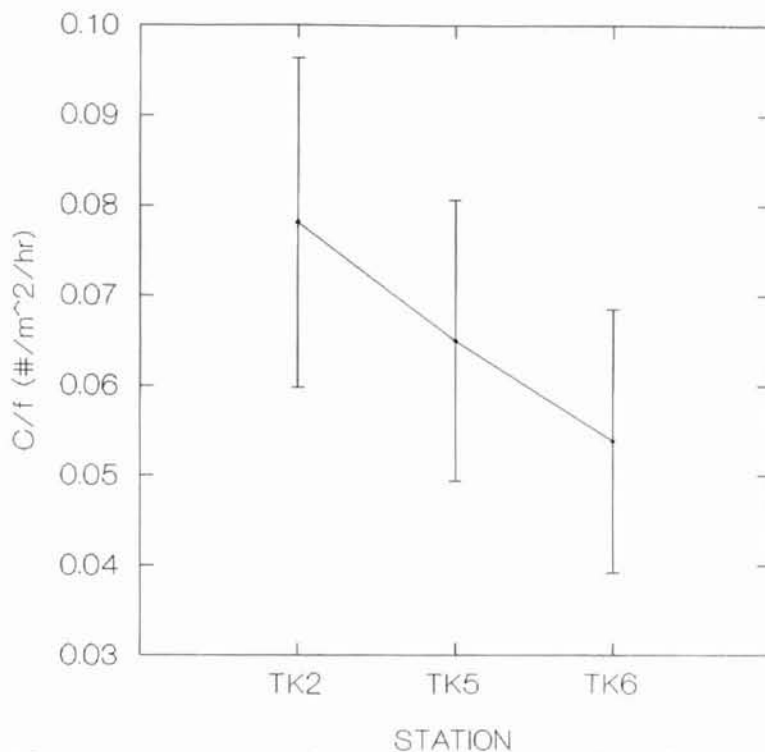


Figure 28. Longitudinal Trend in Gillnet Catch (as number) per Effort (average +/- SEM) .

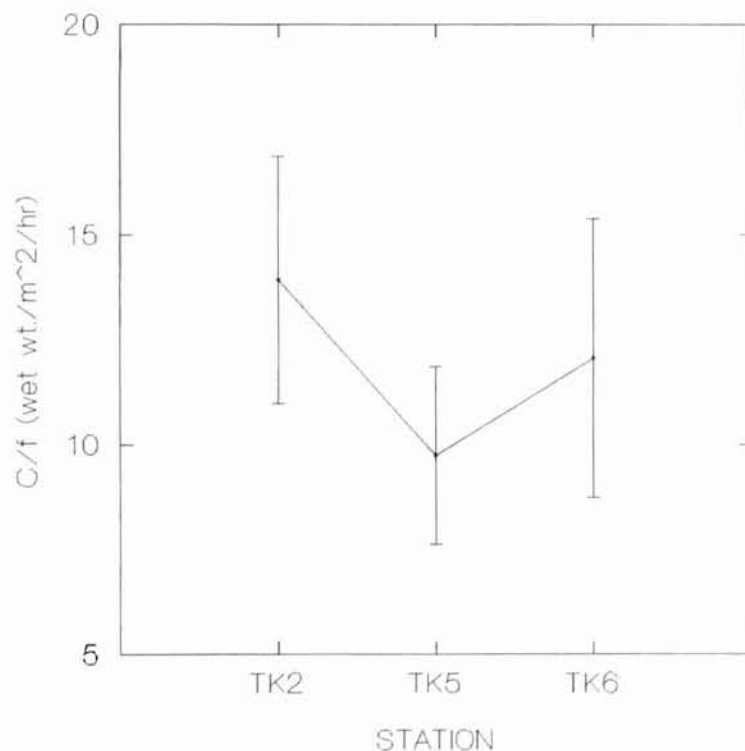


Figure 29. Longitudinal Trend in Gillnet Catch (as wet weight) per Effort (average +/- SEM) .

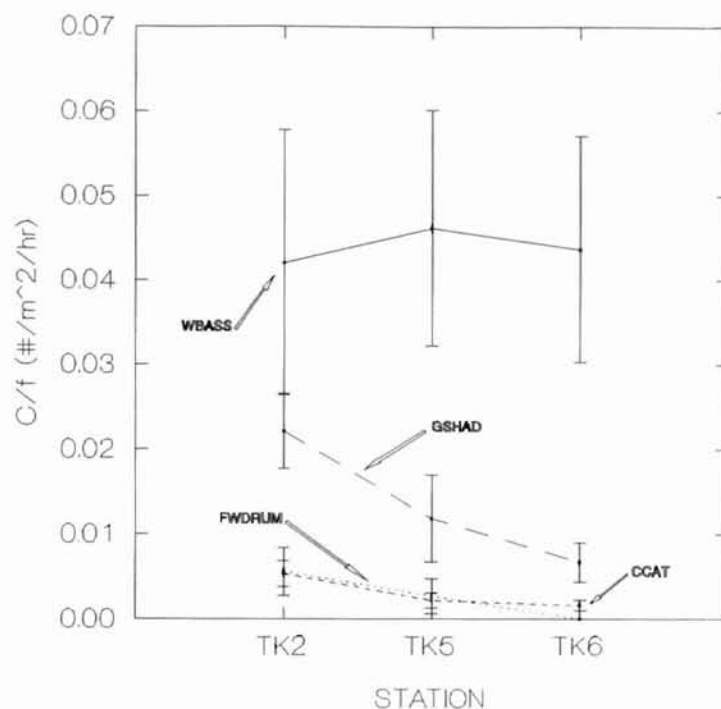


Figure 30. Longitudinal Trends in C/f as Number (average \pm SEM) for Select Fish Species.

statistically different from remaining stations. Channel catfish and drum exhibited declining trends from TK2, but they were not significant ($P = 0.14$ and $P = 0.10$, respectively). Decreasing longitudinal trends for gizzard shad, channel catfish, and drum have been reported for other reservoirs (Eley et al. 1967, Siler 1986).

Longitudinal trends in captured weight were similar to those in number for most species (Figure 31). The trend in white bass was different, however, as it showed an increase from TK5 ($P = .83$). This was attributed to greater frequency of larger individuals captured at TK6. Gizzard shad showed a significant ($P = .02$) downlake decline in captured weight; TK2 was separate from remaining stations.

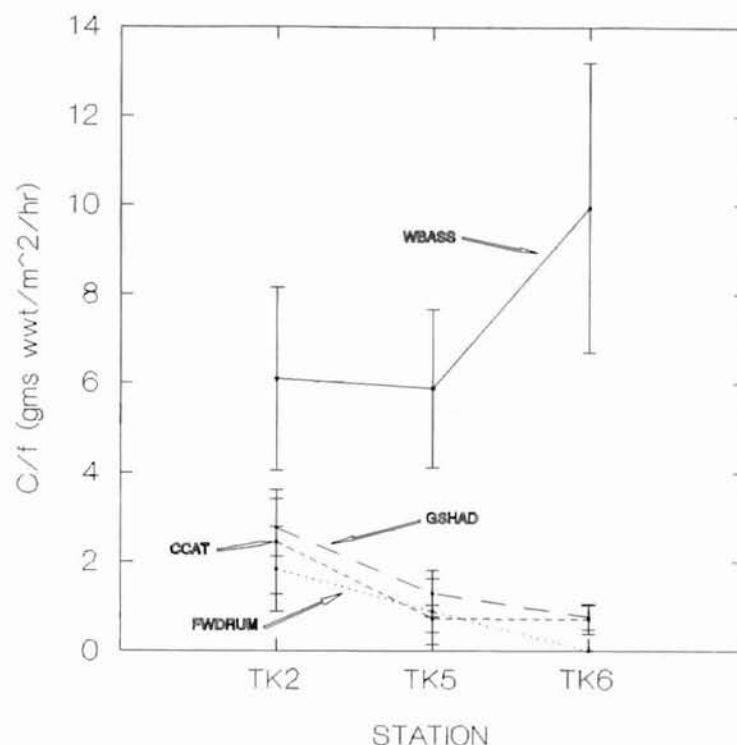


Figure 31. Longitudinal Trends in C/f as Wet Weight (average \pm SEM) for Select Fish Species.

Captured weight of channel catfish declined to TK5 and stabilized ($P = .44$). Weight yield of freshwater drum exhibited a declining trend with thalweg distance ($P = .09$).

Conclusions

Most water quality, fish, and planktonic parameters in Lake Tenkiller exhibited longitudinal trends, and many were significant. Statistical comparisons usually resulted in inference of only two zones (i.e., TK5 and TK6 were statistically similar while different from TK2). This indicated TK5 to be late-transitional in location. Late transitional stations would exhibit characteristics more equitable with lacustrine stations; hence, the frequent

statistical similarity of TK5 and TK6.

Lake Tenkiller plankton and fish exhibited several longitudinal trends. First, chlorophyll concentration for the study duration decreased downlake as opposed to an expected peak at TK5. Secondly, total zooplankton, rotifers, and copepods peaked in density at TK5, while cladocerans increased along the thalweg. Relative frequency of rotifers decreased along the thalweg and that of copepods and cladocerans increased. Thirdly, TPTD, total fish, gizzard shad, drum, and channel catfish numbers and weights generally decreased down the lake. White bass were invariable among stations except for an increase in captured weight at TK6.

Water quality and biotic gradients, as shown in Lake Tenkiller, constitute ambiguity of reservoirs as lentic systems and may explain the limited success of the MEI in reservoir applications (Ryder et al. 1974). A relevant and possibly more successful application would account for longitudinal zonation. This approach would result in at least three values, which would be area-weighted and averaged to represent the system. Thus, as $TDS:Z_{mean}$ decreases from headwaters to dam, fish production (and other parameters) should decline. Eley (1967), Rinne (1981), Siler (1986) and this study show decreasing trends in fish variables with distance from headwaters. For this study, a concomitant decrease in conductivity is also apparent.

Considering the turbidity gradient prevalent among reservoirs, a conductivity-based MEI (derived via discussed

method) may still meet with limited success. In spite of adequate nutrients, algal productivity is light-limited until the transition zone. A conductivity-based MEI would predict higher consumer response than realized until the transition. This would result in outliers which would affect MEI-fish production correlations.

The chlorophyll gradient may serve as a better estimator of reservoir fish (or other consumer) variables. Jones and Hoyer (1982) noted a stronger linear correlation between chlorophyll-a and sportfish harvest than when using total phosphorus, alkalinity, or the conductivity-based MEI. Although correlations were not conducted, total fish variables and chlorophyll appear to exhibit concomitant decreasing trends.

Certain elements of the experimental design should be improved: (1) Study duration should be restricted to stable periods (i.e., stratification). Seasonal transition and resulting destratification during the latter three sampling periods may have overwhelmed spatial trends of some variables (e.g., chlorophyll); (2) More sampling stations should be added to better represent the transition zone and refine trends; (3) Replicate net sets at transects should occur to garner a more robust data set for statistical tests. Although nets were used randomly along transects, intra-transect variability in distribution could have influenced results. Multiple nets per transect and/or increased sample size should decrease the effect of outlying biases which possibly may have masked trends.

Results of this study suggest that reservoirs are spatially heterogenous in habitat and biotic variables along their axes. As seen in Lake Tenkiller, longitudinal trends support the notion of a transition from a riverine to a lacustrine community. Thus, reservoir-wide management decisions cannot be based on data gathered from only one sampling station. Knowledge of longitudinal gradients should not only facilitate more productive sampling but also increase conceptual and practical applicability to reservoirs of such research interests as the MEI.

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APPENDIX A
VERTICAL PROFILES OF WATER QUALITY
AND FISH CATCH

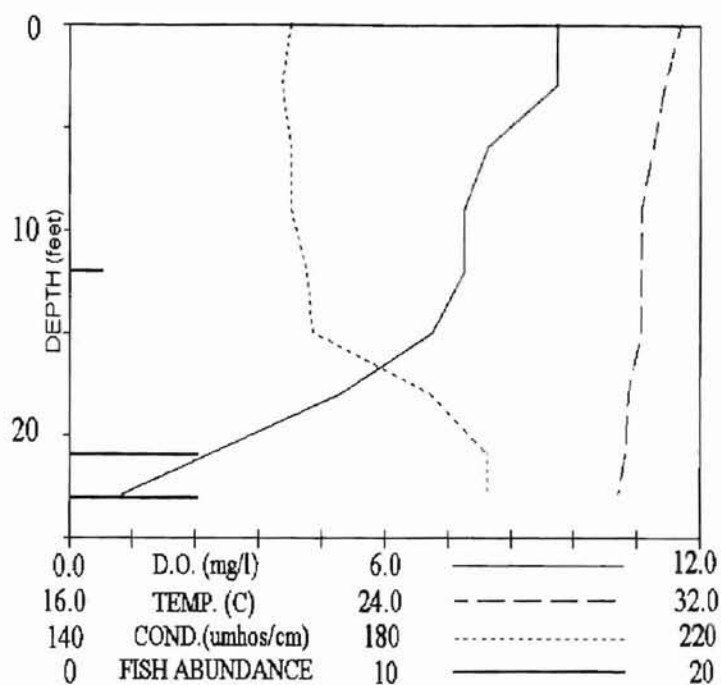


Figure 32. Vertical Profile of Water Quality and Fish Catch for TK2, 16 AUG 93.

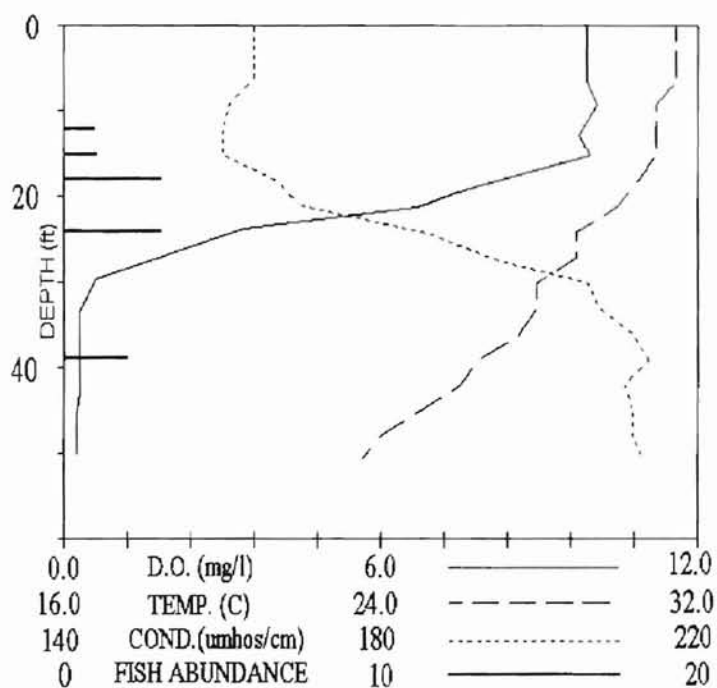


Figure 33. Vertical Profile of Water Quality and Fish Catch for TK5, 16 AUG 93.

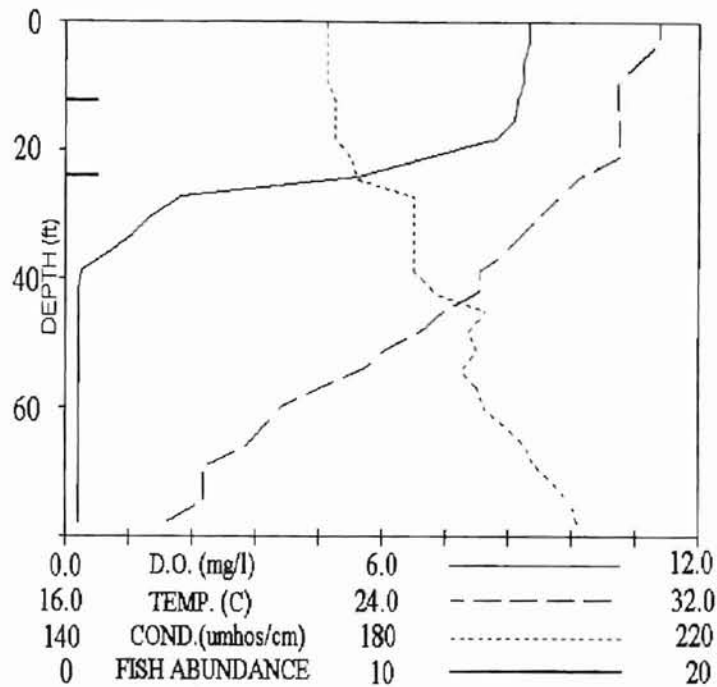


Figure 34. Vertical Profile of Water Quality and Fish Catch for TK6, 16 AUG 93.

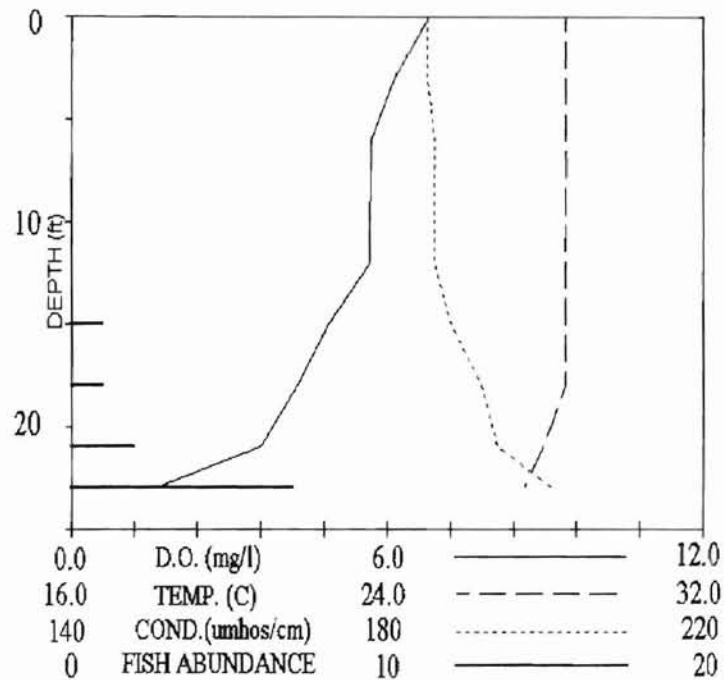


Figure 35. Vertical Profile of Water Quality and Fish Catch for TK2, 2 SEP 93.

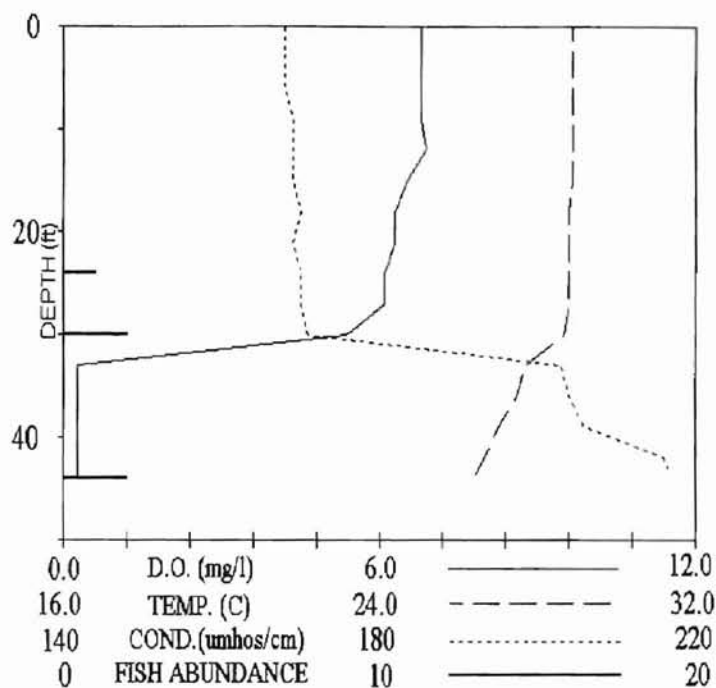


Figure 36. Vertical Profile of Water Quality and Fish Catch for TK5, 2 SEP 93.

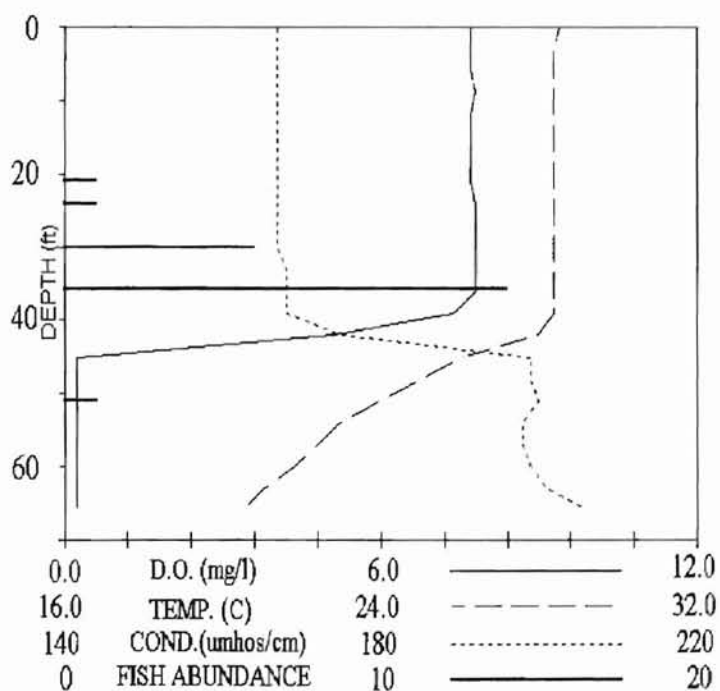


Figure 37. Vertical Profile of Water Quality and Fish Catch for TK6, 2 SEP 93.

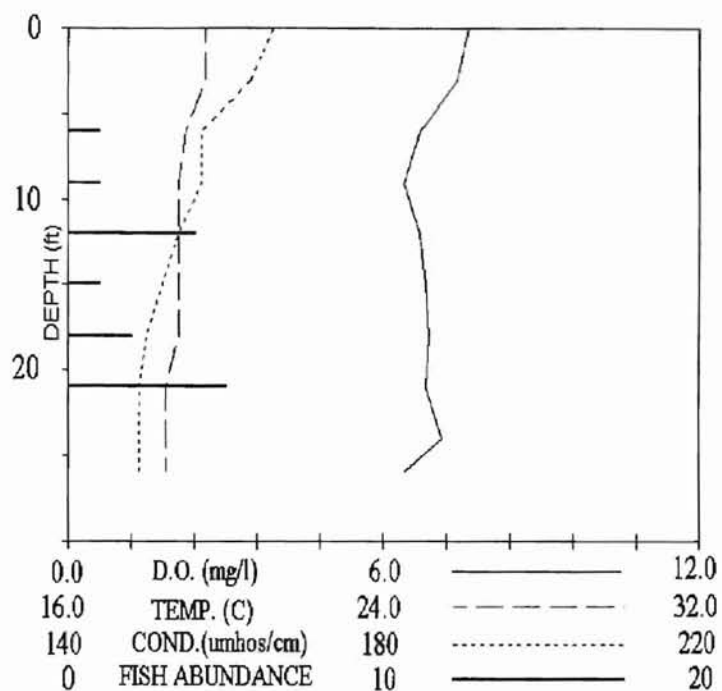


Figure 38. Vertical Profile of Water Quality and Fish Catch for TK2, 16 SEP 93.

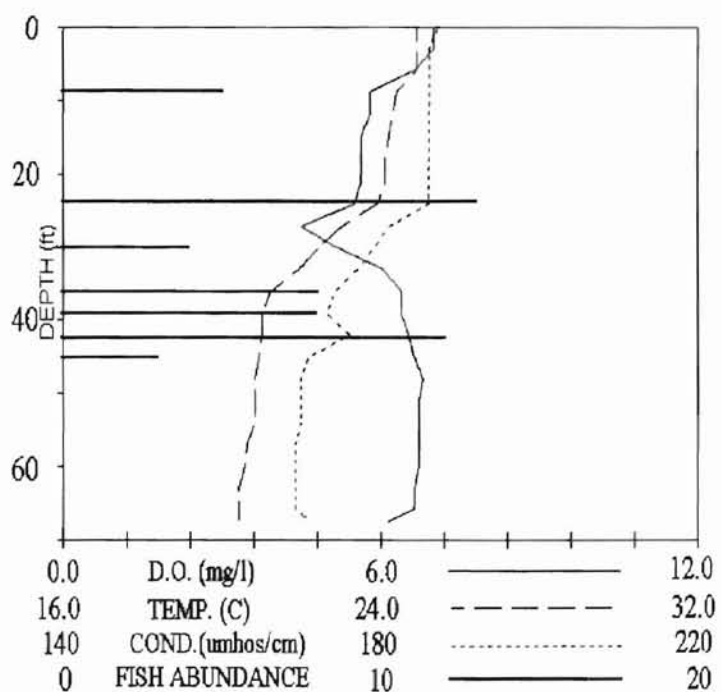


Figure 39. Vertical Profile of Water Quality and Fish Catch for TK5, 16 SEP 93.

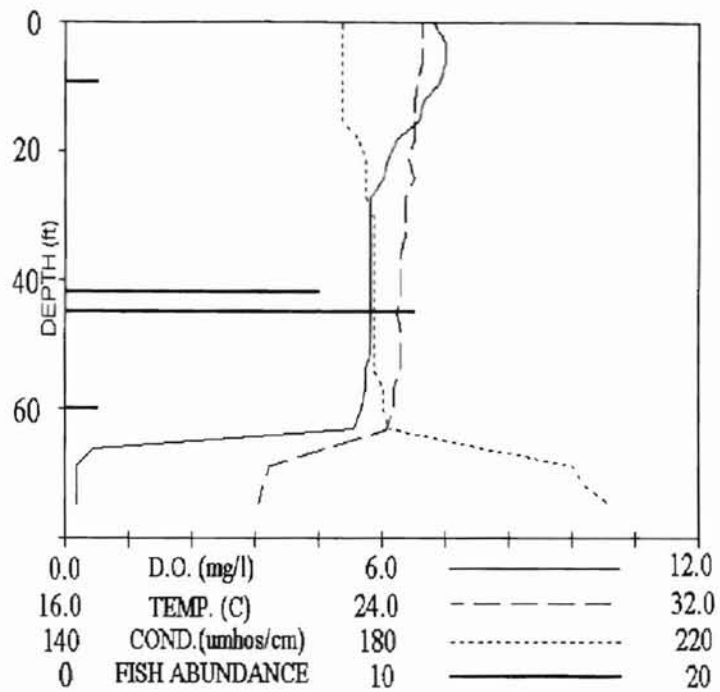


Figure 40. Vertical Profile of Water Quality and Fish Catch for TK6, 16 SEP 93.

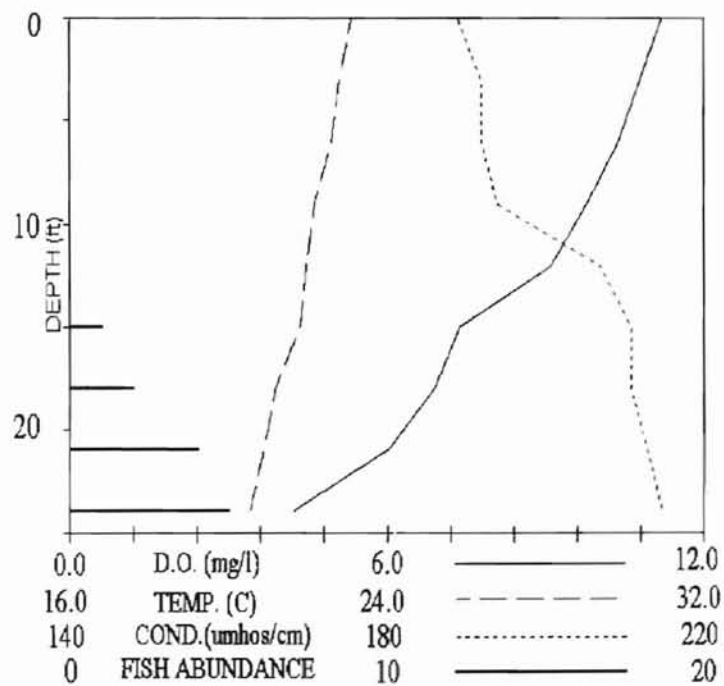


Figure 41. Vertical Profile of Water Quality and Fish Catch for TK2, 30 SEP 93.

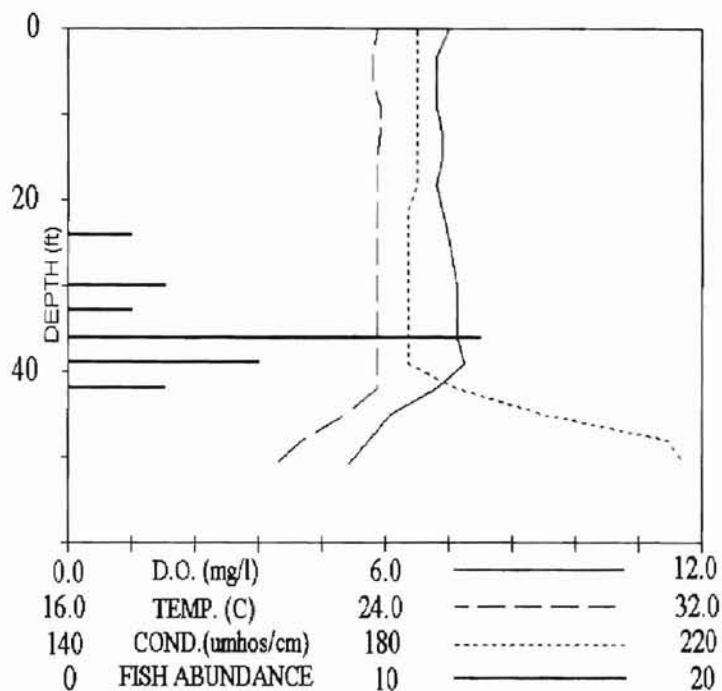


Figure 42. Vertical Profile of Water Quality and Fish Catch for TK5, 30 SEP 93.

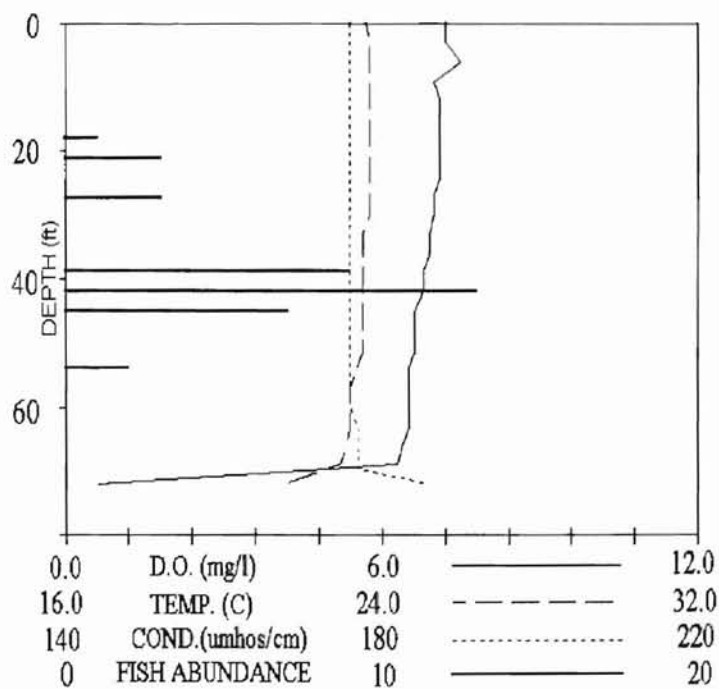


Figure 43. Vertical Profile of Water Quality and Fish Catch for TK6, 30 SEP 93.

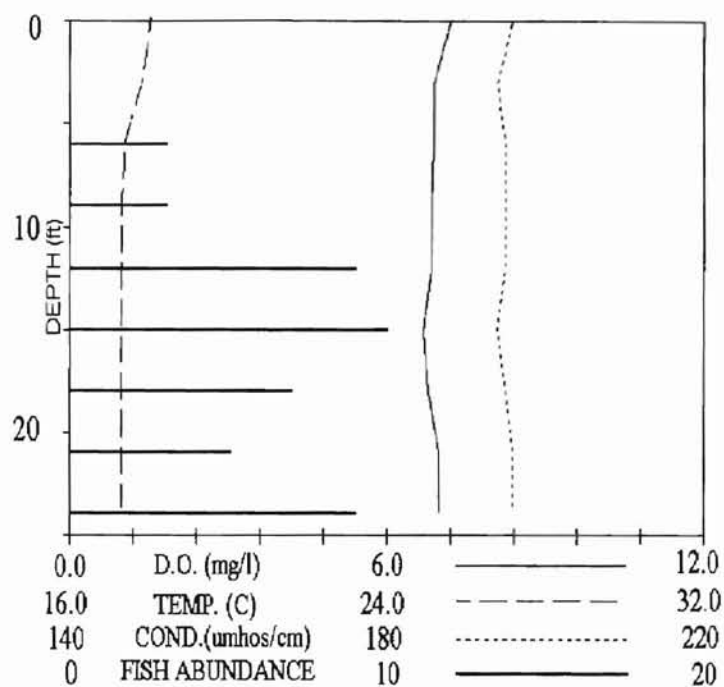


Figure 44. Vertical Profile of Water Quality and Fish Catch for TK2, 21 OCT 93.

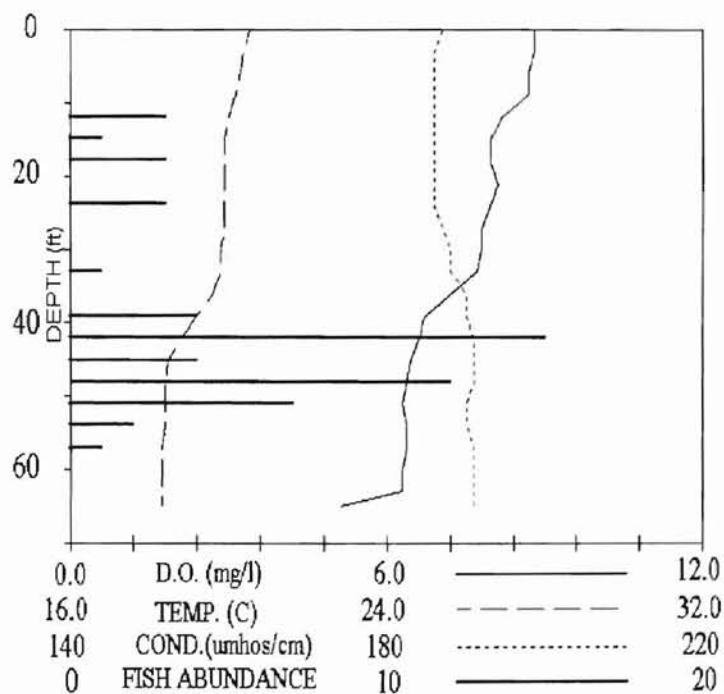


Figure 45. Vertical Profile of Water Quality and Fish Catch for TK5, 21 OCT 93.

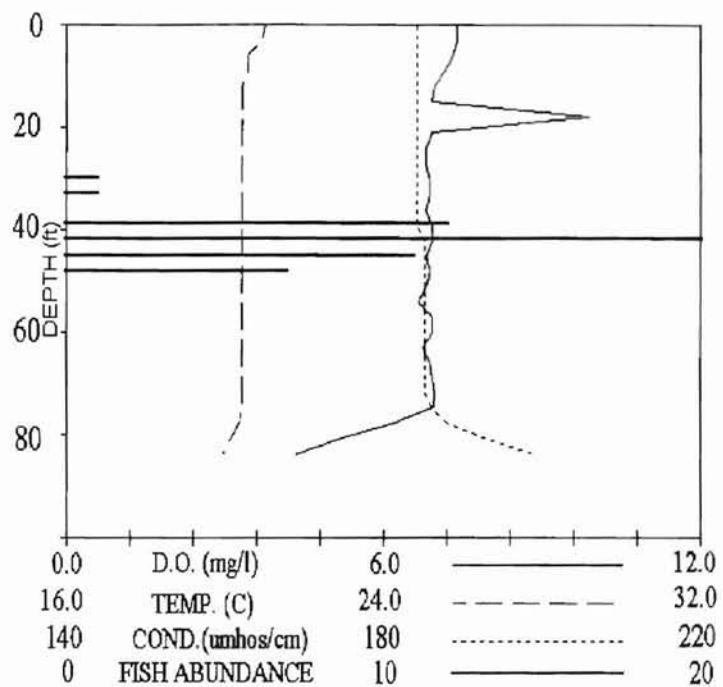


Figure 46. Vertical Profile of Water Quality and Fish Catch for TK6, 21 OCT 93.

VITA

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