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INTRODUCTION

Animal communities develop as a result of the addition of species by immigration and the loss of species by extinction. The species that colonize a newly developing community are those that can reach the area being colonized and survive its physical and biological environment. The process of colonization is influenced by biotic properties such as vagility and dispersal capability, zoogeographic factors, and physical agencies such as wind and water currents that assist dispersal. The survival of colonists is influenced by the character of the physical environment, habitat requirements of the colonists, and nature and intensity of the biological interactions that occur in the developing community.

One of the more controversial aspects of community development concerns the relative importance of deterministic processes, such as biological interactions, versus the action of chance (e.g., random dispersal by water or air currents and chance survival resulting from climatic factors). The dichotomy between these models is indistinct, however, since communities can have deterministic end points dependent upon random initial conditions (Lawton) and since the importance of biotic processes may change as a community matures. It is usually difficult to distinguish between patterns resulting from post-colonization phenomena such as biotic interactions and those produced randomly unless the colonization history of the community is known. The latter is seldom possible under field conditions.

Related to the controversy concerning the relative importance of deterministic and random processes is an interest in the demographic attributes of colonizing species. Typical early colonizing species may posses characteristics, such as high reproductive rates, short generation times, and wide tolerance limits that facilitate the invasion of new communities, leading some researchers to suggest that successful early colonists are typically r-adapted. Features imparting success to early colonist may, however, be less useful as communities develop and biotic interactions increase in intensity. Studies of insular avian communities suggest that species possessing the attributes of good colonists are often absent from communities where species richness is high and biotic interactions presumably more intense. Other researchers, however, believe that a species position on the r - K continuum confers less ability to predict its success as a colonist than an understanding of its ecological requirements in relation to the habitat being colonized.

Patterns of colonization have been described for intertidal, terrestrial arthropod, bird, and mammal communities. Very little, however, has been written concerning patterns of change associated with the development of lentic fish communities. Such communities lend themselves to the study of community development because they are relatively isolated, thus permitting careful monitoring of the order of colonization. While, several researchers have described the changes in fish communities that occur following the impoundment of new reservoirs, these studies have emphasized the management of sport fishes rather than the ecological mechanisms underpinning community development. In addition, the systems under study were heavily fished, which can significantly alter the size and species composition, growth rates, and abundance of their fish populations. Such alterations may obscure the ecological processes characteristic of developing fish communities.

In this study, we sampled the fish community in a new reservoir during the first three years following impoundment. The rate and order in which species were introduced, and their fate was documented by continuous monitoring. Because the reservoir was located on the Savannah River Site, a restricted area owned by the Department of Energy (DOE), it was never fished. The data collected in this study permitted us to address the following questions concerning the development of the L Lake fish community:

1) What types of changes occurred during community development?
2) Was community development a matter of chance or governed by deterministic biological processes?
3) How did early colonizing species differ from the species of later developmental stages?

METHODS AND MATERIALS

Study area

The Savannah River Site encompasses 300 sq mi of the Atlantic Coastal Plain in west-central South Carolina. It is drained by five tributaries of the Savannah River, one of which is Steel Creek. In 1985, the mid reaches of Steel Creek were impounded to create L-Lake, a 400 hectare reservoir intended to serve as a once-through cooling pond for a nuclear reactor. L Lake was filled with water pumped from the Savannah River and a nearby reservoir, discharge from the upper reaches of Steel Creek, and rainfall runoff from the L Lake watershed; it reached normal pool level (approximately 58 m above mean sea level) in October 1985. L-Lake has an average width of approximately 600 m and maximum depth near the dam of approximately 18 m. It extends along the Steel Creek valley approximately 7000 m from the dam to the headwaters. During construction, most of the terrestrial vegetation in the lake bed, with the exception of standing timber in several coves, was cut and hauled away or burned on site. Artificial reefs (tire piles, brush piles, and log piles) were constructed to provide fish habitat in littoral areas.

L-Lake stratifies during spring and summer, mainly due to climatic factors as is typical of most southeastern lakes and reservoirs. However, stratification occasionally occurs during the winter due to density differences between thermal reactor discharges and underlying lake waters. Water quality is within the range of other southeastern lakes for dissolved oxygen, conductivity, total dissolved solids, total suspended solids, total organic carbon, alkalinity, nitrate-nitrogen, silica, calcium, magnesium, potassium, sodium, chloride, hydrogen sulfide, and sulfate. Total phosphorus concentrations and primary productivity, however, are higher than in most other southeastern lakes and reservoirs.

L Lake received thermal effluent during November 1985 - June 1986 and December 1986 - June 1987. The maximum temperature in the study area (i.e., the lower 60% of L Lake by surface area, Figure 1) was 34^{o} C, approximately 2^{o}C higher than in other southeastern reservoirs. While the highest temperatures occurred in June, the greatest elevations occurred during the winter and early spring whe water temperatures were as much as 5 ^{o}C above ambient. Temperatures exhibited little consistent spatial variation within the study area.

<u>Sample design</u>

Adult and juvenile fish were collected by electrofishing. Twenty sampling stations for adult and juvenile fish were established in littoral habitats within the study area (Figure 1). The northern 40% of the lake was not sampled routinely since high temperatures (in excess of 35^{o}C) made it unsuitable for fish and unsafe to sample during periods of reactor operation. The study area was divided longitudinally into five strata of approximately equal size with four sample stations in each strata. Each of the five strata was divided into two substrata corresponding to the left and right banks. The locations of the two sample stations within each substratum were randomly assigned at the start of the study and used for all subsequent sampling. Heavily timbered areas were excluded from sampling because of the difficulty of maneuvering in them during the night when sampling was conducted; heavy standing timber occurred over approximately 8% of the shoreline in the sampling area. Each littoral zone sample station consisted of a 100 m transect parallel to the shoreline and following the one m depth contour.

Electrofishing samples were also collected from 25 artificial reefs distributed throughout the study area. Twelve of the reefs were composed of cinder blocks, twelve of automobile tires, and five of sunken logs and brush. Artificial reefs ranged from 20 - 45 m in length, from 5 - 15 m in width, and were in 1 - 3 m of water. Sampling the fish assemblages on the artificial reefs provided information on species and size groups associated with structurally complex habitats and helped to compensate for our inability to sample the timbered areas in the littoral zone. All electrofishing was conducted during darkness (1800 - 0600 h) when collection efficiency is generally highest for most species.

Electrofishing was conducted at all sample stations and reefs in the sampling area on a monthly basis from January 1986 to December 1988. In addition, electrofishing samples were taken from the northern portion of L-Lake in January 1986, February 1986, March 1986, August 1986, August 1987, and August 1988 to evaluate community development outside the study area. These data will not be reported since they demonstrated nothing of significance.

Larval fish were collected with plankton nets to provide information concerning the reproductive success of some species. Plankton net sampling was conducted weekly during the months of February - June and biweekly during the remaining months. Collections were made by towing the nets horizontally at a depth of approximately 0.5 m along transects parallel to the shoreline. Six transects were sampled in each strata, two in the center of the lake and two at approximately the 2 m depth contours along each bank (Figure 1). Approximately 50 m^3 of water was filtered to obtain each sample. All samples were collected during darkness when the larvae of most species are most likely to be in open water.

In addition to electrofishing and plankton netting, a variety of other sampling techniques (echolocation, hoop netting, gill netting, trammel netting, and seining) were used to collect information on the L-Lake fish community during this study. Extensive programs were also conducted for the assessment of water quality, primary productivity, and phytoplankton, zooplankton, and macroinvertebrate community structure. Since these studies are not central to the main purpose of this paper, their methodologies have not be reported. However, results from some of these studies (along with appropriate citations) will be briefly referenced at a few points in this paper for the purpose of corroboration or to provide useful background information.

Data analysis

The basic data yielded by electrofishing are catch rates (number collected per minute) for each species. Catch rates are assumed to be proportional to the abundance of each species in the littoral zone. This assumption is generally accurate for most species except benthic forms which tend to be underestimated. All catch rates were $\log_e$ transformed for statistical analysis, based on the application of Taylor's Power Law.

Community development involves changes in community composition over time. Changes in community composition are not necessarily manifested as changes in collective properties such as species richness, density, biomass, and diversity; they are, however, manifested as changes in the relationships among species. Multivariate techniques are appropriate for analyzing such changes because they are based on correlations among species abundances. The significance of temporal changes in community structure was analyzed by dividing the three year study into five consecutive six month time periods, averaging the catch rates for each species at each sample station over each six month time period, and conducting a multivariate analysis of variance (MANOVA) of the differences among time periods based on the average species scores. An a priori contrast technique was used to assess the significance of differences between individual time periods following an overall finding of significance by MANOVA. The 0.05 probability level was used in all analyses.

Reciprocal averaging (RA) was used to ordinate the species by time period matrix following MANOVA; this technique was chosen because it is superior to most ordination techniques when community gradients are long and because it maximizes the correlation between samples and species. The latter property permits the derivation of an arranged samples-by-species matrix with its largest values along the matrix diagonal. Two month rather than six month time periods were used for this analysis to provide greater resolution of temporal changes in community structure. Only species that composed at least five percent of at least one time period were used in this analysis and the MANOVA.

RESULTS

Changes in community structure

MANOVA indicated that fish community structure differed significantly ($p \leq 0.05$) among the six month time periods used in this analysis. The a priori contrast technique indicated significant differences between the first time period (January - June 1986) and the remaining time periods. The faunal changes responsible for this difference were analyzed further using RA.

The first RA axes of the ordination of species catch rates on time accounted for 63.3% of the variance in the catch rate data. Scores for the first RA axis were plotted against time to illustrate temporal changes in the structure of the L Lake fish community (Figure 2). RA scores were relatively high during January - June 1986 (time period 1), dropped precipitously in July and August (time period 4), declined slowly between September 1986 and October 1987, and exhibited little consistent change thereafter. The second RA axis was not examined because it accounted for a relatively small proportion of the total variance (21.8), and because it is often subject to distortion (see Gauch 1985 for a discussion of the "horseshoe effect").

The preceding patterns can be interpreted by examining the species weighting the first RA score. The taxa weighting the first RA score positively were the mosquitofish, creek chubsucker, brook silverside, coastal shiner, golden shiner, and dollar sunfish (Table 1). The threadfin shad, gizzard shad, flat bullhead, warmouth, largemouth bass, and bluegill, in contrast, weighted the first RA score negatively. The sharp decline in the RA scores between June and August 1986 resulted from a reduction in the catch of species that weighted the first RA score positively and an increase in the catch of species that weighted it negatively. The relatively slow decline in RA scores between August 1986 and October 1987 reflects a continued but more gradual change in the same direction during the following months.

These taxonomic changes are summarized in Table 2 which shows the simultaneous ordination of species and time periods. This analysis indicates three basic developmental stages in the L-Lake fish community. The first stage (months 1 - 6) was characterized by high densities of mosquitofish, brook silversides, coastal shiner, golden shiner, dollar sunfish, and spotted sunfish. The second stage, was characterized by much lower (and declining) densities of these taxa and by a marked increase in the density of bluegill, and largemouth bass. The dominant taxa in the third stage were bluegill, largemouth bass, and threadfin shad. Other abundant taxa during the third stage were the gizzard shad, warmouth, and flat bullhead. By the third stage, nearly all taxa that were dominant during the first stage had been eliminated from L-Lake, indicating a complete shift in faunal composition during a three year period. It is noteworthy that this change was accomplished with little net change in number of species or diversity indicating that community development is better studied by multivariate techniques than by analysis of collective properties.

An important question concerning the rapid decline in mosquitofish, coastal shiner, creek chubsucker, brooksilverside, spotted sunfish, dollar sunfish, and golden shiner populations that occurred after the first six months is whether this decline represented the die-off of adult fish that emigrated to L Lake and failed to reproduce or of viable, reproducing populations. The creek chubsucker and brook silverside, probably never established a breeding population in L-Lake based on our inability to collect larvae or juveniles of either species. The mosquitofish, golden shiner, and coastal shiner, however, established breeding populations as indicated by the collection of larvae or juveniles in substantial densities (Figures 3, 4, and 5). All of these taxa apparently spawned earlier than usual in L Lake during 1986, presumably because of the affects of elevated water temperatures on the spawning cycle. Spotted sunfish and dollar sunfish were also able to reproduce in L Lake as indicated by the collection of juveniles after May 1986 (Tables 3, 4, and 5). Juveniles collected prior to this may have been residents of Steel Creek prior to the filling of L Lake. Mosquitofish, golden shiner, coastal shiner, dollar sunfish, and spotted sunfish will subsequently be referred to as the "early colonists" in the remainder of this paper.

The sudden decline and extinction of reproducing populations is usually attributed to salient changes in the physical environment or to intense biotic interactions. Dissolved oxygen concentration and temperature are among the most critical physical parameters for fish; neither approached critical levels nor exhibited other types of changes that corresponded with the decline of the colonizing species. Additional physical variables measured concurrently with this study included pH, conductivity, oxidation-reduction potential, light penetration, total dissolved solids, total suspended solids, total organic carbon, dissolved organic carbon, total inorganic carbon, alkalinity, ortho-phosphorus, total phosphorus, nitrite-nitrogen, nitrate nitrogen, ammonia nitrogen, total inorganic nitrogen, total Kjeldahl nitrogen, silica, total and dissolved aluminum, total and dissolved calcium, total and dissolved iron, total and dissolved magnesium, total and dissolved manganese, total and dissolved potassium, total and dissolved sodium, chloride, hydrogen sulfide, and sulphate (Starkel et al. 1988). Like temperature and dissolved oxygen concentration, none of these variables reached detrimental levels or exhibited changes that corresponded with the decline of the colonizing species. In addition, water level and other physical features of L Lake remained constant during the first year.

The only event that clearly coincided with the crash of the early colonists was the sudden expansion of bluegill, redbreast sunfish, and largemouth bass populations. All three taxa (hereafter termed the "successful colonists") exhibited great increases (300-fold for bluegill, eightfold for redbreast sunfish, and 25-fold for largemouth bass) in the period spanning May through August 1986, when the early colonist exhibited their abrupt decline. Of these three taxa, only the redbreast sunfish was relatively abundant before July. Both largemouth bass and bluegill were introduced into L-Lake as juveniles in November 1985 (approximately 4,000 and 40,000 fish, respectively). However, neither taxa was collected in significant numbers until the following spring and summer when juveniles of both species (especially the bluegill) appeared in abundance. The vast majority (97%) of the bluegill collected at this time (July and August) were under 80 mm and probably the progeny of the fish stocked in L Lake (bluegill typically reproduce in their second year). The largemouth bass ranged from 40 - 140 mm in May and from 120 - 280 mm August; they probably included fish spawned in L Lake early in 1986 and fish stocked the previous fall.

Large and sudden increases in standing stock can stress the resources on which populations rely. Food is an important resource that often determines growth rates and carrying capacity in fish communities. Changes in food intake can be evaluated by measuring condition (K), which is essentially a length to weight ratio. Low condition occurs when energy intake is relatively low in relation to energy expenditure. Information was available on the condition of five species of fish during the first year; all exhibited high condition for the first six months followed by an abrupt and statistically significant decrease beginning in July (Figure 6). Declining condition can result from either reduced food intake or increased maintenance costs. Since the physical environment remained unchanged over the period of interest, it is more probable that reduced food intake was the cause.

In the last year of the study, two new taxa appeared in L-Lake. The gizzard shad and threadfin shad were probably introduced as larvae entrained in water that was pumped into L-Lake from the Savannah River where both taxa are abundant. Neither taxa occurred in Steel Creek prior to impoundment. Threadfin and gizzard shad were first observed as juveniles and adults in August 1987. The expansion of these species was not accompanied by decreases in the abundance of other species as was the expansion of the bluegill, redbreast sunfish and largemouth bass.

Characteristics of successful colonists

There were three sources of potential colonists for L Lake: Steel Creek (at least twentyeight species based on pre-impoundment surveys), intentional introductions (two species), and fortuitous introductions (at least three species entrained in water pumped from the Savannah River or a nearby cooling reservoir). Information on the relative abundance of fish in the mid reaches of Steel Creek prior to impoundment is based primarily on electrofishing surveys conducted by Aho et al. (1986) in 1984 and 1985. Presumably successful and unsuccessful colonists of L-Lake differed in terms of demographic, life history, trophic, or other ecological attributes. The potential colonists of L-Lake were compared in terms of parental care of early life stages, fecundity, body size, feeding habits, and spawning habitat requirements. These features were selected because of their ecological importance and because they are fairly well documented for many of the species in Steel Creek and L Lake.

Feeding habits were analyzed by dividing all fish into several broad trophic guilds (insectivore, piscivore, omnivore, and planktivore) based on the major food of adults. Eightyone percent of the early colonists and the species that failed to colonize L-Lake were insectivorous; 8% were piscivorous and 11% were omnivorous (Table 6). In contrast, 22% percent of the species that became established in L-lake were insectivorous, 33% were piscivorous, and 22% were planktivorous. These differences indicate an increase in trophic diversity and predation as the L-Lake fish community developed.

Fecundity was assessed by separating fish into low, medium, and high fecundity groups. Species were classified as low fecundity if they generally produce less than 3,000 eggs per spawning season, medium fecundity if they generally produce 3,000 - 20,000 eggs per spawning season, and high fecundity if they generally produce over 20,000 eggs per spawning season. Exceptions were species known to mature early and produce more than one generation per year; these include mosquitofish and threadfin shad. The mosquitofish produces live young that reach sexual maturity in as little as three months. Adult females produce young as frequently as every two weeks. Threadfin shad generally produce 6,000 - 12,000 eggs per spawning period but may spawn several times per year and grow to reproductive size in the season they were spawned. Both taxa were considered high fecundity in this comparison. Approximately 74% percent of the fish that did not colonize L-Lake were low fecundity and 36% were medium or high fecundity (Table 6). In contrast, all of the successful colonists were medium or high fecundity. The early colonists ranged from low to high fecundity.

Fishes were considered to exhibit parental care if they guarded (i.e., defended from predators) eggs or larvae. Approximately 50% of the species that failed to colonize L Lake, 40% of the early colonists and 78% of the successful colonists exercise parental care (Table 6).

Fish were classified as small if their adult size is generally under 90 mm, medium if between 90 and 200 mm, and large if over 200 mm. Small fish comprised 60% percent of the group that did not produce colonists, 60% of the early colonists, and were absent among the successful colonists (Table 6).

Spawning habitat was divided into several categories: vegetation beds, gravel, sand, hard substrate, submerged objects, and nests. Information on spawning habitat requirements was available for 26 of the potential L-Lake colonists. All but two of the successful colonists were nest builders (Table 6). The threadfin and gizzard shad spawn over vegetation, hard bottoms, and submerged objects. The unsuccessful colonists exhibited a variety of spawning habitat requirements. Some, including the yellow fin shiner, northern hogsucker, tesselated darter, spotted sucker, grass pickerel, and chain pickerel require spawning habitat that was unavailable in L-Lake (e.g., gravel riffles, sandy bottoms, or vegetation beds). While the early colonists also exhibited a variety of spawning habitat requirements, only the creek chubsucker and possibly the brook silverside required habitat (gravel or vegetation beds) unavailable in L-Lake following impoundment.

DISCUSSION

The processes that regulate community development can be broadly categorized in several ways. A basic distinction involves patterns that arise randomly and those produced by the action of "active" ecological processes. Ecological processes can be subdivided into interactive and noninteractive categories; interactive, processes occur among species while noninteractive processes occur within a species or between a species and its environment. One way of determining the importance of interactive biological processes is to observe the responses that follow the introduction of new species or expansion of previously uncommon species. In a community organized by chance or noninteractive biological processes, the introduction of new species would not be expected to affect the resident fauna. A similar lack of response could follow the introduction of new species in other types of communities, if the new species and resident faunas failed to interact or if the interactions were neutral. If, antagonistic interactions (such as predation or competition) occurred with sufficient intensity, however, a reduction in the population size of the resident species would be a possible outcome.

In L Lake, reproducing and relatively well established populations of five species of fish were eliminated following the dramatic expansion of three species. The populations of all the early colonists dropped precipitously with the sudden expansion of the successful colonists and subsequently declined at a lesser rate until largely or completely eliminated from L Lake. There was an absence of concurrent changes in the physical environment likely to have been responsible for the sudden decline of the early colonists. This chain of events indicates the operation of strong, interactive biological processes in L Lake. Strong biological interactions are typical of lake ecosystems and have been posited to be important in the assembly of fish communities in new lakes and reservoirs, but have not been previously observed as directly and clearly as in L Lake.

The nature of the biological interactions responsible for the decline and disappearance of the early colonists can be inferred from the data collected during this study. The expansion of the successful colonists resulted in a relatively sudden 8 - 10 fold increase in the standing stock of fish in the littoral zone of L Lake indicating the potential for increased competition for food. In support of this possibility, food intake decreased after the expansion as indicated by a reduction in the condition of three early colonists and two successful colonists (data were unavailable for other species). Previous research indicates that the species of interest are generalized feeders relying primarily on invertebrates for sustenance; hence may have had overlapping trophic niches.

Even if competition for food was intense, however, it is unlikely to have been the sole cause for the sudden elimination of the early colonists. Condition factors after the expansion of the successful colonist were significantly lower than before the expansion but still close to average levels for the three early colonists for which such comparative information was available (golden shiner, dollar sunfish, and spotted sunfish). In addition, condition factors decreased for both successful colonists and early colonists indicating that both groups suffered reduced food intake, yet the former maintained viable, reproducing populations. Furthermore, it seems very unlikely (and there are no documented cases) that competition alone could cause such drastic declines in species abundance within such a short period of time (amounting to fractions of a generation).

Predation is another interactive biotic process that increased in intensity with the expansion of the successful colonists. Catch rates for largemouth bass, a largely piscivorous species, increased 25-fold between April and August 1986. If this comparison is based on biomass rather than number, the increase is over 100-fold. Potential predators of fish eggs and larvae also increased with the expansion of the early colonists. Bluegill abundance increased over 300-fold between May and August 1986. Bluegill are effective predators of eggs and larvae and, when present in very high densities, can prevent the reproduction of largemouth bass, a large piscivorous species that exercises parental care. Presumably, their impact on species that fail to exercise parental care would be even greater.

If predation on eggs and larvae contributed to the decline of the early colonist, fewer juveniles would be recruited into the population. Examination of the length frequencies of the golden shiner indicates that juveniles quickly disappeared after the expansion of the successful colonists. It is unlikely that this recruitment failure was due to an inability to spawn since the physical conditions for spawning were obviously present (based on previous successful spawnings), and fish health appeared adequate (based on average condition factors). Unlike the golden shiner, the spotted sunfish and dollar sunfish continued to exhibit at least some recruitment during and following the expansion of the successful colonists. These species exercise parental care and would be expected to suffer lower losses of eggs and larvae than the golden shiner.

If predation (either on early life stages or adults) was responsible for the decline of the early colonists but not the successful colonists, it would be reasonable to expect these two groups to differ in ways that affect their vulnerability to predation. Seven of the nine successful colonists were characterized by high fecundity, parental care of early life stages, medium to large body size, and the possession of defensive spines or spiny fin rays. High fecundity imparts obvious advantages if predatory losses are high. Medium to large adult body size is advantageous if the success of predatory attacks is related to the size differential between predator and prey as is typically the case in fish communities. While the spines of the Acanthopterygii serve as fin supports, they also provide defense, and research has shown that soft-rayed fish are more vulnerable to predators than spiny-rayed fish of comparable size. Parental care is "an excellent adaptation to bridge the vulnerable young stage" (Connell) and is of obvious advantage if predation on the early life stages is intense. Parental care as practiced by the species in L Lake, however, also involves oxygenation of the eggs by creating water currents with paired fins or tail. Thus, parental care serves several purposes, only one of which is directly related to defense.

The only invading species that depart from the pattern described above are the threadfin shad and the gizzard shad, neither of which exhibit parental care and both of which are soft rayed. The success of these two species in L Lake during the second and third years is probably related to two somewhat different strategies. The gizzard shad grows very rapidly and attains a large size (over 300 mm). Fishery managers are well aware of its ability to "outgrow" predators and produce large standing stocks of adults that are essentially invulnerable to predation by most native freshwater fishes. It also exhibits very high fecundity. The threadfin shad, on the other hand, attains only moderate size (150 mm) but matures extremely rapidly and is able to produce at least two generations per year. This high biotic potential may permit it to sustain heavy losses yet maintain viable populations. Additional factors that probably contributed to the survival of both species in L Lake are their habitat preference and schooling behavior. The preference of larval and adult shads for pelagic habitat probably reduced contact between them and their predators in L Lake (centrarchids), which are primarily littoral zone inhabitants. A number of studies indicate that schooling imparts protection from predators. Echolocation surveys in L Lake frequently showed discrete aggregations of shad in open water indicating the presence of schooling behavior in L Lake.

The early colonists differed from the successful colonists in several features. The three most abundant early colonists, the golden shiner, coastal shiner, and mosquitofish, are small and soft rayed. These features make them highly vulnerable to a wide variety of predators. Neither of the shiners displays parental care, which could lead to high losses of eggs and larvae to predators of these life stages. The other early colonists, the spotted sunfish and dollar sunfish, are medium size, fish that display parental care. However, the dollar sunfish exhibits very low reproductive potential; it produces only 200 to 400 per clutch, as opposed to its congeners in the successful colonist group which produce up to 50,000 eggs per clutch. The fecundity of the spotted sunfish is unknown; however, they produce unusually large eggs (3 mm in diameter compared with 1.25 mm in diameter for the bluegill) suggesting that clutch size may be low.

Noninteractive as well as interactive biological processes appeared to influence the development of the L Lake fish community. Of the 27 species of fish that occurred in Steel Creek prior to the impoundment of L Lake, 21 apparently failed to establish reproducing populations. Recent research (Meffe and Sheldon) in Steel Creek and several nearby streams indicates that at least seven of the species (tesselated darter, blackbanded darter, Savannah darter, bluehead chub, speckled madtom, northern hogsucker, and yellowfin shiner) that failed to become established in L Lake clearly prefer fast flowing rather than slow flowing or standing water; hence, would not be expected to enter L Lake. Many of the remaining species, while not restricted to flowing waters, require spawning habitat that was unavailable in L Lake. Chain pickerel, redfin pickerel, bluespotted sunfish, and mudminnows generally require aquatic vegetation beds for successful reproduction; aquatic macrophytes were completely absent from L Lake when initial colonization was occurring. Other species, including the spotted sucker and yellow perch probably also lacked appropriate spawning habitat in L Lake. None of these fish were ever collected from L Lake in more than trace amounts. They may have avoided L Lake because of unsuitable habitat or entered L Lake but failed to reproduce. It is noteworthy that nearly all of the species that failed to colonize L Lake possessed either low fecundity or restrictive spawning habitat requirements,

In summary, a variety of noninteractive and interactive biological processes apparently influenced the development of the L Lake fish community. Noninteractive processes and factors, including habitat selection and spawning habitat requirements, may have been instrumental in determining which of the species in the Steel Creek drainage were able to initially colonize L Lake. As standing stocks and predator abundance increased, interactive biological processes including predation and possibly competition probably became of greater importance. A shift from noninteractive to interactive regulatory processes as standing stocks and species number increases may be of general significance. Simberloff and Wilson noted that the development of arthropod communities on previously defaunated islands was initially the result of random or noninteractive biological processes but became increasingly regulated by interactive processes as species richness and population densities rose. Of particular interest in L Lake, however, is the rapidity with which this transition apparently occurred.

While competition may have occurred in L Lake after the expansion of the successful colonists, predation was probably the more important cause of the rapid faunal replacement that we observed. Predation is typically a major organizing factor in lentic communities. The influence of predation by zooplantivorous fishes on the size and species composition of zooplankton communities is a well established fact. It is also clear that predation can have a major influence on the structure of established fish communities; therefore, it is not surprising that it would play a dominant role in the assembly of fish communities in a new reservoir. Regardless of the relative importance of predation versus competition, this study suggests that the assembly of fish communities in new reservoirs (and presumably natural lakes) is a highly deterministic process. All stages of community development appear to have been regulated by biotic processes with relatively predictable outcomes based upon an understanding of the natural histories of the interacting species.

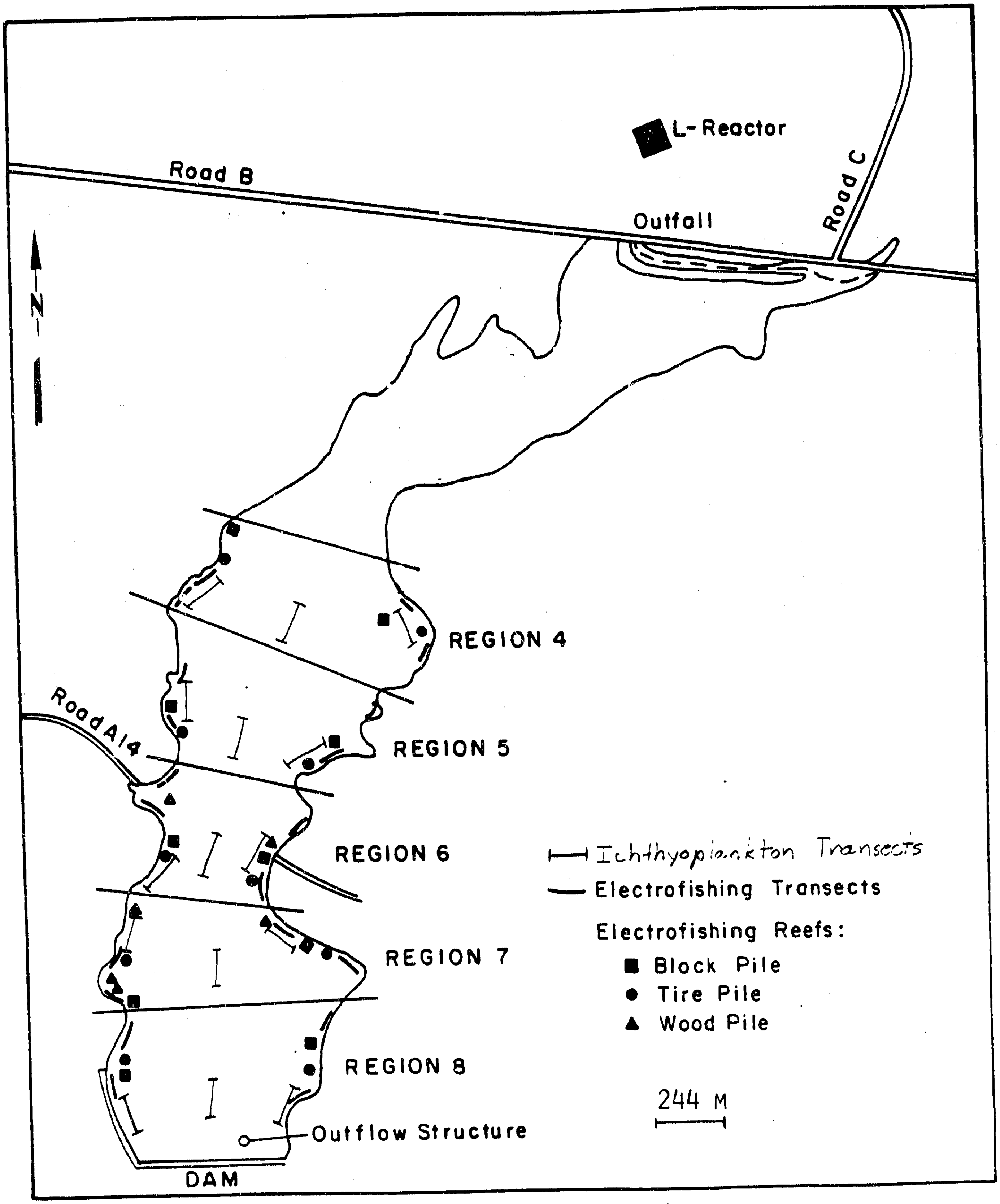


Figure 1. Location of electrofishing and ichthyoplankton transects in L-Lake.

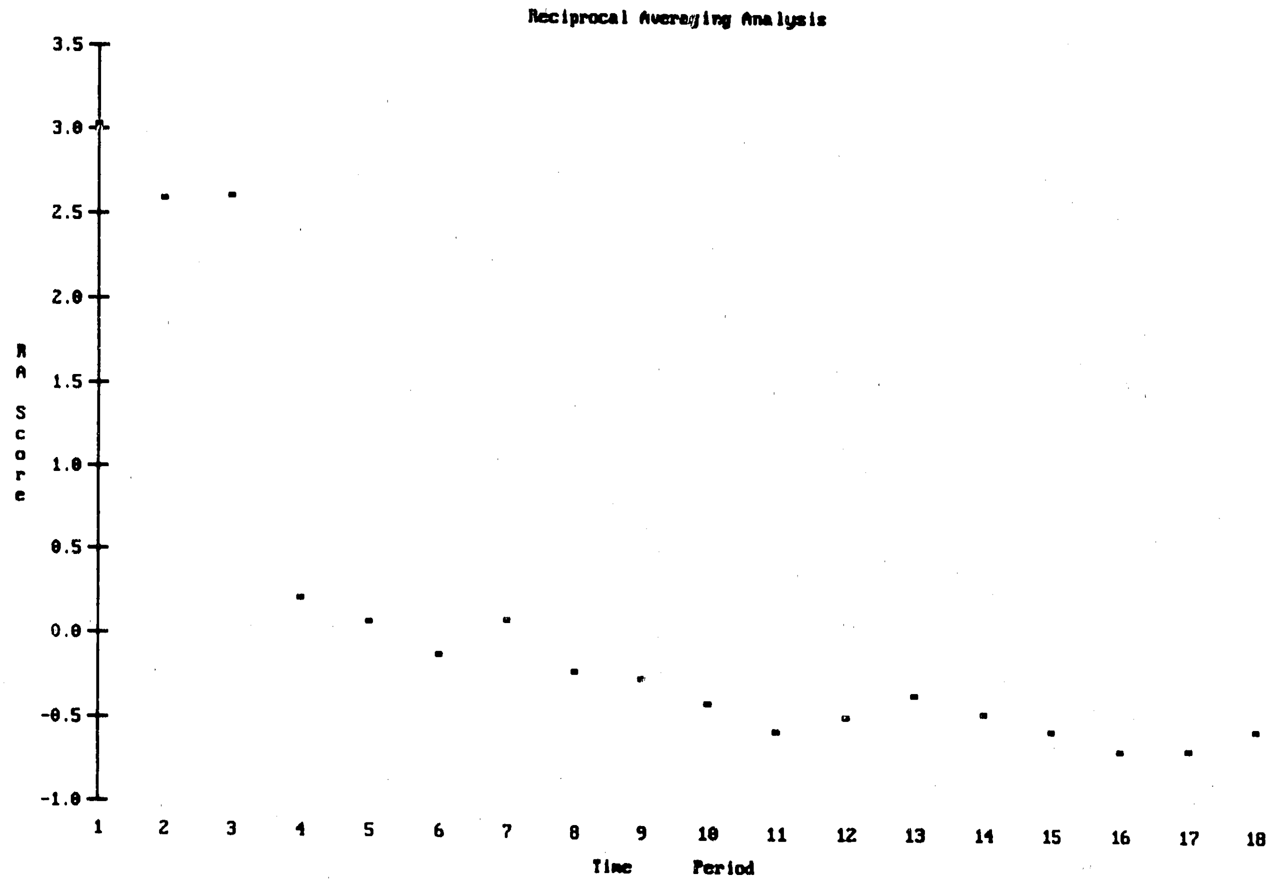


Figure 2. Plot of the first reciprocal averaging score for each two month time period. Time period 1 begins in January 1986 and time period 18 ends in December 1988.

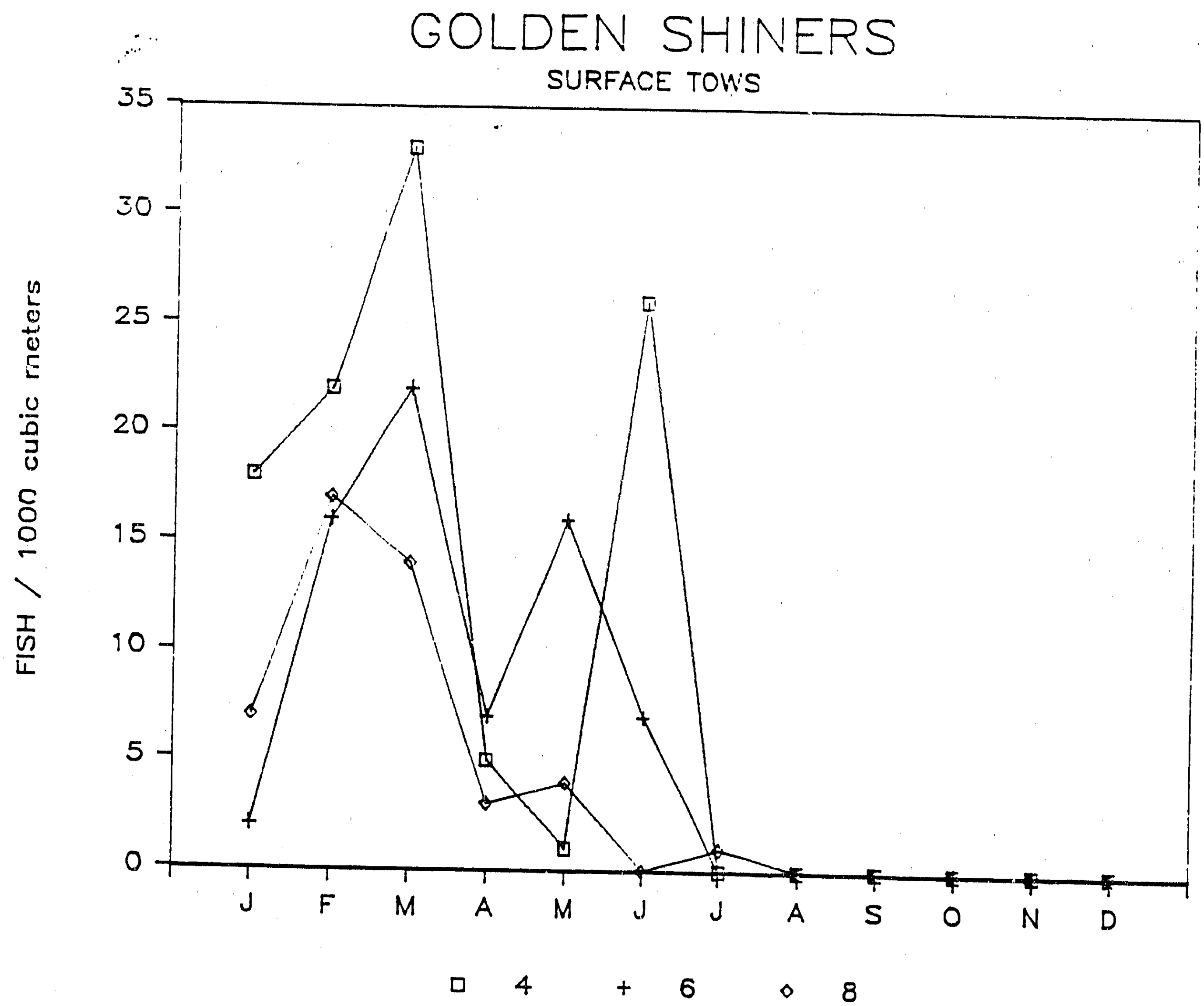


Figure 3 . Average monthly density of golden shiner collected by surface ichthyoplankton tows in Regions 4, 6, and 8 of L-Lake. January - December 1986.

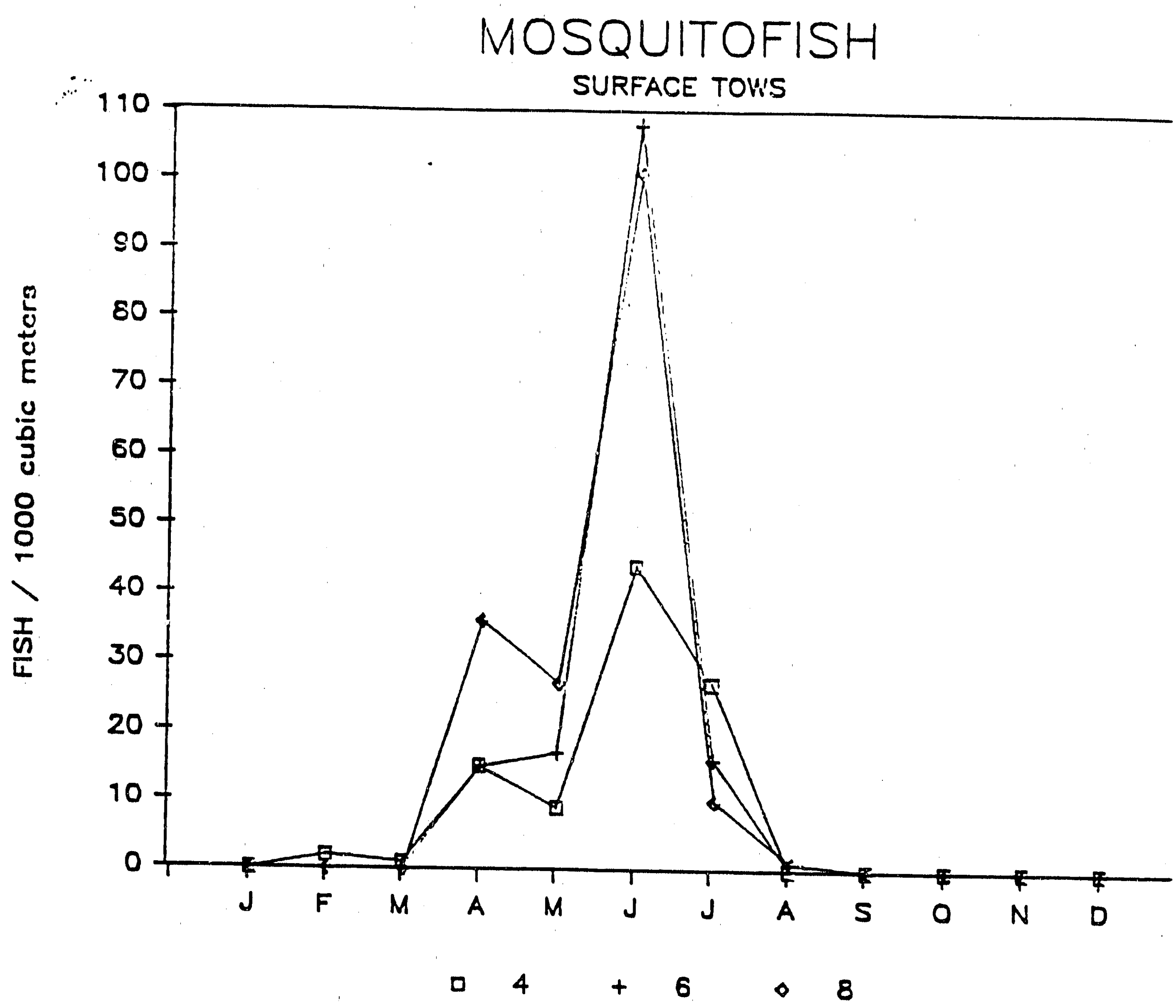


Figure 4 Average monthly density of mosquitofish collected by surface ichthyoplankton tows in Regions 4, 6, and 8 of L-Lake. January - December 1986.

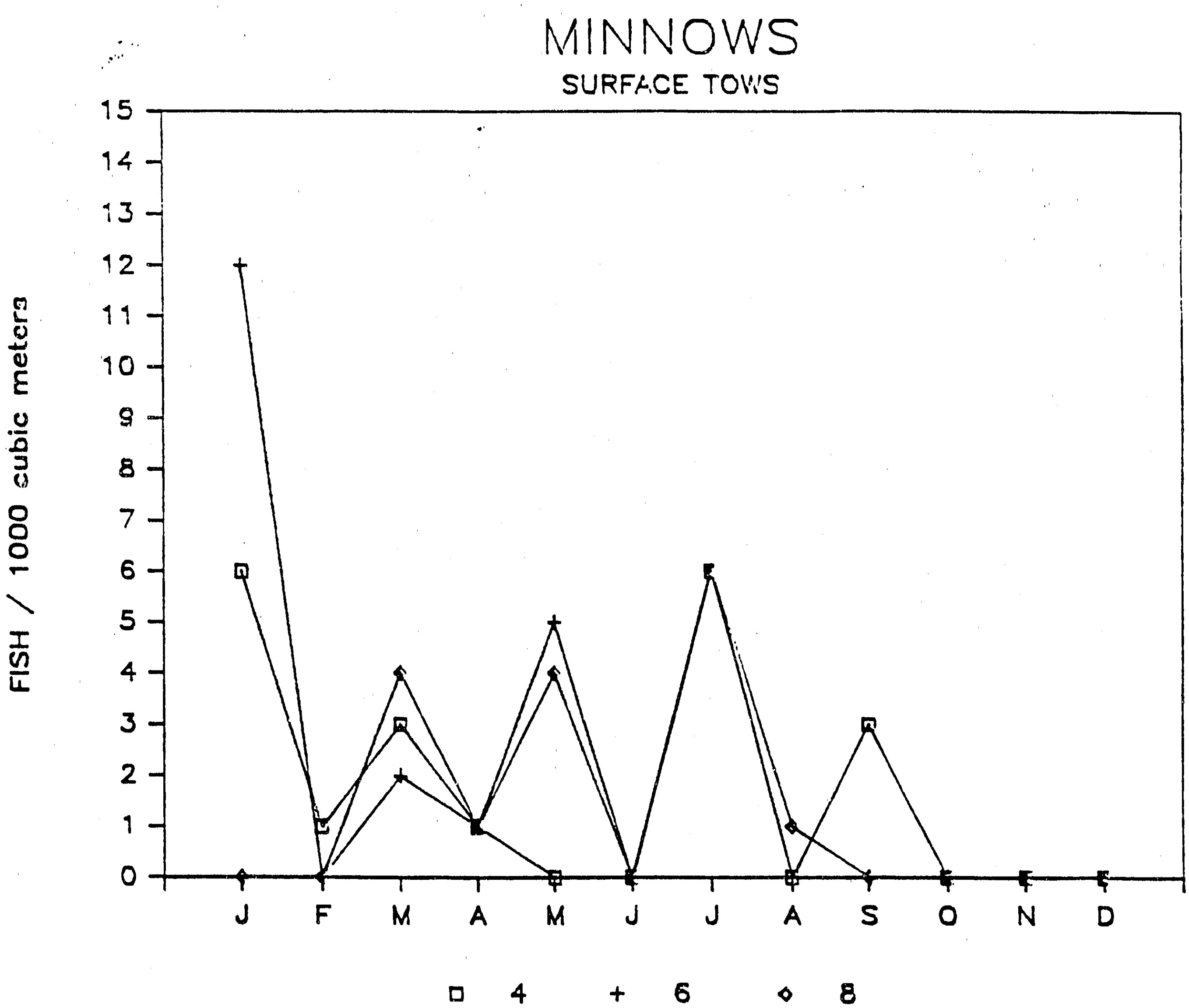
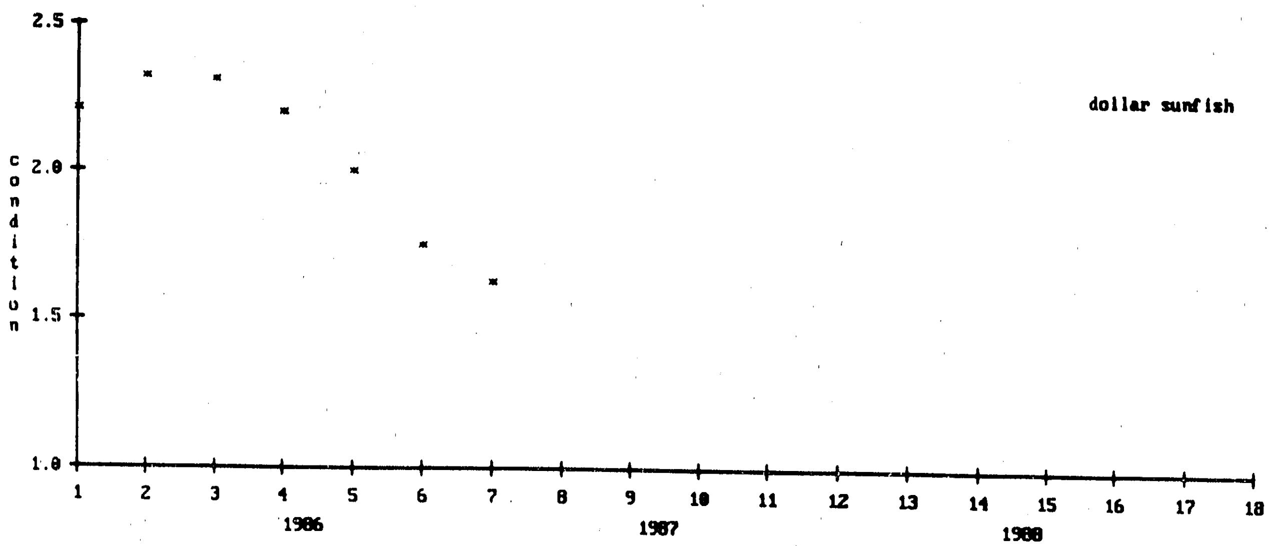


Figure *5* Average monthly density of minnows collected by surface ichthyoplankton tows in Regions 4, 6, and 8 of L-Lake. January - December 1986.



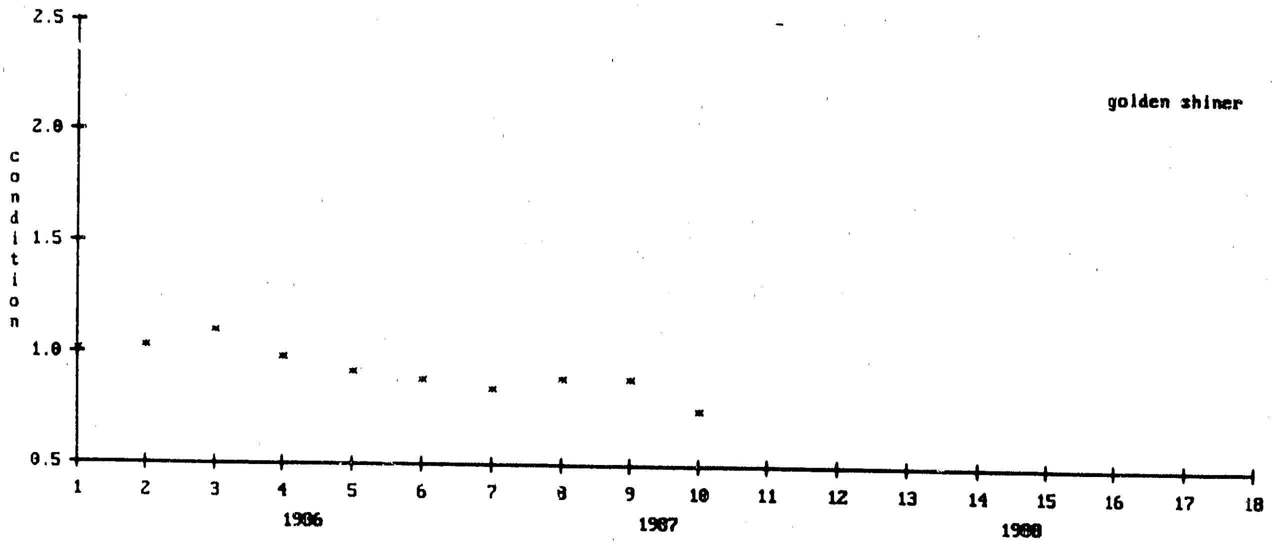


Figure 6. Temporal changes in condition (K) of bluegill, redbreast sunfish, dollar sunfish, golden shiner, and spotted sunfish.

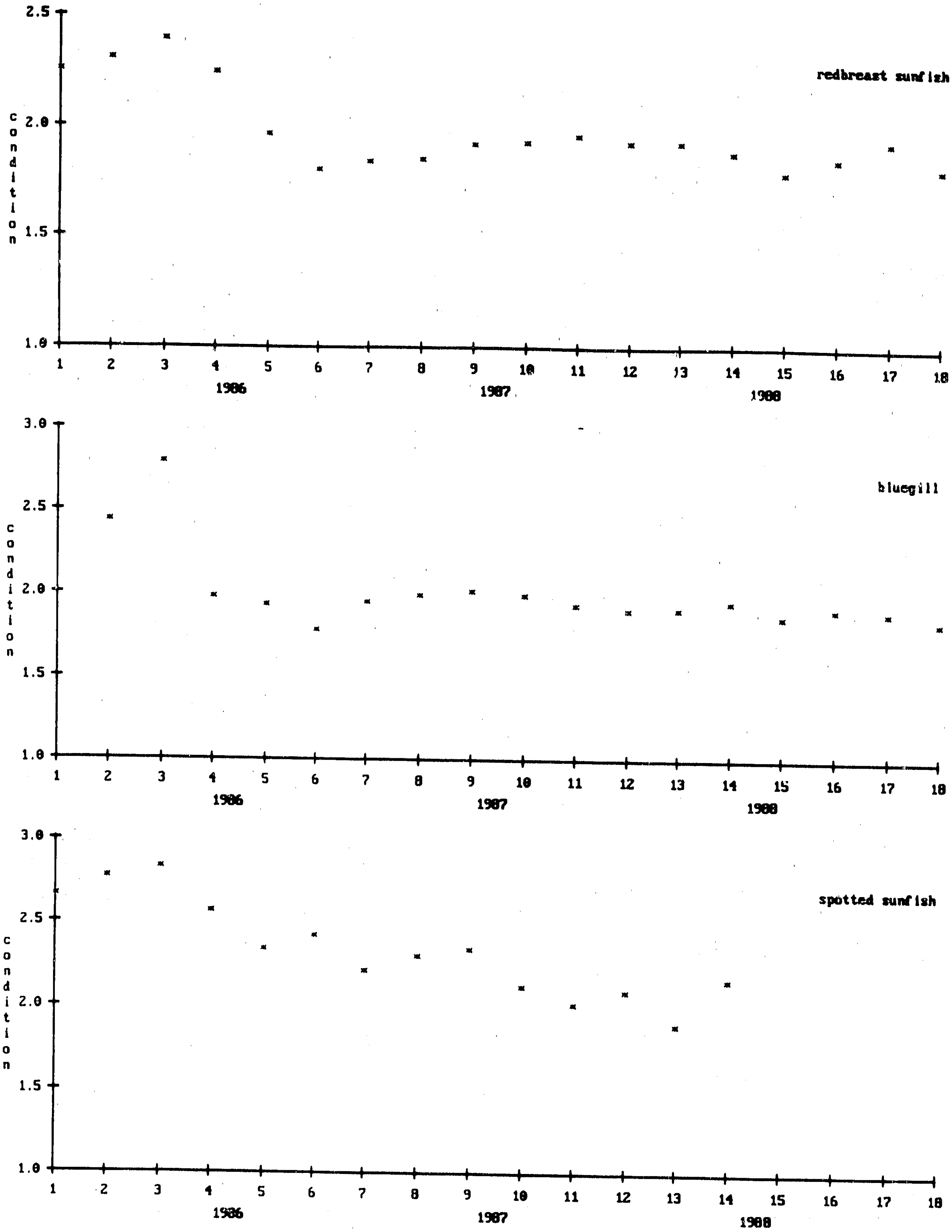


Figure 6. continued

Table 1. Species weights on the first reciprocal averaging axis.

Species	Weighting factor
mosquitofish	4.12
creek chubsucker	3.25
brook silverside	3.08
coastal shiner	2.61
golden shiner	2.58
dollar sunfish	2.45
spotted sunfish	1.49
black crappie	0.40
yellow bullhead	0.36
redbreast sunfish	-0.01
bluegill	-0.39
largemouth bass	-0.39
warmouth	-0.42
flat bullhead	-0.50
gizzard shad	-0.77
threadfin shad	-0.84

Table 2. Species catch rates by time data matrix arranged by reciprocal averaging. Only dominant taxa and catch rates ≥ 0.1 fish/m are shown.

Species	Jan Feb	Mar Apr	May Jun	Jul Aug	Sep Oct	Nov Dec	Jan Feb	Mar Apr	May Jun	Jul Aug	Sep Oct	Nov Dec	Jan Feb	Mar Apr	May Jun	Jul Aug	Sep Oct	Nov Dec
mosquitofish	2.0	0.1	0.9															
creek chubsucker	0.1																	
brook silverside	0.3	0.1																
coastal shiner	1.5	1.0	1.2	0.5	0.6	0.2	0.3											
golden shiner	0.9	0.3	1.0	0.2	0.1	0.2	0.2	0.1										
dollar sunfish	0.3	0.3	0.2	0.2	0.1													
spotted sunfish	0.6	0.2	0.5	0.3	0.3	0.1	0.5	0.1	0.1	0.1	0.1	0.1	0.1					
black crappie			0.1								0.1							
yellow bullhead	0.1						0.1	0.1	0.1					0.1	0.1			
redbreast sunfish	3.4	0.8	1.7	4.9	8.9	6.8	3.9	4.5	7.3	7.0	7.1	7.1	6.0	7.0	5.8	4.2	5.6	5.3
bluegill	0.1		0.1	32.2	52.0	44.7	23.4	11.2	22.7	14.7	12.0	19.8	16.9	11.1	6.6	5.6	8.3	13.1
largemouth bass			0.3	0.5	0.6	1.1	0.5	0.9	0.9	1.1	1.5	1.2	0.9	0.8	0.6	0.8	0.9	0.8
warmouth									0.1	0.1	0.1	0.1		0.1	0.1	0.1	0.1	0.2
flat bullhead						0.1	0.1	0.1			0.1	0.[illegible]	0.1	0.4		0.1	0.1	0.1
gizzard shad										0.2	0.2	0.1	0.1	0.2	0.2	0.2	0.2	0.1
threadfin shad									0.1	0.4	9.8	2.4	0.4	1.5	4.7	13.5	14.1	3.7

Table 3.

Length frequency of dollar sunfish collected in L Lake, grouped by two-month time periods

Length Class	1986 JAN FEB	MAR APR	MAY JUN	JUL AUG	SEP OCT	NOV DEC	1987 JAN FEB	MAR APR	MAY JUN	JUL AUG	SEP OCT	NOV DEC	1988 JAN FEB	MAR APR	MAY JUN	JUL AUG	SEP OCT	NOV DEC
51-60				4														
61-70	7	2	2	2														
71-80	18	4	1	3			1			2								
81-90	38	16	2						1	2	1				1			
91-100	20	31	11		2									2				
101-110	18	33	25	6	3													
111-120	6	14	13	37	20	4	7	2		1								
121-130	1	4	4	17	6	2	2	2	1									
131-140		1	1	1			1						1					
141-150				1	1													
151-160			1															
161-170																		
171-180																		
181-190																		

Table 4.

Length frequency of golden shiners collected in L Lake, grouped by two-month time periods

	1986						1987						1988					
Length Class	JAN FEB	MAR APR	MAY JUN	JUL AUG	SEP OCT	NOV DEC	JAN FEB	MAR APR	MAY JUN	JUL AUG	SEP OCT	NOV DEC	JAN FEB	MAR APR	MAY JUN	JUL AUG	SEP OCT	NOV DEC
41-50	1	2																
51-60	5	1	2					1										
61-70	44	10	17	2														
71-80	4141	18	52	3	1		4		1									
81-90	45	19	31				1											
91-100	30	17	31	3	1				1	1								
101-110	40	22	27	7	2					3		1						
111-120	26	18	18	12	4					2	1							
121-130	14	24	12	11	4	1	1				2	1	2					
131-140	21	8	13	8	6	3	4					2		2				
141-150	4	10	20	16	3	6	3	2				1	1		1			
151-160	1	4	8	9	3	6	6	2	1	1						1		
161-170	1	3	6	17	6	7	6		2									
171-180		2	2	28	10	9	4	2	6	3					1			
181-190	1	3	4	22	8	14	12	6	4	2			1	1		1		
191-200				4	6	9	13	2			1		1	1		2		
201-210	1			2	1	5	6	2										
211-220					1	2		1						2				
221-230								1										
:																		
310-320															1			

Table 5.

Length frequency of spotted sunfish collected in L Lake, grouped by two-month time periods

Length Class	1986 JAN FEB	MAR APR	MAY JUN	JUL AUG	SEP OCT	NOV DEC	1987 JAN FEB	MAR APR	MAY JUN	JUL AUG	SEP OCT	NOV DEC	1988 JAN FEB	MAR APR	MAY JUN	JUL AUG	SEP OCT	NOV DEC
51-60					2													
61-70	2		1	1	1		1						1			1		
71-80	14	1					1		3	1	3		4			1	1	
81-90	36	11	1		1			1		1	4	6	3	5		3	1	
91-100	60	13	5	2	1						1	2	3	1	1		1	5
101-110	66	18	6	1		1				1			2			1	2	2
111-120	26	29	14	7	2		2			1								1
121-130	20	31	23	13	4		6			1							1	
131-140	15	19	36	16	9	3	5	3	1	3	1	1	1	2		1		
141-150	7	20	39	70	21	6	18	3	3	7	1	1	3	1				
151-160	6	11	25	109	41	9	29	9	6	13	4	8	2	1				
161-170	1	6	5	77	24	15	42	14	15	6	2	6	5	1	1		1	
171-180	1	1	1	16	8	4	9	5	4	3		1						
181-190			1	2		2												

Table 6. Ecological characteristics of fishes that colonized L Lake and failed to colonize L Lake.

Species	Abundance[a] SC	LA	LB	Parental[b] care	Spawning[c] require-ments	Fecundity[d]	Size[e]	Food[f]
yellowfin shiner	A			N	GR	L	S	I
bluehead chub	A			N		L	S	I
northern hogsucker	M			N	GR	H	L	I
brown bullhead	R			Y	N	M	M	O
margined madtom	R			Y	N	L	S	I
speckled madtom	M			Y	N	L	S	I
tadpole madtom	R			Y	N	L	S	I
pirate perch	M			Y		L	S	I
redfin pickerel	R			N	V	L	M	F
chain pickerel				N	V	H	L	F
Savannah darter	R			Y		L	S	I
blackbanded darter	M			Y		L	S	I
tesselated darter	M			Y		L	S	I
rosyface chub	R			N		L	S	I
creekchub	R			Y	NG	M	M	I
bluespotted sunfish	R			Y	NV	L	M	I
yellow perch	R			N	SVG	H	M	I
mudminnow	R			N	V	L	S	I
spotted sucker	R			N	R	H	L	O
mosquitofish	M	A		L		H	S	I
creek chubsucker	R	R		N	VG	H	M	O
brook silverside		M		N	VG	M	S	I
coastal shiner	R	A		N		M	S	I
golden shiner	R	A		N	VH	H	M	I
dollar sunfish	R	M		Y	N	L	M	I
spotted sunfish	M	A	R	Y	N		M	I
black crappie		R	R	Y	N	H	L	F
yellow bullhead	R	R	R	Y	N	M	L	O
redbreast sunfish	M	A	A	Y	N	M	M	I
bluegill		R	A	Y	N	H	M	I
largemouth bass	R	R	M	Y	N	H	L	F
warmouth	R		M	Y	NVC	H	M	F
flat bullhead	R		R	Y	N	M	L	O
gizzard shad			M	N	H	H	L	P
threadfin shad			A	N	H	H	M	P

[a] Abundance in Steel Creek (SC) before impoundment, L Lake during Jan-Jun 1986 (LA), and L Lake during Jun 1986-Dec 1988 (LB).
[b] Parental care exercised (Y), not exercised (N), or live birth (L).
[c] Substrate or habitat required for spawning; gravel (G), aquatic vegetation (V), sand (S), hard substrate (H), riffle area (R), cover (C), nest constructed by parent (N).
[d] Reproductive potential based on clutch size, time to maturity, and spawning frequency: low (L), medium (M) or high (H).
[e] Adult body size: small (S, <90), medium (M, 90 -200), large (L, >200).
[f] Primary food of adults: insects (I), fish (F), plankton (P), omnivorous (O).

END

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