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Bart, Henry Leonard, Jr.

**STABILITY AND RESILIENCY OF FISH ASSEMBLAGES IN AN OZARK
STREAM**

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THE UNIVERSITY OF OKLAHOMA

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STABILITY AND RESILIENCY OF FISH ASSEMBLAGES

IN AN OZARK STREAM

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

DOCTOR OF PHILOSOPHY

by

HENRY L. BART, JR.

Norman, Oklahoma

1985

STABILITY AND RESILIENCY OF FISH ASSEMBLAGES
IN AN OZARK STREAM

A DISSERTATION

APPROVED FOR THE DEPARTMENT OF ZOOLOGY

By

Loren G. Puse
William M. Matthews
Gay D. Hill
M. M. Mace
Paul J. Saunders

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PREFACE

This dissertation has been prepared in the style of a manuscript to be submitted to Ecology.

STABILITY AND RESILIENCY OF FISH ASSEMBLAGES
IN AN OZARK STREAM

Henry L. Bart Jr.

Department of Zoology, University of Oklahoma, Norman, OK 73019

Running Head: FISH-ASSEMBLAGE STABILITY AND RESILIENCY

Abstract. Predictions of alternative hypotheses of assemblage structure concerning equilibrium states were tested for fish assemblages from spatially repeated sets of habitats in an Ozark stream. Equilibrium characteristics (stability and resiliency) were elucidated through manipulation experiments conducted within habitats over a 15-mo period and Mantel tests for associations among the correlation patterns of the fish assemblages within habitats across sites.

Fish assemblages from main channel riffle habitats varied independently with little evidence of stability. Assemblages from backwater inlet and pool habitats varied seasonally with respect to stability and resiliency. Results were inconsistent across sites for inlet assemblages. In backwater pools, a consistent pattern of stable and resilient fish-assemblage structure was noted in summer and fall. The pattern corresponds with a predictable pattern of resource limitation, and suggests equilibrium structure based on occurrences of interspecific competition. However, the summer-fall period coincided with the period of post-larval recruitment. During this period pool assemblages were dominated by young-of-year of species that occurred across habitat types, suggesting that the pattern of stability and resiliency was dependent on ephemerally high abundances of fish recruits. Life history characteristics of the species considered here support an interpretation of the pattern as independent coexistences of species.

Key words: stability; resiliency; assemblage structure; stream fishes; manipulations; equilibrium states; species individualism

10-year index entries: stability and resiliency of fish assemblages in streams; manipulations of stream-fish assemblages; equilibrium structure vs. independent coexistences.

INTRODUCTION

Emphasis in community ecology has recently been placed on critical tests designed to determine the importance of interspecific competition in natural assemblages of species (Connor and Simberloff 1979, Strong et al. 1979, Wiens and Rotenberry 1980, Lawton and Strong 1981, Grossman et al. 1982, Sale and Williams 1982). Direct evidence of competition may be unobtainable due to its pervasiveness and the complexity of other factors involved (Diamond 1978, Quinn and Dunham 1983, Roughgarden 1983). However, competition theory allows testable predictions about the structure of assemblages (Connell 1980, 1983, Simberloff 1983, Strong 1980, 1983, Wiens 1983). Strong (1983) proposed species individualism (independent coexistence of species as a function of different autecological factors) as the logical basis for the null hypothesis of assemblage structure. A goal of the critical approach to the study of community ecology is determining whether interspecific competition modifies individual species existences in particular cases (Strong 1983, Wiens 1983).

Competition theory predicts equilibrium structure for assemblages in stable environments (Connell 1978). Predictions concerning equilibrium states vary under temporally variable environmental conditions based on the frequency and intensity with which competition occurs (Wiens 1977). Some ecologists maintain that even infrequent, historical episodes of competition are sufficient to produce patterns of assemblage structure that reflect equilibrium conditions (Connell 1980).

Theoretically, competitive equilibrium conditions would never be achieved under species individualism because the necessary interspecific interactions would not occur. Consequently, nonequilibrium structure is predicted for assemblages of independently coexisting species.

From a quantitative perspective (i.e., abundances of species), equilibrium systems display stability in the face of a disturbing force, and resiliency (or elasticity) when perturbed by the force (Connell and Sousa 1983). Equilibrium structure would be suggested if the relative abundances of species remained stable over time and returned to their original state following a perturbation. Nonequilibrium systems should not satisfy either of these conditions. However, as Strong (1983) stated, there are contexts in which stable associations could be expected for independently coexisting species that are affected by the same overwhelming autecological factors. Adaptive life history characteristics of the species involved must be considered to determine whether such conditions prevail.

In this study I tested the equilibrium prediction of competition theory for fish assemblages from spatially repeated sets of habitats in an Ozark stream. Stream habitats typically represent distinct zones of adaptation for many fishes. They contain groups of similarly adapted species with a potential for interaction (Schlosser 1982, Herbold 1984). A number of recent studies suggest that fishes associated with stream habitats display predictable patterns of assemblage structure and equilibrium states (based on interspecific competition) when the habitats themselves are stable or predictable (Gorman and Karr 1978,

Baker and Ross 1981, Schlosser 1982, Herbold 1984, Moyle and Vondracek 1985). The present study is based on a null hypothesis of independent species coexistence (individualism) and nonequilibrium assemblage structure. I conducted a series of manipulation experiments within habitats, tested for associations among overall assemblage structure patterns, and examined life history characteristics of the species involved to determine whether habitat assemblages exhibit equilibrium structure produced by occurrences of interspecific competition.

STUDY AREA

The study area consisted of three sites within a 5-km stretch of Flint Creek in Delaware County, Oklahoma (Fig. 1). Flint Creek is a 3rd order, predominantly spring-fed tributary of the Illinois River, draining western portions of the Ozark Plateau in Arkansas and Oklahoma. The region is characterized by a hilly topography of alternating flint and limestone layers (Blair and Hubble 1947). Flint Creek flows throughout the year and has a relatively stable thermal regime.

Aquatic vegetation consists mainly of waterweed (Elodea sp.) and a variety of unidentified filamentous and rock encrusting algal species. Patchy growths of watermoss (Fontinalis sp.), pondweed (Potamogeton sp.), and coontail (Ceratophyllum sp.) occur with stands of waterweed in backwater habitats off the main channel. In summer and fall water primrose (Jussiaea diffusa) and watercress (Nasturtium officinale) form dense growths along the stream margins. Duckweed (Lemna sp.) blankets the surface in quiet areas during spring. The predominant riparian vegetation includes American elm (Ulmus americana), sycamore (Platanus

occidentalis) and hackberry (Celtis occidentalis).

METHODS

Fishes were sampled monthly from three contiguous habitats at each site over a 15-mo period from March 1983 to May 1984. Habitat types included main channel riffles, and backwater inlets and pools located adjacent to the riffles. Physical characteristics of the habitats and seasonal variation in habitat characteristics are summarized (Fig. 2). The sampling period encompassed five seasons (two springs, summer, fall and winter). Within each season one "high-effort" removal sample and two routine "census-release" samples were obtained. In removal sampling an attempt was made to capture (or at least displace) all fishes from the habitat areas. Removal samples were separated by 2-mo intervals to allow recolonization of the habitats. Routine censuses were conducted to obtain information on assemblage structure. I made every effort to return the assemblage intact.

With the exception of removal samples from riffle habitats, all fish samples were collected with 3.3-mm mesh seines of a variety of sizes (1.2-m and 1.8-m depths; and lengths of 6.1, 7.6, and 15.2 m). The size of seine employed varied with habitat depth and width. The number of seine hauls necessary to obtain a representative sample of the habitat assemblages in routine censusing was determined in a preliminary study conducted in February 1983. Numbers of individuals and species captured in each of eight consecutive seine hauls were recorded. The results (Table 1) suggest that three seine hauls was a sufficient minimum number in all habitats. Total individuals were obtained in six

or fewer seine hauls. All species were collected in two to three seine hauls. Assemblage structure obtained after one or two seine hauls was significantly correlated ($P < .01$) with that obtained after the sixth seine haul.

In all habitats the first seine haul was taken in the direction of flow to maximize initial catch (Hendricks et al. 1980). When seining over large substrates, the bottom of the seine was fitted with a slightly shorter length of 13-mm thick chain to agitate the substrate in advance of the net. This increased the representation of benthic fishes in individual seine hauls and prevented other species from escaping capture by darting beneath the net or substrate surface.

Census and removal techniques in inlet and pool habitats were identical. This involved blocking the entrances to the habitats with appropriately sized nets and making a series of seine sweeps through the area. When removing fishes from inlets and pools, seining continued until catch dropped to zero. To obtain removal samples from riffle habitats a 1.2 x 1.2 x 1.8-m, 3.3-m mesh bag net (fitted with 1.2 x 1.8-m panels and supported by steel rods) was used to block the downstream end of the habitat. The riffle sampling area was then repeatedly shocked with a 12-volt DC backpack electrofisher. Substrates were agitated by foot during shocking periods to free fishes trapped under rocks.

During routine censusing, captured fishes were kept in fiberglass containers (Frigid Unit Model 29-A) filled with habitat water. After sampling, the fishes were identified, categorized into one of five age

classes (scored for the predominant age class present when age classes overlapped), counted, and released into their original habitats. Very few deaths occurred as a result of this procedure (less than 0.5%). Fishes captured during removal sampling were preserved in 10% formalin and returned to the laboratory for future processing. Identifications are based on Miller and Robison (1971) with the following exceptions. Campostoma oligolepis occurred syntopically with C. anomalum at all sites, but I could not identify females and nonbreeding individuals to species in the field. Both species are included in a single taxonomic category (Campostoma spp.). The specimens of Ambloplites captured in Flint Creek agreed with A. arionomus which is known to occur in the Illinois River (R.C. Cashner personal communication). The Ozark minnow is referred to Notropis nubilis following Robins et al. (1980).

Fishes were sampled in daylight hours to avoid diel variation in catch. Care was taken not to disturb the habitats in an appreciable way during sampling, thus minimizing changes in assemblage structure due to habitat alteration. Each habitat was scored for 14 characteristics: water temperature (C); current rate (cm/s); maximum depth (cm); habitat area (maximum width times length); percent of habitat surface covered by leaf litter (LEAVES); logs and branches (TREES); particulate organic matter (POM); Elodea; filamentous algae (ALGAE); rock-encrusting algae (CRUSTS); proportion of substrate comprised of mud and silt; gravel; rubble; and larger stones. Hester-Dendy samplers were placed in each habitat and sampled monthly to obtain crude estimates of invertebrate biomass. Biomass was recorded (in grams) as the volume (milliliters) of

preserving fluid displaced by the collected invertebrates.

A total of 130 fish samples and 133 sets of habitat characteristics were obtained. A hard freeze in January 1984 prevented fish sampling from all pool habitats and inlets at sites 2 and 3. Habitat data was not obtained for the pool at site 1 and the inlet at site 3. Due to the missing samples, there are no winter comparisons for inlet and pool habitats in certain analyses.

ANALYTICAL DESIGN

Fish assemblage data consists of abundances and age class representation of species observed or removed from each habitat for each month of the sampling period (Appendix). Comparison of the removal sample with the preceding census sample within each season provided the estimate of stability. To assess assemblage resiliency, I compared the removal sample with the subsequent census sample. I used Kendall's tau rank correlation statistic to test the significance of these comparisons, expecting stable or resilient assemblage structure to result in significant correlations (Grossman et al. 1982). The results of these comparisons suggested equilibrium structure if stability and resiliency was found across similar habitats from different sites. Nonequilibrium structure was suggested if there was no consistent evidence of stability and resiliency.

The rank correlation procedure used here is appropriate in assemblage structure analyses where it is expected that sampling error accounts for part of the variability in the actual abundances of species (Grossman et al. 1982). However, significance tests in rank correlation

analyses are based on the null hypothesis that all rankings are equally likely. In assemblage-structure comparisons this translates into an even probability that any species can occupy a given rank (Jumars 1980, 1983). There is an increased probability of type I error when rare or uncommon species are included in comparisons because their stable lower positions in assemblages cause rankings to depart from equiprobability. This type of uneven distribution of individuals among species is a reasonable expectation for natural assemblages independent of competitive influences which could produce the same result (Jumars 1980).

Prior to rank analysis, I excluded species that occurred in less than 40% of the samples from each habitat, unless occurrence was seasonally consistent and the species comprised greater than 1% of the total catch (Ross et al. 1985). This limitation resulted in a 33-63% reduction in species included for particular habitats (Table 2). I calculated Kendall's concordances (W) among ranks of the remaining species over all of the samples from each habitat to test for equiprobability. I expected equally probable rankings of species over time to result in zero or nonsignificant concordance values. The results of these tests (Table 2) suggest rank stability for all riffle assemblages (significant concordances, $P < .005$). However, nonsignificant to marginally significant concordances were obtained for most inlet and pool assemblages, suggesting rank equiprobability. Although the probability of type I error causes Kendall's tau to be conservative when it suggests stability or resiliency for riffle assemblages (Grossman et

al. 1982), this is probably not the case for inlet and pool assemblages. There was no evidence of underlying stability over the 15 mo period when fish samples from the three habitats at each site were pooled (nonsignificant concordances, $P > .05$).

In the second major set of analyses, matrices of Kendall's tau correlations among all pairs of samples from each habitat were compared using a matrix regression technique known as the Mantel test. This procedure, originally developed to determine the spatial and temporal clustering of rare diseases (Mantel 1967), has recently been applied to a variety of systematic and behavioral problems (Sokal 1979, Douglas and Endler 1983, Schnell et al. 1985). The test employs a t -statistic computed from the sum of products of corresponding cells in two matrices (Z scores or congruence values), minus an expected value of Z based on a hypothesis of random permutations, divided by the standard error in Z .

I used the Mantel procedure to test for significant associations: (a) among fish-assemblage correlation matrices (FAM) from similar habitat types at different sites (expected to show independent correlation patterns under species individualism); (b) between FAM and each of three matrices of correlations among corresponding habitat characteristics (HCM); and between FAM and three hypothetical correlation matrices with specific regions corresponding to high positive correlation values. In comparisons involving FAM from similar habitat types, significant positive associations indicated congruence in overall correlation patterns and were considered evidence of equilibrium structure. Comparisons between FAM and HCM were used to determine

whether fish -assemblage structure was a function of habitat stability.

Hypothetical patterns (Fig. 2) included: (1) a pattern of stability within all seasons (high correlations along the diagonal and in the corner of a triangular matrix); (2) a pattern of stability during spring (high correlations at the ends of a triangular matrix); and (3) a pattern of stability, centered around fall, from midsummer to midwinter (high positive correlations in the middle of a triangular matrix). Consistent agreement with a particular hypothetical pattern in comparisons within habitat types indicated a specific pattern of seasonal stability and resiliency. Cells in the hypothetical matrices corresponding to high positive correlations had values of one (darkened cells, Fig. 2). All other cells had zero values.

Principal components analysis was performed to indicate degrees distinctiveness in the habitats and seasonal variation in habitat characteristics. Prior to analysis, each character was standardized (to mean = 0 and standard deviation = 1) over the 133 samples of habitat data. The first two components derived from the analysis accounted for 50% of total character variance. The results (Fig. 3) are reported as separate projections of standardized habitat data from each site on components 1 and 2. Points representing habitat data from each season are connected to illustrate seasonal variation.

All statistical computations were performed on the IBM 3081 Computer at the University of Oklahoma. Statistical Analysis System procedures (SAS, Barr et al. 1976) were used to compute abundance ranks (ties were assigned the mean of the ranks they occupied) and Kendall's

tau values. Kendall's W values (corrected for ties) were computed with SPSS-x programs (SPSS Inc. 1983). Mantel tests were performed with GEOVAR computer programs written by David M. Mallis and furnished by Robert R. Sokal. A matrix algebra procedure in GEOVAR was used to convert correlations to distances (each element subtracted from unity) prior to Mantel comparisons. Standardization of habitat data and principal components analysis were performed with NT-SYS computer programs (Rohlf et al. 1972).

RESULTS

The three habitats at each site were distinct based on the results of the principal components analysis (Fig. 3). Riffles and pool showed the greatest separation. In general, riffles were shallow with large substrates and relatively high flow. Pools were deep, mud and silt bottomed, and heavily vegetated. Inlets were intermediate in these respects, were generally smaller in size, and tended to overlap pools at some sites. All of the habitats showed the same pattern of seasonal variation, usually involving size differences. The habitats were smaller and less variable from fall to winter. They tended to be larger and more variable in spring and summer. There were no drastic changes in habitat characteristics during the study period.

Distinct patterns of stability and resiliency were indicated across habitat types based on the results of the manipulation experiments (Table 3). The results were inconclusive for most of the comparisons involving winter samples in inlet and pool habitats. The fish assemblage from riffle site 1 showed evidence of stability in fall and

winter comparisons. There was no evidence of resiliency for any season in riffle habitats. Stable and resilient fish-assemblage structure was suggested from spring to fall for inlet site 3, and in summer for inlet site 1. Resilient structure was indicated for inlet site 1 in winter. Pool assemblages showed a consistent pattern of stability and resiliency from summer to fall. There was evidence of stability in winter at pool site 3 (one of only two winter comparisons). Stability was also suggested for one pool assemblage in spring (pool site 1).

Overall, the results of the manipulation experiments suggest nonequilibrium structure for riffle assemblages, equilibrium structure for some inlet assemblages during different seasons, and equilibrium structure for all pool assemblages during summer and fall. A similar pattern of perturbation resiliency is indicated across habitat types when correlation values from removal-census comparisons are used descriptively (Fig. 4). In general, resilience to perturbations was higher from summer to fall and lower in spring (no information for inlets and pools in December and January), implying that an underlying seasonal factor is controlling assemblage structure in all habitats.

The results of the Mantel tests suggest independent correlation patterns across sites for riffle and inlet assemblages. Associations among FAM for each of these habitat types were nonsignificant (Table 4). The comparison of FAM for inlet sites 1 and 3 produced a positive t -value that was close to statistical significance (1.828, with the 0.05 level at 1.960), suggesting the correlation patterns were similar. High positive t -values were obtained for all comparisons among FAM from pool

habitats (two of the three comparisons were significant). Correlation patterns of pool assemblages were very similar across sites (Fig. 5).

Associations between FAM and HCM were nonsignificant for all riffle habitats (Table 5). Riffle FAM were not positively associated with either of the hypothetical patterns. Significant positive associations were obtained for comparisons between FAM and HCM for inlet sites 2 and 3, suggesting that stability and resiliency in the fish assemblages was related to habitat stability. The FAM for inlet site 1 was significantly associated with the seasonal hypothesis. The FAM for inlet site 3 was significantly associated with the spring hypothesis. Pool FAM consistently agreed with the fall hypothesis (highly significant associations for pool sites 1 and 3, and a high positive association for pool site 2), suggesting similar patterns of stable and resilient structure from late summer to early winter for all pool assemblages.

Variation in fish density and resource availability was examined to determine whether the patterns support the results of the manipulation-study comparisons and Mantel tests. Vegetation was considered a trophic resource because of the prevalence of herbivorous minnows in Flint Creek. Patterns of variation in fish density and trophic resources were independent of the patterns of stability and resiliency suggested for inlet and pool habitats. Fish density tended to be higher from summer to fall in some inlet and pool habitats (inlet site 2 and pool sites 1 and 2, Fig. 6). Invertebrate biomass varied across sites, but was generally higher in spring and lower from summer to winter (Fig. 7).

Vegetation coverage was extremely variable in inlet habitats (Fig. 8). There was high vegetation coverage in pools from spring to summer, and lower coverage in winter. None of the invertebrate biomass or vegetation coverage patterns was significantly correlated with fish density, suggesting that the patterns are unrelated.

Fish assemblages from the different habitats were not distinct based on species occurrences. Of the 20 species considered, 15 (75%) occurred across habitat types (Table 6). Seventeen (85%) of the included species occurred in riffles, all 20 in inlets, and 18 (90%) in pools, suggesting little interspecific variation in habitat use. The total turnover time of the habitat assemblages (based on the longevity of the longest-lived species occurring in each habitat type) is approximately 5 yr. Most species produced sufficient young during the study period to replace existing adults. However, percentages of species showing complete life cycles within particular habitat types were small (24% in riffles; 40% in inlets; 28% in pools), suggesting that most species have minimum areas that are larger than the habitat areas studied. For some species (indicated in Table 6), minimum areas are apparently larger than the three habitat areas combined.

Most species used backwater pool habitats as young, but completed their life cycles in inlets, riffles, or other main-channel habitats. A large percentage of pool species occurred as young (83%), but only a third occurred in breeding condition. Breeding individuals were more commonly associated with inlet and riffle habitats. The mean age-class composition of pool assemblages usually corresponded to younger age

classes (Fig. 9). Riffles and inlets were inhabited by older individuals of the same species. The pattern suggests intraspecific variation in habitat use with similar habitat associations (occurrence in backwater pools) among early life history stages.

Young-of-year fishes tended to be concentrated in backwater pools during summer and fall months. The most common species in pool assemblages were usually represented as young or juveniles from summer to fall (Fig. 10). For most of these species, occurrence as young was positively correlated with abundance. Abundances of common pool species typically reached peak levels in summer and fall months, and tended to be lower during other parts of the year (Fig. 11).

DISCUSSION

Evidence from the manipulation study and comparisons of correlation patterns (Mantel tests) demonstrates a consistent lack of stability and resiliency for fish assemblages from main channel riffle habitats in Flint Creek. Thus, it provides little support for a conclusion of equilibrium structure for riffle assemblages. The same evidence suggests that fish assemblages from backwater inlet and pool habitats exhibit stable equilibrium structure during different periods of the year.

Unstable assemblage structure is predicted for fishes associated with shallow mainstream habitats (Schlosser 1982). Shallow riffle areas are generally more exposed to temporal variability in flow regime, a factor linked to the most important habitat descriptors (Horwitz 1978) and known to affect reproductive success (Schlosser 1982, Herbold 1984).

In cases where fish assemblages from riffle habitats were found to be stable (Herbold 1984, Moyle and Vondracek 1985), the study sites were located below dams or flood control structures, which undoubtedly have a stabilizing effect on flow. Flint Creek riffle habitats are not protected from temporal variability in flow regime. This factor seems to be a reasonable explanation for the lack of stability and resiliency that was demonstrated for riffle fish assemblages. Schlosser (1982) hypothesized that recolonization dynamics and other independent species responses to environmental variability are more important than competitive exclusion and predation as determinants of assemblage structure in environmentally unstable stream habitats.

In contrast, deeper or less exposed stream habitats are generally more stable environmentally (Horwitz 1978), and tend to have more stable or predictable fish assemblages (Gorman and Karr 1978, Horwitz 1978, Schlosser 1982). Recent studies suggest equilibrium conditions and niche diversification for fish assemblages associated with stable stream habitats (Baker and Ross 1981, Moyle and Vondracek 1985; but see Herbold 1984). Flint Creek inlet and pool habitats are generally deeper and located off the main channel of flow. Thus, it is conceivable that the stability and resiliency documented for the associated fish assemblages represents equilibrium structure resulting from interspecific competition in these presumably more stable habitat types.

Inlet and pool fish assemblages exhibited seasonally variable stability and resiliency. A consistent pattern of summer to fall equilibrium structure was indicated for pool assemblages. The pattern

of equilibrium structure in some seasons that was suggested for inlet assemblages was inconsistent across sites. A seasonally variable action of interspecific competition is predicted in streams based on resource availability and the degrees to which species are crowded in habitats due to restrictions in flow. In warmwater streams, competitive interactions among fishes are predicted as most likely from summer to fall; the period when trophic resources are typically lowest (Schlosser 1982) and fish densities are presumably highest (Moyle and Vondracek 1985). The pattern of equilibrium structure suggested for pool assemblages fits the prediction.

Correlations between fish-density patterns and corresponding patterns of variation in trophic resources were nonsignificant for all inlet and pool habitats. Significant negative correlations were expected if the habitats exhibited predictable periods of more or less likely competition. Although weak, the correlations between fish density and trophic structure were negative for pools. For inlets, fish density was positively associated with vegetations amounts, suggesting responses to greater resource availability if vegetational resources are more important. The patterns of stability and resiliency noted for inlet and pool fish assemblages could have resulted from sporadically occurring competitive bottlenecks associated with harsh environmental conditions (Wiens 1977). In such a case, inferences based on short-term resource-availability patterns would be meaningless.

A strong case for equilibrium fish assemblage structure in inlet habitats cannot be made based on the inconsistent evidence of stability

and resiliency. The consistent summer-to-fall pattern of stable and resilient assemblage structure noted for backwater pool habitats does suggest equilibrium conditions resulting from occurrences of interspecific competition during periods of resource limitation. The niche diversification hypothesis predicts coexistence at equilibrium as a function of restrictive use of habitats (or subdivisions of habitats) by particular species (Connell 1978). There was little fidelity in the use of pool habitats by particular species during the suggested equilibrium period. Instead, pool assemblages were comprised of younger age classes of species that occurred across habitat types, suggesting intraspecific, rather than interspecific, variation in habitat use.

Life history characteristics of species comprising pool assemblages support a different interpretation of the pattern of stability and resiliency. For most of the species considered here, late spring to early fall is the period of post-larval recruitment. During this period fish recruits are typically available in large numbers. Abundances of the most common pool species peaked in association with their occurrence as young, and declined as population structure shifted to older age classes. There was consistent evidence of stability and resiliency in pools when young were available in large numbers (summer to fall), but little or no evidence for this when assemblages were made up of smaller or variable numbers of older individuals. This alternatively suggests that the pattern of stability and resiliency was dependent on the large numbers of fish recruits present from summer to fall.

Assemblages from all habitats showed decreased age structure and

increased resiliency during summer, suggesting that the ability to recover from perturbations was enhanced by the influx of new recruits into the assemblages. Resilience remained at high levels through fall in pools. Associations of young-of-year fishes with these habitats also persisted through fall. Backwater pool habitats may represent favorable areas for the growth and survival of young. Young in pools were effectively isolated from adults which tended to use other habitats more extensively during summer and fall. Intraspecific competition between young and adults may be avoided by the different patterns of habitat association.

Fish recruit abundances are typically highest from summer to fall in warmwater streams (Schlosser 1982). The decline in abundances after this period is attributed to the high (type III) mortality rates among younger age classes of most stream fishes (Schlosser 1982, Yant et al. 1984). Conclusions of equilibrium structure and niche diversification in stream-fish studies confined to this so-called period of likely competition would be suspect if the stable pattern resulted from temporarily high abundances of young fishes. Long-term investigation would not remedy the problem if the timing and success of reproduction is similar from one year to the next. This may not be the case in general for midwestern streams (Grossman et al. 1982, Schlosser 1982; but see Herbold 1984), but it is apparently true for warmwater streams in the west (Moyle and Vondracek 1985).

The patterns of fish-assemblage structure noted for Flint Creek habitats are interpreted as products of nonequilibrium, independent

species coexistences; in spite of the evidence which suggests equilibrium structure in some instances. The one consistent pattern of stability and resiliency could be dependent on adaptive life history characteristics of species that are responding in similar ways (but individually) to the same overall autecological factors (Strong 1983). While historical occurrences of interspecific competition (and some influence by these events on assemblage composition) cannot be ruled out, such an argument is not necessary to explain any of the patterns observed here.

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Table 1. Results of preliminary study conducted in February 1983 to determine the number of seine hauls necessary to obtain a representative sample of fish assemblages in routine censusing.

Habitat	Seine haul number [‡]																	
	1			2			3			4			5			6		
	A	S	K	A	S	K	A	S	K	A	S	K	A	S	K	A	S	K
R1	11	25	.77	72	75	.91	89	100	1.0*	94	100	1.0	100	100	1.0	100	100	1.0
R2	47	67	.81*	70	79	.72	92	100	1.0	98	100	1.0	100	100	1.0	100	100	1.0
R3	14	67	-1.0	50	100	1.0*	79	100	1.0	79	100	1.0	86	100	1.0	100	100	1.0
I1	52	82	.80*	79	100	.84	90	100	1.0	96	100	1.0	97	100	1.0	100	100	1.0
I2	44	70	.82*	71	90	.76	85	100	.95	90	100	1.0	96	100	1.0	100	100	1.0
I3	39	54	.44	75	82	.78*	86	91	.85	100	100	1.0	100	100	1.0	100	100	1.0
P1	66	100	.87*	83	100	.93	96	100	1.0	98	100	1.0	98	100	1.0	100	100	1.0
P2	52	100	.32	81	100	1.0*	90	100	1.0	97	100	.95	100	100	1.0	100	100	1.0
P3	46	86	.75	79	100	.90*	86	100	.97	92	100	1.0	99	100	1.0	100	100	1.0

[‡] A = % cumulative abundance; S = % cumulative species; K = Kendall's tau correlation with relative abundances of species obtained after the 6th seine haul.

* $p < .01$

Table 3. Seasonal estimates of stability and resiliency (Kendall's tau correlations) across sites for fish assemblages from riffle, inlet, and pool habitats in Flint Creek.

Season	Site	Riffle		Inlet		Pool	
		Stability	Resiliency	Stability	Resiliency	Stability	Resiliency
Spring	1	0.408	0.183	0.065	0.341	0.619*	0.056
	2	0.184	0.116	0.218	0.051	0.300	-0.170
	3	0.533	0.385	0.425*	0.517*	0.134	0.375
Summer	1	0.913	0.667	0.680**	0.566*	0.791*	0.867*
	2	0.024	0.141	0.480	0.491	0.580*	0.560*
	3	0.385	0.528	0.561**	0.541**	0.156	0.612*
Fall	1	1.000*	0.548	0.000	0.019	0.741**	0.857**
	2	0.510	0.322	0.231	-0.113	0.651**	0.607**
	3	0.038	0.483	0.575**	0.568**	0.663**	0.737**
Winter [‡]	1	1.000*	0.548	0.458	0.524*	NC	0.390
	2	0.514	0.333	NC	NC	NC	NC
	3	-0.084	0.601	0.286	NC	0.741**	NC

** $P < .01$

* $P < .05$

[‡] NC = no comparison

Table 2. Numbers of observed and included species in each habitat, criteria for inclusion, and results of tests for rank equiprobability (Kendall's W values).#

Habitat	OS	IS	RS	TI	MO	MI	W	P
R1	12	4	60	94.7	46.7	7.7	0.657	.0008
R2	15	10	33	97.5	46.7	1.6	0.260	.0009
R3	15	8	47	96.4	40.0	1.4	0.299	.0026
I1	17	11	35	87.3	40.0	1.1	0.142	.0825
I2	16	8	50	93.2	57.1	2.8	0.259	.0127
I3	22	14	36	97.1	42.9	1.6	0.095	.1852
P1	19	7	63	92.0	28.6	1.0	0.185	.2055
P2	22	12	45	98.2	50.0	0.7	0.167	.0168
P3	23	12	48	97.3	28.6	1.5	0.144	.0438

#OS=observed species; IS=included species; RS=% reduction in species; TI=% total catch represented by included species; MO=minimum % occurrence of an included species; MI=minimum % total catch of an included species; W=Kendall's concordance; P=significance.

Table 4. Results of Mantel tests (t -values)
 for comparisons of fish assemblage matrices.
 among sites for each habitat type.

Sites compared	Fish assemblage matrices		
	Riffles	Inlets	Pools
1-2	-1.424	0.545	1.678
2-3	1.053	1.422	2.140*
1-3	-0.557	1.828	2.963**

** $\underline{p} < .01$

* $\underline{p} < .05$

Table 5. Results of Mantel tests (t values) from comparisons of fish assemblage matrices for riffles, inlets, and pools at each site with corresponding habitat characteristic matrices, and the three hypothetical matrices.

Matrices compared	Riffles			Inlets			Pools		
	1	2	3	1	2	3	1	2	3
Habitat characteristics	0.996	0.242	-0.136	-0.548	2.509*	3.279**	2.381*	1.466	0.554
Seasonal hypothesis	-2.040	0.413	0.438	2.151*	1.687	1.334	0.110	0.316	1.050
Fall hypothesis	0.791	0.589	-2.115	-0.637	0.789	0.315	3.790**	1.859	3.119**
Spring hypothesis	-2.130	0.154	0.660	1.642	-0.079	2.127*	-1.026	-1.030	-1.723

** $P < .01$

* $P < .05$

Table 6. Summary of life history information for the 20 included species from the three habitat types.

Species	Label	Age classes [#]			Longevity (years)
		Riffles	Inlets	Pools	
<u>Campostoma</u> spp.	CAMPO	ALL	ALL	1-4	3
<u>Notropis nubilis</u>	NUBIL	3-5	3-5	ALL	2
<u>Nocomis asper</u> *	NOCOM	1-3	1-4	1-3	3
<u>Cottus carolinae</u>	COTTU	ALL	1-4	1-4	4
<u>Etheostoma spectabile</u>	SPECT	2-5	ALL	1-4	3
<u>Phoxinus erythrogaster</u>	PHOXI	2-4	2-5	ALL	2
<u>Gambusia affinis</u>	GAMBU	3	ALL	ALL	1
<u>Notropis pilsbryi</u>	PILSB	ALL	ALL	1-4	3
<u>Notropis rubellus</u>	RUBEL	2-5	2-5	1-4	2
<u>Etheostoma punctulatum</u>	PUNCT	ALL	ALL	ALL	3
<u>Noturus exilus</u>	NOTUR	2-5	3-4	—	2
<u>Semotilus atromaculatus</u> *	SEMOT	2-3	2-4	1-3	3
<u>Labidesthes sicculus</u>	LABID	3	ALL	2-3	1
<u>Lepomis megalotis</u>	MEGAL	—	ALL	1-3	5
<u>Lepomis macrochirus</u>	MACRO	—	ALL	1-4	5
<u>Fundulus olivaceus</u>	OLIVA	—	1-4	ALL	2
<u>Ambloplites ariommus</u> *	AMBLO	2	1-4	1-4	5
<u>Fundulus catenatus</u>	CATEN	1	4	2-5	3
<u>Micropterus dolomieu</u> *	DOLOM	2	1-3	2	5
<u>Etheostoma zonale</u> *	ZONAL	3-4	3-4	—	3

[#] 1=young; 2=juvenile; 3=intermediate; 4=adult; 5=breeding; ALL=complete life cycle (all age classes)

* Species not represented by all age classes across the three habitat types combined.

FIGURE LEGENDS

Fig. 1. Map of the study area showing the location in northeastern Oklahoma and the proximity of the three collecting sites.

Fig. 2. Hypothetical matrices used in Mantel tests, with specific regions (darkened cells) corresponding to high positive correlations (values of 1) within seasons, in fall, and in spring.

Fig. 3. Projections of standardized habitat data (by sites) on the first two components derived from a single PCA; involving all samples and sites. Samples from a given site are depicted on the same axis.

Fig. 4. Patterns of perturbation resilience across months for Flint Creek riffle, inlet, and pool assemblages, based on Kendall's tau correlations (y-axis) between removal and census samples.

Fig. 5. Patterns of Kendall's tau correlation among all pairs of samples for fish assemblages from riffle, inlet, and pool habitats at each site. Darkened cells represent correlations that were significant at or below the 0.05 level. Shaded cells represent January comparisons for which results were not obtained due to missing samples.

Fig. 6. Variation in fish density across a 15-mo period from March(1) to May(15) for inlet and pool habitats.

Fig. 7. Variation in invertebrate biomass for the three inlet (I1-I3) and three pool (P1-P3) habitats, showing correlations with fish

density (at bottom).

Fig. 8. Variation in vegetation coverage for inlet and pool habitats, showing correlations with fish density (at bottom).

Fig. 9. Mean age class composition across months for assemblages from Flint Creek riffle, inlet and pool habitats at each site. Numbers on the y-axis refer to age groups (young, juvenile, intermediate, adult).

Fig. 10. Variation in age class representation for the most common species in pool assemblages at each site. Species labels are abbreviations for scientific names (presented in Table 6).

Fig. 11. Variation in abundances of the most common species in pool assemblages at each site.

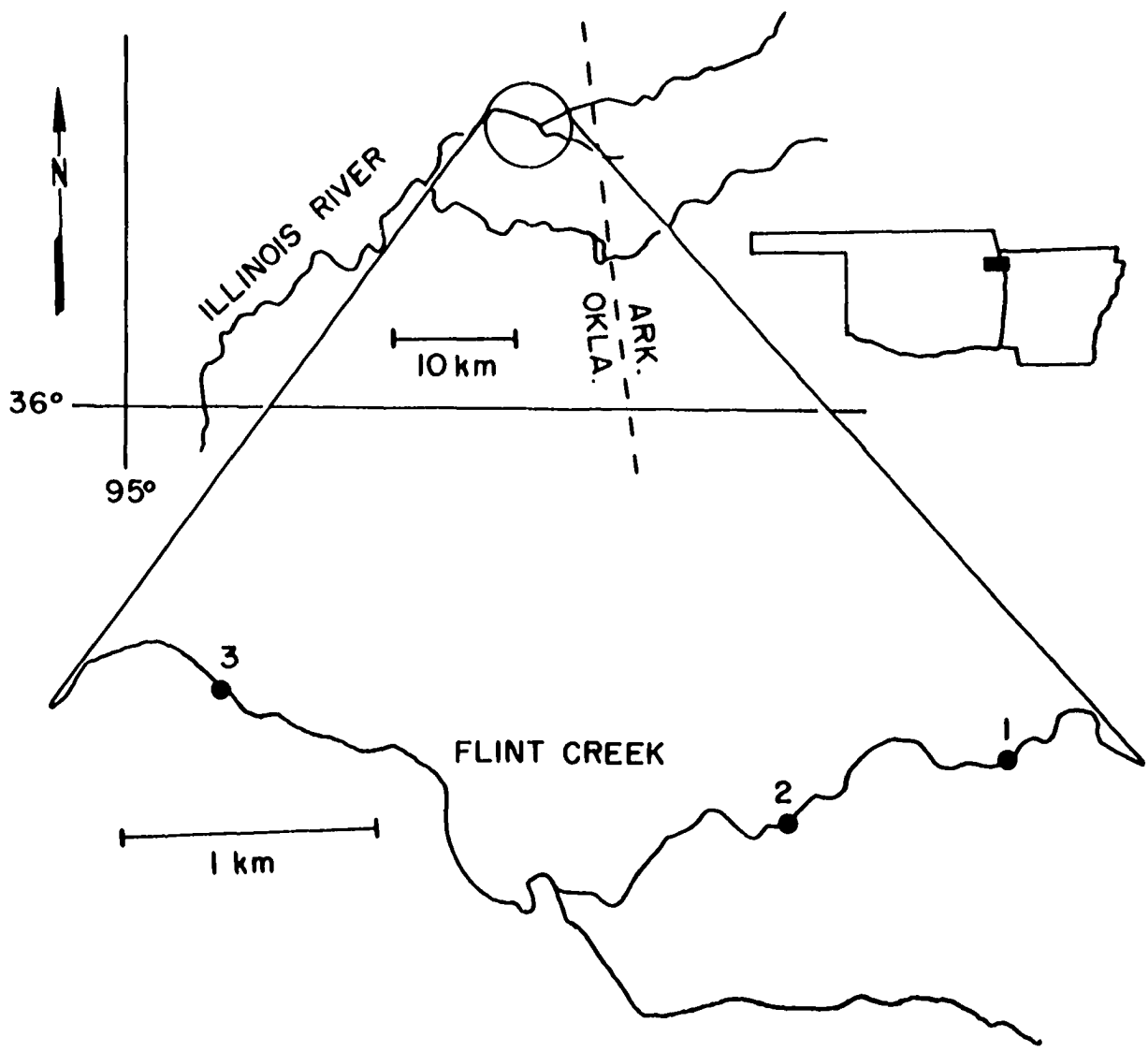


Fig. 1

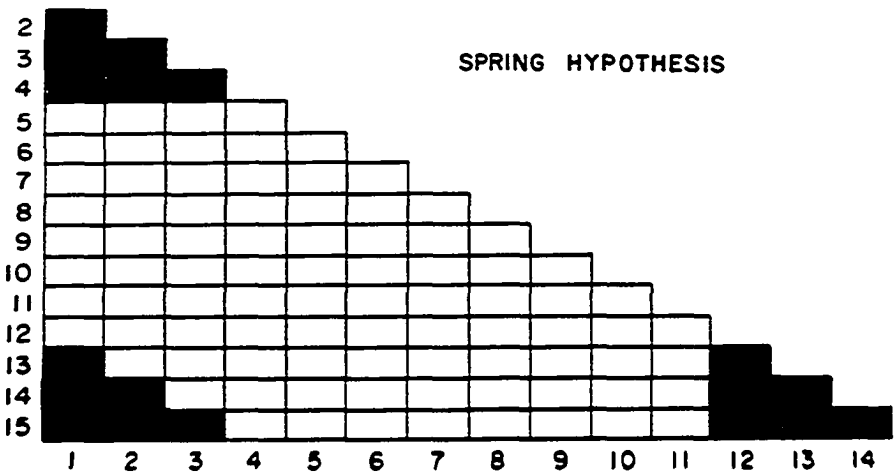
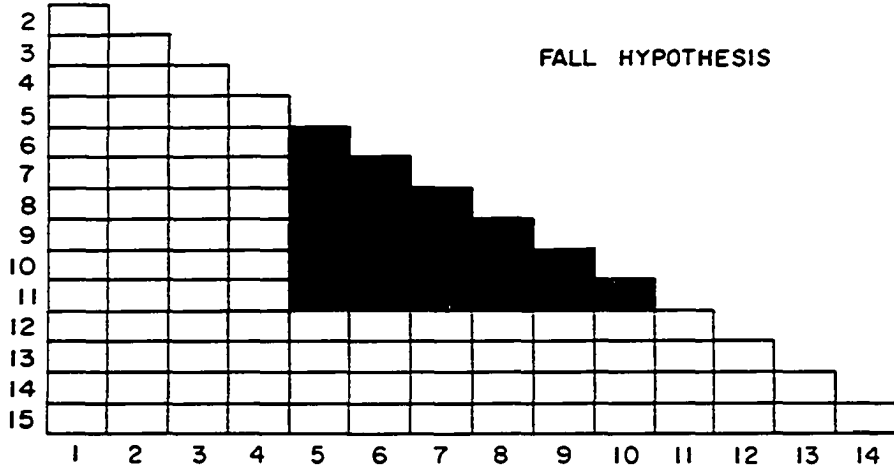
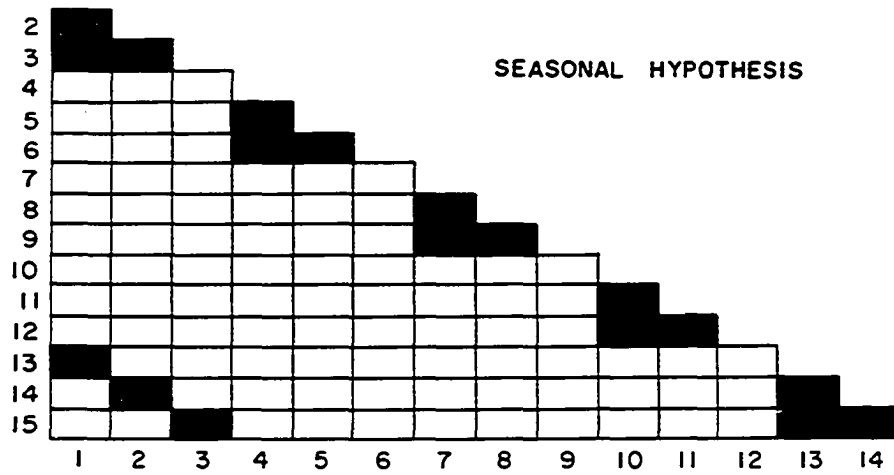


Fig. 2

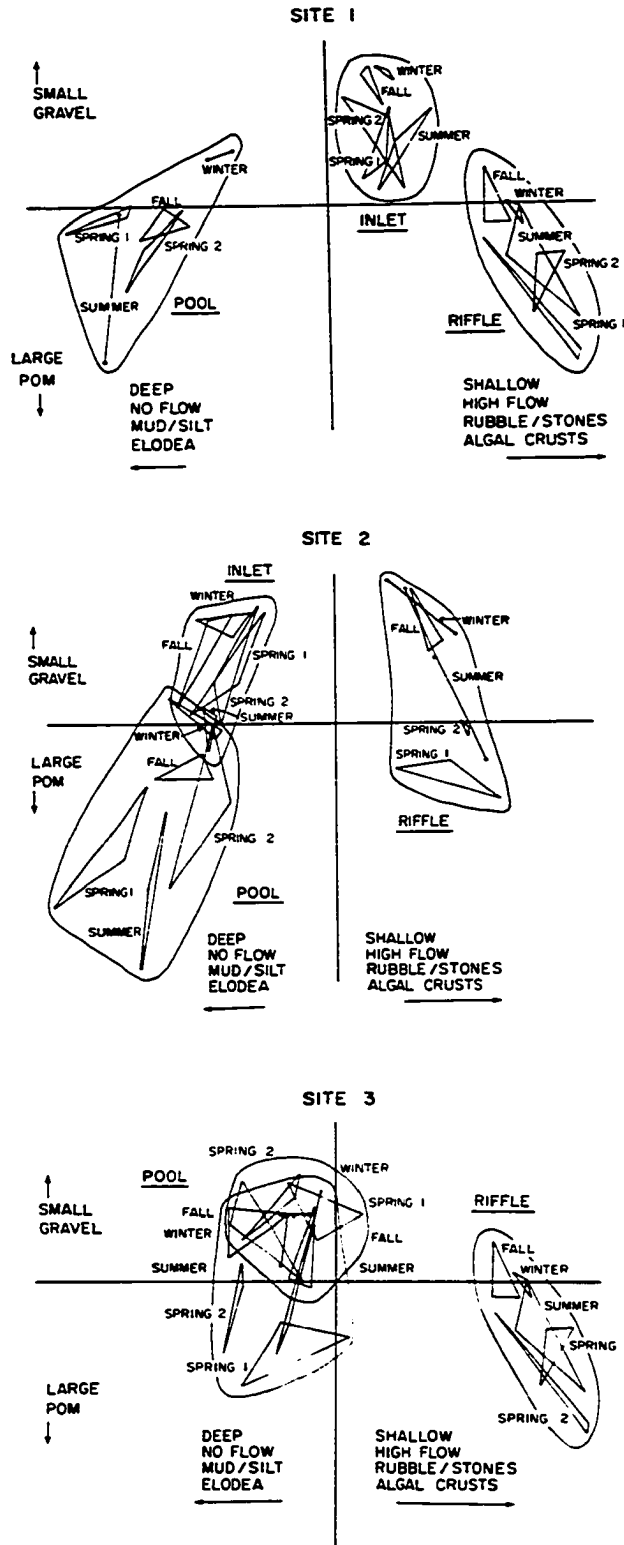
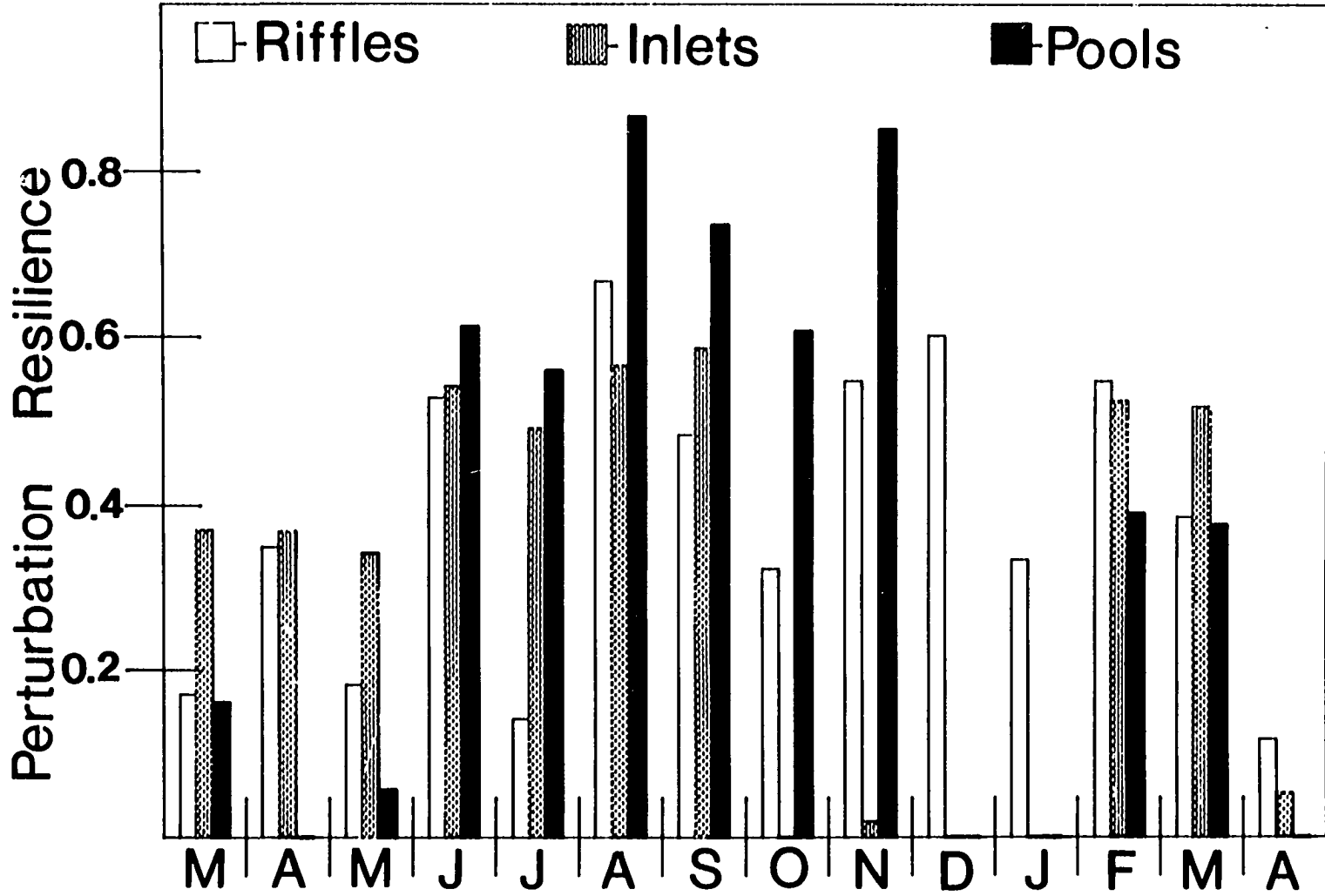


Fig. 3

Fig. 4



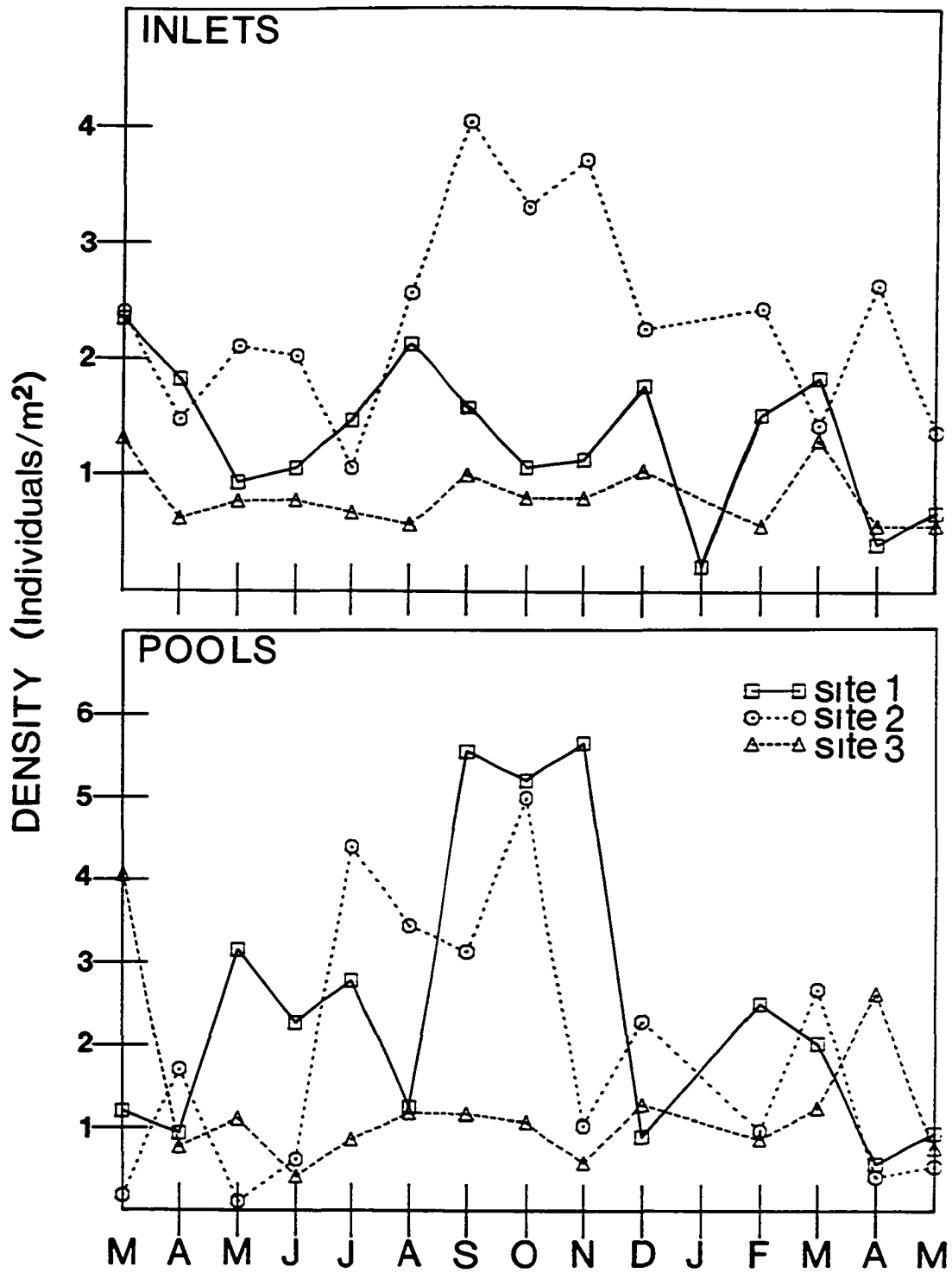


Fig. 5

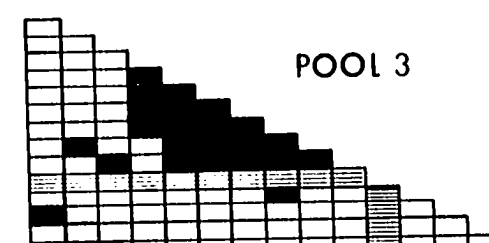
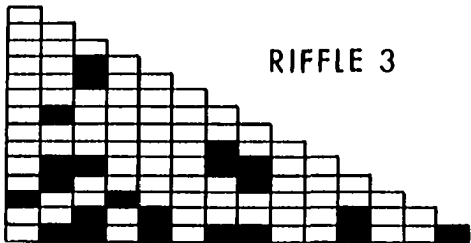
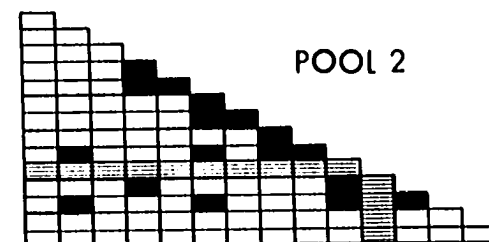
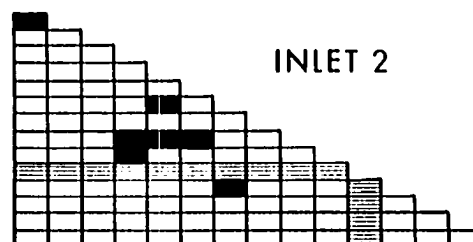
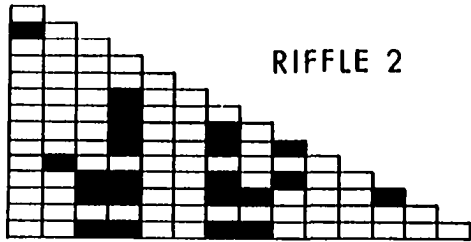
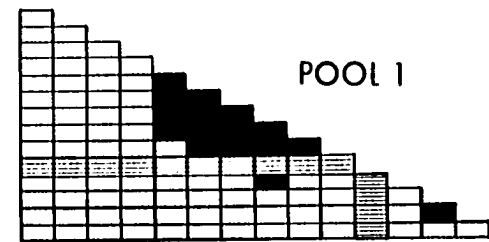
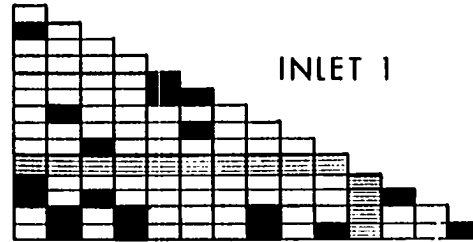
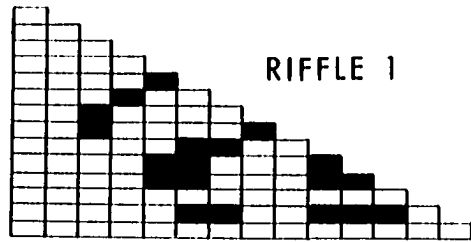


Fig. 6

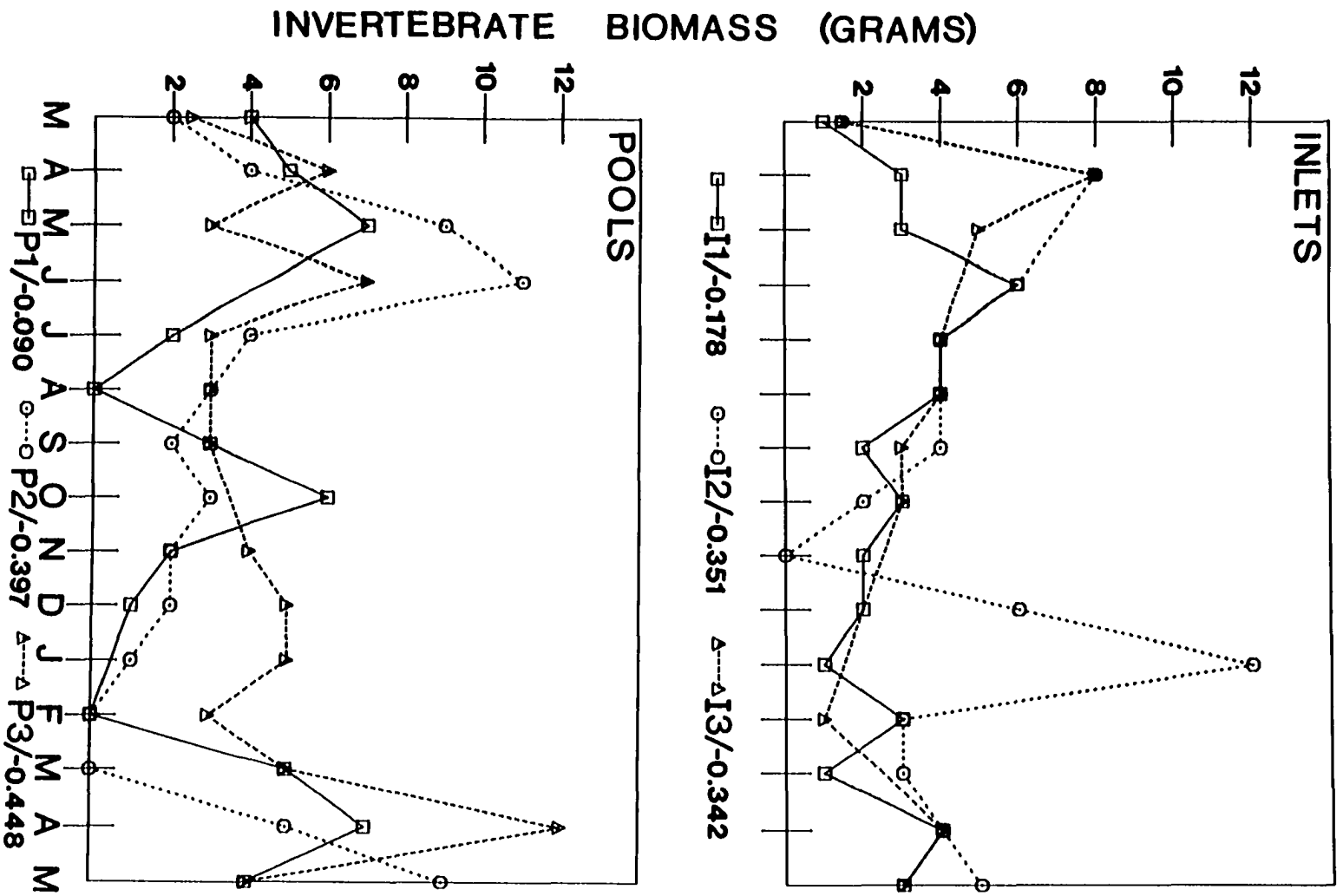


Fig. 7

PERCENT HABITAT COVERED WITH VEGETATION

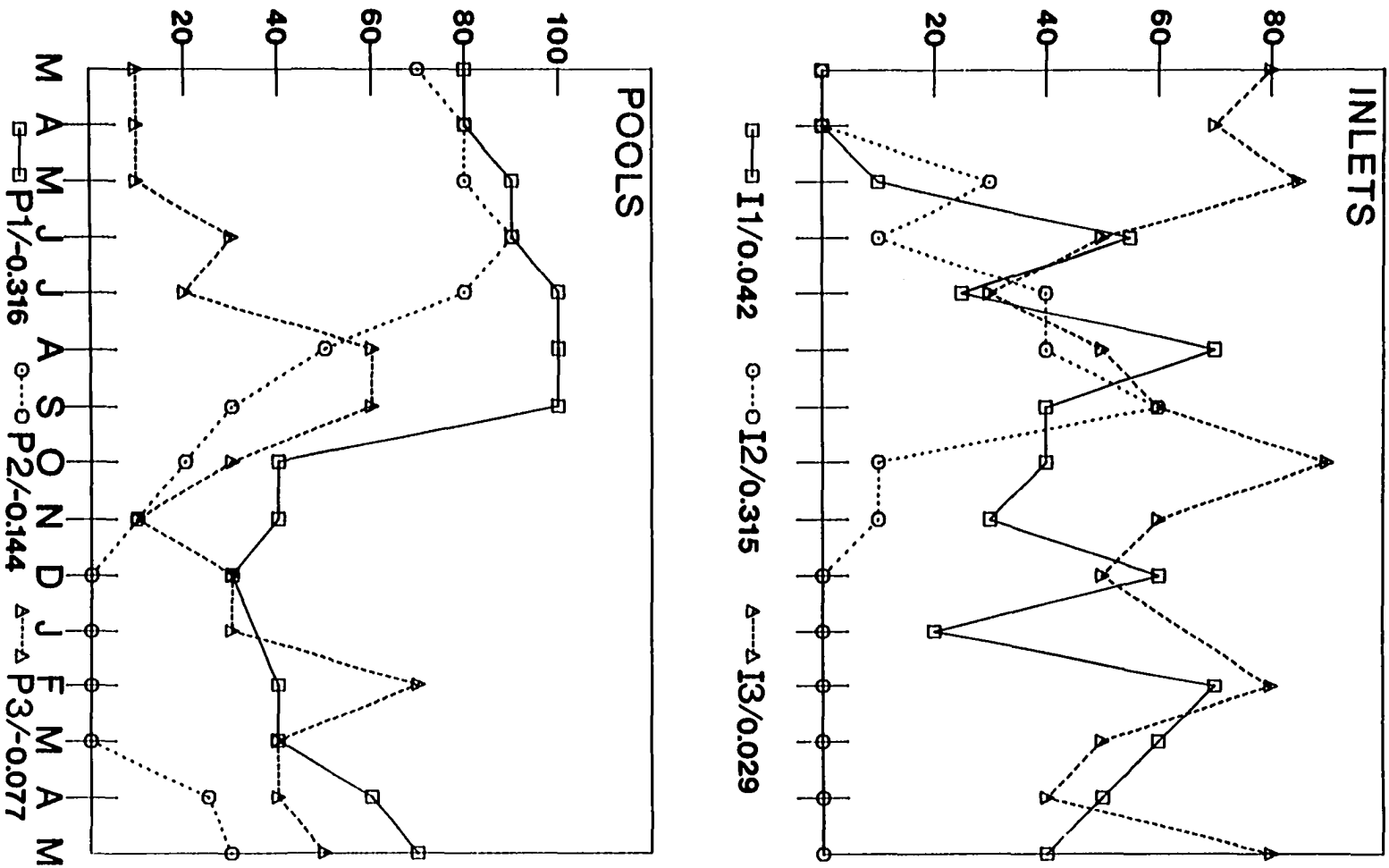


Fig. 8

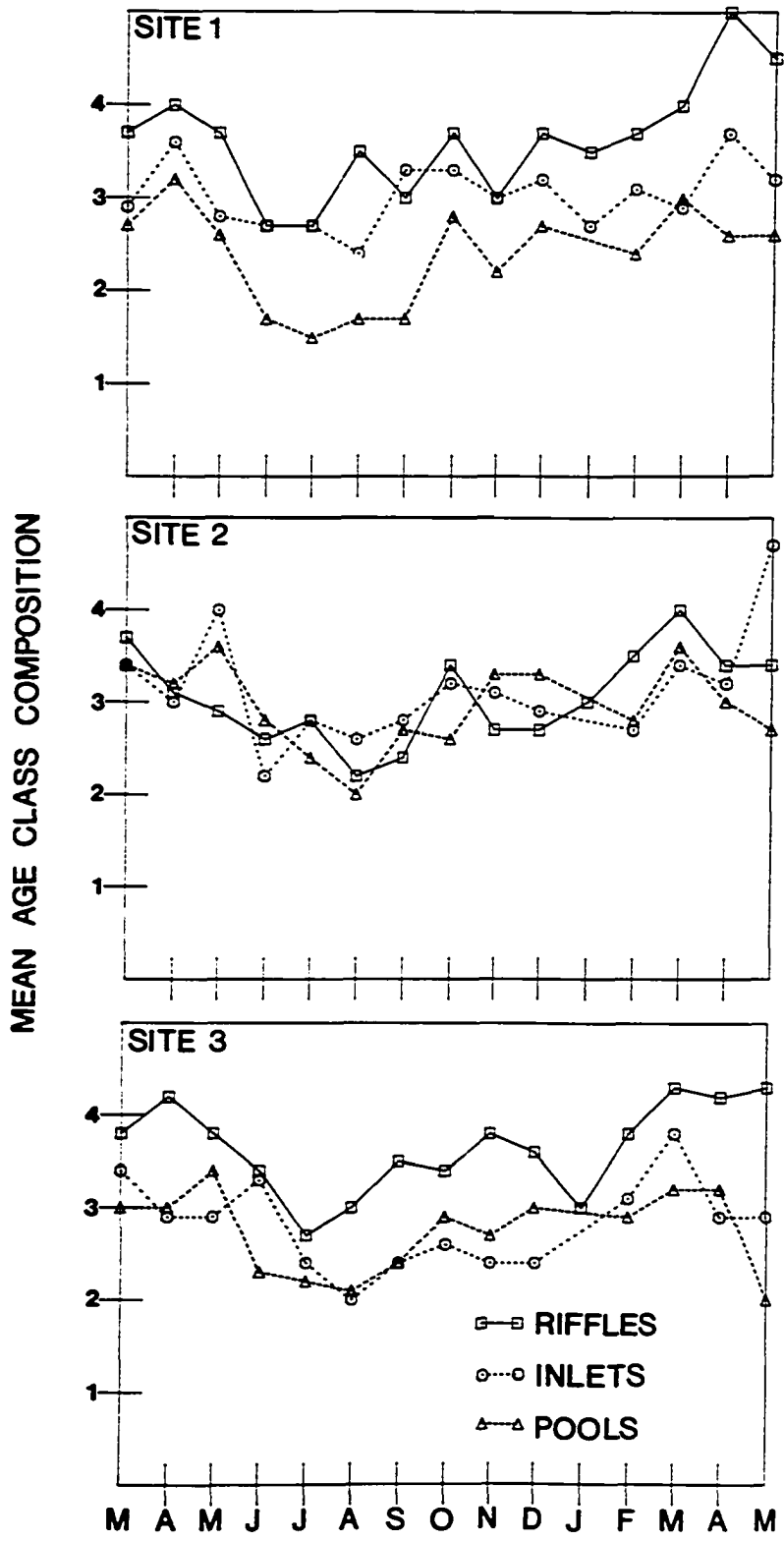


Fig. 9

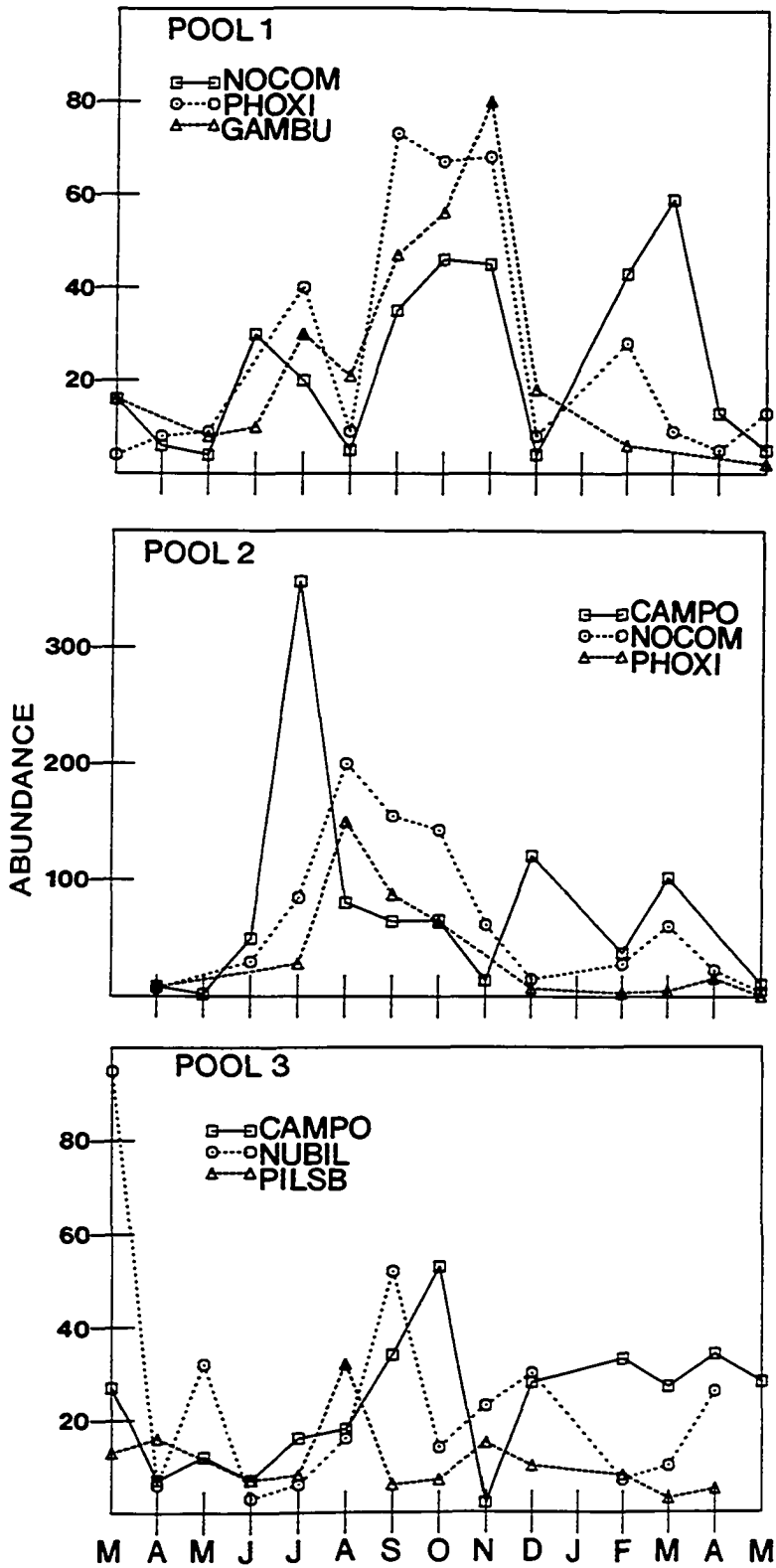


Fig. 10

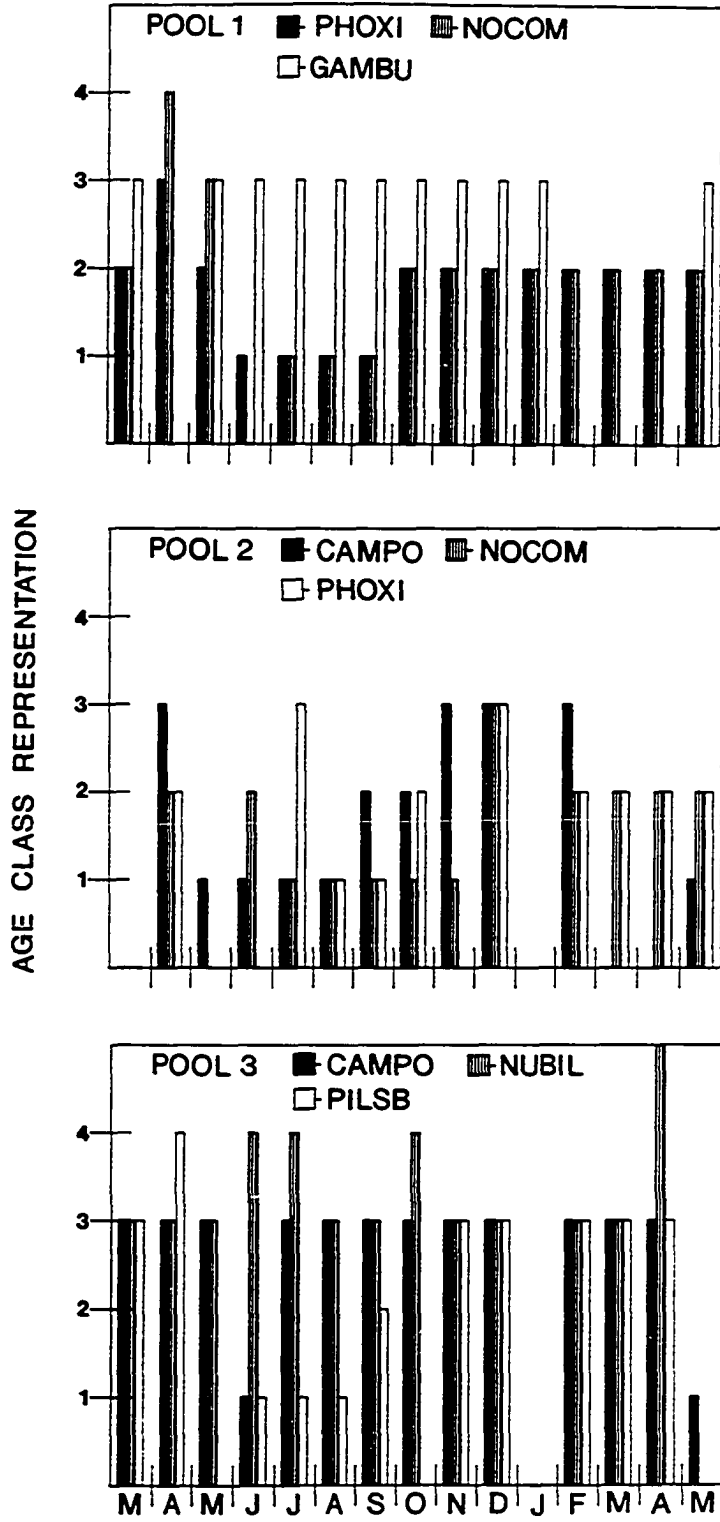


Fig. 11

APPENDIX

Fish assemblage data for each habitat, showing species abundance and age class representation (in parentheses), total abundance, and mean age-class composition for each month of the sampling period. Species labels are abbreviations for scientific names (presented in table 6).

Species	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
<u>Site 1 Riffle Assemblage</u>															
COTTU	6(3)	1(3)	61(4)	7(2)	4(2)	290(3)	6(2)	11(3)	49(2)	10(3)	11(3)	73(3)	8(3)	4(3)	27(3)
SPECT	29(5)	1(5)	16(5)	7(4)	4(4)	52(4)	5(4)	1(4)	8(4)	4(4)	2(4)	11(4)	13(5)	2(5)	13(5)
NOTUR	7(3)	--	23(4)	--	3(4)	42(4)	--	2(4)	10(3)	1(4)	--	5(4)	--	--	16(5)
CAMPO	--	--	1(2)	1(2)	2(1)	31(3)	1(3)	--	3(3)	--	--	--	--	--	36(5)
total	42	2	101	15	13	415	12	14	70	14	14	89	21	6	92
x age	3.7	4	3.7	2.7	2.7	3.5	3	3.7	3	3.7	3.5	3.7	4	4	4.5
<u>Site 2 Riffle Assemblage</u>															
CAMPO	15(3)	13(3)	13(3)	110(1)	18(3)	4(3)	10(2)	208(3)	16(2)	10(3)	1(2)	10(3)	41(4)	17(4)	10(3)
SPECT	108(5)	17(5)	28(3)	17(3)	6(3)	3(3)	15(4)	40(3)	35(4)	36(3)	5(4)	30(4)	26(5)	9(4)	6(5)
COTTU	6(4)	24(1)	19(1)	20(1)	29(2)	1(2)	8(2)	43(3)	2(3)	6(3)	5(3)	11(3)	5(3)	16(1)	13(1)
NUBIL	56(4)	4(4)	23(5)	9(4)	2(4)	8(3)	1(4)	17(4)	4(4)	--	--	15(4)	18(4)	13(4)	5(5)
NOCOM	--	2(2)	4(2)	5(3)	11(1)	11(1)	19(2)	17(3)	7(3)	5(2)	--	14(2)	2(3)	10(3)	10(2)

RUBEL	22(4)	4(4)	9(5)	--	13(4)	8(4)	--	9(4)	--	--	--	--	3(4)	17(4)	4(2)
PILSB	1(3)	5(3)	--	--	9(1)	2(1)	--	19(3)	1(2)	--	--	--	2(4)	30(3)	1(5)
SEMOT	--	--	4(3)	2(3)	7(3)	--	--	--	5(2)	3(2)	--	--	--	1(3)	2(2)
NOTUR	--	6(3)	--	--	9(4)	1(4)	--	10(4)	--	--	1(4)	--	--	14(5)	2(5)
PUNCT	1(4)	--	3(1)	8(3)	2(3)	--	--	2(4)	1(2)	4(2)	--	4(5)	1(5)	--	1(4)
total	209	75	103	171	106	38	53	365	61	54	12	84	98	127	54
x age	3.7	3.1	2.9	2.6	2.8	2.2	2.4	3.4	2.7	2.7	3	3.5	3.4	3.4	3.4

Site 3 Riffle Assemblage

COTTU	125(5)	3(4)	4(1)	81(3)	12(2)	1(2)	47(3)	4(3)	7(4)	7(3)	14(3)	11(3)	109(5)	4(4)	1(4)
CAMPO	3(3)	26(4)	7(3)	10(3)	20(1)	7(3)	134(3)	8(3)	--	13(3)	16(3)	1(3)	6(4)	4(3)	4(4)
SPECT	19(4)	28(5)	6(5)	23(4)	6(4)	3(4)	21(4)	4(4)	1(4)	2(4)	12(3)	19(5)	14(5)	3(5)	1(5)
NOTUR	24(3)	--	--	18(4)	--	--	59(3)	1(4)	--	7(4)	--	1(4)	11(4)	--	--
PILSB	30(4)	--	3(5)	2(1)	2(1)	2(1)	5(3)	--	1(4)	6(4)	--	--	7(4)	3(3)	--
NUBIL	--	--	--	2(4)	2(4)	1(3)	14(4)	--	1(4)	--	--	--	2(4)	1(5)	--
RUBEL	--	--	5(5)	5(4)	4(4)	4(4)	3(4)	--	--	--	--	--	--	2(5)	--
ZONAL	--	1(4)	--	1(4)	--	1(4)	1(4)	4(3)	5(3)	1(4)	--	1(4)	--	--	--
total	201	58	25	142	46	19	254	21	15	36	42	33	149	17	6
x age	3.8	4.2	3.8	3.4	2.7	3	3.5	3.4	3.8	3.6	3	3.8	4.3	4.2	4.3

Site 1 Inlet Assemblage

SPECT	75(5)	19(5)	23(5)	9(3)	6(4)	10(1)	5(4)	5(4)	17(4)	22(3)	7(4)	18(4)	43(5)	3(5)	4(5)
CAMPO	13(2)	4(4)	17(3)	28(1)	32(1)	21(3)	8(3)	9(3)	4(3)	43(3)	2(2)	6(2)	31(2)	3(4)	12(3)
GAMBU	--	--	--	2(3)	16(3)	33(3)	40(3)	--	9(3)	--	--	1(3)	--	--	--

NUBIL	--	37(5)	--	12(4)	1(4)	--	1(4)	22(4)	1(4)	4(3)	--	--	--	5(5)	7(5)
PUNCT	17(5)	1(3)	4(3)	--	--	2(4)	--	1(4)	8(4)	6(4)	--	19(5)	20(5)	--	1(5)
NOCOM	3(2)	5(3)	--	3(3)	3(3)	4(2)	12(3)	4(3)	9(3)	--	--	11(2)	21(2)	2(2)	1(2)
GOTTU	--	4(1)	1(1)	3(2)	2(2)	5(2)	--	--	7(3)	10(3)	1(2)	15(3)	13(3)	2(4)	3(1)
PILSB	1(2)	22(5)	--	2(1)	1(1)	--	--	4(3)	--	6(3)	--	2(2)	4(2)	8(5)	11(5)
SEMOT	2(2)	4(3)	6(3)	4(3)	2(3)	1(3)	--	--	3(2)	1(2)	--	--	5(2)	3(3)	1(3)
DOLOM	--	--	--	--	1(2)	2(1)	4(2)	3(2)	2(1)	--	--	--	1(2)	2(2)	1(2)
OLIVA	2(2)	--	1(2)	2(4)	2(4)	2(3)	1(4)	--	--	1(4)	--	1(4)	--	--	--
total	113	96	52	65	66	80	71	48	60	93	10	91	138	28	41
x age	2.9	3.6	2.8	2.7	2.7	2.4	3.3	3.3	3	3.2	2.7	3.1	2.9	3.7	3.3

Site 2 inlet Assemblage

NUBIL	43(3)	26(4)	66(5)	4(4)	13(4)	5(4)	52(4)	12(4)	44(4)	27(4)	--	36(4)	8(4)	18(4)	45(4)
CAMPO	--	--	2(3)	50(1)	5(4)	44(1)	19(3)	21(3)	33(3)	14(3)	--	6(2)	12(3)	--	--
PILSB	6(3)	17(3)	1(5)	15(1)	7(1)	3(4)	4(2)	12(3)	8(2)	11(3)	--	11(3)	17(2)	4(2)	--
NOCOM	9(3)	2(2)	--	--	3(1)	15(1)	29(4)	16(2)	7(3)	--	--	13(2)	--	--	--
SPECT	8(5)	1(3)	--	--	1(4)	--	4(4)	22(4)	5(4)	10(3)	--	4(4)	4(5)	1(4)	--
RUBEL	13(2)	11(3)	4(5)	--	--	1(4)	--	2(4)	6(3)	1(2)	--	1(2)	9(3)	--	2(5)
PUNCT	1(5)	--	--	1(4)	--	--	1(3)	15(3)	6(3)	9(3)	--	5(3)	--	--	1(4)
SEMOT	1(3)	--	1(3)	1(3)	3(3)	4(2)	4(2)	4(3)	8(3)	7(2)	--	1(2)	--	1(3)	--
Total	81	57	74	71	32	72	113	104	117	79	--	77	50	74	48
x age	3.4	3	4.2	2.2	2.8	2.6	2.8	3.2	3.1	2.9	--	2.7	3.4	3.2	4.7

Site 3 Inlet Assemblage

CAMPO	43(3)	20(3)	12(1)	7(1)	9(4)	2(2)	3(3)	13(3)	23(3)	46(2)	--	9(3)	75(5)	5(2)	2(1)
NUBIL	11(3)	10(3)	9(5)	2(4)	6(4)	3(3)	24(4)	7(4)	18(4)	32(3)	--	4(3)	32(4)	15(5)	17(5)
NOCOM	10(3)	28(3)	14(3)	9(3)	8(1)	15(1)	9(2)	27(2)	4(2)	4(3)	--	11(2)	17(4)	25(2)	8(2)
RUBEL	6(4)	8(3)	29(5)	24(4)	26(4)	1(4)	9(4)	4(4)	24(3)	15(4)	--	--	3(3)	15(5)	7(5)
LABID	3(4)	--	2(4)	--	1(4)	12(1)	9(2)	12(3)	--	13(3)	--	17(3)	3(4)	2(4)	11(3)
COTTU	8(4)	1(1)	5(1)	8(3)	1(1)	--	--	2(2)	1(2)	1(2)	--	2(2)	12(3)	4(1)	25(1)
SPECT	31(4)	1(3)	--	1(4)	--	1(3)	--	--	2(4)	2(1)	--	16(4)	10(4)	--	--
PILSB	11(3)	10(4)	1(5)	5(4)	1(4)	--	1(2)	1(3)	7(3)	6(3)	--	4(4)	6(4)	4(3)	1(3)
GAMBU	--	--	--	--	2(2)	7(1)	18(3)	16(3)	--	5(3)	--	--	--	--	1(4)
MEGAL	2(3)	11(3)	20(2)	--	1(2)	--	--	--	1(2)	3(4)	--	--	6(4)	--	3(2)
AMBLO	1(2)	4(3)	4(2)	6(3)	3(1)	3(1)	3(2)	1(2)	1(3)	1(1)	--	2(4)	2(4)	--	--
MACRO	--	--	--	--	--	5(1)	3(1)	4(2)	7(1)	1(1)	--	3(2)	4(4)	2(1)	--
PUNCT	19(5)	1(4)	1(1)	1(4)	--	--	--	--	3(4)	--	--	--	3(4)	--	--
OLIVA	--	1(2)	--	--	--	3(1)	11(2)	2(2)	1(1)	1(2)	--	--	2(2)	--	--
Total	145	95	97	63	58	52	90	89	93	130	--	68	175	72	75
x age	3.4	2.9	2.9	3.3	2.4	2.0	2.4	2.6	2.4	2.4	--	3.1	3.8	2.9	2.9

Site 1 Pool Assemblage

PHOXI	4(2)	8(4)	9(3)	--	40(1)	9(1)	73(1)	67(2)	68(2)	8(2)	--	28(2)	9(2)	5(2)	13(2)
NOCOM	16(2)	6(3)	4(2)	30(1)	20(1)	5(1)	35(1)	46(2)	45(2)	4(2)	--	43(2)	59(2)	13(2)	5(2)
GAMBU	16(3)	--	8(3)	10(3)	30(1)	21(3)	47(3)	56(3)	80(3)	18(3)	--	6(3)	--	--	2(3)

CAMPO	2(2)	15(3)	37(2)	60(1)	10(1)	--	--	9(3)	2(2)	1(2)	--	9(2)	3(2)	2(2)	20(1)
SPECT	5(3)	16(3)	54(5)	--	--	--	--	8(3)	7(3)	4(3)	--	4(3)	10(5)	1(5)	1(4)
PUNCT	5(4)	10(3)	7(1)	--	--	--	--	1(4)	--	1(4)	--	--	2(5)	--	1(4)
MEGAL	--	5(3)	2(2)	--	--	--	--	--	1(1)	--	--	--	6(2)	4(2)	3(2)
total	48	60	120	100	100	35	155	187	203	36	--	90	89	25	45
x age	2.7	3.2	2.6	1.7	1.5	1.7	1.7	2.8	2.2	2.7	--	2.4	3	2.6	2.6

Site 2 Pool Assemblage

NUBIL	--	201(4)	--	19(4)	49(5)	26(3)	37(3)	303(3)	17(4)	144(4)	--	38(4)	201(4)	6(2)	6(4)
CAMPO	--	9(3)	2(1)	50(1)	357(1)	81(1)	65(2)	66(2)	14(3)	121(3)	--	38(3)	102(3)	--	11(2)
NOCOM	--	7(2)	--	30(2)	85(1)	200(1)	155(1)	143(1)	62(1)	15(3)	--	28(2)	61(2)	23(2)	4(2)
PHOXI	--	8(2)	--	--	28(3)	150(1)	88(1)	64(2)	--	7(3)	--	3(2)	5(3)	16(2)	1(2)
GAMBU	--	--	--	--	15(3)	1(3)	8(3)	21(4)	10(3)	1(4)	--	--	--	--	33(4)
SEMOT	5(4)	--	--	--	1(1)	1(2)	7(3)	40(2)	4(3)	4(3)	--	5(2)	4(3)	2(2)	--
SPECT	5(3)	3(4)	3(5)	1(4)	3(4)	1(3)	1(3)	6(3)	2(4)	1(4)	--	5(3)	4(5)	8(4)	6(3)
MACRO	1(2)	1(2)	3(3)	1(3)	8(3)	3(3)	2(3)	12(3)	--	--	--	--	--	2(3)	10(3)
PILSB	--	1(2)	--	--	2(1)	2(1)	1(4)	--	--	11(3)	--	5(3)	19(3)	1(3)	--
GATEN	2(4)	10(5)	--	--	--	--	--	17(3)	5(4)	5(3)	--	1(3)	1(4)	--	1(3)
PUNCT	10(4)	3(4)	5(4)	--	3(1)	--	1(3)	--	--	--	--	6(3)	2(5)	2(5)	3(1)
OLIVA	0	1(4)	2(5)	--	9(3)	--	1(4)	--	2(4)	--	--	--	1(4)	2(4)	6(4)
Total	23	244	15	101	560	465	329	672	116	309	--	143	400	62	81
x age	3.4	3.2	3.6	2.8	2.4	2.0	2.7	2.6	3.2	3.3	--	2.8	3.6	3	2.7

Site 3 Pool Assemblage

CAMPO	27(3)	7(3)	12(3)	7(1)	16(3)	18(3)	34(3)	53(3)	2(3)	28(3)	--	33(3)	27(3)	34(3)	28(1)
NUBIL	95(3)	6(3)	32(3)	3(4)	6(4)	16(3)	52(3)	14(4)	23(3)	30(3)	--	7(3)	10(3)	26(5)	--
PILSB	13(3)	16(4)	--	7(1)	8(1)	32(1)	6(2)	7(2)	15(3)	10(3)	--	8(3)	3(3)	5(3)	--
NOCOM	20(2)	3(2)	8(3)	7(1)	1(1)	8(1)	5(2)	17(2)	1(2)	6(2)	--	10(2)	12(2)	30(2)	--
PUNCT	77(5)	--	--	5(4)	--	--	--	--	--	1(4)	--	--	34(5)	1(4)	2(1)
GAMBU	--	--	6(4)	6(3)	33(3)	23(3)	1(2)	2(2)	1(3)	7(2)	--	1(2)	--	--	16(4)
RUBEL	16(3)	19(3)	24(3)	--	1(1)	1(4)	--	--	3(3)	10(3)	--	--	5(2)	10(3)	--
SPECT	35(3)	7(4)	8(5)	--	--	--	--	--	--	2(3)	--	10(4)	10(5)	1(5)	--
COTTU	2(4)	--	3(3)	--	--	--	--	--	--	--	--	--	2(3)	15(1)	18(1)
LABID	--	14(3)	--	--	--	--	--	1(3)	3(3)	3(3)	--	--	6(3)	7(3)	--
MEGAL	6(2)	2(2)	--	--	--	--	--	--	--	--	--	--	9(2)	7(3)	9(3)
PHOXI	1(2)	--	--	--	--	1(1)	--	4(2)	1(2)	3(3)	--	11(3)	1(4)	--	--
total	292	74	93	35	65	99	98	98	49	118	--	80	119	136	64
x age	3	3	3.4	2.3	2.2	2.1	2.4	2.9	2.7	3.0	--	2.9	3.2	3.2	2.0