Ecology of Freshwater Fish 1993: 2: 23–30
Printed in Denmark · All rights reserved

ECOLOGY OF
FRESHWATER FISH
ISSN 0906-6691

Fish populations in tropical floodplain pools: a re-evalution of Holden's data on the River Sokoto

Chapman LJ, Chapman CA. Fish populations in tropical floodplain pools: a re-evaluation of Holden's data on the River Sokoto. Ecology of Freshwater Fish 1993: 2: 23–30. © Munksgaard, 1993

L. J. Chapman[1], C. A. Chapman[2]
[1]Museum of Comparative Zoology and
[2]Peabody Museum, Harvard University,
Cambridge, Massachusetts, USA

Abstract – In this study we asked whether the fish populations of residual pools in a seasonally fluctuating African river varied between years. We used a series of data on the fish of the permanent floodplain pools of the River Sokoto, Nigeria compiled by M. J. Holden (1963) to address this objective. Holden provided estimates for the size and biomass of fish populations in 12 permanent dry season pools over a period of 2 to 3 years. On average, only 22% of the species present in a pool were absent from that pool in the following sampling period. Despite low inter-annual variability in the species composition of the pools, rank correlation analysis indicated significant variation in the relative numbers and biomass of the 10 most numerically abundant species in most pools. Altering the spatial scale of analysis to include all possible combinations of 2 and 6 pools did not affect the results. Indices of similarity also indicated relatively high annual variability in the relative abundance of species in the pool communities. We suggest that habitat selection may contribute to the continued occurrence of fish species in pools from year to year, and such factors as changes in the overall abundance of fish species in the system and haphazard trapping during flood decline may contribute to annual variation in their relative abundance.

Key words: floodplain; tropical fish; community ecology; Africa

L. J. Chapman, Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, USA

Accepted for publication February 16, 1993

Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

In many larger tropical rivers, forests and savannas become flooded over large areas during the wet season, producing enormous areas of seasonally available habitat for aquatic organisms. For example, in African floodplain rivers, the area of dry season aquatic habitat averages 28% of that available in the wet season (range = 5–59%) (Welcomme 1979). In the shallow basin of the central Amazon, annual variation in water levels from 7 to 13 m produces inundation that may extend laterally 20 to 100 km (Junk 1970; Goulding 1980). The annual cycle of events in these systems is predictable, in that flooding occurs annually, although the onset, magnitude, and duration may vary from year to year.

During the wet season, many fish move into newly inundated areas. Some species exhibit long defined migrations, others make only local movements, and some species tend to remain in their home pools (Lowe-McConnell 1964, 1975; Welcomme 1979; Goulding 1980). When flood waters recede, fishes retreat to the main river or remaining floodplain pools (Lowe-McConnell 1964, 1975; Welcomme 1979; Junk, Soares & Carvalho 1983). As the dry season progresses, fish densities can become dramatically high in desiccating pools, and catastrophic mortality of fishes trapped in temporary dry season pools can occur (Lowe-McConnell 1964, 1975; Bonetto et al. 1969; Roberts 1972). Some of the studies that discuss the habitat characteristics and ecology of fishes living in tropical floodplain rivers include Daget (1957), Lowe-McConnell (1964, 1975), Welcomme (1979), Goulding (1980) and Winemiller (1987).

The enormous areas of new habitat created by flooding and the large-scale movements of fish produce a dynamic annual reconstruction of communities. Spawning success, migration, habitat selection, mortality and the random trapping of fish in pools are likely to produce strong annual variation in the species density and diversity of dry season pools. However, there are few studies that quantitatively document the distribution of species among tropical floodplain pools over more than 1 year. One notable exception is the study by Holden (1963) that examined the composition of fish communities in 12 dry-season floodplain pools in the River Sokoto. Holden estimated the size and biomass of the fish populations shortly after pools became separated through an intensive mark and recapture program. Values for 10 of the pools were estimated over a period of 2 to 3 years. In this study we determined whether the populations of residual pools vary between years with respect to the fish species present (species composition) and the relative numbers of the most abundant species (stability). In addition, we considered factors that may influence annual variation in the distribution and abundance of fish species among pools.

A variety of recent studies examine the stability and persistence of stream fish assemblages (Grossman, Moyle & Whitaker 1982; Rahel, Lyons & Cochran 1984; Grossman et al. 1985; Ross, Matthews & Echelle 1985; Matthews 1986; Grossman, Dowd & Crawford 1990). Although we use similar analyses as these studies, we do not purport to be able to consider the relative importance of deterministic and stochastic factors in shaping the community. In this study we simply take a similar statistical approach to examine the degree to which the structure of the fish communities in dry-season pools changes over a 2- to 3-year period. We follow Connell & Sousa (1983), Ross et al. (1985), and Matthews (1986) in considering stability as constancy in the relative abundance of groups (in this case, species) over time. We use the percentage of fish species in a pool that were found in the same pool in the next sampling period to represent inter-annual variation in species composition. We consider the effect of both the number of species in the analyses and spatial scale on our interpretations. The number of species included in the analysis can affect the results in concordance tests (Rahel et al. 1984; Grossman et al. 1985; Matthews 1986). Often, rarer species are excluded from the analysis of assemblage stability (Grossman et al. 1982; Ross et al. 1985; Matthews 1986; Matthews, Cashner & Gelwick 1988). In our analysis of the relative abundance of fishes in the River Sokoto pools, we use the 10 most abundant species to define the assemblage in a given pool, but also consider the results when all of the species in a pool are included. Connell & Sousa (1983) suggest that the assemblage is less likely to be found to be stable if the study is conducted over a large area than a small area, because increasing the spatial scale dampens out the fluctuations of subpopulations. We consider the problem of spatial scale by varying the number of pools used to define the assemblage and then assessing changes in the relative abundance of fish species.

Material and methods

The River Sokoto is a tributary of the River Niger, flowing from Funtua northwest of the town of Sokoto, Nigeria and then southwest into the Niger (Holden 1963). From an area 160 km southwest of Sokoto, the river flows south through a large seasonal floodplain (about 8 km wide). When the waters recede into the dry season riverbed (minimum width of 30 m), the floodplain dries, leaving a series of permanent pools. The pools remain isolated for approximately 4 months depending on the onset, magnitude, and duration of the rains. Holden describes in detail the pool characteristics

Table 1. Characteristics of the pools studied by Holden (1963) in the River Sokoto

Pool	Year	Area (m^2)	Volume (m^3)	Average depth (m)	Maximum depth (m)	Standing crop (kg)
Auwuru	1955	710	720	1.0	3.25	37
Dan Akwati	1956	2520	2890	1.2	4.75	72
	1957	2520	2890	1.2	4.75	188
Dan Kube	1955	950	1710	1.8	5.25	73
	1956	950	1710	1.8	5.25	145
	1957	1480	1980	1.3	5.25	151
Dan Kube Mai Tukunyia	1955	1920	2290	1.2	3.75	47
	1957	1920	2290	1.2	3.75	26
Fesafari	1954	37450	41100	1.1	2.00	2307
	1956	37450	37500	1.0	1.75	1394
	1957	37450	37500	1.0	1.75	1154
Kai Kai	1955	5120	4930	1.0	3.25	386
	1956	5120	4930	1.0	3.25	519
	1957	5120	4930	1.0	3.25	892
Maiarake	1955	1120	1130	1.1	3.25	172
	1957	1120	1130	1.1	3.25	43
Me Kawa	1957	1730	1360	0.8	3.75	–
Melissa	1956	25400	12700	0.5	0.50	255
	1957	25400	12700	0.5	0.50	511
Sambo ka Face	1955	1530	1250	0.8	2.25	68
	1957	1530	1250	0.8	2.25	317
Shafu Shuni	1956	19350	16100	0.8	1.75	815
	1957	19350	16100	0.8	1.75	918
Tamfarka	1956	12890	8080	0.6	1.25	100
	1957	12890	8080	0.6	1.25	224

we have summarized in Table 1. The 5 most abundant species in the system were *Sarotherodon galilaeus, Oreochromis niloticus, Alestes dentex, Hemichromis fasciatus* and *Alestes nurse*.

Holden (1963) selected 12 pools varying in size from 0.07 to 4.7 ha that were partially free of vegetation to facilitate seining. The pools were closed to local fishermen, and fishes were captured using draw nets. Holden does not report the mesh size of the nets that were used, but states that, in 1955, 1956, and 1957, small mesh nets (<2.5 cm) provided samples of all fish of a markable size. Fish as small as 6 cm (total length, TL) are reported; however, tagged fishes were generally greater than 10 cm, with the exception of *Alestes*, where the minimum length was approximately 15 cm (Holden 1963; M. J. Holden, personal communication). Fish were marked by fin-clipping or by applying numbered plastic tags. In general, Holden derived mark-recapture estimates using the triple catch method or the negative method (Bailey 1952) or using the Lincoln index when a large number of fish were marked but recaptures were insufficient. When few fish were captured and marked and no fish were recaptured, the number of fish marked was reported as the corrected estimate of population size. Estimates were corrected to allow for marking mortality. When corrected figures gave an estimated population that was less than the number of fish marked, the latter was reported as the corrected population estimate. We use the corrected estimates for all analyses. The pools remained cut off for about 4 months, February to May, depending on the speed that the flood waters subsided, the date of the onset of the rains and the location and morphometry of the pools. Population estimates were generally initiated in mid-March and tagging reached a peak in April, with the estimate completed in a maximum of 4 weeks (Holden 1963; M. J. Holden, personal communication). This left an interval of 1 to 2 months between the completion of the estimates and reconnection of the pools by rising flood waters. The river level and rainfall patterns were very similar during the different years of the study, with little rain falling in October (approximate inter-annual range for the month of October = 2–3 cm) and no rain falling in November.

Holden provides estimates of fish numbers, biomass and staining crop. Records were kept on all species caught except *Petrocephalus bovei*, which was usually killed by seining, and *Tetraodon fahaka*. *Protopterus annectens* occurs in the area but aestivates in a cocoon during the dry season and was not captured. In addition, because of the mesh size used, cyprinidontoids and small *Barbus* would not have been caught (M. J. Holden, personal communication). With these exceptions, the samples are believed to have approximated the fish community composition in the pools (M. J. Holden, personal communication). If a fish species was noted to occur in a pool, but their biomass was small and considered as being negligible in the standing crop, Holden did not present a biomass estimate. We assigned these species the lowest ranking for biomass.

Following Grossman (1982) and Matthews (1986), the stability of the assemblage structure was examined for each pool by comparing the relative abundance of fish species from any paired collections (i.e. year 1 *vs* 2, year 2 *vs* 3 and year 1 *vs* 3). The Spearman's rank correlation (r_s) was used to compare the relationship between paired collections. Since the analysis included many comparisons, we adjusted the alpha level to ensure that all tests would detect significance at the 0.05 level using the Dunn-Sidak formula (Ury 1976; Grossman et al. 1985). Following Matthews et al. (1988), Morisita's index (Morisita 1959; Wolda 1981) and Schoener's index (Schoener 1968; Linton, Davies & Wrona 1981, referred to as PSI in Matthews et al. 1988) were used to measure the similarity of fish assemblages between any two sampling dates. Both indices were used because Morisita's index can overestimate and Schoener's index can underestimate the true similarity (Linton et al. 1981).

To examine the influence of the number of taxa included in the assemblage on the analysis of stability, we repeated the above analysis with only those fish species that were found in any given pool in the years compared and with the 10 most numerically abundant species for each pool over the years studied.

The problem of selecting an appropriate spatial scale was addressed by varying the number of pools used in the correlational analysis for the 10 most abundant species. First, we took all possible combinations of 2 different pools for the 7 pools that were sampled on 2 consecutive years (1956–1957). Second, we took all possible combinations of 6 different pools from the same 7 pools, and Spearman's rank correlation was used to determine the relationship between the relative numerical abundance of fishes between years for the pooled collections.

Results

The percentage of fish species in a pool that were found in the same pool the next sampling period varied from 50% to 100%, with an average of 78% (±12%, SD, Table 2). Thus, on average, only 22% of the species present in a pool at time 1 were

Table 2. The percentage change in the species composition of the River Sokoto pools (no. of species from sample 1 that were found in sample 2, expressed as a percentage of sample 1)

Pool	Years	No. of species in sample 1	No. of species in sample 2	% of sample 1 in sample 2
Auwuru	1955	21	–	–
Dan Akwati	1956–1957	14	19	11/14 (78.6%)
Dan Kube	1955–1956	20	13	12/20 (60.0%)
	1956–1957	13	12	10/13 (76.9%)
	1955–1957	20	12	10/20 (50.0%)
Dan Kube	1955–1957	21	22	15/21 (71.4%)
Mai Tukunyia Fesafari	1956–1957	21	22	18/21 (85.7%)
Kai Kai	1955–1956	19	17	14/19 (73.7%)
	1956–1957	17	21	15/17 (88.2%)
	1955–1957	19	21	15/19 (78.9%)
Maiarake	1955–1957	18	20	14/18 (77.8%)
Me Kawa	1957	16	–	–
Melissa	1956–1957	20	22	16/20 (80.0%)
Sambo ka Face	1955–1957	21	21	17/21 (81.0%)
Shafu Shuni	1956–1957	26	27	23/26 (85.2%)
Tamfarka	1956–1957	13	21	13/13 (100%)

absent from that pool at time 2. For the 2 pools that were sampled over 3 consecutive years, the repeated occurrence of species was higher between 1956 and 1957 (76.9% and 88.2% for Dan Kube and Kai Kai, respectively) than between 1955 and 1956 (60.0% and 73.7% for Dan Kube and Kai Kai, respectively).

In contrast to the relatively low variability in the species composition of individual pools, there were fluctuations in both the number and biomass of particular fish species between sampling periods in many pools. However, the degree of concordance was highly variable among pools and differed depending on the number of species used to define the assemblage. When the species assemblage was defined as the species that occurred in a specific pool in the years compared, 43% of the correlations were significant at $P<0.05$ for ranks of abundance based on numbers, and 29% of the correlations were significant when the probability level was adjusted for multiple tests (Table 3). With respect to ranks of abundance based on biomass, 36% of the rank correlations were significant at $P<0.05$, and 21% of the correlations were significant with the corrected probability value. When we considered only the 10 most numerically abundant species in each pool, the concordance among years with respect to the relative abundance of fish species declined. Only 14% and 29% of the correlations were significant at $P<0.05$ for ranks of abundance based on numbers and biomass, respectively. When adjusted for multiple comparisons, only one correlation was significant for ranks of abundance based on numbers, and no correlations were significant for ranks based on biomass.

The results of the rank correlation analysis were supported by indices of faunal similarity. On average, faunal similarity changed among years and varied greatly among pools. Morisita's index based on numbers of fish estimated to be present in pool populations averaged 0.62, but ranged from 0.26 to 0.93 among pools and sampling periods, whereas Schoener's index averaged 0.50, but ranged from 0.27 to 0.76 (Table 3).

We examine the effects of spatial and temporal variability among pools by graphically presenting the relative numerical abundance of the species in each pool for 2 sampling periods (Fig. 1). There were great differences in the relative abundance of some fish species both among pools and within pools over time. For example, in 1955, the estimated population of *Alestes nurse* in Kai Kai was 1987, representing 22.4% of the fish community. In 1956, the estimated population size had declined to 6 fish representing less than 1% of the community. In Dan Kube *Alestes dentex* increased from an estimated 30 fish, representing 8% of the community in 1955, to an estimated 756 fish, representing approximately 48% of the community, in 1956.

To examine the effects of spatial scale on the analysis of change in the relative abundance of fishes, we considered rank correlations between the numbers of the 10 most abundant species within groups of two pools. We used all 21 possible combinations of the 7 pools sampled in both 1956 and 1957. Only 14% of the relationships were significant at $P<0.05$, and no correlations were significant when the probability level was adjusted for multiple comparisons, indicating that for this system, enlarging the spatial scale to include two pools did not decrease the shifts in the relative abundance of species. We then enlarged the spatial scale to include all possible combinations of 6 of the 7 pools sampled in 1956 and 1957. None of the 7 possible combinations was significant.

To identify factors that may account for the variation in stability among pools, we considered relationships between each of the similarity indices and a series of pool characteristics (pool area, maximum depth, mean depth, standing crop, vegetation characteristics and pool volume; Table 1). These analyses were conducted in 2 ways: relating Morisita's index and Schoener's index to the pool characteristics at time 1, and relating the indices to the pool characteristics at time 2. None of the relationships were significant at $P>0.14$. A stepwise regression including all continuous variables was used to identify possible interactive effects; no variables entered into the regression at $P<0.05$. Thus, there was no evidence to indicate that variation in the similarity indices among pools was related to pool characteristics.

Table 3. The relationship between species abundance for paired collections from River Sokoto floodplain pools for all species within a given pool during the years compared and the 10 most abundant species within a specific pool, Morisita's index of similarity for fish assemblages, and Schoener's index of similarity

		r_s (all species) (one pool)		r_s (10 species)		Morisita's index	Schoener's index
Pool	Dates	Numbers	Biomass	Numbers	Biomass	Numbers	Numbers
Auwura	1955	–	–	–	–	–	–
Dan Akwati	1956–1957	0.21	0.01	0.52	0.21	0.54	0.44
Dan Kube	1955–1956	0.30	0.20	0.09	0.04	0.52	0.48
	1956–1957	0.60*	0.67*	0.67*	0.68*	0.92	0.74
	1955–1957	0.20	0.13	0.02	−0.12	0.53	0.35
Dan Kube Mai Tukunyia	1955–1957	0.07	0.07	−0.21	0.01	0.26	0.27
Fesafari	1956–1957	0.79**	0.74**	0.61	0.73*	0.93	0.76
Kai Kai	1955–1956	0.45*	0.38	0.25	0.51	0.62	0.49
	1956–1957	0.73**	0.63**	0.83**	0.79*	0.72	0.65
	1955–1957	0.30	0.34	0.01	0.10	0.59	0.49
Maiarake	1955–1957	0.27	0.10	−0.13	−0.02	0.71	0.44
Me Kawa	1957	–	–	–	–	–	–
Melissa	1956–1957	0.20	0.23	0.35	0.40	0.36	0.32
Sambo ka Face	1955–1957	0.19	0.37	0.24	0.04	0.56	0.39
Shafu Shuni	1956–1957	0.75**	0.64**	0.53	0.67*	0.73	0.57
Tamfarka	1956–1957	0.68**	0.56*	0.43	0.45	0.64	0.54
Total no. $P<0.05$ (*)		6	5	2	4	mean=0.62	0.50
corrected (**)		4	3	1	0		

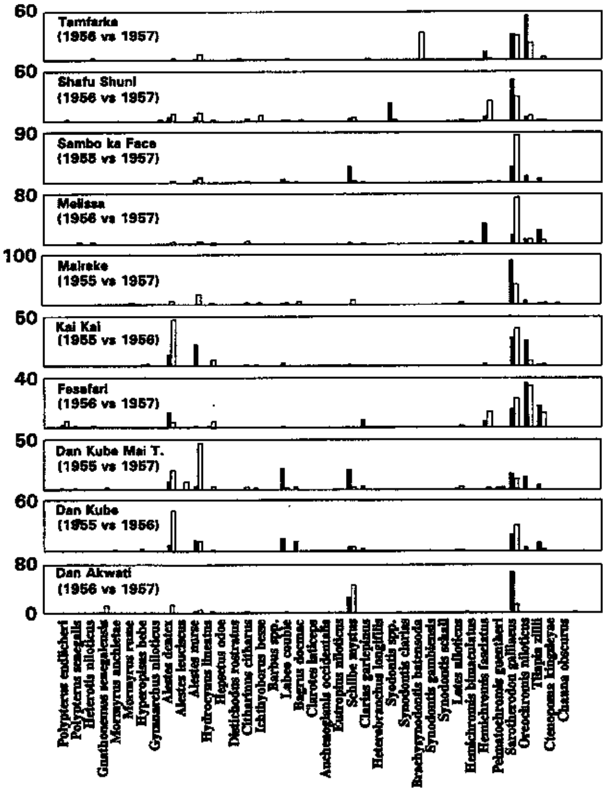

Fig. 1. The relative abundance (%) of the fish species found in the floodplain pools of the River Sokoto, expressed as a percentage of the total number of fish estimated to be in an individual pool in a given year. For pools sampled for more than 2 years, the first 2 years are included in the figure.

Discussion

Species composition

Despite the vast annual changes in the physical environment of the River Sokoto and the fish movements associated with seasonal flooding, the species composition of the dry season pools in the River Sokoto remained similar between years. On average, only 22% of the species present in a pool during a given dry season were absent from that pool the following sampling period, 1 or 2 years later. This compares favorably with studies of temperate stream assemblages, which have reported little inter-annual variability in species composition (Ross et al. 1985; Matthews 1986; Matthews et al. 1988). For example, Matthews et al. (1988) found that only 18% of the fish species in an upland stream in Oklahoma were absent from collections in 2 or more of the 5 years of study. Lowe-McConnell (1967) examined floodplain pools in the Rupununi district of Guyana and found that different kinds of pools tended to have the same types of fish year after year. The continued occurrence of fish species in pools from year to year may be related to habitat selection (for example, Holden describes substrate preferences for some species), homing or the sedentary nature of some species.

Relative abundance: analytical considerations

Although species composition of pools was similar between sampling periods, the relative abundance of fish species exhibited marked fluctuations in many pools. Most pools showed no concordance among years in the relative abundance of the 10 most abundant species. However, the degree of stability exhibited by an assemblage may vary with the number of species used to define the assemblage (Rahel et al. 1984; Matthews 1986). When we defined the assemblage as the species that appeared in specific pools over the course of the study, the concordance among years in the relative abundance of fishes increased. It seems reasonable to conclude that there were significant fluctuations in the relative abundance of species in many pools of the River Sokoto, but that the number of species used to define the assemblage affected our assessment of the degree of change.

Similarity indices are useful in comparing the relative stability among sites, but because they have no associated significance levels, they are less useful as a criterion for indicating the similarity of a particular assemblage between years. However, Matthews et al. (1988) reviewed studies that used similarity indices to consider a general range of values that represent low or high similarity and concluded that most authors judge values greater than about 0.7 as indicative of a stable assemblage. In the River Sokoto system, Morisita's index of similarity averaged 0.62 between sequential samples of pools and Schoener's index averaged 0.50, indicating relatively low similarity of fish assemblages among years. However, the indices were highly variable, and low or high similarity was not necessarily pool specific. For example, Morisita's index for Dan Kube was 0.53 (low) for 1955–1956 and 0.92 (high) for 1956–1957.

The number of years of sampling in this study is small and may not reflect long-term patterns. Ross et al. (1985) found that the relative abundance measures of fishes in a small midwestern stream in Oklahoma showed significant fluctuations. With additional surveys from the same stream, Matthews et al. (1988) produced a temporally expanded data set that showed significant rank correlation of abundance for the common species. A long-term data set on the fishes of tropical floodplain pools will be necessary to draw conclusions about the long-term stability of pool assemblages.

It has been argued that, if one examines the stability of a small assemblage (such as one station in a flowing stream or one floodplain pool), it is unlikely to be stable (Connell & Sousa 1983). However, if one considers a larger spatial scale (such as several stations in a stream), it is much less likely to show significant change in the relative abundance of species. With respect to the floodplain pools of the River Sokoto, increasing the spatial scale did not affect the results. It is quite possible that if one continued to increase the spatial scale to include a greater number of pools, increased stability would be observed. However, in the floodplain pools, the characteristics of individual pools and changes in the relative abundance of species within specific pools have important consequences for the survival of individuals and populations. If fish move to different pools during the floods, individuals may encounter different fish assemblages over the course of their lives.

Finally, errors are inherent in all mark-recapture estimates and may have contributed to the variation observed. However, Holden (1963) believed that his estimates reflected actual changes in the fish populations that were supported by his observations on how easy or difficult it was to catch a species in a certain year or place.

Potential correlates of fluctuations in abundance

A variety of factors may contribute to annual fluctuations in the relative abundance of species in floodplain pools. Spawning success, migration, habitat selection, mortality and the random trapping of individuals as waters fall may all interact to produce a dynamic system of interacting variables that results in annual fluctuations in the number of fishes within areas of the floodplain and main rivers. It has been suggested that annual variation in ecological conditions, which allows some species to become more abundant in some years than ecologically similar species, may be important in allowing high numbers of species to coexist (Lowe-McConnell 1967).

In highly seasonal tropical waters, there seems to be strong selection for high fecundity, rapid development, fast growth and short life cycles (Lowe-McConnell 1967, 1975, 1984). When spawning success varies between species, this can produce changes in the relative numbers of species within pools. Holden notes that 5 non-migratory species (*H. fasciatus, S. mystus, S. galilaeus, O. niloticus* and *T. zillii*) exhibited the highest densities in 1955 (mostly young of the year), which he attributed to high reproductive success. The onset and duration of flooding may affect spawning success and mortality. An early rise in water level may allow smaller fishes to escape dry season water holes where there may be a high concentration of predators by the end of the dry season. Floods of a longer duration may improve the situation for multiple spawners such as *Tilapia* and *Oreochromis* spp. (Holden 1963). Thus, much of the annual variation in the relative abundance of fishes within a specific residual pool may reflect overall change in the relative abundance of species within the entire system.

Movement during flooding also influences the distribution pattern and relative numbers of fish in floodplain pools. Many fish move over the floodplain in response to rising flood waters. However, as waters fall, fish return to the main river or distribute themselves among the remaining dry season refuge pools. Very little is known about the pattern of movement by floodplain fishes as the flood waters recede; however, unpredictability in the magnitude and duration of seasonal flooding is one factor that may contribute to the trapping of individuals in pools that they would otherwise not select. For example, Holden suggests that the rate of fall of the flood waters is a decisive factor in the distribution of some migratory species in the River Sokoto (such as *C. gariepinus, H. lineatus* and *L. niloticus*). The faster rate of decline in 1956–1957 seemed to result in larger numbers of migrating fish being trapped in 1957 than during the other sampling periods.

If the selection of pools based on habitat characteristics contributes to the overall pattern of fish distribution, changes in the habitat characteristics of pools may influence stability in the system. For example, in 1956, Melissa had a cover of vegetation, which had largely disappeared when it was sampled in 1957. This may have contributed to the very low index of similarity between 1956 and 1957 (Morisita's index = 0.36; Schoener's index = 0.32).

Implications for seasonal studies

It could be argued that the results of the River Sokoto study may have differed if pools had been sampled at the very end of the dry season. It is possible that pressure on food resources and space may increase as the dry season progresses, altering the proportion of different species that survive. In the floodplain pools of the Rupununi savanna (Guyana), Lowe-McConnell (1964) found that conditions of intense crowding at the end of the dry season were expressed by a scarcity of small fish and high proportion of predators, the latter presumably responsible for the disappearance of many of the smaller forms. Many authors have noted the dry season to be the most limiting with respect to food resources for some trophic groups (Lowe-McConnell 1964; Zaret & Rand 1971; Welcomme 1979; Bayley 1988). However, in the permanent pools of the River Sokoto included in this study, the surface area of the pools once disconnected did not change to a great degree between the time of sampling and initiation of the next flood (M. J. Holden, personal communication). The interflood interval of the River Sokoto is about 4 months, whereas in other floodplain areas it can be longer. The greatest percentage of fishes (numbers and weight) were herbivores. Predatory species were not very abundant in most pools and, in many cases, potential prey species were too large to be eaten by those predators present (M. J. Holden, personal communication). In addition, aerial predators were not common (M. J. Holden, personal communication). Thus, in general, the time of sampling in most of the River Sokoto pools probably made no great difference to estimates of community composition. Exceptions include pools in which there were large populations of predatory fish such as *Hydrocynus lineatus*. For example, in Dan Kube in 1957, the *H. lineatus* comprised an estimated 40% of the fish biomass. In such pools, one might anticipate high loss of prey fish over the dry season.

Resumen

1. Basandonos en el re-análisis de series de estimas de tamaño y biomasa de poblaciones de peces de 12 pozas estacionales del río Sokoto (Nigeria), sobre un período de 2 a 3 años – datos obenidos por M. J. Holden (1963) – hemos encontrado que, entre años, aparece una alta repetición de las mismas especies en las pozas, sin embargo, en la may or parte de éstas, la abundancia relativa de las poblaciones fluctúa significativamente entre años.
2. Aunque el conocimiento actual sobre los patrones de movimientos de los peces en respuesta a los flujos de agua recesivos está limitado, parece que el patrón final puede ser el resultado de selección de habitat, éxito reproductivo, capturas al azar de los peces en las pozas y variaciones en las tendencias migratorias.
3. Durante la estación seca, cuando el agua desciende y las pozas residuales llegan a aislarse, no hay potencial para que los peces confinados puedan re-distribuirse entre ellas. Cada poza, contiene una comunidad de peces que puede vivir junta hasta el siguiente período de inundación.
4. Las variaciones en la composición de los ensamblajes entre años sugiere la necesidad de un alto grado de flexibilidad comportamental por parte de los peces que habitan estos ríos de inundación tropicales.

Acknowledgements

This research was funded by an NSERC Post-Graduate Fellowship, a McConnell Memorial Fellowship to LJC, NSERC Post-Doctoral Fellowships to CAC and LJC and NSERC operating grants to D.L. Kramer and L. Lefebvre. We wish to express our gratitude to Michael Holden first for collecting such an extensive data set, and subsequently for asssisting us with the interpretation of the data and for comments on the manuscript. We also wish to thank D.L. Kramer, G. Grossman, and the reviewers for constructive comments on this manuscript. Initial work on the manuscript was carried out at McGill University in Montreal, Canada.

References

Bailey, N.T.J. 1952. Improvements in the interpretation of recapture data. Journal of Animal Ecology 21: 120–127.

Bayley, P.B. 1988. Factors affecting growth rates of young tropical floodplain fishes: seasonality and density-dependence. Environmental Biology of Fishes 21: 127–142.

Bonetto, A.A., Cordiviola de Yuan, E., Pignalberi, C. & Oliveros, O. 1969. Ciclos hidrologicos del Rio Parana y las poblaciones de peces contenidas en las cuencas temporarias de su valle de inundacion. Physis (Buenos Aires) 29: 213–223.

Connell, J.H. & Sousa, W.P. 1983. On the evidence needed to judge ecological stability or persistence. American Naturalist 121: 789–824.

Daget, J. 1957. Donnees recentes sur la biologie des poissons dans le delta central du Niger. Hydrobiologia 9: 321–347.

Goulding, M. 1980. The fishes and the forest. Berkeley: University of California Press.

Grossman, G.D., Dowd, J.F. & Crawford, M. 1990. Assemblage stability in stream fishes: a review. Environmental Management 14: 661–671.

Grossman, G.D., Moyle, P.B. & Whitaker, J.O. 1982. Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: a test of community theory. American Naturalist 120: 423–454.

Grossman, G.D., Freeman, M.C., Moyle, P.B. & Whitaker, J.O. 1985. Stochasticity and assemblage organization in an Indiana stream fish assemblage. American Naturalist 126: 275–285.

Holden, M.J. 1963. The populations of fish in dry season pools of the River Sokoto. Colonial Office Fishery Publications 19: 1–65.

Junk, W.J. 1970. Investigations on the ecology and production-biology of the 'floating meadows' (Paspalo-Echinochloetum) on the middle Amazon. I. The floating vegetation and its ecology. Amazoniana 2: 449–495.

Junk, W.J., Soares, G.M. & Carvalho, F.M. 1983. Distribution of fish species in a lake of the Amazon River floodplain near Manaus (Lago Camaleao), with special references to extreme oxygen conditions. Amazoniana 7: 397–431.

Linton, L.R., Davies, R.W. & Wrona, F.J. 1981. Resource utilization indices: an assessment. Journal of Animal Ecology 50: 283–292.

Lowe-McConnell, R.H. 1964. The fishes of the Rupununi savanna district of British Guiana, South America. I. Ecological groupings of fish species and effects of the seasonal cycle on the fish. Journal of the Linnean Society (Zoology) 45: 103–144.

Lowe-McConnell, R.H. 1967. Some factors affecting fish populations in Amazonian waters. Atas do Simposio a Biota Amazonica 7: 177–186.

Lowe-McConnell, R.H. 1975. Fish communities of tropical freshwaters. London: Longman.

Lowe-McConnell, R.H. 1984. Ecological aspects of seasonality in fishes of tropical waters. Symposium of the Zoological Society of London 44: 219–241.

Matthews, W.J. 1986. Fish faunal structure in an Ozark stream: stability, persistence and a catastrophic flood. Copeia 1986: 388–397.

Matthews, W.J., Cashner, R.C. & Gelwick, F.P. 1988. Stability and persistence of fish faunas and assemblages in three midwestern streams. Copeia 1988: 945–946.

Morisita, M. 1959. Measuring of interspecific association and similarity between communities. Memoirs of the Faculty of Science, Kyushu University, Series E (Biology) 3: 65–80.

Rahel, F.J., Lyons, J.D. & Cochran, P.A. 1984. Stochastic or deterministic regulation of assemblage structure? It may depend on how the assemblage is defined. American Naturalist 124: 583–589.

Roberts, T.R. 1972. Ecology of fishes in the Amazon and Congo basins. Bulletin of the Museum of Comparative Zoology 143: 117–197.

Ross, S.T., Matthews, W.J. & Echelle, A.A. 1985. Persistence of stream assemblages: effects of environmental change. American Naturalist 126: 24–40.

Schoener, T.W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. Ecology 49: 704–726.

Ury, H.K. 1976. A comparison of four procedures for multiple comparisons among means (pairwise contrasts) for arbitrary sample sizes. Technometrics 18: 89–97.

Welcomme, R.L. 1979. Fisheries ecology of floodplain rivers. New York: Longman.

Winemiller, K.O. 1987. Tests of ecomorphological and community level convergence among neotropical fish assemblages. Ph.D. Thesis. Austin: University of Texas.

Wolda, H. 1981. Similarity indices, sample size, and diversity. Oecologia 50: 296–302.

Zaret, T.M. & Rand, A.S. 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. Ecology 52: 336–342.