BACKWATER FISH COMMUNITIES IN THE COLORADO RIVER, GRAND CANYON FINAL REPORT

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Executive Summary

This report examines fish community composition of backwaters in the Colorado River, Grand Canyon, from 1991-1999. It summarizes data collected by Arizona Game and Fish Department during Glen Canyon Environmental Studies Phase II from 1991-1995 and Interim Monitoring from 1996-1997, and during U.S. Fish and Wildlife Service fish monitoring from 1998-1999.

Backwaters are important rearing areas for native Colorado River fishes (bluehead sucker *Catostomus discobolus*, flannelmouth sucker *C. latipinnis*, speckled dace *Rhinichthys osculus* and the endangered humpback chub *Gila cypha*). Their importance has increased in the Colorado River in Grand Canyon because of the constantly cold water released from Glen Canyon Dam. However, backwaters are also inhabited by non-native fishes, such as fathead minnow *Pimephales promelas*, channel catfish *Ictalurus punctatus*, common carp *Cyprinus carpio*, plains killifish *Fundulus zebrinus*, rainbow trout *Oncorhynchus mykiss* and red shiner *Cyprinella lutrensis*, which may compete with and/or prey on larval and juvenile native fishes.

A total of 37,506 fish were captured in 548 samples during 1991-1999. Fathead minnow was the most dominant species overall (38.4%) and speckled dace (23.8%) was second most dominant. Bluehead sucker comprised 12.5% of the total catch, humpback chub 10.6% and flannelmouth sucker 9.3%. Nine other species (all non-native fishes) comprised the remaining 2% of the catch and included black bullhead *Ameiurus melas*, brown trout *Salmo trutta*, channel catfish, common carp, green sunfish *Lepomis cyanellus*, plains killifish, rainbow trout, red shiner and yellow bullhead *Ameiurus natalis*.

In the Upper Reach (below the Little Colorado River; River Miles 60-75) 18,561 fish were captured in 249 samples. Fathead minnow was the most dominant species, comprising 51.3% of the catch and humpback chub (21.2%) was the second most dominant species. Common species included speckled dace (9.8%), bluehead sucker (7.2%), flannelmouth sucker (4.6%) and plains killifish (1.4%).

In the Lower Reach (River Miles 164-225), 18,945 fish were captured in 299 sampling sites. Speckled dace was the most dominant species, comprising 37.6% of the catch in this reach. Fathead minnow (25.8%), bluehead sucker (17.7%) and flannelmouth sucker (13.9%) were also dominant in Lower Reach backwaters. Only 45 humpback chub were captured in the

Lower Reach, comprising 0.2% of the catch.

During spring (March - May), 15,013 fish were captured in 285 sampling sites. Fathead minnow was the most dominant fish in backwaters during spring, comprising 46.7% of the catch. Speckled dace was the second most dominant species, comprising 23.5% of the catch. Bluehead sucker (9.6%), humpback chub (7.7%) and flannelmouth sucker (7.5%) were common. Speckled dace was the most dominant species (27.7%) of the 13,077 fish caught during summer (June - August). Fathead minnow, (22.6%), bluehead sucker (21.6%) and flannelmouth sucker (13.3%) were also dominant and humpback chub (8.1%) were common. Fathead minnow (47.8%) was the most dominant species of the 9,117 fish from 132 sampling sites during fall (September - November). Speckled dace (19.4%) and humpback chub (17.9%) were also dominant, while flannelmouth sucker (6.6%), bluehead sucker (4.6%) and plains killifish (1.8%) were common. Only 299 fish were captured from 23 sites during winter (December - February) sampling. Humpback chub was the most dominant species, comprising 43.1% of the winter catch. Fathead minnow (28.1%) was also dominant and speckled dace (9.4%), flannelmouth sucker (5.7%), rainbow trout (3.3%), red shiner (2.0%), plains killifish (1.7%) and common carp (1.0%) were common.

Bluehead suckers were a more common component of the backwater fish community in the Lower Reach (17.7%) than the Upper Reach (7.2%). They comprised a greater proportion of the backwater fish community during summer (21.6%) and a smaller proportion during winter (0.7%). Flannelmouth suckers were also more common in the Lower Reach (13.9%) than the Upper Reach (4.6%). In a given year, they also comprised a greater proportion of the backwater fish community during summer (13.3%) and less in winter (5.7%). Humpback chub were a much more dominant component of the backwater fish community in the Upper (21.2%) than the Lower Reach (0.2%). They tended to comprise a larger percentage of the fish community in backwaters during summer (8.1%), fall (17.9%) and winter (43.1%). Speckled dace were a dominant component of the backwater fish community in both the Upper (9.8%) and Lower reaches (37.6%). They appear to be more dominant in the Upper Reach during summer and appear to be less dominant during winter in the Lower Reach. Fathead minnows were more dominant in the Upper Reach (51.3%), but were also a major component of the Lower Reach (25.8%), as well. They generally comprised a greater percentage of the spring (46.7%) and fall (47.8%) backwater fish community than during summer (22.6%) or winter (28.1%). Plains

killifish were more abundant in the Upper (1.4%) than the Lower Reach. (0.3%). While they were rarely a dominant member of the fish community, their composition was fairly consistent. Red shiners were more abundant in the Upper (0.2%) than the Lower Reach (0.1%). Red shiners were rare to non-existent in Colorado River backwaters until 1996. In 1998, they became more abundant, comprising 20.3% of the backwater fish community and comprised 80% of the one backwater sampled in winter of 1999. Common carp were more abundant in the Lower (0.5%) than the Upper Reach (0.2%). Since 1991, their percent composition of the backwater fish community has remained low in the Upper Reach. In the Lower reach, their percent composition has generally decreased, since they comprised 10.4-14.6% of the backwater fish community from summer 1991 - spring 1992.

Larval and juvenile life history stages of most Grand Canyon fishes require warm water to grow quickly. Nearshore areas provide sheltered water that is warmer than the main channel. Of these refugia, backwaters are the warmest, most sheltered and most productive. Eight species of fish were commonly captured in backwaters and are the main components of the backwater fish community. These species probably rely on this habitat for at least a part of their life cycle, and include bluehead sucker, flannelmouth sucker, humpback chub, speckled dace, fathead minnow, plains killifish, red shiner and common carp. The percentage of the fish community that each comprised varied between reaches and among seasons and was likely dependent upon where they were able to spawn in Grand Canyon and their thermal tolerances.

Backwaters in the Colorado River are very important habitats for native fishes at crucial stages of their life history. The composition of the fish community, particularly the abundance of non-native fishes, in these habitats is likely to affect native fishes through competition, predation and other behavioral interactions. Experimental manipulations, such as low steady flows or temperature controls should be cautiously tested, as these alterations may benefit non-native more than native species. More studies of the dynamics of backwaters, the use of backwaters by native and non-native fishes and the interactions among the fishes that inhabit them is necessary for the successful management of fish populations in Grand Canyon.

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Introduction

Backwaters in Grand Canyon are pockets of water partially isolated from the main channel by a sand bar and usually form immediately downstream from a channel constriction, such as a debris fan (Rubin et al. 1990; Schmidt 1990; Schmidt and Graf 1990). This partial isolation allows backwaters to warm more and become more productive than the main channel of the Colorado River (Arizona Game and Fish department 1996). Because of this, backwaters have been shown to be important rearing areas for native Colorado River fishes (Holden 1978; Valdez and Clemmer 1982; Carter et al. 1985; Maddux et al. 1987; Minckley 1991; Angradi et al. 1992; Arizona Game and Fish Department 1996). Their importance has increased in the Colorado River in Grand Canyon because of the constantly cold water released from Glen Canyon Dam. Larval and small juvenile fishes emigrating from warm spawning tributaries into the cold Colorado River are unlikely to survive unless they find a suitable backwater (Arizona Game and Fish Department 1996; Lupher and Clarkson 1994; Childs and Clarkson 1996). However, backwaters are also inhabited by non-native fishes which may compete with and/or prey on larval and juvenile native fishes (Arizona Game and Fish Department 1996).

Most native fish spawning occurs in only a few tributary streams, from which they often emigrate at a very early age. Therefore, the reaches of Colorado River below those streams are important for survival of juvenile native fishes. Arizona Game and Fish Department (1996) found a relationship between density of juvenile native fishes in the Colorado River and the proximity of spawning tributaries. In particular, the areas downstream of the Little Colorado River and below Kanab and Havasu creeks contained high densities of juvenile native fishes. All four extant native species (bluehead sucker *Catostomus discobolus*, flannelmouth sucker *C. latipinnis*, speckled dace *Rhinichthys osculus* and the endangered humpback chub *Gila cypha*) spawn in Little Colorado River (LCR), which is the only significant spawning site for humpback chub. The LCR and neighboring reach of the Colorado River contain all common non-native species, including fathead minnow *Pimephales promelas*, channel catfish *Ictalurus punctatus*, common carp *Cyprinus carpio*, plains killifish *Fundulus zebrinus*, rainbow trout *Oncorhynchus mykiss* and red shiner *Cyprinella lutrensis*. Kanab and Havasu creeks are important spawning areas for bluehead and flannelmouth suckers and main channel spawning is also possible in the lower canyon, particularly in areas with warm springs.

This report examines fish community composition of backwaters in the Colorado River, Grand Canyon, sampled from 1991-1999. It summarizes data collected by Arizona Game and Fish Department during Glen Canyon Environmental Studies Phase II from 1991-1995 and Interim Monitoring from 1996-1997, and during U.S. Fish and Wildlife Service fish monitoring from 1998-1999.

Study Site

The Colorado River in Grand Canyon was divided into two reaches for examination: the Upper Reach stretched fro, RM[1] 60-75 and the Lower Reach from RM 164-225 (Figure 1). Arizona Game and Fish Department (1996) found these to be the two most important reaches of the Colorado River in Grand Canyon for juvenile native fishes. The Upper Reach is characterized by the junction of the Colorado and Little Colorado Rivers at RM 61.5. The Little Colorado River is the largest contributor of sediment in Grand Canyon (Andrews 1991) and this reach often contains large numbers of backwaters in eddies formed behind debris fans or large boulders. Juvenile native fishes captured in the Lower Reach were most likely spawned in Kanab and Havasu creeks, which enter the Colorado River at RM 143.5 and RM 156.93, respectively. This reach is relatively wide and slow (Schmidt and Graf1990) and long, narrow backwaters are often formed in large eddies (Arizona Game and Fish Department 1996).

Grand Canyon backwaters are ephemeral habitats which appear and disappear with changes in river discharge and their morphology (area and volume) and longevity depend on antecedent flows and successional changes caused by sedimentation and scouring (Arizona Game and Fish Department 1996; Parnell et al 1997). Therefore, backwater sampling sites in Grand Canyon cannot be standardized and were sampled as they were present.

Methods

Backwaters were sampled by seining with an appropriately sized bag or straight seine with mesh of ≤0.32 mm (0.125 inch). Seining was conducted from the mouth (connection to the main channel) to the foot (furthest from the main channel) and from 1-8 seine hauls were

[1]The standard method for noting Colorado River locations in Grand Canyon is river mile (RM) downstream from Lees Ferry and side of river ('L' or 'R') when facing downstream.

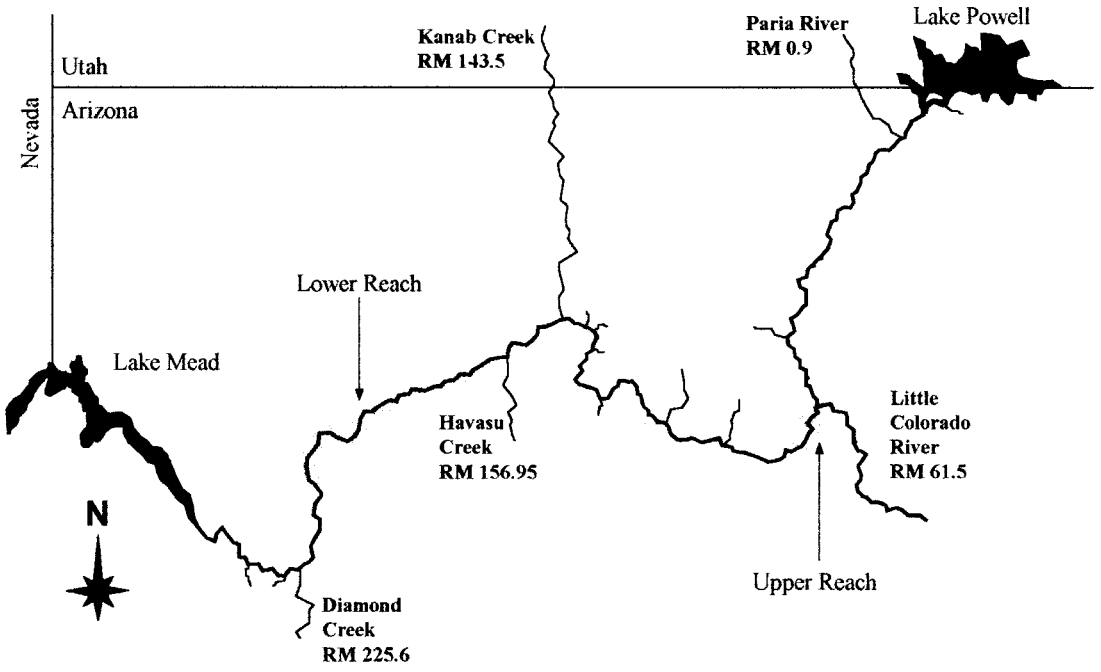

Figure 1. Colorado River in Grand Canyon, with Upper (RM 60-75) and Lower (RM 164-225) reaches and mentioned tributaries.

conducted at each site. Captured fish were identified to species and enumerated. Occasionally (when air temperature was so high as to be stressful to handled fish or when very small fish were captured that were difficult to identify quickly), fish were identified only to family (suckers) or not identified. Unidentified suckers were included in these analyses but other unidentified fish were not included. Percent composition of each species were calculated for each sample (sampling location and date). Mean percent compositions were then calculated for each species within each reach and season (spring = March - May; summer = June - August; fall = September - November; winter = December - February). Abundance of each species was classified as dominant (>10% of the total catch), common (1-10% of the total catch) and rare (<1% of the total catch). No comparisons were made by year because of inconsistent sampling times among years. Sites in which no fish were captured were not included in these analyses.

Table 1. Number of fish caught and percent of total catch for each species and number of backwater sites sampled in the Upper and Lower reaches of the Colorado River, Grand Canyon, during Arizona Game and Fish Department and U.S. Fish and Wildlife Service sampling, 1991-1999.

	Upper Reach RM 60 - 75		Lower Reach RM 164 - 225		Total	
Species	N	%	N	%	N	%
Bluehead Sucker	1,338	7.2	3,344	17.7	4,682	12.5
Flannelmouth Sucker	848	4.6	2,632	13.9	3,480	9.3
Humpback chub	3,933	21.2	45	0.2	3,978	10.6
Speckled Dace	1,816	9.8	7,128	37.6	8,944	23.8
Unidentified Suckers	615	3.3	666	3.5	1,281	3.4
Black Bullhead	0	0.0	1	<0.1	1	0.0
Brown Trout	0	0.0	1	<0.1	1	0.0
Channel Catfish	2	<0.1	8	<0.1	10	0.0
Common Carp	40	0.2	100	0.5	140	0.4
Fathead Minnow	9,523	51.3	4,887	25.8	14,410	38.4
Green Sunfish	0	0.0	2	<0.1	2	0.0
Plains Killifish	262	1.4	64	0.3	326	0.9
Rainbow Trout	145	0.8	53	0.3	198	0.5
Red Shiner	38	0.2	13	0.1	51	0.1
Yellow Bullhead	1	<0.1	1	<0.1	2	0.0
Total	18,561		18,945		37,506	
Number of Sites	249		299		548	

Results

A total of 37,506 fish were captured in 548 samples in the two study reaches during 1991-1999 (Tables 1 and 2). Fathead minnow was the most commonly caught species overall (38.4%) and speckled dace (23.8%) was second most common. Bluehead sucker and humpback chub were also dominant, while flannelmouth sucker and unidentified suckers were common. Nine other species of non-native fishes were rare, combining to comprise the remaining 2% of the catch and included black bullhead *Ameiurus melas*, brown trout *Salmo trutta*, channel

catfish, common carp, green sunfish *Lepomis cyanellus*, plains killifish, rainbow trout, red shiner and yellow bullhead *Ameiurus natalis*.

Reach

Fathead minnow and speckled dace were the most commonly captured species in the two sampling reaches (Table 1). Fathead minnow dominated the Upper Reach and speckled dace the Lower Reach.

Upper Reach

A total of 18,561 fish were captured in 249 samples in the Upper Reach (Table 1). Fathead minnow was the most commonly captured species, comprising 51.3% of the catch. Humpback chub was also dominant. Common species included speckled dace, bluehead sucker, flannelmouth sucker and plains killifish. Unidentified suckers comprised 3.3% of the catch. Channel catfish, common carp, rainbow trout, red shiner and yellow bullhead were rare.

Lower Reach

A total of 18,945 fish were captured in 299 sampling sites in the Lower Reach (Table 1). Speckled dace was the most commonly captured species, comprising 37.6% of the catch in this reach. Fathead minnow, bluehead sucker and flannelmouth sucker were also dominant species. Unidentified suckers comprised 3.5% of the catch. Only 45 humpback chub were captured, comprising 0.2% of the catch. Also rare in this reach were black bullhead, brown trout, channel catfish, common carp, green sunfish, plains killifish, rainbow trout, red shiner and yellow bullhead.

Season

The dominant species varied seasonally (Table 2). Fathead minnow was the most commonly caught species during spring and fall, speckled dace during summer and humpback chub was most common in the winter catch.

Spring

A total of 15,013 fish were captured in 285 sampling sites during spring (Table 2).

Fathead minnow was the most commonly captured fish in backwaters during spring, comprising 46.7% of the catch. Speckled dace was also dominant, comprising 23.5% of the catch. Common species included bluehead sucker, humpback chub and flannelmouth sucker. Unidentified suckers comprised 3.0% of the total catch. Black bullhead, channel catfish, common carp, plains killifish and rainbow trout each comprised <1% of the total catch.

Summer

Speckled dace was the most commonly caught species (27.7%) of the 13,077 fish caught during summer (Table 2). Fathead minnow, bluehead sucker and flannelmouth sucker were also dominant and humpback chub were common. Unidentified suckers comprised 6.0% of the summer catch. Common carp, plains killifish, rainbow trout, red shiner and yellow bullhead were rare.

Fall

Fathead minnow (47.8%) was the most commonly captured species of the 9,117 fish from 132 sampling sites during fall (Table 2). Speckled dace and humpback chub were also dominant. Flannelmouth sucker, bluehead sucker and plains killifish were common. Unidentified suckers comprised only 0.3% of the fall catch. Brown trout, channel catfish, common carp, green sunfish, rainbow trout, red shiner and yellow bullhead were rarely captured.

Winter

Only 299 fish were captured from 23 sites during winter sampling, (Table 2). Humpback chub was the most commonly captured species, comprising 43.1% of the winter catch. Fathead minnow was also a dominant species. Speckled dace, flannelmouth sucker, rainbow trout, red shiner, plains killifish, and common carp were common. Bluehead sucker (0.7%) were rare.

Species

Use of backwaters varied among species by both reach and season. These differences are largely explained by the life history, temperature preferenda and distribution of each species. The species discussed below are important components of the backwater fish community and/or rely on backwaters to complete their life cycles in the Colorado River in Grand Canyon.

Bluehead Sucker

Bluehead sucker was a dominant component of the backwater fish community in the Lower Reach (17.7%) but only common in the Upper Reach (7.2%) (Figure 2). They generally comprised a greater proportion of the fish community in backwaters during the summer months (21.6%) and a smaller proportion during the winter (0.7%). Bluehead sucker were particularly abundant during the summers of 1993 and 1994.

Flannelmouth Sucker

Flannelmouth sucker was also dominant in the Lower Reach (13.9%) and common in the Upper Reach (4.6%) (Figure 3). In a given year, they also comprised a greater proportion of the backwater fish community during summer (13.3%) and less in winter (5.7%). They were particularly abundant in Lower Reach backwaters during the summers of 1995 and 1996.

Humpback Chub

Humpback chub were a dominant component of the backwater fish community in the Upper Reach (21.2%) but rare in the Lower Reach (0.2%) (Figure 4). They tended to comprise a larger percentage of the fish community in backwaters during summer (8.1%), fall (17.9%) and winter (43.1%). Humpback chub appear to have been more abundant in 1991, 1993, 1998 and 1999 than in other years.

Speckled Dace

Speckled dace was a common component of the backwater fish community in the Upper Reach (9.8%) and increased to dominant in the Lower Reach (37.6%) (Table 5). They appear to be more abundant in the Upper Reach during summer and less abundant during winter in the Lower Reach, but there is little discernable seasonal pattern in their backwater abundance. The years of 1991, 1996 and 1998 appear to have been strong years for speckled dace in the Upper Reach, while they consistently comprised 30-50% of the fish community in the Lower Reach.

Fathead Minnow

Fathead minnows were dominant in both reaches, comprising 51.3% fo the backwater fish community in the Upper Reach and 25.8% in the Lower Reach (25.8%) (Figure 6). They

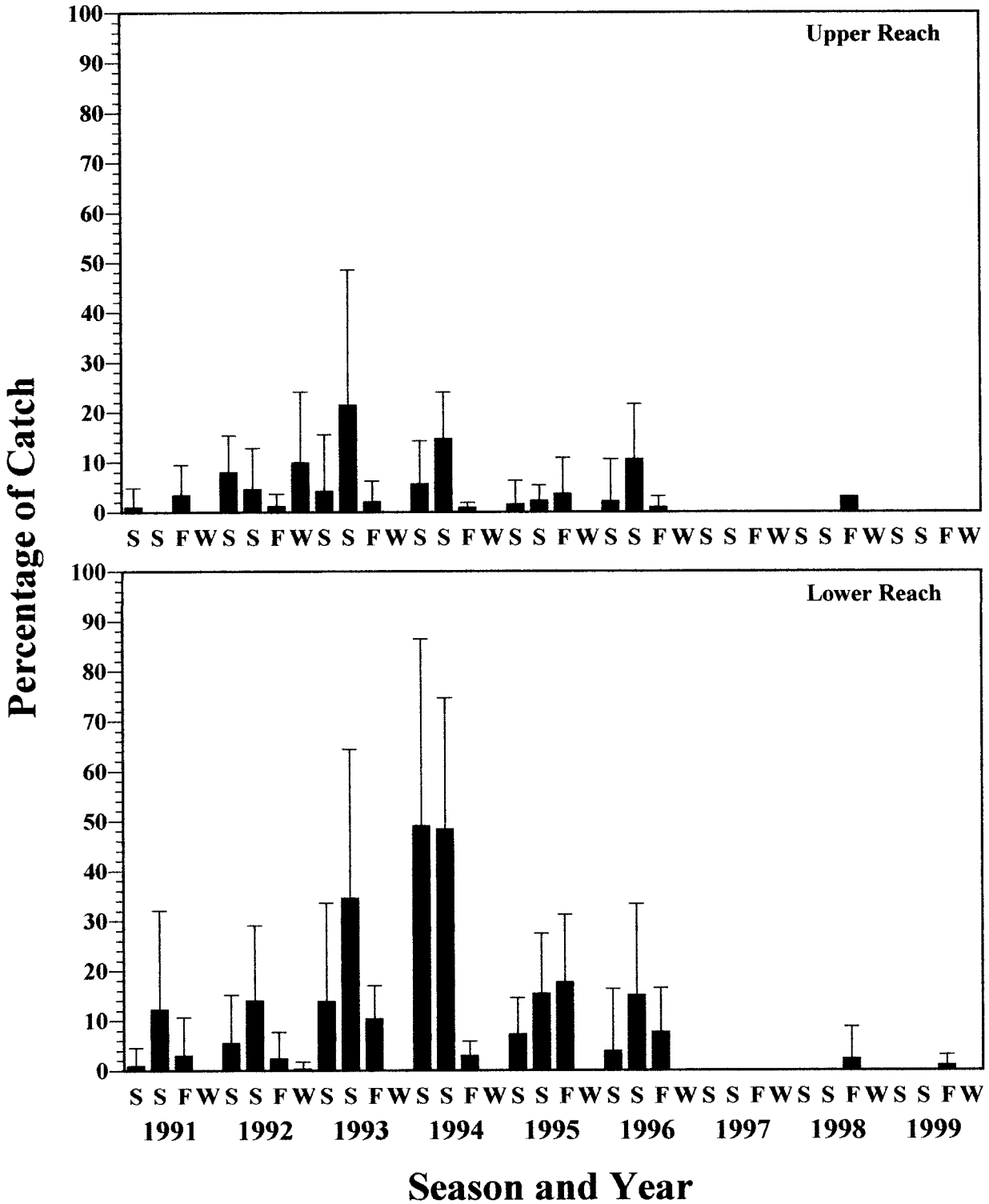

Figure 2. Percentage of catch from backwaters in the Upper (RM 60-75) and Lower (RM 164-225) reaches of the Colorado River, Grand Canyon, comprised by bluehead sucker during spring, summer, fall and winter, 1991-1999.

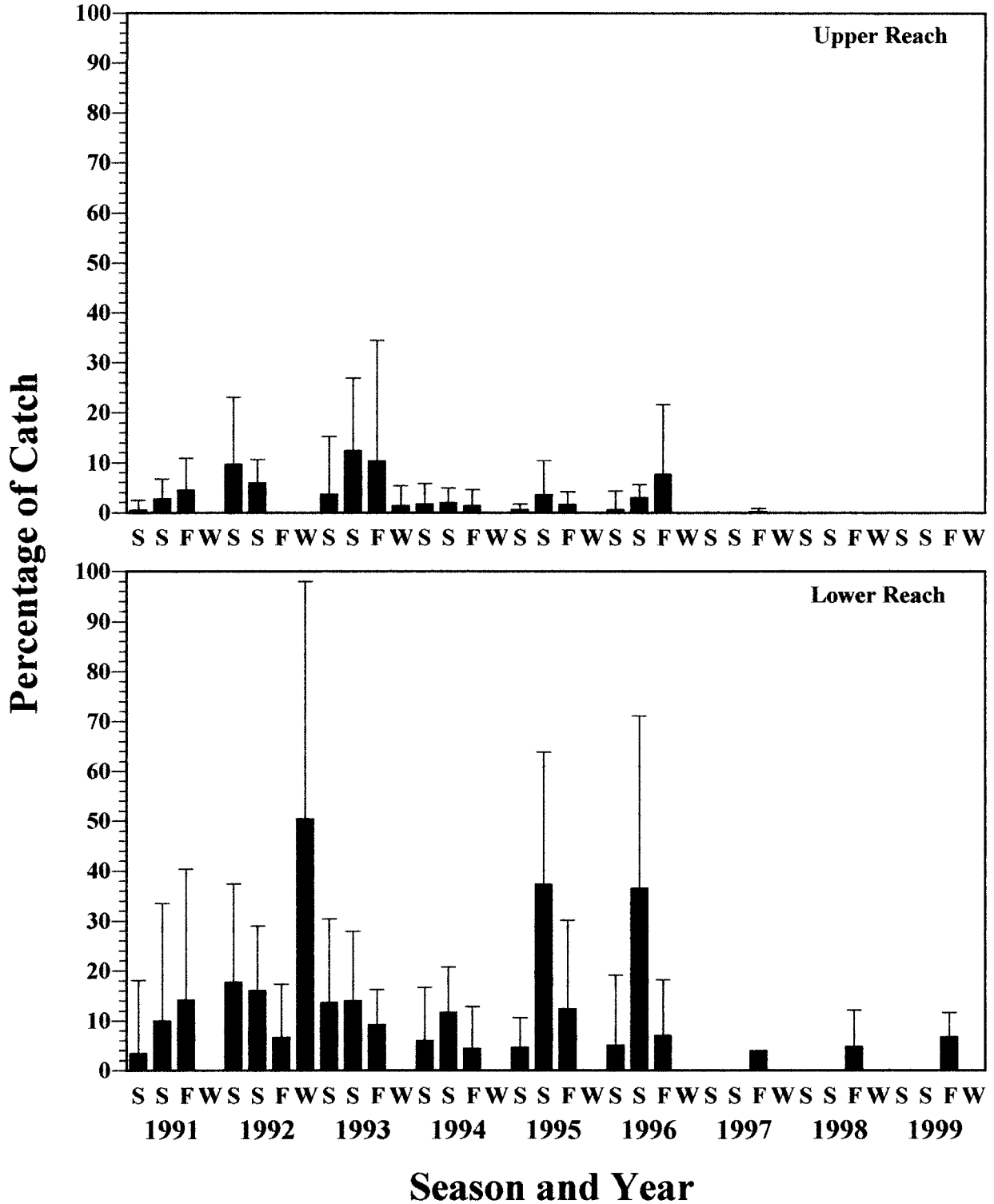

Figure 3. Percentage of catch from backwaters in the Upper (RM 60-75) and Lower (RM 164-225) reaches of the Colorado River, Grand Canyon, comprised by flannelmouth sucker during spring, summer, fall and winter, 1991-1999.

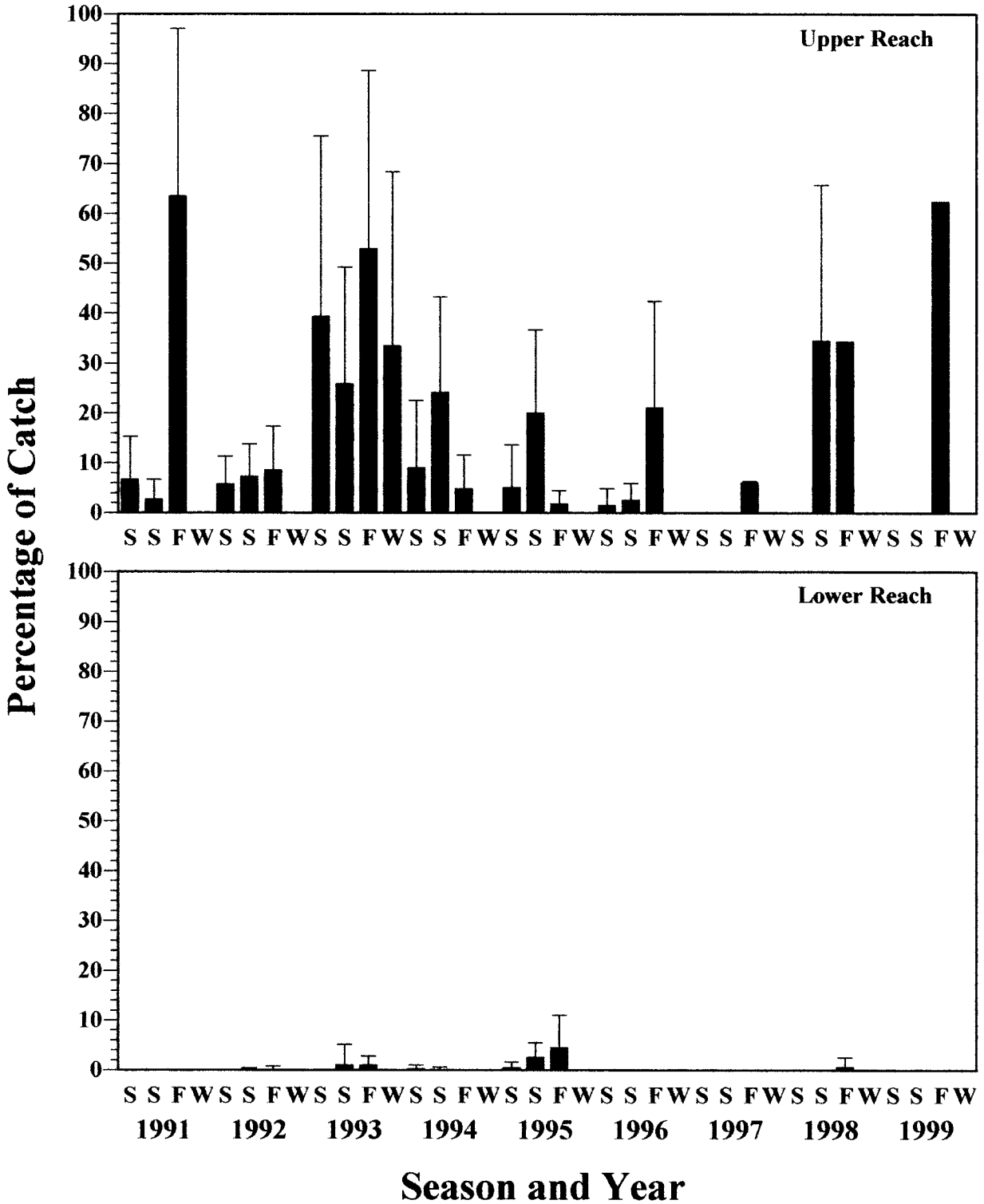

Figure 4. Percentage of catch from backwaters in the Upper (RM 60-75) and Lower (RM 164-225) reaches of the Colorado River, Grand Canyon, comprised by humpback chub during spring, summer, fall and winter, 1991-1999.

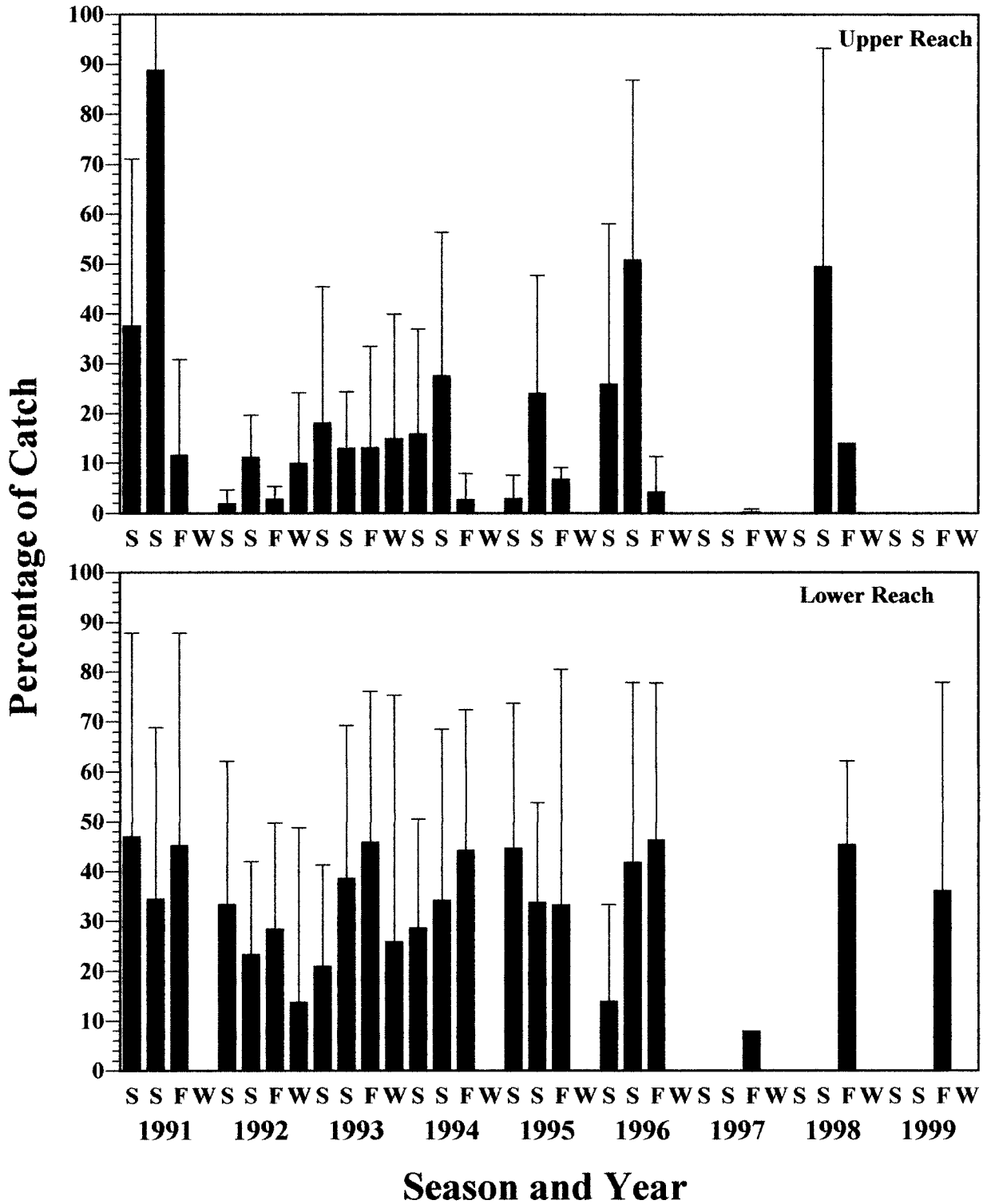

Figure 5. Percentage of catch from backwaters in the Upper (RM 60-75) and Lower (RM 164-225) reaches of the Colorado River, Grand Canyon, comprised by speckled dace during spring, summer, fall and winter, 1991-1999.

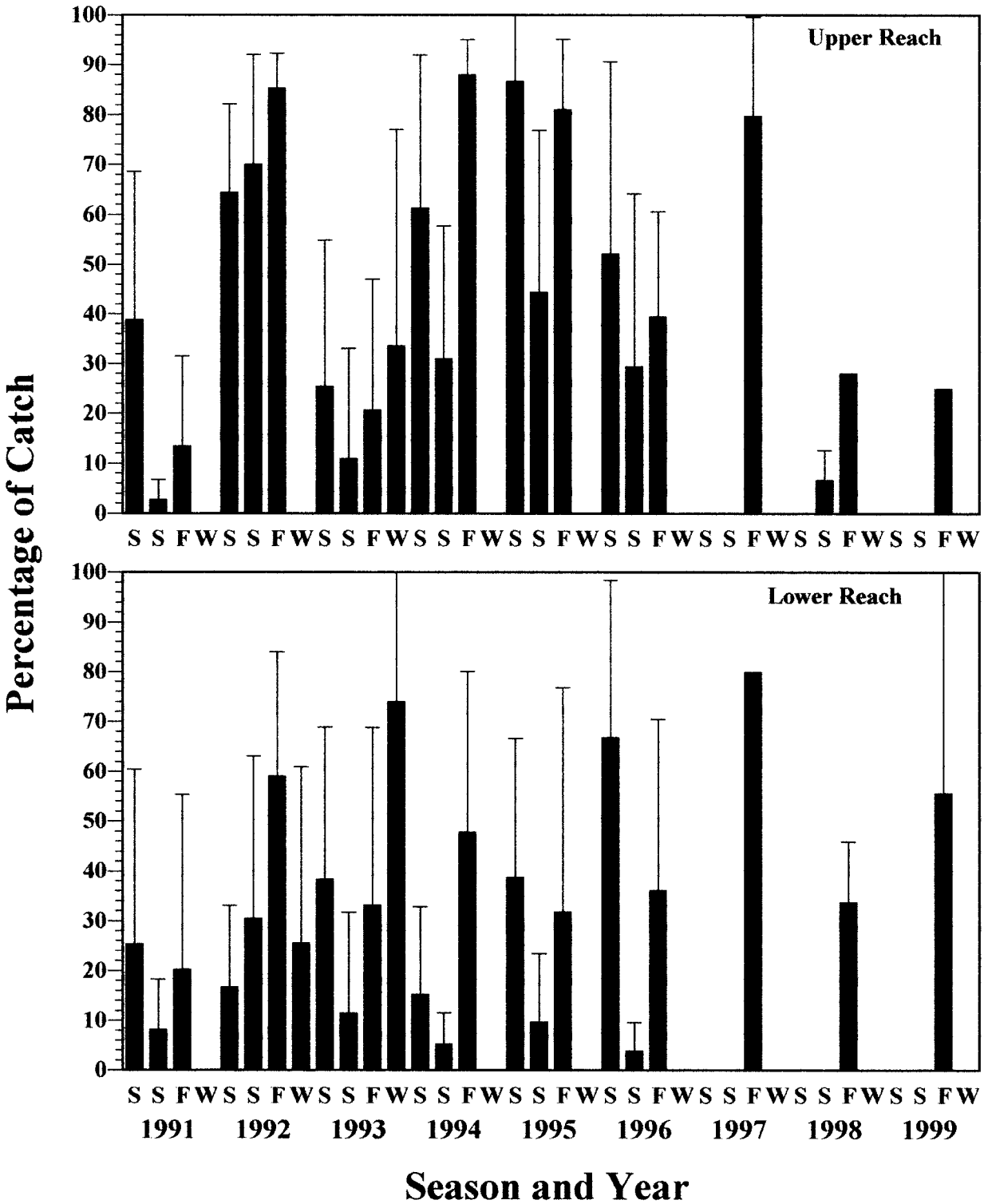

Figure 6. Percentage of catch from backwaters in the Upper (RM 60-75) and Lower (RM 164-225) reaches of the Colorado River, Grand Canyon, comprised by fathead minnow during spring, summer, fall and winter, 1991-1999.

generally comprised a greater percentage of the backwater fish communities during spring (46.7%) and fall (47.8%) than during summer (22.6%) or winter (28.1%). However, their abundance in backwaters varied greatly, with seasonal means ranging from 0 - 86.7%.

Plains Killifish

Plains killifish were common in the Upper Reach (1.4%) but rare the Lower Reach (0.3%) (Figure 7). While they were rarely a dominant member of the fish community in any backwater, their composition was usually a few present in any backwater. However, they comprised 80% of the fish community in the eight backwaters sampled during the winter of 1992 and 24.3% of the community during fall of 1996.

Red Shiner

Red shiners were more common in the Upper (0.2%) than the Lower Reach (0.1%) but were rare in both reaches (Figure 8). Red shiners were not found in Colorado River backwaters until 1996. In 1998, they increased in abundance, comprising 20.3% of the backwater fish community, and comprised 80% of the one backwater sampled in the winter of 1999.

Common Carp

Common carp were rare in both reaches: 0.5% in the Lower (0.5%) and 0.2% in the Upper Reach (Figure 9). Since 1991, their abundance in the backwater fish community has remained low in the Upper Reach. In the Lower reach, their abundance has generally decreased, since they comprised 10.4-14.6% of the backwater fish community from summer 1991 - spring 1992.

Other Species

Six other species were captured in backwaters, most of which were extremely rare and/or could not be considered to be reliant on backwaters. Rainbow trout was the most common of these species, comprising 0.5% of the backwater fish community. Rainbow trout were more abundant in backwaters in the Upper (0.8%) than the Lower Reach (0.3%). Black bullhead, yellow bullhead, channel catfish, brown trout and green sunfish each comprised <0.01% of the backwater fish community.

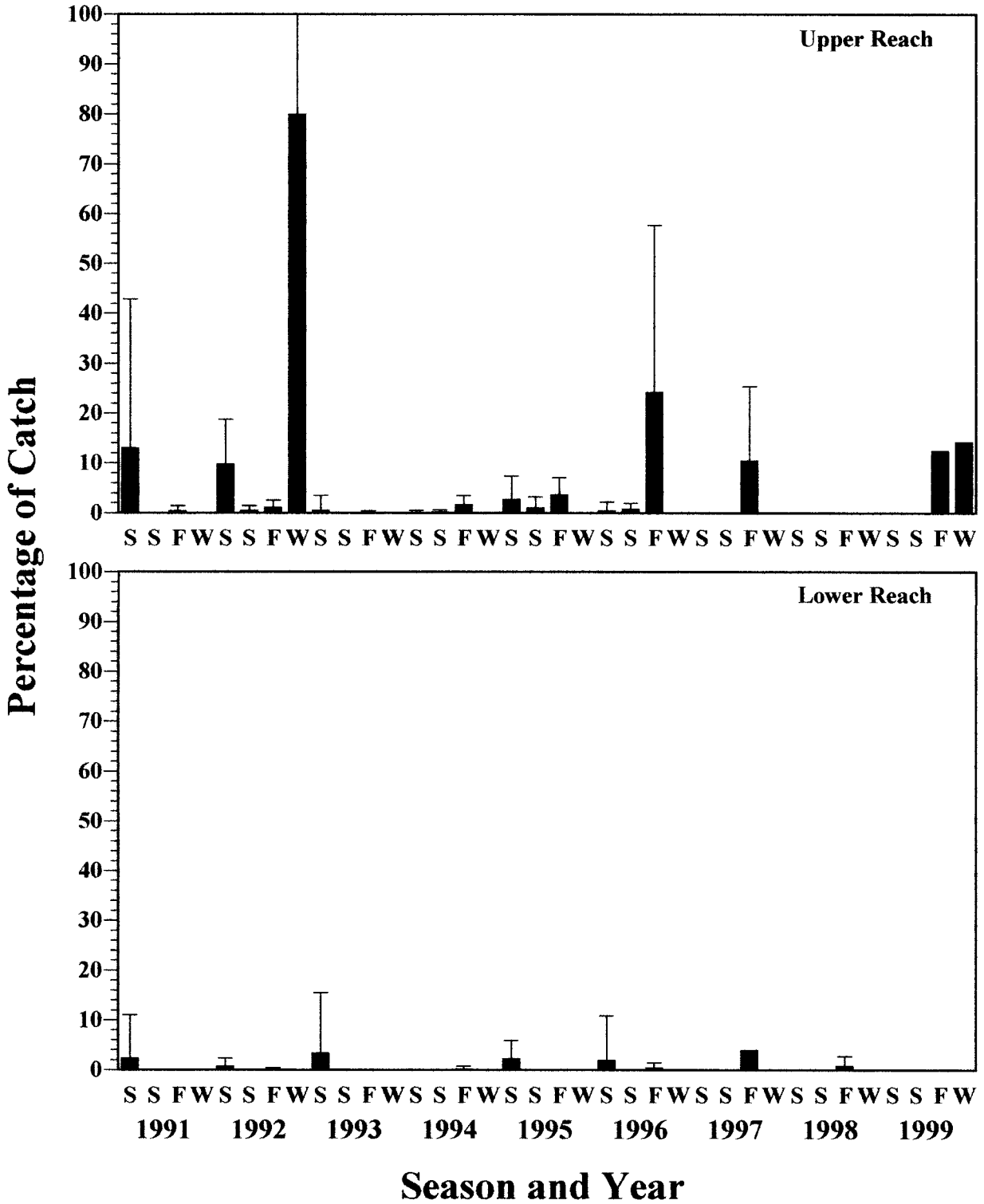

Figure 7. Percentage of catch from backwaters in the Upper (RM 60-75) and Lower (RM 164-225) reaches of the Colorado River, Grand Canyon, comprised by plains killifish during spring, summer, fall and winter, 1991-1999.

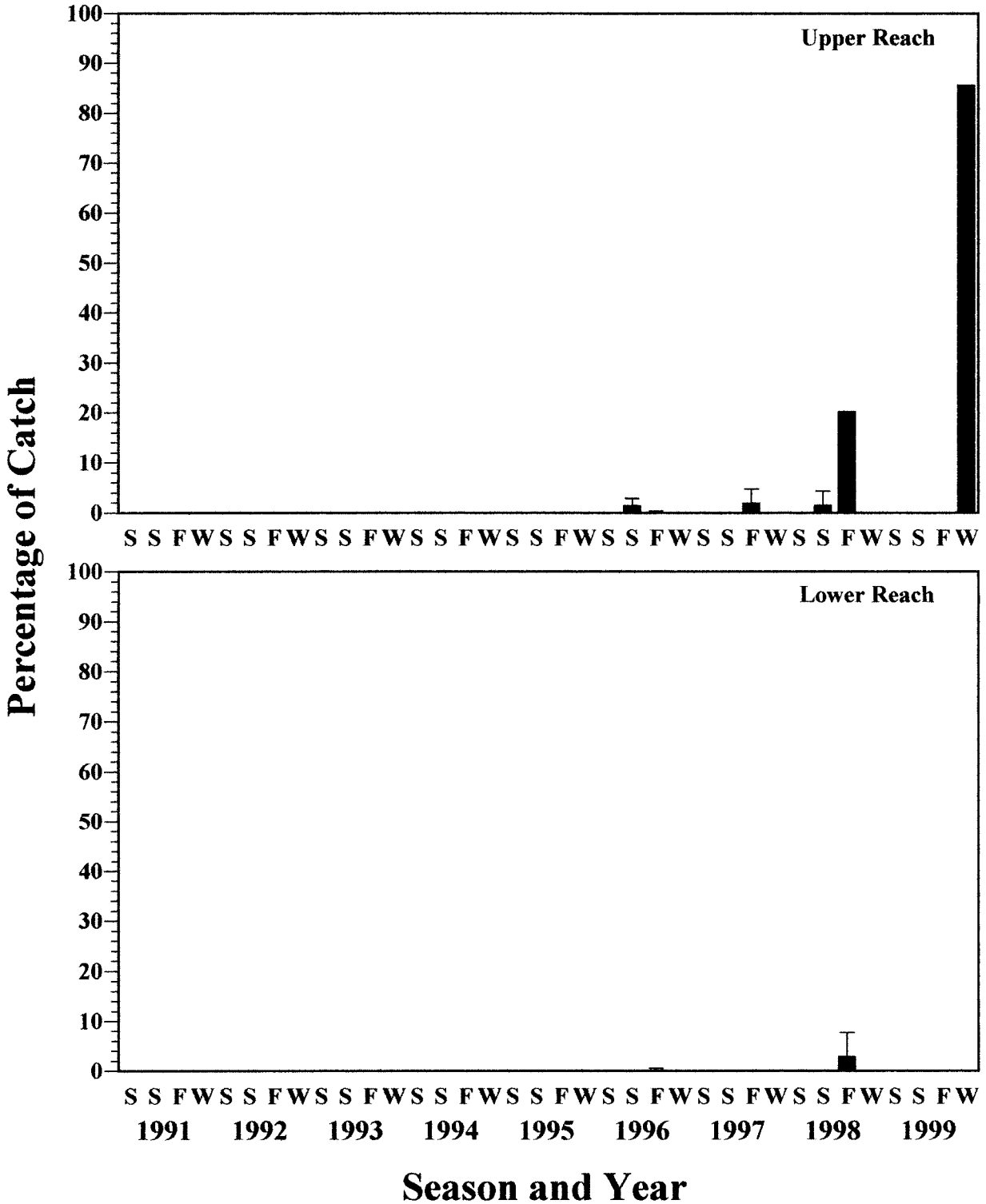

Figure 8. Percentage of catch from backwaters in the Upper (RM 60-75) and Lower (RM 164-225) reaches of the Colorado River, Grand Canyon, comprised by red shiner during spring, summer, fall and winter, 1991-1999.

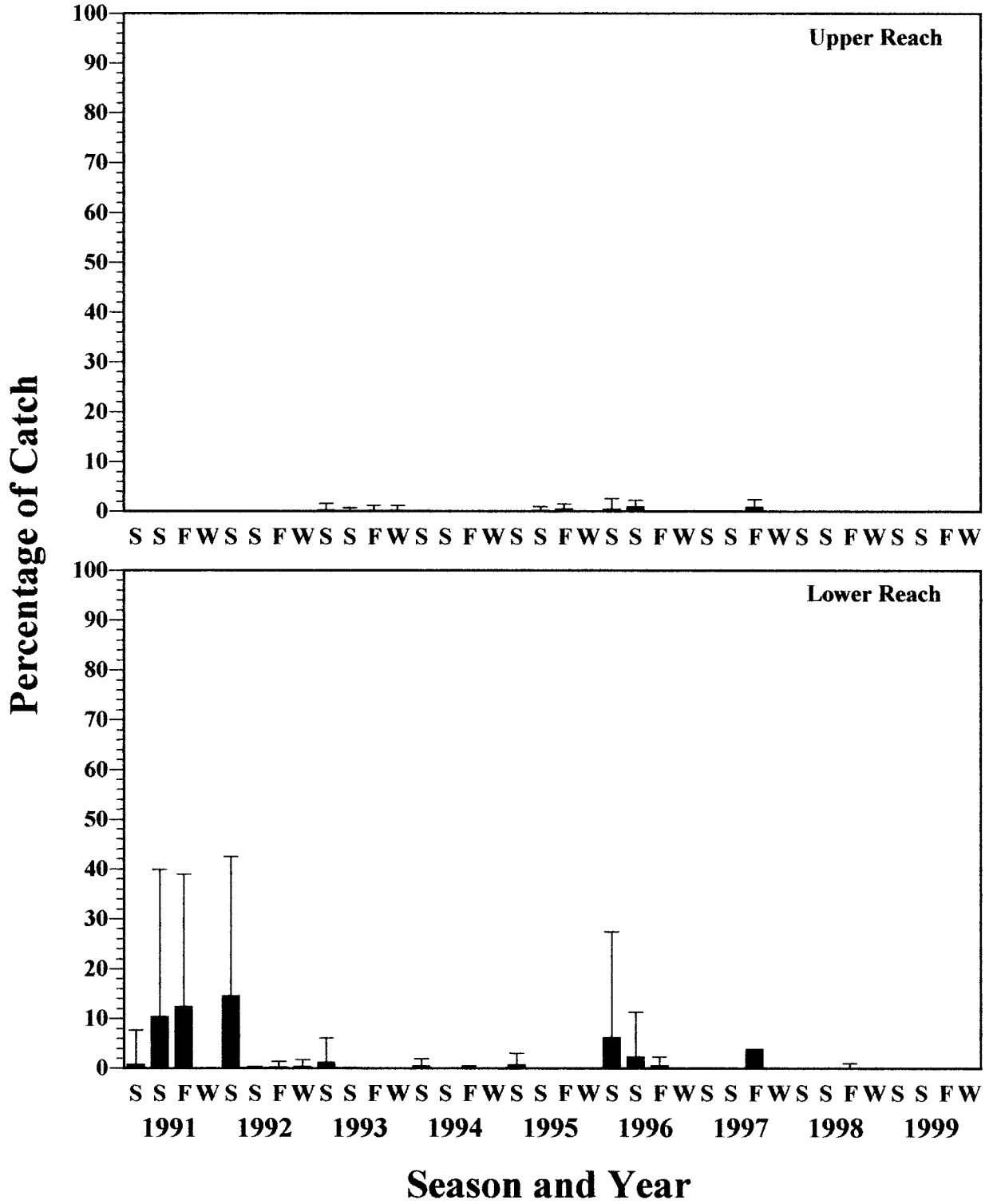

Figure 9. Percentage of catch from backwaters in the Upper (RM 60-75) and Lower (RM 164-225) reaches of the Colorado River, Grand Canyon, comprised by common carp during spring, summer, fall and winter, 1991-1999.

Discussion

Larval and juvenile life history stages of most Grand Canyon fishes, particularly native fishes, require warm water to grow quickly and reduce their exposure to predation. Nearshore areas contribute to growth and recruitment of early life history stages of native species by providing sheltered water that is warmer than the main channel and backwaters are the warmest, most sheltered and most productive of these refugia (Arizona Game and Fish Department 1996). However, backwaters in Grand Canyon are ephemeral habitats and their appearance and longevity depend on river discharge, antecedent flows and successional changes caused by sedimentation and scouring (Arizona Game and Fish Department 1996; Parnell et al 1997). Therefore, backwater sampling sites in Grand Canyon were sampled as they are present and cannot be standardized.

Eight species of fish (bluehead sucker, flannelmouth sucker, humpback chub, speckled dace, fathead minnow, plains killifish, red shiner and common carp) were commonly captured in the sampled backwaters and are the main components of the backwater fish community. Common carp and red shiner were less abundant than the other species, but they were included in this discussion because they were common or dominant for a portion of the sampling period and are capable of affecting species composition in a backwater through competition, predation or agonistic behavior (Carlander 1969 and references therein; Greger and Deacon 1988; Ruppert et al. 1993; Muth and Snyder 1995; Arizona Game and Fish Department 1996). These species probably rely on warm shoreline habitats, of which backwaters are the warmest and most productive (Arizona Game and Fish Department 1996), for at least a part of their life cycle. The percentage of the fish community that each comprised varied between reaches and among seasons and was likely dependent upon where they are able to spawn in Grand Canyon and their thermal tolerances.

Reach

Differences in fish communities among reaches was probably due to thermal preferenda of each species and where they are able to spawn. For example, humpback chub were rare in Lower Reach backwaters because there are no documented spawning sites in Grand Canyon below the LCR. However, Arizona Game and Fish Department (1996) reported that it was likely that there is limited humpback chub spawning in the lower part of the canyon, based on the

capture of very small (<25 cm) humpback chub in backwaters over 100 river miles downstream from the LCR.

The main spawning area in the Upper Reach is the Little Colorado River, in which all four extant native fishes and most non-native fishes spawn (Maddux et al. 1987; Gorman 1994; Robinson 1996). In the Lower Reach, Kanab and Havasu creeks probably supply the majority of the larval and juvenile suckers to backwaters. Mainstem spawning by suckers appears to be possible in the Lower Reach, particularly in areas with warm springs, although this has not been documented. Mainstem/backwater spawning is likely in both reaches by speckled dace and small non-native fishes. Larval and very small juvenile speckled dace, plains killifish and fathead minnows have been captured in backwaters to which it is unlikely that they drifted or swam (Arizona Game and Fish Department 1996). Additionally, fathead minnows twice deposited eggs on a water quality instrument deployed in the backwater at RM 60.85L in May 1994 (Hoffnagle 1996).

Juvenile bluehead and flannelmouth suckers were dominant in the Lower Reach but only common in the Upper Reach. This may have been due to the large numbers of suckers spawned in Kanab and Havasu creeks and which emigrate from these tributaries soon after swimming up from the gravel. These species also spawn in the LCR, but there many of the fish may remain in the LCR for a longer period of time. In the Paria River, young flannelmouth suckers often remain in the Paria until they are flushed out by late spring or monsoon floods (Hoffnagle and Sponholtz 2000).

Temperature likely plays a large role in the distribution of fishes in Grand Canyon. Arizona Game and Fish Department (1996) reported that both backwaters and the main channel Colorado River were warmer in the lower canyon than below the LCR. Maximum mean monthly backwater temperature in the Upper Reach was 14.9° C, while in the Lower Reach it rose to 19.1° C, with a maximum recorded backwater temperature of 28° C.

Season

Seasonal differences in the backwater fish communities appear to be explained by differences in life history characteristics of each species and their thermal tolerances. Bluehead and flannelmouth suckers were more abundant during summer because they drift from spawning tributaries in late spring and early summer and find backwaters in which to rear. Both species

feed similarly (zooplankton and benthic invertebrates) and often school together until they reach approximately 50 mm in length (Arizona Game and Fish Department 1996). Humpback chub spawn in the LCR and largely remain there until the late summer and early fall monsoon period, when many disperse into the Colorado River (Valdez and Ryel 1995; Arizona Game and Fish Department 1996), which explains their increase in the percentage of the fish community during fall and winter. Fathead minnow and plains killifish are year round residents of backwaters and changes in their percentage of the fish community may be caused by the arrival and departure of native species, as well as their own reproduction.

Species

Use of backwaters varied among species by both reach and season. These differences in use are largely explained by the life history, temperature preferenda and the availability of spawning areas for each species.

Bluehead Sucker

Bluehead sucker was a more common component of the backwater fish community in the Lower Reach than the Upper Reach and during spring and summer than fall or winter. Bluehead suckers spawn in most tributaries of the Colorado River from the Little Colorado River and continuing downstream, including many small and ephemeral streams (Arizona Game and Fish Department 1996). They drift from these tributaries soon after hatching and inhabit warm, slow habitats. Juveniles feed on benthic invertebrates and zooplankton in soft-bottomed habitats, such as those found in backwaters and they are often found schooling in backwaters with similar-sized flannelmouth suckers (Arizona Game and Fish Department 1996). However, when they reach approximately 50 mm total length, they develop a cartilaginous scraper on their lower jaw, which they use to scrape algae and diatoms from rocks, often in fast water (Minckley 1991; Arizona Game and Fish Department 1996). Prior to the closure of Glen Canyon Dam, bluehead suckers may have primarily inhabited tributary streams (Woodbury 1959), in which they were able to find algae and diatom-covered rocks to feed but which were probably rare in the muddy Colorado River. However, the closure of Glen Canyon Dam caused the mainstem water to become clear providing habitat more to the liking of bluehead suckers on rocky shorelines and riffles. Bluehead suckers appear to have taken advantage of this change in habitat and expanded

their range into the mainstem Colorado River.

Flannelmouth Sucker

Flannelmouth sucker was also a more common component of backwaters in the Lower Reach than the Upper Reach and during summer months. Flannelmouth suckers spawn in the larger tributaries of the Colorado River in Grand Canyon and also drift soon after hatching (Minckley 1991; Arizona Game and Fish Department 1996). They school with similar-sized bluehead suckers in backwaters and along protected shorelines, feeding on similar invertebrate prey items (Arizona Game and Fish Department 1996). As they reach 50-100 mm in total length, they also leave the backwaters, probably because they appear to prefer the darker conditions of muddy or deep water (Valdez and Ryel 1995; Arizona Game and Fish Department 1996). However, unlike bluehead suckers, they continue to feed on soft bottoms throughout their life and are commonly captured in the mouths of tributaries and in backwaters, into which they migrate during the night (Arizona Game and Fish Department 1996).

Humpback Chub

Humpback chub distribution is very much tied to the LCR, as is evidenced by their skewed distribution between the Upper and Lower reaches. Nearly all humpback chub spawning in Grand Canyon occurs in the LCR and the only area in which they are known to recruit into the adult spawning population is the LCR and nearby reaches of the Colorado River (Valdez and Ryel 1995). Humpback chub that disperse downstream past Lava Chuar Rapid (RM 65.5) are not known to return to the LCR to spawn and are, therefore, lost from the effective spawning population in Grand Canyon.

Young-of-the-year humpback chub drift from the LCR throughout the spring and summer (Robinson et al. 1998) and these fish must quickly find warmer water, as they do not appear to withstand the instantaneous decrease in temperature (~10° C) from the LCR to the Colorado River (Lupher and Clarkson 1994). It appears unlikely that these early-dispersing fish survive to adulthood unless backwaters are abundant. However, a larger emigration occurs during the monsoon floods of late summer and early fall (Arizona Game and Fish Department 1996). By this time, juvenile humpback chub have grown sufficiently large that they appear to be able to withstand the temperature change and navigate in the swift current of the mainstem Colorado

River. These small fish inhabit sheltered shoreline habitats, such as talus and vegetated shorelines, as well as backwaters, which provide them with increased food supplies and cover from predation (Valdez and Ryel 1995; Converse 1996; Hoffnagle et al. 1999). Additionally, there is evidence that humpback chub particularly use backwaters as feeding areas at night (Hoffnagle 1996), showing a diel habitat use pattern similar to that seen in the LCR (Stone 1999).

Speckled Dace

Speckled dace are distributed throughout Grand Canyon, inhabiting all perennial and many seasonal streams (Arizona Game and Fish Department 1996). They inhabit most shoreline habitats, particularly those with sandy bottoms and some boulders, such as debris fans and backwaters (Arizona Game and Fish Department 1996; Hoffnagle et al 1999). They comprised a lower percentage of the fish community during winter, which may reflect their preference for warmer water. During the winter, backwaters are usually colder than the main channel (Arizona Game and Fish Department 1996) and is likely that these fish simply move to relatively warmer habitats. Similarly, speckled dace leave the Paria River during winter, when the Paria is colder than the Colorado River, but return as soon as the Paria warms in spring (Hoffnagle and Sponholtz 2000).

Fathead Minnow

Fathead minnows are also found throughout the Colorado River in Grand Canyon and its larger tributaries. They are year round residents of backwaters and have been documented spawning there (Hoffnagle 1996). They are abundant in backwaters, particularly during winter because they prefer low velocities. The experimental flood in Grand Canyon caused their abundance to decrease dramatically (Hoffnagle et al 1999). However, they are very prolific and by then end of the summer their numbers in the backwaters and other nearshore habitats rebounded, from reproduction and immigration from tributary refugia, to exceed that found before the flood. Changes in seasonal composition of fathead minnows in backwaters likely reflects changes in their numbers caused by reproduction and changes in numbers of native fishes, which appear to only use backwaters for part of their life history. Fathead minnows may affect backwater use by native fishes because they have a similar diet to that of small native

fishes (Arizona Game and Fish Department 1996) and they may prey on larvae, as well (Dunsmoor 1993).

Plains Killifish

Plains killifish are regularly found in backwaters and tributaries with slow water habitats (Arizona Game and Fish Department 1996). They do not appear to withstand high current velocity, as was demonstrated by the experimental flood, which appeared to have completely removed them from the mainstem Colorado River (Hoffnagle et al. 1996). However, due to immigration from tributary refugia and reproduction in backwaters that were unusually stable in 1996 (due to unusually steady discharge from Glen Canyon Dam), they comprised 24.3% of the backwater fish community by September 1996. Plains killifish comprised a higher percentage of the backwater fish community in the Upper Reach than the Lower Reach and are rarely found upstream from the LCR (Arizona Game and Fish Department 1996). This indicates that they may have invaded Grand Canyon from the upper LCR drainage during flooding and are colonizing downstream. Diet of plains killifish overlaps those of small native fishes, but the low abundance of plains killifish make it unlikely that they are significant competitors of native fishes (Arizona Game and Fish Department 1996).

Red Shiner

Red shiners are usually not a dominant or even common species in any backwater, but their numbers have been increasing and it is an aggressive fish that is capable of influencing the backwater fish community. Red shiners have been present in Grand Canyon since at least 1971 (Miller and Smith 1972), but have been rare from 1991-1996 (Arizona Game and Fish Department 1996; Brouder and Hoffnagle 1998; Hoffnagle 2000). However, they have become more abundant since 1996 in the LCR (Hoffnagle et al. 1997; Brouder and Hoffnagle 1998) and since 1998 in the Colorado River. Their increasing abundance in the mainstem is undoubtedly related to their increased abundance in the LCR, but the presence of small red shiners in backwaters far downstream from the LCR is indicative of reproduction in backwaters, as well. Red shiners are competitors and predators of larval and juvenile native fishes and should be considered a threat to native species (Greger and Deacon 1988; Ruppert et al. 1993; Muth and Snyder 1995).

Common Carp

Carp were introduced into Arizona prior to 1885 (Minckley 1973) and into the Colorado River drainage in Utah around 1888 (Sigler and Sigler 1996). They were the second most common species of fish (behind channel catfish) captured in Glen Canyon in 1958 (Woodbury 1959). The closure of Glen Canyon Dam cooled the waters to below that preferred by common carp (27-32° C), even below that avoided (24° C) by carp (Coutant 1977), which reduced their distribution to the LCR and lower portions of Grand Canyon (Valdez and Ryel 1995). However, they are strong swimmers and are sporadically captured throughout Grand Canyon (Valdez and Ryel 1995). They are also capable of taking advantage of suitable habitat when they find it and were reported spawning in a backwater at RM 55.5R in 1996 (Parnell et al. 1997). Larger carp likely use backwaters only for feeding, but will spawn there if suitable substrate , such as vegetation or other debris (Swee and McCrimmon 1966) is available. Young-of-the-year probably spend more time in these habitats. Diet of carp, particularly small carp, overlaps with that of native fishes and they are likely competitors (Carlander 1969 and references therein; Arizona Game and Fish Department 1996).

Other Species

The other species captured in backwaters over this period were captured in low numbers and appear to use backwaters only intermittently. Each of these species, with the exception of green sunfish, probably move into backwaters only to feed and many of them have been documented preying on native fishes (Marsh and Douglas 1997).

Rainbow trout was the most common of these species and comprised a greater percentage of the overall fish community than red shiner and common carp. Rainbow trout appear to move into backwaters to feed at night and young trout may spend a substantial amount of time there. However, the generally warmer temperatures of backwaters are not suited to trout and it is likely that they use backwaters only opportunistically. One brown trout, which was probably there to feed, was also captured in a backwater in the Lower Reach.

Green sunfish are regularly found only in Kanab Creek in Grand Canyon, where they can be very common if there have been no recent floods (Hoffnagle et al. 1998 a; b). In Kanab Creek, they probably feed heavily upon larval bluehead and flannelmouth suckers until the suckers leave the stream. It is highly unlikely that green sunfish are able to withstand the cold

temperature and fast current of the Colorado River and any that are flushed from Kanab Creek must find a backwater or perish.

Channel catfish were introduced into the Colorado river drainage in Utah in 1888 (Sigler and Sigler 1996) and was the most common species of fish caught in Glen Canyon in 1958 (Woodbury 1959). As with common carp, the closure of Glen Canyon Dam caused a reduction in their numbers and distribution when temperature dropped well below their preferred range of 25-30° C (Coutant 1977). They are now common only in the Little Colorado River (Hoffnagle et al. 2000) and the lower canyon (Valdez and Ryel 1995). Channel catfish are important predators of native fishes in the LCR (Marsh and Douglas 1997). Black and yellow bullhead are also predators of small fish (Carlander 1969 and references therein; Marsh and Douglas 1997), but are very rare in Grand Canyon.

Conclusions

Backwaters of the Colorado River in Grand Canyon are very important habitats for native and non-native fishes during the crucial early stages of their life history. Some species (e.g., bluehead sucker, flannelmouth sucker and speckled dace) may rely on them for growth to a size sufficient to withstand the rigors of the main channel. Other species (e.g., humpback chub and common carp) may rely on them more as a source of abundant food for juvenile and older fish. Fathead minnow and, particularly, plains killifish and red shiner may rely on them for their entire life. The composition of the fish community in backwaters, particularly the abundance of non-native fishes, is affected by two main factors: 1) the ephemeral nature of this habitat under the artificial flow regime caused by Glen Canyon Dam and 2) the abundance of non-native fishes, which affect native fishes through competition, predation and other behavioral interactions.

Current thought in Grand Canyon fisheries management is geared towards manipulating changes in habitat to benefit native fishes (Valdez and Carothers 1998; Valdez et al. *in press*). These manipulations include controlled floods, steady flow periods, installation of a temperature control device and removal of non-native fishes (Valdez and Carothers 1998). Hoffnagle (1996; *in press*) found that backwaters warm appreciably under a regime of steady flows and that ph, dissolved oxygen and conductivity vary, as well. Removal of non-native fishes will be an ongoing process, but may reduce predation on young native fishes. Experimental manipulations,

such as low steady flows or temperature controls may be useful tools. However, all of these potential management actions should be examined scientifically and with much forethought, planning and caution since these actions may be detrimental to native species by benefitting non-native more than native species. Therefore, any use of these tools should be well thought-out with well developed hypotheses and study plans and not be conducted in haste, simply to fulfill bureaucratic mandates. More studies of the dynamics of backwater creation and longevity, the use of backwaters by native and non-native fishes and the interactions among these fishes are needed before the Colorado River in Grand Canyon can be successfully managed for native fishes.

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