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TROPHIC INTERRELATIONS AMONG INTRODUCED FISHES IN THE LOWER COLORADO RIVER, SOUTHWESTERN UNITED STATES [1]

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Analysis of 1,050 stomachs of 18 species of fishes from the lower Colorado River mainstream indicates a relatively simplified food web based on autochthonous detrital materials, algae, and macrophytes. Aquatic insects, clams, and crayfish eaten by larger fishes fed directly on detritus or particles filtered from the water. Threadfin shad and red shiner, both depending principally on detritus as food, were major forage for piscivores.

INTRODUCTION

The lower Colorado River has one of the most highly modified channels in western North America. The most characteristic feature of aquatic habitats in arid zones, extreme variability in time and space, has been suppressed, and this notoriously fluctuating, formerly turbid stream now flows under essentially complete control by mainstream and tributary impoundments. Its native fishes, highly endemic but comprising only about nine species, are extirpated from the mainstream, or are rare. A new fauna, consisting of exotic species, is becoming established. So far, 44 non-native taxa have been recorded from the reach between Davis Dam and the U. S. and Mexican Boundary, 20 of which are locally or regionally abundant (Minckley 1979, Nicola 1979). Most published data on fishes of the river consist of faunal listings (Evermann 1931, Miller 1961, Miller and Lowe 1967, Bradley and Deacon 1967), general discussions of the fisheries (Moffett 1942, Dill 1944, Jonez *et al.* 1951, Wallis 1951, Kimsey 1958), keys for identification (Miller 1952, Winn and Miller 1954, Minckley 1971*a*), and numerous shorter works dealing with species introductions, and observations on distribution and ecology (reviewed by Minckley 1973 and Moyle 1976). Part of an ecological survey of the mainstream lower Colorado River, conducted from 1974 through 1976, was to identify general food relations within the fish fauna. Food habits of 18 species of fishes were studied to obtain an outline of trophic structure for the system. Edwards (1974) reported on foods of striped bass, *Morone saxatilis,* and his data are also summarized herein.

DESCRIPTION OF THE AREA

The study area was delimited upstream by Davis Dam and below by the International Boundary. The Colorado River forms the border between Nevada and Arizona to the north, California and Arizona through much of the study reach, and Baja California Norte, Mexico, and Arizona, at the southern extreme (Figure 1). The International Boundary lies about 120 km upstream from the Gulf of California. Historically, the only perennial tributaries entering this 453-km reach are the Gila and Bill Williams rivers. The former is now maintained below dams by return flow from irrigation and domestic wastewaters except in periods

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of unusually high runoff (Brown, Carmony, and Turner 1978). The latter is also impounded and sometimes ceases to flow at its mouth. Local precipitation seldom exceeds 12 cm per year, summer air temperatures often rise to greater than 40°C, and winter temperatures rarely drop below freezing for more than a few hours.

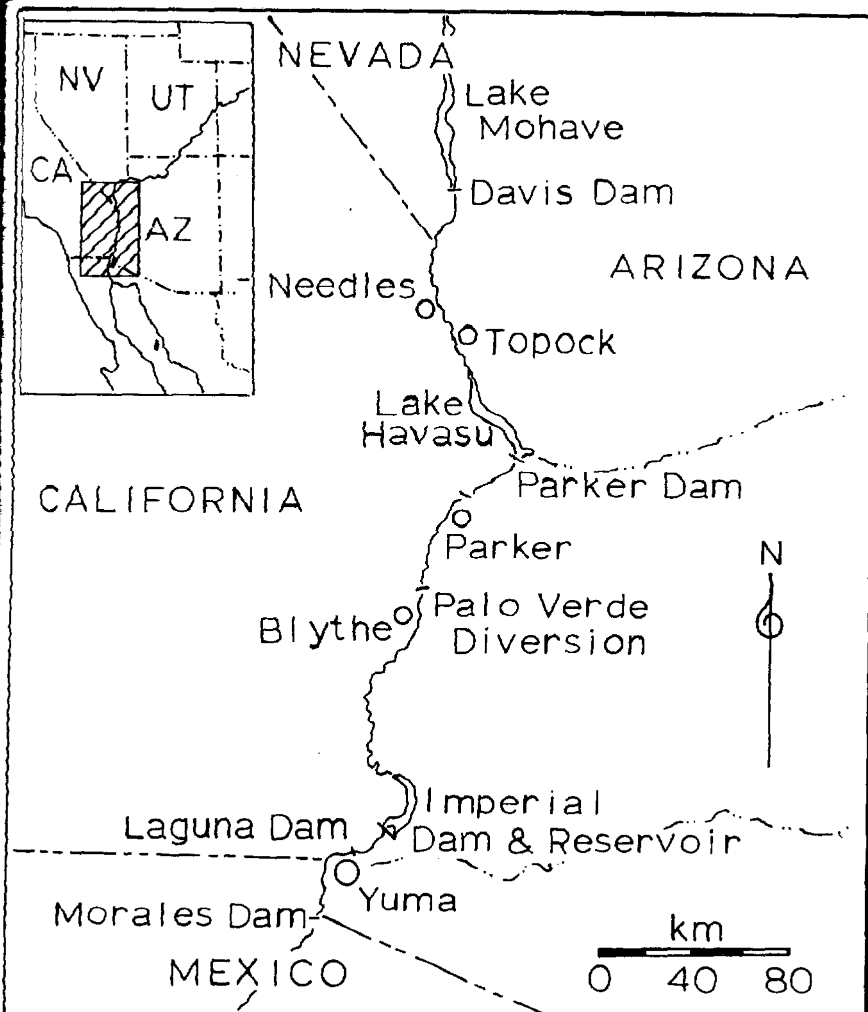

FIGURE 1. Map of the lowermost Colorado River, southwestern United States, with some place names mentioned in text.

Terrain along the river ranges from precipitous cliffs, where the stream has eroded through mountain ranges, to low, broad floodplains. Slopes and terraces are stony along mountain fronts. Lower terraces and floodplains are composed of fine sands and silts.

The sparse natural vegetation of the region is classified as Sonoran desertscrub (lower Colorado River subdivision; Brown and Lowe 1980). Plant communities especially those of riparian zones, are highly modified by agricultural development, by alteration of stream banks and channels, and through other direct influences of early and later settlers (Ohmart, Deason, and Burke 1977).

METHODS AND MATERIALS

An attempt was made to use fishes from throughout the reach, and from different seasons, to obtain comprehensive coverage. However, this was realized only for some of the more common species such as carp, *Cyprinus carpio;* red shiner, *Notropis lutrensis;* channel catfish, *Ictalurus punctatus;* largemouth bass, *Micropterus salmoides;* and bluegill, *Lepomis macrochirus,* where 11 to 50 individuals were studied each season. Foods of other fishes were studied in spring through autumn. All rainbow trout, *Salmo gairdneri,* were obtained from fishermen and from Arizona Game and Fish Department personnel near Davis Dam. Most smallmouth bass, *Micropterus dolomieui,* examined were caught by anglers near Blythe, California. Threadfin shad, *Dorosoma petenense;* flathead catfish, *Pylodictis olivaris;* yellow bullhead, *Ictalurus natalis;* sailfin molly, *Poecilia latipinna;* mosquitofish, *Gambusia affinis;* warmouth, *Chaenobryttus gulosus;* striped mullet, *Mugil cephalus* (the only native fish taken); and the mouthbrooder, *Sarotherodon mossambica,* all were from the reach below Blythe. Redear sunfish, *Lepomis microlophus;* green sunfish, *L. cyanellus;* and black crappie, *Pomoxis nigromaculatus,* were obtained near Parker and/or Yuma, Arizona. Specimens taken by hook and line or with various seines were sacrificed for analysis to avoid prolonged restraint and loss of food items through continuing digestion which occurs in fishes taken in gill, trammel, and hoop nets of various sizes and meshes (Minckley 1979).

Food habits were determined by examination of stomach contents under appropriate magnifications. In species with ill-defined stomachs (*e.g.* carp) the anterior few centimetres of digestive tract was examined. Stomachs were excised from larger fishes, after ligation of the esophagus and pyloric regions, and preserved in 10% formalin. All stomachs were tagged for later identification. Small fishes were preserved intact in the field and their viscera removed in the laboratory.

Data were reduced as "frequency of occurrence," which tends to underestimate importance of large items and over-estimate importance of small items. However, this technique develops comparative data, expressed as percentage, among diverse species, and avoids ambiguities of assigned (estimated) "points" (Hynes 1950) or attempted reconstruction of live volumes of animals from fragments present (Ricker 1937). Stomach contents were teased apart in water and identified through use of keys of Edmondson (1959) and Usinger (1956). Reference collections were used to identify fishes and larger crustaceans.

RESULTS

General Food Habits

Detritus formed the major proportion of stomach contents of threadfin shad, red shiner, mouthbrooder, sailfin molly, and striped mullet (Table 1), and was common in carp, channel catfish, and yellow bullhead. Most detritus was identifiable as fibrous particles of higher plants, typically aquatic macrophytes. A small percentage was dark, gelatinous material identical in appearance to *gytjja*-like organic deposits along the channel and in backwaters of the river. A liberal occurrence of sand in stomachs of detritivores indicated direct feeding from the bottom. Amorphous detrital materials in stomachs of carp and channel catfish often included unicellular algae, some of which was likely recorded as phytoplankton (Table 1). The high incidence of Asiatic clams, *Corbicula fluminea*, in stomachs of these fishes, and field observation of carp feeding upon and among clams, indicates probable use of pseudofeces of the mollusk (Prokopovich 1969) by the fishes as food. This material, bypassed by a clam when particulates exceed its capacity for ingestion, includes a large percentage of detritus, plus organisms bound in a mucoid secretion. Detritus in stomachs of sailfin molly and mouthbrooder was associated with the high frequency of occurrence of benthic (or epiphytic) algae, and in the case of the latter, with substantial amounts of higher plant tissues. Both of these fishes often grazed within beds of aquatic plants.

Although much of the algae eaten by fishes in the lower Colorado River could easily have been ingested while foraging for other items, rainbow trout contained considerable volumes of *Cladophora glomerata*, a large filamentous alga that formed a major component of organic drift observed and caught on nets near Davis Dam. Drifting algae may be taken as an innate feeding response by visually-oriented fishes such as hatchery-reared trout, or may be consumed indiscriminately by facultative planktivores such as threadfin shad and striped mullet. Some algal species that appeared to be true phytoplankters (desmids and some diatoms) were found in stomachs of the last two species (Table 1).

Zooplankton in stomachs of rainbow trout, threadfin shad, red shiner, and bluegill included cladocerans and copepods characteristics of limnetic populations in Colorado River reservoirs, presumably having been entrained through penstocks into the channel. Zooplankters in stomachs of carp, largemouth bass, green sunfish, and black crappie also included ostracods and thus included near-bottom or benthic microcrustaceans. Only trout and shad contained what might be considered more than trace amounts of zooplankton.

Benthic invertebrates were present in stomachs of essentially all fishes examined, with chironomid dipteran larvae almost universally represented. Rainbow trout from below Davis Dam ate about equal amounts of chironomid and simuliid dipteran larvae and also contained a substantial frequency of hydropsychid trichopteran larvae. Carp fed on chironomids, ephemeropteran nymphs, trichopteran larvae, and a few odonate naiads. The last three groups only occurred in stomachs of fishes from below Parker Dam. Red shiners ate chironomids, and a few ephemeropterans and trichopterans. The low frequency of occurrence of chironomids in channel catfish (5.1%) indicated little dependence on benthic insects. No other insect groups were used by channel catfish, which is surprising in light of findings in other streams (*e.g.* Bailey and Harrison 1948). Yellow bullheads used chironomids extensively, but young flathead catfish ate only large odonates and trichopterans.

Most mosquitofish examined had eaten tiny, soft-bodied larvae of chironomids, culicids, dixids(?), and undetermined insect groups. About 43% fed on terrestrial invertebrates (aphids, ants, and spiders) and aerial adults of aquatic insects (included with terrestrial insects in Table 1). Sailfin mollies did not feed on animal materials (see, however, Harrington and Harrington 1961).

TABLE 1. Summary of Frequency of Occurrence of Various Food Items in Stomachs of Fishes from the Lower Colorado River, 1974–76, as Percentages of All Stomachs Examined for Each Species.

Items in stomachs	*Salmo gairdneri*	*Dorosoma petenense*	*Cyprinus carpio*	*Notropis lutrensis*	*Ictalurus punctatus*	*Ictalurus melas*	*Pylodictis olivaris*	*Gambusia affinis*	*Poecilia latipinna*	*Micropterus dolomieui*	*Micropterus salmoides*	*Chaenobryttus gulosus*	*Lepomis cyanellus*	*Lepomis macrochirus*	*Lepomis microlophus*	*Pomoxis nigromaculatus*	*Morone saxatilis*	*Sarotherodon mossambicus*	*Mugil cephalus*
Number of stomachs	38	49	135	79	137	16	23	42	52	27	189	16	51	47	34	29	100	65	21
Total lengths, limits in millimetres	152–440	37–193	175–864	33–56	236–737	93–325	178–813	21–37	27–64	118–432	99–560	82–155	75–205	78–213	85–305	173–327	540–893	95–289	381–495
Percentage empty	18.4	0.0	7.8	11.4	16.1	12.5	39.1	2.4	0.0	29.6	11.6	31.3	31.6	0.0	5.9	0.0	45.0	0.0	0.0
Inorganic Materials																			
Sand, gravel, etc.	–	*81.8*	*30.4*	*3.8*	–	–	–	*2.4*	*19.4*	–	*3.7*	*12.5*	*2.0*	*2.1*	*8.8*	–	–	*20.0*	*95.2*
Vegetative Materials																			
Detritus	–	*98.0*	*42.2*	*62.0*	*32.9*	*12.5*	–	–	*100.0*	–	–	–	–	–	–	–	–	*63.1*	*100.0*
Macrophytes	*2.6*	–	*1.5*	–	*40.9*	*18.8*	–	–	–	–	–	–	–	–	–	*41.4*	–	*44.6*	*4.8*
Benthic and epiphytic algae	*42.1*	*16.3*	*3.7*	*2.5*	*8.0*	–	–	*54.8*	*82.7*	–	–	–	–	–	*5.9*	–	–	*27.7*	*14.3*
Phytoplankton	–	*16.3*	*33.3*	–	*0.7*	–	–	–	–	–	–	–	–	–	–	–	–	–	*14.3*
Animal Materials																			
Crustacea	*34.3*	*20.4*	*7.4*	*26.6*	*24.8*	*56.3*	*26.1*	–	–	*29.6*	*15.3*	–	*7.8*	*63.8*	–	*10.3*	*7.0*	–	–
Copepoda	29.0	20.4	0.7	21.5	–	–	–	–	–	–	10.6	–	7.8	51.1	–	6.9	–	–	–
Cladocera	5.3	4.1	3.0	11.4	–	–	–	–	–	–	4.8	–	–	19.1	–	3.4	–	–	–
Ostracoda	–	–	0.7	–	–	–	–	–	–	–	1.6	–	2.0	–	–	3.4	–	–	–
Decapoda																			
Astacidae	5.3	–	3.7	–	21.2	56.3	26.1	–	–	29.6	3.7	12.5	3.9	–	–	6.9	7.0	–	–
Paleomoneidae	–	–	–	–	3.7	–	–	–	–	–	8.5	6.2	7.8	–	–	41.4	–	–	–

Benthic Insecta	*26.3*	*26.5*	*33.3*	*24.1*	*5.1*	*37.5*	*8.7*	*61.9*	–	*29.6*	*9.0*	*43.8*	*35.3*	*46.8*	*8.8*	–	–	*16.9*	*4.8*
Ephemeroptera	–	–	1.5	3.8	–	–	–	–	–	29.6	–	–	–	–	–	–	–	–	–
Odonata																			
Zygoptera	–	–	–	–	–	–	–	–	–	–	2.1	31.2	9.8	–	–	–	–	1.5	–
Anisoptera	–	–	0.7	–	–	–	8.7	–	–	–	1.6	12.5	5.8	–	–	–	–	–	–
Megaloptera	–	–	–	–	–	–	–	–	–	11.1	–	–	–	–	–	–	–	–	–
Trichoptera	18.4	–	3.0	1.3	–	–	4.4	–	–	3.7	0.5	–	–	–	–	–	–	–	–
Diptera																			
Tipulidae	–	–	0.7	–	–	–	4.4	–	–	–	–	–	–	–	–	–	–	–	–
Culicidae	–	–	–	–	–	6.2	–	45.2	–	–	–	–	2.0	4.2	–	–	–	–	–
Simuliidae	23.7	4.1	–	–	–	–	–	–	–	3.7	–	–	–	–	–	–	–	–	–
Chironomidae	26.3	–	33.3	24.1	5.1	37.5	–	9.5	–	3.7	9.0	6.2	35.3	46.8	8.8	–	–	16.9	4.8
Dixidae (?)	–	–	–	–	–	–	–	26.2	–	–	–	–	–	2.1	–	–	–	–	–
Undetermined taxa	2.6	4.1	2.2	5.1	–	–	–	19.0	–	–	–	–	–	8.5	–	–	–	1.5	–
Terrestrial																			
Invertebrates	–	–	–	–	–	–	–	*42.9*	–	–	–	*12.5*	*9.8*	*2.1*	–	–	–	*3.1*	–
Hymenoptera																			
Formicidae	–	–	–	–	–	–	–	16.7	–	–	–	12.5	3.9	–	–	–	–	–	–
Homoptera																			
Aphididae	–	–	–	–	–	–	–	9.5	–	–	–	–	–	–	–	–	–	–	–
Araneida																			
Undetermined taxa	–	–	–	–	–	–	–	–	–	–	–	–	7.8	–	–	–	–	–	–
Undetermined taxa	–	–	–	–	–	–	–	21.4	–	–	–	–	2.0	–	–	–	–	–	–
Mollusca	–	–	*46.7*	–	*29.2*	*6.3*	–	–	–	–	*1.6*	–	–	–	*58.8*	–	–	*26.2*	–
Sphaeriidae	–	–	46.7	–	29.2	6.3	–	–	–	–	1.6	–	–	–	55.9	–	–	23.1	–
Physidae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5.9	–	–	3.1	–
Oligochaeta	–	–	*6.7*	*3.8*	*1.5*	*37.5*	–	–	–	–	–	–	–	–	–	–	–	*1.5*	–
Vertebrata	*34.2*	–	*2.2*	–	*19.7*	–	*43.5*	–	–	*11.1*	*55.0*	*25.0*	*5.8*	–	*2.9*	*55.2*	*51.0*	–	–
Salmonidae																			
Salmo gairdneri	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	13.0	–	–
Clupeidae																			
Dorosoma petenense	34.2	–	2.2	–	5.1	–	4.3	–	–	–	53.4	–	–	–	2.9	20.7	35.0	–	–

TABLE 1. Summary of Frequency of Occurrence of Various Food Items in Stomachs of Fishes from the Lower Colorado River, 1974–76, as Percentages of All Stomachs Examined for Each Species.—Continued

Items in stomachs	*Salmo gairdneri*	*Dorosoma petenense*	*Cyprinus carpio*	*Notropis lutrensis*	*Ictalurus punctatus*	*Ictalurus melas*	*Pylodictis olivaris*	*Gambusia affinis*	*Poecilia latipinna*	*Micropterus dolomieui*	*Micropterus salmoides*	*Chaenobryttus gulosus*	*Lepomis cyanellus*	*Lepomis macrochirus*	*Lepomis microlophus*	*Pomoxis nigromaculatus*	*Morone saxatilis*	*Sarotherodon mossambicus*	*Mugil cephalus*
Cyprinidae																			
Cyprinus carpio	–	–	–	–	–	–	4.3	–	–	–	–	–	3.9	–	–	–	1.0	–	–
Notropis lutrensis	–	–	1.4	–	7.3	–	13.0	–	–	3.7	7.9	18.8	–	–	–	34.5	–	–	–
Ictaluridae																			
Ictalurus punctatus	–	–	–	–	–	–	4.3	–	–	–	–	–	–	–	–	–	–	–	–
Poeciliidae																			
Gambusia affinis	–	–	–	–	–	–	–	–	–	–	–	18.8	–	–	–	–	–	–	–
Poecilia latipinna	–	–	–	–	–	–	–	–	–	–	–	6.2	–	–	–	–	–	–	–
Centrarchidae																			
Micropterus salmoides	–	–	–	–	–	–	–	–	–	–	0.5	–	–	–	–	–	3.0	–	–
Lepomis cyanellus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.0	–	–
Undetermined species	–	–	–	–	2.9	–	4.3	–	–	7.4	1.6	–	2.0	–	–	–	–	–	–
Undetermined fishes	–	–	–	–	3.6	–	–	–	–	–	1.1	–	2.0	–	–	–	–	–	–
Ambystomatidae																			
Ambystoma tigrinum	–	–	–	–	0.7	–	–	–	–	–	–	–	–	–	–	–	2.0	–	–
Undetermined vertebrates (?) ..	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6.0	–	–

Smallmouth bass stomachs contained large numbers of ephemeropteran nymphs and megalopteran larvae. Odonate naiads, including both damsel- and dragonflies, were taken by juvenile largemouth bass, warmouth, and green sunfish. Included were species of clambering damselfies typically found in beds of aquatic plants (see also Weaver and Zeibell 1976). Chironomids also were taken by the last three fishes. Bluegill depended strongly on chironomids, along with zooplankton (Table 1). Redear sunfish ate chironomid larvae only infrequently.

Mouthbrooder and striped mullet contained a few tiny chironomid larvae that may have been consumed along with detritus (especially in the latter). Mouthbrooder, however, contained a few terrestrial insects and a number of other benthic groups.

Introduced palaemoneid shrimp, *Palaemonetes paludosus,* are common in the lower Colorado River, but contributed to the diet of only five fish species. Black crappie appeared to select the food item. Largemouth bass, warmouth, and green sunfish all fed on shrimp at about the same proportion. Channel catfish contained them at a frequency of only 3.7%. Perhaps its semi-transparent body makes the shrimp relatively immune to all except special predators, especially when in dense aquatic vegetation.

The introduced crayfish, *Procambarus clarki,* was a major food of almost all large carnivores, especially catfish and smallmouth bass. Rainbow trout, carp, largemouth bass, warmouth, green sunfish, and black crappie also ate the decapod. Edwards (1974) reported crayfish from striped bass stomachs. Introduced softshelled turtle, *Trionyx spiniferus,* also depended heavily on them (present in 10 animals dissected, along with odonate naiads as the only other food item).

Asiatic clams were eaten by carp, channel catfish, yellow bullhead, redear sunfish, largemouth bass, and mouthbrooder (Table 1). In all but redear sunfish, clams were digested without breakage of valves, with the shell simply passing through the intestinal tract. The redear sunfish is especially adapted for crushing mollusks, with molariform teeth on its pharyngeal bones; however, less than 20% of shells in redear stomachs had been physically damaged. Crushing of clams is obviously not requisite to digestion since shells in hindguts of redear sunfish and other species alike were devoid of flesh. Consumption of clams by carp was spectacularly high in some instances, with some fish containing more than 30. Some clams eaten by carp and channel catfish exceeded 2.5 cm across the valves, but most were less than 1.0 cm.

Rainbow trout, two of the catfish, and all sunfishes excepting bluegill contained other fishes. Channel and flathead catfishes, largemouth bass, warmouth, and black crappie were the most piscivorous species. Edwards (1974) demonstrated that striped bass in the Colorado River were also voracious piscine predators (Table 1).

Threadfin shad was the exclusive fish eaten by trout. Largemouth bass also ate shad, followed by red shiner, unidentified sunfish, unidentified fish, and other largemouth bass. Channel catfish fed on shad and red shiner, unidentified centrarchids, and other unidentified fish. Flathead catfish ate mostly red shiner and mouthbrooder. Four flathead catfish each had eaten a single fish, each of a different species (threadfin shad, carp, channel catfish, and undetermined centrarchid). The warmouth was a specialized piscivore, feeding on poeciliids and red shiner. Green sunfish were more opportunistic, eating small carp and unidentified fishes. Only one redear sunfish took a juvenile shad, but black crappie ate them frequently, along with red shiner. Striped bass ate threadfin shad, rainbow trout, crayfish, centrarchids, carp, tiger salamander, *Ambystoma tigrinum,* and unidentified animal material (Edwards 1974). The salamander is a common bait animal along the Colorado River (Minckley 1971*b*); and a single specimen also was eaten by a channel catfish (Table 1).

Percentages of empty stomachs in fishes of the lower Colorado River were related to principal food habits. No empty stomachs were found among detritivores and facultative planktivores. Species that depended upon a broader food base, including significant frequencies of benthic invertebrates, also had relatively low percentages of empty stomachs. Large piscivores tended to have a high incidence of empty stomachs (*e.g.* flathead catfish, 39.1%). Edwards (1974) reported 45% of 100 stomachs of adult striped bass as empty. Smallmouth bass, warmouth, and green sunfish also had an incidence of empty stomachs that exceeded 20%, but largemouth bass displayed a wider food base and all but 11.6% contained foods.

SPATIAL VARIATION

Trophic structure within the fish community of the lower Colorado River differs substantially in different reaches of stream. Near Davis Dam, waters of the upstream reservoir (Lake Mohave) provide a major proportion of basic foodstuffs. Substantial amounts of plankton and detritus pass through the dam and this is reflected in a large proportion of filter-feeding invertebrates (*e.g.* simuliids) in stomachs of fishes from that reach. Threadfin shad also drawn through the dam form a major portion of the food supply for striped bass (Edwards 1974), and likely for larger rainbow trout. Cold water resulting from hypolimnic releases from Davis Dam exclude many temperate (and obviously tropical) species of fishes from that area. Primary production is relatively high, since aquatic vegetation is abundant (no quantitative data available), but essentially no fishes are present to utilize that level in the food web.

Downstream in Topock Gorge, deep, swift areas continue to be influenced by hypolimnic water from Lake Mohave. A few major backwaters provide habitat for temperate fishes. It seems likely that this reach is relatively devoid of foods for piscivores, since red shiners were rare and threadfin shad almost non-existent (Minckley 1979).

Lake Havasu is a relatively stable, mainstream reservoir that differs greatly from the remainder of the reach under consideration. Few stomachs of fishes were examined from the lake (none of those presented in Table 1), but food relations seemed similar to those described by Rinne, Minckley, and Bersell (1981) from reservoirs in central Arizona. Fishes were distributed relative to their food supplies: planktivorous threadfin shad were most abundant near nutrient inputs, thus near phyto- and zooplankton concentrations, and piscivorous largemouth bass tended to be near threadfin shad. Benthic predators were more generally distributed within the reservoirs, in keeping with a more general distribution of benthic invertebrates. Zooplankton was not studied in Lake Havasu, but Chlorophyll *a* concentrations were highest near nutrient inputs at the uppermost end of the lake and in the Bill Williams River arm (Portz 1973, Minckley 1979). Benthic invertebrates in Lake Havasu were also similar in diversity and general abundance to those elsewhere in low desert impoundments (Rinne *et* *al.* 1981), with fewer animals and biomass where currents were present (Minckley 1979, Cowell and Hudson 1967), presumably in response to changes in sediments (Schulback and Sandholm 1962). Shoreline populations of benthic invertebrates were locally dominated by Asiatic clams, reflecting high plankton populations in the lake. These were eaten by carp, channel catfish, and redear sunfish, at frequencies comparable to those in the river channel (based on qualitative examination of stomachs).

Epilimnetic penstock intakes in Parker Dam allow warm water to flow downstream, thus enhancing habitat for warmwater fishes in the river below Lake Havasu. Particulate materials, including plankton, in turn enhance filter-feeding benthic animals, as do hard bottoms and an abundant micro- and macroflora. Macrophytes, benthic algae, and phytoplankton made up a significant part of the diet of all but centrarachids near Parker, Arizona, with phytoplankton being derived in part from the pseudofeces of Asiatic clams. Detritus, both from auto- and allochthonous sources, also was present in stomachs of many species at high frequencies, especially threadfin shad, carp, and channel catfish. Benthic insects, consisting mostly of chironomid dipteran larvae, comprised major parts of the diet of all species present. Other invertebrates, excepting clams and crayfish, were broadly represented, but far less significant than chironomids. Clams were eaten by specialists (carp, channel catfish, and redear sunfish), forming major parts of their diets. Crayfish were generally taken by piscivores, with the exception of smallmouth bass, who appeared to feed selectively upon them. Other fishes were important in the diets of six species, and especially so for channel and flathead catfishes, largemouth bass, and black crappie. Fishes lowest in the food web of the system, threadfin shad and red shiner, were eaten by other fishes most frequently, and were the most abundant species in the river (Minckley 1979). Other prey species were mostly juvenile centrarchids, for the most part secondary consumers in the system.

In the lowermost reaches, detritivory became a major mode of life for sailfin molly, striped mullet, and mouthbrooder. Accumulation of organic materials from upstream, resulting from high rates of production, lack of flooding, and in part from diminution in discharge as a function of progressive water use, allows these fishes to maintain and expand their populations. However, constraints of temperature upstream (too low in winter or near Davis Dam) for the molly and mouthbrooders, and distance from the sea plus intervening barriers for the mullet, undoubtedly limit their over-all distribution more than food.

DISCUSSION AND CONCLUSIONS

Although the Colorado River provides a relatively low food diversity, food habits of introduced fishes of the Colorado River do not differ substantially from those of the same species within their native ranges (see reviews in Calhoun 1966). Many abundant forage species are introduced (probably not so for most insects and oligochaetes) and are characterized by high reproductive rates and high-density, monospecific populations. These features are also evident in the new fish fauna, with many species now populating transitory habitats where populations may explode, stunt, then eventually stabilize at low levels or disappear.

The food web of the Colorado River is based upon autochthonous materials. Fishes in other large rivers often depend upon allochthonous inputs. In the

Missouri River (Berner 1951), 54% of materials ingested by fishes was of terrestrial origin. The sparse terrestrial vegetation of most of the Colorado River basin, and relatively large size of the stream in proportion to its narrow, water-limited riparian zone, diminishes the importance of allochthonous input. As emphasized by Minshall (1978), autochthonous conditions are far more prevalent in open, western streams than has been generally recognized.

Organic and inorganic transport in the Colorado River are curtailed by reservoirs, excepting for downstream passage of plankton and associated suspended debris through penstocks. These materials and nutrients not trapped by impoundments (Paulson and Baker 1980), nonetheless form a basis for downstream production. The few backwaters that remain along the river appear highly productive, supporting large standing crops of plankton, rooted aquatic vegetation, and fishes (Minckley 1979, Nicola 1979), all of which are flushed into the channel by almost-tidal fluctuations in the stream resulting from hydroelectric generation and pulses of irrigation deliveries. Less modified reaches of the river and those which are relatively stabilized have proportionately more backwater habitat. In-stream productivity is also locally high, enhanced by current under abundant insolation without interference of shading by turbidity or riparian vegetation, and is at present further augmented by addition of nutrients through return flow of irrigation systems. A trophic economy based upon autochthonous detritus establishes quickly under such conditions.

Introduced forage species that have survived and flourished in the lower Colorado River mainstream all depend heavily upon detritus or primary producers, or upon secondary consumers such as zooplankton, chironomids, or other invertebrates. Large fishes with less piscivorous tendencies feed directly upon detritus- or plant-dependent clams or crayfish. The introduced fish fauna thus appears to have relatively simple food interrelations.

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