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Ecology of the coporo, *Prochilodus mariae* (Characiformes, Prochilodontidae), and status of annual migrations in western Venezuela

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Synopsis

Deforestation, overfishing, pollution, and construction of dams have severely impacted migratory fishes of western Venezuela. The coporo, *Prochilodus mariae* (Prochilodontidae), has supported the largest commercial fishery among the species that have seasonal long-distance migrations between rivers of the Andean piedmont and the llanos floodplains. During the period July 1988 to November 1990, coporo ecology was studied in the Río Boconó and the Boconó-Tucupido reservoir in estado Portuguesa. Coporo females mature at age 2 at 23 cm SL. Relatively few coporos were captured from the reservoir and the R. Boconó upstream. No coporos were encountered in the river > 3 km upstream from the reservoir nor in hypoxic regions of the reservoir > 4 m deep. In the river segment immediately downstream (0–4 km) from the Boconó Dam, the stock was comprised of mostly juveniles (78% < 17 cm SL), and this size/age structure was relatively stable over time. In recent years, overfishing downstream from the dam has reduced the densities and sizes of coporos in the R. Boconó. The river segment 4–16 km below the dam was comprised of 78% adults. Few coporos > 3 yr and > 30 cm SL were found in the rivers, whereas none were < 4 yr and < 30 cm in the reservoir. Detritus was consumed more than algae by coporos in the reservoir and by adults relative to juveniles among river-dwelling fish. In both reservoir and river fish, gonadal development was initiated during late November and peaked during May-June. We found no evidence of successful reproduction in the reservoir, and mature adults in the lower river segment disappeared during June, presumably having migrated to the floodplains of the low llanos for spawning. From mid-November 1989 until March 1990, coporo 'ribazóns' (schools of ascending migrants) of diminishing densities were surveyed from the R. Apure upstream to the R. Boconó. 'Ribazóns have been eliminated or greatly diminished in nearly 80% of the principal rivers of the Andean piedmont in western Venezuela. Management options to assist this economically and ecologically important species are discussed.

Introduction

Seasonal fish migrations are a conspicuous feature of South American rivers. Fishes migrate in search of seasonal refuges, feeding habitats, and spawning areas, but the magnitude of migrations depends up-on the species, life-cycle interval, seasonal habitat variation, and the geomorphology and habitat heterogeneity of river basins. Some fishes undertake long-distance migrations. For example, some of the large catfishes of importance to river fisheries undertake migrations of hundreds to thousands of kilometers between the presumptive spawning grounds in the western Amazon and feeding habitats near the Amazon River's mouth in the east (Goulding 1988, Bayley & Petrere 1989, Barthem et al. 1991). The most conspicuous of the long-distance migrants are the prochilodontid fishes of the genera *Prochilodus* (called 'coporo' in northern South America, 'sábalo' in the south, and 'curimbatá' in Brazil) and *Semaprochilodus* (called 'bocachico' in Spanish and 'jaraqui' in Portuguese). These fishes are abundant in the major river basins of South America where they feed on detritus, algae, and associated microorganisms (Bowen 1983, Bowen et al. 1984). Prochilodontids are important prey for piscivores and thus constitute an important link for the transfer energy and biomass from basal production to species higher in the food web (Jepsen et al. 1997, Winemiller 1996b). *Prochilodus* feeding has been shown to have strong direct and indirect effects on benthic community structure and ecosystem processes like sedimentation and nutrient cycling (Flecker 1992, 1996). Prochilodontids support important commercial and subsistence fisheries throughout South America (Bayley & Petrere 1989, Novoa 1989, Welcomme 1990).

The prochilodontid life cycle is complex, and the direction and degree of longitudinal migrations varies depending on species and geographic location. In the western Orinoco basin of South America, most adult *Prochilodus* migrate from dry-season habitats in tributary rivers and streams of the llanos and Andean piedmont to their wet-season spawning and feeding habitats in lowland channels and floodplains of the mainstem rivers (Lilyestrom 1983). These downstream migrations, at first, consist of relatively uncoordinated movements by solitary fish and small aggregations, and fish eventually congregate for spawning in river channels and areas of the flooded savanna during the rising and high flood water (late May-June). Migrating prespawning males and courting males emit a low-pitched, drumming sound that presumably attracts ripe females. Fertilized eggs, embryos and larvae drift with the river's current some distance downstream and eventually end up in the floodplain lagoons where juveniles feed on rich invertebrate and algal production. During the falling-water period, conspicuous large schools of coporos with other species (the 'ribazón') migrate upstream in tributary rivers that originate in the Andes Mountains. Much like salmon, prochilodontids can traverse many natural channel barriers, such as low water falls and rapids. Yet, dams constructed for hydroelectric power generation and flood control block migration, and fish ladders appear to be largely ineffective (Quirós 1989, Winemiller et al. 1996). Even low dams created for diversion of irrigation water can impede the upstream passage of a great many migrants, and those that manage to scale these dams expend considerable energy and risk injury (Winemiller et al. 1996).

In western Venezuela, large-scale deforestation has caused dewatering of river channels in the Andean piedmont with negative impacts on migratory coporo, *Prochilodus mariae* (Lilyestrom & Taphorn 1978, Lilyestrom 1983, Winemiller et al. 1996). Dams now obstruct nine Andrean piedmont rivers in western Venezuela, and new dams are planned for several of the remaining unimpounded rivers. The construction of the Boconó Dam during the early 1980s blocked coporo migrations in the Río Boconó and R. Tucupido (R. Orinoco drainage basin). Prior to the construction of the dam, large schools of migrating coporo were a major resource exploited by fishers of the R. Boconó (Chapman 1980), but in the years following dam construction, coporo migrations declined markedly. The purpose of our investigation was to document features of the habitat of the R. Boconó, coporo population structure, and major movements of the coporo in western Venezuela.

Study area

We studied coporos in the R. Boconó, including the unimpounded upper reaches in the Andean piedmont, the Boconó-Tucupido Reservoir, the lower

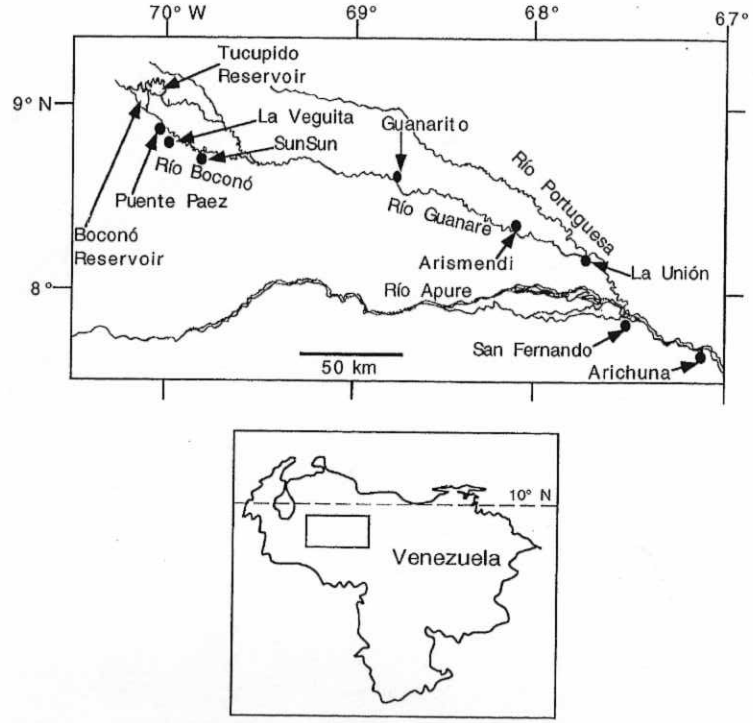

Figure 1. Map showing the Río Boconó study region and the longitudinal river gradient where the coporo ribazón was monitored i western Venezuela.

R. Boconó from the Boconó Dam to the R. Guanare-Chorrosco, and the lower R. Guanare from the mouth of the R. Boconó to its juncture with the R. Portuguesa. This area covers the northwest portion of Portuguesa state, the northeast portion of Barinas state, and the southeast portion of Trujillo state, from 9°32′ N, 70°08′ W to 8°43′ N, 69°43′ W in western Venezuela (Figure 1). From its source in the Jabón and Turnal páramos at an elevation of approximately 3450 m, the Río Boconó runs approximately 170 km through páramo, piedmont, and llanos to its juncture with the R. Guanare at approximately 240 m elevation. Annual rainfall averages 2.1 m in the river's drainage basin, and most of the rain falls during the period May through August (Figure 2).

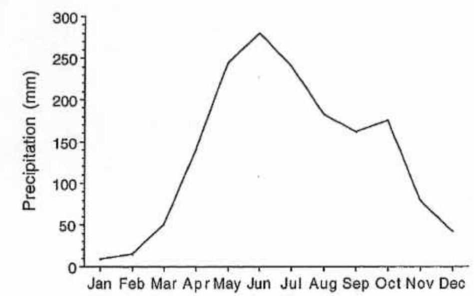

Figure 2. Plot of monthly rainfall (1989) for the Río Bocon drainage basin in western Venezuela (data based on daily san pling by the Minesterio del Ambiente y Recursos Naturale Renovables-Zone 8).

Materials and methods

From November 1988 to October 1989, water quality parameters were measured monthly from samples taken from the following locations: (1) entrance of the river into the reservoir, (2) center of the reservoir- surface, (3) center of reservoir-mid-depth, (4) center of reservoir-bottom, (5) turbine entrance-surface, (6) turbine entrance- mid-depth, (7) turbine entrance-bottom, (8) turbine exit, (9) Río Bocon6 at Puente Paez, and (10) R. Boconó at La Veguita. Water samples were taken from the reservoir from a boat with a 2.0 l Kenmerer water sampler between 8:00 and 13:00 h. The following parameters were estimated at each site: temperature (°C), dissolved oxygen (mg l^{-1}), phosphate (mg l^{-1}), pH, total solids (mg l^{-1}), and turbidity (NTU). Temperature was measured in the field with a thermometer. Water samples for dissolved oxygen measurements were placed in clean 500 ml glass containers, fixed for later Winkler titration in the laboratory, and placed on dry ice. Water samples for other physico-chemical measurements were placed in clean plastic 2000 ml containers on dry ice for transport to the laboratory. No more than 6 h elapsed between the time the first sample was collected at a site and the time when the samples were processed in the laboratory at UNELLEZ in Guanare. Standard titration methods were used for phosphate and pH. River gauge data were not available to us, however monthly discharge from the Boconó Dam appeared to be strongly correlated with the seasonal pattern of rainfall.

Fish samples were collected from four zones of the study area on an approximate monthly schedule during the period July 1988 – November 1989. In an attempt to collect a sample that was representative of the local population structure in light of the particular habitat conditions present, several different sampling methods were used, and the results compared here. No single sampling method could have been used at all sites, for example, some sites had too much flow or volume for the use of rotenone or a large seine net, whereas others were too deep to use a castnet. The first zone was the R. Boconó above the Boconó Reservoir where collections were made with different seines (0.2, 0.5, 1, and 4 cm bar mesh; 2 × 3–10 m) and castnets (2 m diameter; 1, 2, 3, and 6 cm bar mesh). The second zone was the Boconó Reservoir where fish were collected with the same seines and castnets, plus with a monofilament nylon gillnet (0.5 and 1 cm mesh; 2 × 50 m) and a multifilament nylon gillnet (4 and 8 cm mesh; 2 × 50 m). Rotenone was used on six occasions to obtain samples from the reservoir. The third zone was the river channel from just below the Boconó Dam to a point 4 km downstream from the town of La Veguita (Figure 1), and the fourth zone was the channel from that point to the river's juncture with the R. Guanare. Fish were collected from the last two zones with seines (1, 2, 4, and 8 cm mesh; 2 × 6.7–10 m), castnets (2, 4, 6, and 8 cm mesh: 2–3 m diameter), and a multifilament nylon gillnet (2 and 4 cm mesh; 2 × 50 m). Collections were made from the shoreline in all four zones, but a boat was also used in deeper waters of the two lower zones. During the high water period, we discontinued our regular sampling effort below the fourth zone (R. Guanare juncture), because fish densities per unit area were so low that sampling was inefficient (sampling of the ribazón during the falling water period was the exception; see below). All coporos were immediately measured and weighed in the field. Depending on the size of the catch, each specimen was dissected for examination of gonad condition, scales were removed for age analysis in the laboratory, and the stomach was removed and preserved in 10% formalin for stomach contents analysis in the laboratory. Twenty scales were removed from the anterior region of the right flank just above the lateral line. Whenever the catch was too large to process rapidly in the field, the remaining undissected specimens were preserved in 10% formalin and returned to the laboratory for later examination.

Scales were placed in 1% KOH solution for 15 days prior to examination under a dissecting microscope. Annual growth checks (annuli) were readily apparent on scales almost without exception, and, in almost all cases, false annuli were easily distinguished from true annuli based on fine-scale structural features. According to Lilyestrom (1983), annuli are formed during the annual ascending migrations, a period when fish cease feeding (Dahl et al. 1963) and may lose up to 15% of their body weight (Godoy 1959). Additional annuli may be associated with spawning or poor feeding by individuals trapped in isolated floodplain lagoons (Bayley 1973), but these factors probably influenced very few of our fishes given that none with > 3 annuli were documented from locations downstream from the Boconó Dam. Age and size of maturation were estimated based on (1) size at age data based on scale annuli (the mean from 20 scales for each individual) and (2) the minimum size of maturation based on the occurrence of ripe gonads in migrating fish during the late dry season prior to the initiation of wet-season spawning. The condition index was calculated as $K = 100‰ W/L^3$ for body weight in grams and standard length in centimeters.

For each retained specimen, a single sample of the gut contents was removed from the thin-walled cardiac stomach located just anterior to the muscular pyloric stomach (Bowen 1983) and placed on a wet-mount slide for examination under a dissecting microscope. The percentages of algae (diatoms and filamentous algae) and mud (amorphous and vegetative detritus) was estimated for each sample. These percentages then were averaged across fish grouped according to life-cycle interval and zone.

From 12 November 1988 until March 1989 (i.e., the falling water period) and in collaboration with commercial fishermen of the region, we monitored the annual upstream migration of coporos and other fishes (ribazón) from the R. Apure in the low llanos near the town of Arichuna to the Boconó Dam in the piedmont. The fishermen follow the annual ribazón in order to maximize their catch, so consequently, we were able to follow the upstream migration by tracking the movements of the local fishers. We accompanied a group of commercial fishermen along a segment of the R. Apure from the mouth of Caño Boqueron (at the town of Arichuna) to the mouth of the R. Portuguesa then up the Portuguesa to the R. Guanare and up the Guanare to the town of Arismendi (Figure 1). From Arismendi, we acompanied a different group of fishermen, some commercial and others subsistence, up the R. Guanare and R. Boconó to the town of Sun Sun. We sampled fishes ourselves in the upstream segment of the R. Boconó between Sun Sun and Puente Páez. Within each region, we monitored

the species composition of the fishermen's catches. Data were summarized for the following river segments: (1) R. Apure within the reach as defined above, (2) R. Portuguesa within the reach as defined above, (3) R. Guanare from its mouth at the R. Portuguesa to Arismendi, (4) R. Portuguesa from Arismendi to the mouth of the R. Boconó, (5) R. Boconó from its mouth at the R. Guanare to Sun Sun, (6) R. Boconó from Sun Sun to La Veguita and (7) R. Boconó from La Veguita to Puente Páez. Overall, 107 days were registered in this field survey, 26 214 fishes were identified from commercial and subsistence catches, and the survey spanned 449 river km. For the most part, fishermen used seine nets of 5 cm mesh and castnets of 6 cm mesh.

Results

Water quality

Dissolved oxygen, suspended solids, and turbidity varied between sites and seasons in the R. Boconó (Table 1). Dissolved oxygen ranged between 4.7 and 6.8 mg l^{-1} at the river entrance into the reservoir (site 1) and between 3.1 and 7.0 mg l^{-1} in the river below the dam (sites 8, 9, 10). Dissolved oxygen declined markedly with depth in the reservoir's central region (sites 3, 4, 5) and near the dam (sites 6, 7, 8). The highest DO recording for the reservoir (6.4 mg l^{-1}) was during March at the surface (central) and the lowest DO (1.0 mg l^{-1}) was during April at the bottom (central). The DO depth gradient was less pronounced at both of the reservoir locations during July compared with November and March (Table 1). During the wet season, bottom DO increased to 3.6 mg l^{-1} where it remained except for a decline to 1.25 mg l^{-1} during September. Dissolved oxygen levels were similar in the regions of the river inflow and outflow (between ca. 5–7 mg l^{-1}), except during the early wet season when DO was elevated near the river entrance (6.0–6.75 mg l^{-1}) and depressed at the dam outflow (3.1–4.7 mg l^{-1}).

During November, suspended solids and turbidity were greatest at the river entrance and near the bottom of the reservoir near the dam (Table 1), and the lowest values were recorded at the surface of

Table 1. Comparison of water quality parameters at different stations in the Río Boconó drainage during three seasons: falling-water season (November), dry season (March), and wet season (July). tr indicates < 0.01 mg l^{-1}.

Site	8 November 1988						14 March 1989						18 July 1989					
	Temp. (°C)	DO (mg l^{-1})	PO_4 (mg l^{-1})	Solids (mg l^{-1})	pH	Turbidity (ntu)	Temp. (°C)	DO (mg l^{-1})	PO_4 (mg l^{-1})	Solids (mg l^{-1})	pH	Turbidity (ntu)	Temp. (°C)	DO (mg l^{-1})	PO_4 (mg l^{-1})	Solids (mg l^{-1})	pH	Turbidity (ntu)
1. entrance	20.5	4.7	tr	844	7.8	396	22.5	5.7	tr	138	8.2	4	21.0	6.8	tr	438	7.7	145
2. surface	26.5	5.1	tr	152	7.9	78	26.0	6.4	tr	96	8.3	3	26.0	5.5	tr	108	7.6	4
3. mid	23.5	3.3	0.18	242	7.9	306	23.0	2.3	0.10	102	8.2	17	23.0	2.7	0.18	118	7.6	5
4. bottom	22.5	3.2	0.24	394	7.8	498	24.0	1.8	0.07	182	8.2	64	24.0	2.4	0.06	201	7.5	86
5. surface	26.5	5.5	tr	100	7.9	13	24.5	6.0	tr	102	8.2	3	25.0	5.6	tr	219	7.7	160
6. mid	23.5	2.1	0.20	212	7.8	188	23.5	2.1	tr	210	8.1	162	23.0	4.2	0.12	358	7.8	365
7. bottom	23.7	1.5	0.25	950	7.4	650	23.5	2.3	0.08	296	8.2	325	22.0	3.3	0.12	437	7.8	356
8. outflow	23.1	5.7	tr	288	7.9	240	24.5	6.2	tr	175	8.2	91	23.0	3.1	0.06	245	7.8	140
9. river	25.9	5.5	tr	284	8.2	180	25.5	7.0	tr	156	8.3	72	23.0	4.0	tr	154	7.8	51
10. river	24.0	5.4	tr	230	8.0	213	24.5	6.9	tr	178	8.3	84	24.0	4.7	tr	164	7.8	125

the reservoir. The same pattern was observed during March and July, except that the river entrance site had low suspended solids and turbidity during March, and surface water near the dam was moderately turbid (219 mg l^{-1} solids, 160 NTU) during July. March is the late dry season, and reduced runoff accounts for the reduced turbidity of the river upstream from the dam. During other periods of the year, the reservoir accumulates suspended solids and reduces turbidity of water in the river downstream.

Water temperature ranged from a low of 20.5 °C at the river entrance during November to a high of 26 °C at the surface of the reservoir (site 2) during July (wet season). The river downstream from the reservóir was always warmer than the river at its entrance into the reservoir (Table 1). Surface waters in the reservoir tended to be 2–3 °C warmer than water at mid-depth and the bottom. pH varied 0.2 to 0.4 units between sites on a given sampling date. Average pH was lowest during July (7.7) and highest during March (8.2), and pH varied little with depth.

Spatial patterns in coporo population structure

Within the Boconó Reservoir, coporos were associated primarily with shallow nearshore habitats with DO > 5.0 mg l^{-1}. Based on our seine and gillnet data from the reservoir, 80% of the coporos were captured from shallow habitats, 20% were captured from the area near the dam, and none were captured in gillnets set in deeper waters near the middle of the reservoir (Figure 3). About 40% of the coporos were captured in the region of the river entrance, a shallow zone where many coarse suspended sediments are deposited.

Females matured at annulus 2 and approximately 23 cm SL, and most males attained maturity at annulus 2 and approximately 17–23 cm SL, values consistent with the findings of Lilyestrom (1983). All of the coporos captured from the Boconó Reservoir and the river above the reservoir were adults 4–8 years of age (Table 2), which corresponds with spawning prior to the final closure of the Tucupido Dam (1984). Coporos were not abundant in the Boconó upstream from the reservoir, and all of our

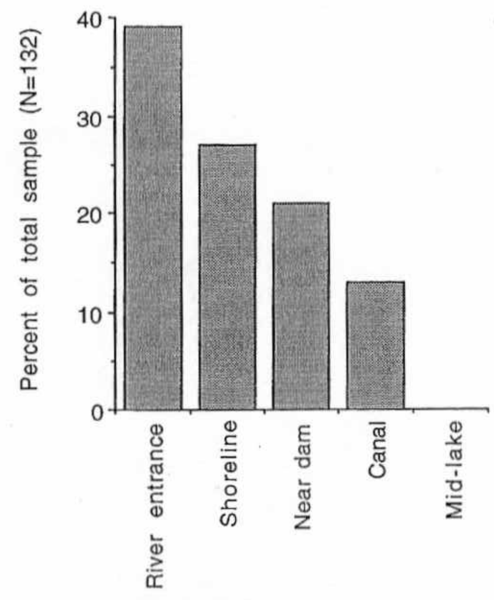

Figure 3. Percentages of coporos caught in different regions of the Boconó Reservoir.

samples were captured within 3 km of the reservoir. The lengths of fish from the reservoir and river upstream ranged from 34.2 to 44.0 cm SL with weights ranging from 993 to 2487 g. Fish from the reservoir and river upstream were larger than fish from the river downstream from the dam (Figure 4), and immature fish were captured in the downstream reaches (Table 2). Immature coporos (< 23 cm SL) dominated the samples from the reach just below the dam, an area where age 1+ fish are blocked during their attempts at upstream migration. No coporos older than age 3 were documented in our samples from the downstream reaches of the river. The

Table 2. Number of coporo (*Prochilodus mariae*) of different size intervals caught in different zones of the Río Boconó.

Zone	Juveniles (< 17 cm)	Maturing (17–23 cm)	Adults (> 23 cm)	Total
A. Up-river	0	0	27	27
B. Reservoir	0	0	132	132
C. Below dam	273	37	41	351
D. Down-river	31	27	159	217

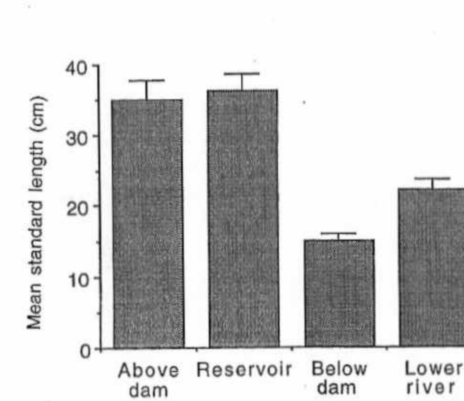

Figure 4. Mean standard length of coporos caught in differen zones of the Río Boconó (bars indicate 1 standard error). The conversion for SL to total length for the coporo is TL = 2.003 + 1.152SL with r^2 = 0.99 (Lilyestrom 1983).

average lengths and weights at age for these fish were as follows: 15.9 cm SL and 116 g at annulus 1 22.9 cm and 273 g at annulus 2, and 27.1 cm and 395 g at annulus 3. Monthly variation in the mean length of coporos was relatively small and revealed no temporal trend for samples from either above or below the dam.

Condition and reproductive state

The body weight-length relationship from a sample of 206 coporos pooled across all four survey zones was W(g) = 0.024 L $(cm)^{3.0}$ with r^2 = 0.985. An exponent of 30 implies that condition is independent of length (LeCren 1951). Based on samples from the lower reaches of the R. Boconó, the average condition (K) of coporos was lowest during the wet season and greatest during the middle-dry season (Figure 5). The increase in condition during the dry season was associated with development of visceral fat deposits, and the decline in condition during April was associated with a reduction in visceral fat and gonad development in adults. Most coporos of both sexes had well developed gonads by May. Coporos from the reservoir and river upstream always registered large condition values (mean K = 8.0, SE = 2.5) and contained large deposits of visceral fat. Immature fishes from the river downstream rarely

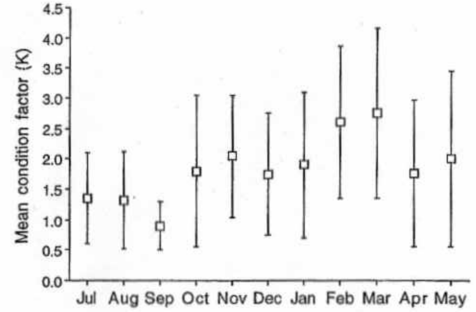

Figure 5. Monthly variation in mean condition factor (K) for Río Boconó coporos during 1988–1989 (bars indicate ±1 standard error).

contained large visceral fat deposits and mean K was 1.95 (SE = 2.3).

Nearly all coporos achieved gonadal maturation by June. Coporos in the reservoir achieved the same level of gonadal maturation during the same time period as those from the furthest downstream region of the river (La Veguita-R. Guanare). However, successful reproduction by the reservoir fish appears to be very unlikely based on the absence of immature and young adult fish. During July 1988 and again during June 1989, one of us (ABD) observed schools of coporos in the shallow (< 3 m) slow moving water in the region of the river entrance into the reservoir. The low grunting sound characteristic of courting males was detected from above the water's surface. These schools did not disperse even after several throws of a castnet in their midst. The females did not emit sounds, and they occupied areas of faster flowing water. No spawning behavior was ever observed in the reservoir, so it is unknown whether the apparent reproductive failure in the reservoir is due to failure to spawn or mortality of early life intervals due to lack of suitable habitat.

In the river reach just downstream from the dam, no adults with mature gonads were encountered. The zone further downstream yielded fish with maturing gonads beginning in December and with fully mature gonads during May and June (based on examination of 87 individuals). No evidence of spawning within this zone was obtained, and the capture of adults in this reach declined abruptly during July. These ripe adults must have migrated downstream to spawn in river channels and floodplains located downstream in the drainage basin.

Diet

Overall, immature coporos consumed more algae and less mud (fine amorphous detritus) than adult size classes. The adults from the river upstream and reservoir zones consumed material that was identified as mud containing only trace amounts of diatoms and filamentous algae (Table 3). This apparent lack of algivory was despite that attached algae were abundant on submerged woody debris and other substrata within these zones. In the river reach just below the dam, juveniles consumed only algae, large juveniles (17–23 cm SL) consumed mostly algae but also a small fraction of mud, and adults consumed mostly algae and about 30% mud by volume. In the river zone furthest downstream, juveniles consumed mostly algae plus 25% mud, large juveniles consumed mostly mud and a small fraction of algae, and adults consumed only mud. The greatest number of empty stomachs was found

Table 3: The volumetric percentage of algae and mud in diets of coporo (*Prochilodus mariae*) of different size intervals caught in different zones of the Río Boconó.

Zone	N stomachs with food	N empty stomachs	Juveniles (SL < 17 cm)		Maturing (SL 17–23 cm)		Adults (SL > 23 cm)	
			algae	mud	algae	mud	algae	mud
A. Up-river	25	2	–	–	–	–	0	100
B. Reservoir	66	45	–	–	–	–	0	100
C. Below dam	248	5	100	0	88	12	79	21
D. Down-river	123	43	75	25	14	86	0	100

in fish from the reservoir and the furthest downstream river reach, and almost all of these were adults taken during the period of the ascending migration (November–February).

Composition of the ribazón

During the early dry season (November–March), the floodplains east of San Fernando de Apure drain their waters into tributaries of the R. Apure and R. Arauca. Caño Boqueron is one such tributary and its mouth at the R. Apure (near Arichuna) served as the starting point for our study of the ascending fish migration (ribazón) of 1988–1989. We began monitoring on 12 November 1988 at Arichuna and terminated on 30 March 1989 about 1 km upstream from Puente Paez on the R. Boconó. According to some of the local fishermen, most of the fishes of this ribazón originate from the Apure floodplains near Arichuna, and a minor component comes from the floodplains lying further upstream at Camaguán (lower R. Portuguesa just below La Unión), Chiriguare (lower R. Guanare below Arismendi), and the lower R. Boconó. Other fishermen believe that the ribazón originating at Arichuna progresses upriver in the main channel of the R. Apure, and that few enter the R. Portuguesa. According to these fishermen, most fishes of the R. Portuguesa-Guanare-Boconó ribazón originate from the floodplains of Camaguán. Ribazón samples from the lower river reaches were easier to obtain and contained more fishes (Table 4). The abundance of fishes in our survey samples declined markedly between the R. Guanare (N = 6101) and lower R. Boconó (N = 1788).

Coporos sampled from the early ribazón at the R. Apure and Portuguesa averaged 30.9 cm SL, and those from the later stages of the ribazón at the R. Guanare and Boconó averaged 24 cm. Most of the late ribazón coporos from the upstream reaches were approaching age 2 and the length at which maturation occurs (23 cm SL). Several species comprised the ribazón, but the coporo was by far the most important (Table 4). The percent contribution by the coporo to the total number of fishes sampled ranged from 83.9 to 39.8, and declined from downstream to upstream river segments. The anostomids

Table 4. Species composition of the ribazon (percentage of individuals) captured by commercial fishermen in 7 reaches of the Río Boconó-Río Apure migration route.

Common name	Species	Apure	Portuguesa	Guanare-1	Guanare-2	Boconó-1	Boconó-2	Boconó-3
	Prochilodontidae:							
Coporo	*Prochilodus mariae*	83.94	64.54	63.96	53.84	51.12	52.61	39.84
	Characidae:							
Palambra	*Brycon whitei*			0.11	0.79	6.37	8.77	11.72
Cachama	*Piaractus brachypomus*	0.15	1.41	1.89	0.90	2.85	1.85	
Palometa	*Mylossoma duriventris*	8.85	14.46	13.86	21.50	9.79	8.94	
Saltador	*Salminus hilarii*					1.69	2.34	
	Anostomidae:							
Mije	*Leporinus friderici*	5.42	9.18	6.17	13.34	17.45	11.13	15.63
Tusa	*Schizodon isognathus*	4.27	3.32	7.00	11.30	14.67	28.91	
	Doradidae:							
Bagre sierra	*Oxydoras niger*	1.46	5.36	9.33	0.38	0.22		
	Pimelodidae:							
Bagre dorado	*Brachyplatystoma rouseauxi*	0.03						
Bagre hipi	*Goslina platynema*	0.01						
Bagre cupido	*Hemisorubim platyrhynchos*	0.05	0.14	0.58	0.18	0.62		0.78
Bagre rayado	*Pseudoplatystoma fasciatum + P. trigrinum*	0.06	0.64	0.78	2.07	0.28	0.34	0.78
Total number surveyed		7692	5823	4489	6101	1788	593	128
Total kg surveyed		49	48	105	179	38	19	11

Leporinus friderici and *Schizodon isognathus* were the next most abundant species in the ribazón. *Leporinus,* an omnivore, showed no longitudinal trend in relative abundance, but *Schizodon,* an herbivore, tended to increase in relative abundance in upstream reaches. The omnivorous characid *Brycon whitei* entered the ribazón in the R. Guanare and gradually increased in relative abundance in upstream reaches. None of the catfishes in the ribazón were abundant, and all five of the pimelodid catfishes are large piscivores that exploit coporos and other species of the ribazón.

On 28 November in the R. Apure 8 km downstream from San Fernando de Apure, we estimated an approximate density of 1 040 000 individuals ha^{-1}, of which 863 200 were coporos. These estimates are based on an average of 29 fish m^{-3} (24 coporos) at an average water depth of 3 m. We obtained these values from 40 successive samples from a seine net measuring 150 × 4 m (3.5 cm mesh) that was used to encircle an area between two boats. The school of fishes from which we obtained these samples occupied an area approximately 2.5 km along the length of the river channel with an average width of approximately 36 m. Based on this rough estimate of 9.0 ha occupied by the school, we estimate 9 360 000 total fishes, of which 7 758 800 were coporos. Using the same methodology, we estimated 360 000 fishes, of which 198 000 were coporos, in the R. Guanare just downstream from Arismendi. This school occupied and area of approximately 500 m × 30 m where the depth averaged ca. 2 m. Upstream from this location, the river channel is narrower and some fishermen use gillnets set perpendicular to the river channel. In response to the net obstructions in these upstream river reaches, the ribazón disperses into scattered groups and individuals. From January to April, no large fish schools were observed in the R. Boconó. In contrast, based on 935 throws of a 2 m diameter castnet, 0.083 coporos per throw were obtained in the R. Boconó. Based on 612 throws with the same castnet, an average of 8.0 coporos per throw were captured in the R. Apure, Portuguesa, and Guanare during November, December, and part of January.

Discussion

The life-cycle of the coporo is complex, yet well suited to exploit large-scale patterns of spatial and temporal variation in the western llanos of Venezuela. Migration is a response to seasonal changes in habitat availability and quality at the landscape level. Extensive wet-season flooding of the low llanos (the floodplains of the lower R. Apure and the flat savannas to the south) provides a vast and rich habitat for adult foraging and the feeding, growth, and survival of larvae and juveniles. As coporos migrate, sometimes more than 300 km, from river channels to inundated floodplains, their gonads mature and energy stored as fat is consumed (Saldaña & Venables 1983). As the floodplains gradually dry up during September-December, fishes must return to the river channels. A portion of the floodplain fish may remain resident in lagoons until the next annual flood, and the decision to migrate or remain may be associated with body condition relative to the energetic demands of migration (Saldaña & Venables 1983). The size and density of ascending schools (ribazóns) diminishes as the fish move upstream. The coporos of the ribazóns appeared to actively migrate primarily during the night, yet they remained densely congregated with movement by day.

The annual ecological events and major movements of coporos in western Venezuela are summarized in Figure 6. This scenario is similar to that described for *Prochilodus* and *Semaprochilodus* species in the central Amazon (Goulding 1980, Ribeiro 1983, Vazzoler et al. 1989, Vazzoler & Amadio 1990). Presumably, the primary function of the ribazón is dispersal of the regional population within rivers and streams of the R. Apure basin of western Venezuela. We hypothesize that this dispersal behavior is a density-dependent response to food and/or space limitations in river channels during the dry season. We did not observe feeding behavior by migrating coporos of the early ribazón within the R. Apure and Portuguesa, but we observed feeding behavior by coporos after the schools had dispersed in the R. Guanare and Boconó during the latter stages of the 1988–1989 ribazón. According to our findings for the R. Boconó, it appears that most of the copo-

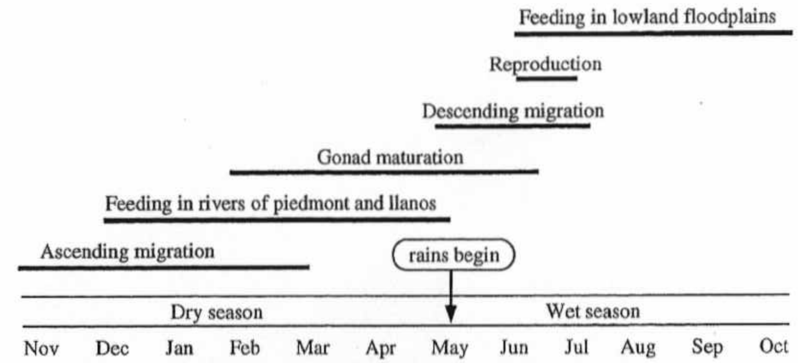

Figure 6. Summary of the annual cycle of ecological periods and movements of coporos in western Venezuela.

ros that attempt to penetrate the upper river reaches in the piedmont are smaller individuals of age 1–2 yr. Smaller coporos consumed greater fractions of algae, therefore, smaller fish may move further upstream in search of algal growth on hard substrates. Conversely, larger coporos consumed greater fractions of fine detritus, and these silty deposits would be more abundant in lower velocity habitats of lower river reaches.

Ribazóns also could function to reduce predation. Coporos, and to a much lesser extent omnivorous and hebivorous characiforms, far outnumbered piscivores (principally *Pseudoplatystoma* spp.) in the ribazón. As the floodplains dry up and fish densities increase in river channels and lagoons, predator-prey encounter rates increase. Schooling can function to reduce the threat of predation mortality for individuals, but migration to locations higher in the watershed with less extensive floodplains should further reduce predation risk. Whereas some large predators probably migrate for some distance in pursuit of the ribazóns, others appear to remain in the lowlands at 'feeding stations', areas where tributaries that drain the floodplains deliver their contents to the main river channels. The saltador, *Salminus hilarii,* was the only piscivorous characid captured with the ribazón, and this species frequently migrates far into the piedmont in a manner similar to the coporo. The abundance of the omnivorous palambra, *Brycon whitei,* in the ribazón increased with successive upstream samples, and indication that this species does not migrate as far int the lowlands during the wet season as the coporo.

All coporos of the Boconó Reservoir and uppe R. Boconó were adults, but neither migration no evidence of successful reproduction was observe there during our study. We made 17 surveys and in terviewed 12 local residents along the river abov the reservoir, and no fish migration was document ed. Limited movement apparently occurs within th reservoir during the dry season when courtin males were observed in the shallow upper region o the reservoir. Coporos do not seem to use most o the volume of the reservoir, rather they seem to b restricted to relatively shallow areas with DO : 3.5 mg l^{-1}. Coporos of the reservoir were larger an older (age 4–8) than those captured downriver (ag 1–3). The coporos above the dam appear to be a isolated stock that probably will be extirpated with in the next decade as the last old individuals di Without access to the floodplains of the lowland the species appears incapable of completing its lif cycle. This situation contrasts sharply with that c the Itaipú Reservoir in Brazil/Paraguay where sea sonal floodplains lie upstream from the reservoi within the upper Río Paraná basin (Agostinho et a 1993). *Prochilodus scrofa* from Itaipú migrate up stream to the floodplains for spawning and feeding and this behavior probably has a genetic/evolution ary basis due to the unusual river basin geomor phology in this region. A similar situation may exis in Guri Reservoir on the R. Caroní basin in easter Venezuela. *Prochilodus rubrotaeniatus* of Guri ap parently spawn in the floodplains in the region above the reservoir where the R. Caroní and Parguaza enter (Alvarez et al. 1986).

Regulation of a relatively stable reservoir level has created problems for coporos downstream. First, wet-season flooding has been greatly reduced in the floodplains of the lower R. Boconó, which seem to have provided an historical spawning habitat for at least a small fraction of the coporos of the region. Second, since the initiation of electrical generation at the Boconó Dam in 1987, the modified instream flow and water chemistry could disrupt coporo migratory behavior. Third, the dam blocks upstream migration so that fishes now gather below the dam for variable periods of time and are more vulnerable to capture by fishermen.

In recent years, coporo ribazóns have diminished greatly in western Venezuela. Chapman (1980) described great numbers of migrating coporos in the R. Boconó, as well as their great importance in the diet of the local people. Now only scattered schools of immature fish and few adults ascend through this region. According to our interviews with local residents along the lower R. Boconó, the coporo migrations have been sporadic and very small since the closure of the dam during the mid-1980s.

We interviewed local people and assessed environmental impacts in each of the principal Andean piedmont rivers of the Apure basin. We asked people living along each river to describe the state of the most recent ribazón. People in 15 areas reported no ribazón, and people in five areas reported very small migrations of scattered individuals (Table 5). Only one river in Portuguesa State and three rivers in Barinas State were reported to have relatively large ribazóns in recent years. All four of these rivers lacked major environmental impacts, whereas 19 of the 20 rivers in which ribazóns had been reduced or eliminated showed obvious anthropogenic impacts. Nine of these rivers had impoundments that obstruct upstream migration, seven had severely reduced instream flows primarily due to large-scale deforestation in their watersheds, and five received major contamination from urban and agricultural sources.

Notwithstanding the issue of the obstruction to migration posed by the dam, the R. Boconó does not now have the environmental conditions required to support migratory coporo. The coporo densities below the dam during the dry season are probably artificially high and food may be limiting as indicated by the low condition values for this stock. During the dry season in the area just below the dam, we estimated a density of 1506 coporos in an area of approximately 0.05 km^2 (i.e., 0.03 m^{-2}). These fish did not seem to congregate nor did they attempt to enter the turbines or ascend the dam wall. We have noted the latter at other dams with spillways (e.g., R. Guanare). Repeated failed attempts to scale dams undoubtedly leads to exhaustion and injury. Dissolved oxygen periodically falls below 3.5 mg l^{-1} in the area just below the Boconó Dam (Table 1), and this might induce stress in coporos.

Solutions that would allow migratory fishes to coexist with dams are needed, because plans for widespread dam construction exist for most of the major river basins of South America (Fearnside 1989, Quirós 1989, Barthem et al. 1991). Fish passages have proved largely ineffective for Neotropical migratory fishes (Quirós 1989). Pool and weir-type fish ladders seem to be effective to only 8–10 m, and it is difficult to attract migratory fishes to the entrance (Quirós 1989, personal observations at the R. Guanare). Borland-type fish locks have been installed in at least one dam in Argentina, but their handling capacity is so low that they probably do little to aid large schools of ascending fishes, and they are only effective to heights of 25 m (Quirós 1989). The high handling capacity required for migratory *Prochilodus* would require a fish elevator, but the potential effectiveness of this expensive technology is unknown and debatable (Quirós 1989). Despite our current lack of information on Neotropical fish response to fish passages, many of the countries of South America already have laws requiring the construction of fish passages in new dams (Quirós 1989).

Table 5. Summary of the current condition of rivers and coporo ribazons in the Río Apure drainage basin of western Venezuela.

River	Condition	Ribazón
Estado Cojedes:		
Río Tinaquillo	contaminated	absent
Río San Carlos	reduced flow (< 1 m^3 s^{-1})	very small
Río Cojedes	obstructed, contaminated	absent
Estado Portuguesa:		
Río Sarare	contaminated	absent
Río Acarigua	reduced flow (< 2 m^3 s^{-1})	very small
Río Ospino	dry	absent
Río Guache	reduced flow (< 1.2 m^3 s^{-1})	absent
Río Las Marías	reduced flow (< 0.5 m^3 s^{-1})	very small
Río Portuguesa	normal	normal
Río Guanare	obstructed	absent
Río Tucupido	obstructed, dry	absent
Estado Barinas:		
Río Boconó	obstructed	absent
Río Masparro	obstructed	absent
Río Santo Domingo	obstructed	absent
Río Paguey	normal	very small
Río Canagua	moderately contaminated	absent
Río Socopo	normal	normal
Río Michay	reduced flow	very small
Río Suripa	normal	normal
Río Curbaty	normal	normal
Estado Tachira:		
Río Caparo	obstructed	absent
Río Doradas	obstructed	absent
Río Uribante	obstructed	absent
Río Torbes	contaminated	absent

R. Smith (unpublished undergraduate thesis, 1987, UNELLEZ, Guanare) proposed construction of a series of canals and ponds along the margins of river channels to create additional habitat for coporos in impoundment tailwaters. The design would permit migratory fishes to enter and exit the refuge from the river and provide auxillary feeding habitat during the dry season. During years when population densities exceed the carrying capacity of the refuge, a portion of the fish stocks could be harvested easily. Such a refuge system of earthen canals and ponds probably would cost less and require less maintenance than fish passage devices of questionable utility. To increase refuge carrying capacity, enrichment of algal stocks and detritus could be achieved using standard aquaculture methods.

Another possible solution is to block access to impounded rivers at their mouths, so that most of the ascending fishes are shunted toward unimpounded tributaries with appropriate habitat. In a manner similar to that employed by llanos gillnet fishermen, small mesh (< 4 cm) blocknets might be positioned across the mouth of the R. Guanare so that ascending coporos would be forced to ascend the R. Guanare Viejo (a south bank tributary) or the R. Portuguesa. Unfortunately, very few unimpacted rivers remain in western Venezuela to receive rerouted migrants (Table 5).

In addition to dams, reduced instream flows and pollution, overfishing poses a serious threat to coporo stocks in western Venezuela. Coporo fishing has a long tradition in the llanos, but true commercial fishing began in the llanos during the 1950s. During our survey of the ribazón, one of us (ABD) interviewed fishermen and fish buyers, and all stated that the fish catch was declining with each passing year. Fishing had been especially poor in the upper and middle reaches of the basin during the five years preceeding our study. As stocks decline, illegal fishing methods are used increasingly. Near the mouth of the R. Portuguesa, gillnets, including many of illegal mesh sizes, are set perpendicular to the river channel. These nets catch some of the ascending coporos, but probably reroute many more fish upstream in the R. Apure channel. Gillnets also block the R. Guanare, especially in places where the channel is narrow and there is little access to the river by land. Clearly, more effective enforcement of fishing regulations will be required, if coporo stocks are to remain viable in the remaining unimpacted rivers of western Venezuela.

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Incomplete mixing of limed water and acidic runoff restricts recruitment of lake spawning brown trout in Hovvatn, southern Norway

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Synopsis

Repeated liming of Hovvatn during the 1981–1995 period assured successful reintroduction of lake spawning brown trout, *Salmo trutta.* Poor natural recruitment to the population was associated with low survival during early life stages (before hatching) as shown by the 0.5, 3.5, 0.9 and 1.0% of live embryos found in natural redds during the 1992–1995 period, respectively. The low survival was most likely caused by the combination of shallow spawning areas (<2.0 m) and acidic runoff (pH 4.0–4.8) which overlayed the limed part of the water body during the ice covered period. It is therefore concluded that this type of episodic acidification poses a major threat to lake spawning salmonids, and that it can retard or inhibit biotic recovery towards preacidified conditions expected as a result of liming. Addition of limestone gravel (8–32 mm) onto spawning grounds was an efficient alternative liming strategy as 33–36% live embryos were found in this substrate. Conversely, the trout actively avoided additions of shellsand, a behaviour most likely caused by the small particle size of shellsand (3–7 mm) relative to natural spawning gravel.

Introduction

Acidification is one of the major environmental problems in Scandinavia. In Norway, fish losses caused by acidification are extensive as more than 2500 populations, including 2129 populations of brown trout, *Salmo trutta* , have been lost (Hesthagen et al. 1994). Large-scale liming is used to mitigate the acidification process (Hindar & Rosseland 1991, Henrikson & Brodin 1995) and is also applied, although to a lesser extent, in other affected areas in Europe and North America (Olem 1991).

Lakes are most often limed by direct application of limestone powder onto the lake surface. Indigenous fish populations threatened by acidification or reintroduced fish may thereby be protected. The reacidification process starts immediately after liming as acidic runoff water enters the lake from the untreated catchment area. Although lakes are normally relimed before the whole water body reacidifies, incomplete mixing between limed water and acidic inflows, often associated with snowmelt or heavy rain, can produce distinct water chemical gradients. A vertical pH gradient is established during winter or spring when inverse thermal stratification prevents the cold, acidic runoff in the surface layer from mixing with the more circumneutral (i.e. limed) water deeper in the water column (e.g. Hultberg & Andersson 1982, Booth et al. 1986, Hasselrot et al. 1987, Gubala & Driscoll 1991, Abrahamsson 1993). Similar gradients have also been reported from unlimed lakes during the early phases