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Factors affecting growth rates of young tropical floodplain fishes: seasonality and density-dependence

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Synopsis

Deviations of growth increments from a model describing average growth of 12 common fish species, mostly juveniles, were compared with hydrological variables and biomass density (ranging from 1 g m^{-2} to 83 g m^{-2}) of potentially competing species of similar size ranges (guilds). Seasonal effects on growth were highly significant for omnivores but not for detritivores. Omnivores exhibited faster growth during the rising water season, and higher growth rates were associated with periods of increased rates of flooding during this season, which could be associated with increased availability of food. No species exhibited density-dependent growth when all seasons were considered together. During the rising-water-level season, no inverse relationship between growth and biomass density was found in any of the 11 species tested at $p = 0.05$. During the short falling-water season, 2 of 8 species tested did exhibit density-dependent growth but a sign test of correlation coefficients from all species was not significant. These two significant results were from four omnivores tested. However, density-dependent growth was not indicated when the data were pooled within either detritivore or omnivore guilds by hydrological season. It was concluded that with the possible exception of juvenile omnivores during the limited falling-water season, density-dependent growth, and by implication interspecific competition, had no effect in regulating the species' populations investigated in the floodplain environment. Conversely, the importance of a seasonal hydrological regime in maintaining growth rates, at least for omnivores, was evident.

Introduction

Little is known about what may regulate fish populations and production in floodplains associated with tropical rivers. The effects of hydrological season and the density of potentially competing species on a key variable, growth rate, are examined in this paper.

Factors controlling fish growth in seasonally flooded environments have been reported in temperate areas (Viosca 1943, Stroud 1948, Starrett & Fritz 1965) but rarely for adults in tropical latitudes (Dudley 1974, Kapetsky 1974), although seasonal feeding (Goulding 1980) and growth (Welcomme 1979) in adult tropical floodplain fishes have been recognized. The effects of physical factors or the density of potential competitors on growth rates are little known in floodplain systems. Studies of any aspect of the dynamics of young tropical floodplain fish in the context of their communities are lacking.

In other ecosystems, density-dependent growth rates have been documented for temperate juvenile fish in riverine (Legget 1977) and marine habitats (Raitt 1939, Iles 1968, 1973). This phenomenon has been reported occasionally for adult fish in relatively undisturbed lakes (Hile & Deason 1934, Hile 1936) and frequently for heavily manipulated lentic populations (Beckman 1941, Stroud 1948, Bennett 1954, LeCren 1958, Grice 1959). Some researchers have failed to detect the phenomenon even when population size has changed considerably (Hickling 1946, Starrett & Fritz 1965), and even a positive correlation of growth rate and population density has been documented in a temperate river (Kawanabe 1958).

Variation in growth rate was measured in a subset of common, largely juvenile, central Amazon floodplain species of high biomass and productivity. The considerable seasonal variation in flooding results in different habitats and feeding opportunities. Therefore, deviations from average growth patterns were related to densities of guilds (potentially competing species groups) occupying subsets of habitats within hydrological seasons, in addition to analysing differences between seasons.

The environment

The littoral zone in the central Amazon floodplain (Fig. 1) changes predictably with hydrological season. Small fish, accompanied by piscivores and other large fish, follow the advancing water's edge as the level rises, exploiting food sources in the newly inundated areas (see also Chapman et al. 1971). Nutrients are released from the ground and contribute to the rapid aquatic macrophyte and periphyton growth which keeps up with the advancing water. Associated with these macrophytes are the largest concentrations of invertebrates reported from the area (Junk 1973), and ultimately, a rich source of detritus derives from the aquatic and terrestrial vegetation and phytoplankton. Although oxygen levels are generally tolerable close inshore, locally dense concentrations of macrophytes and detritus are often associated with deoxygenation (Junk et al. 1983).

As the rate of increase slows or stops at high water level, oxygen drops as the vegetation decays, as reported by Dudley (1974) and Chapman et al. (1971) in Africa. Also, the processes of increasing food production and availability are probably slowed down. However, absolute quantities of food available to fish must be positively influenced by the fourfold increase in water area compared with the low water season in the area concerned (Bayley 1983).

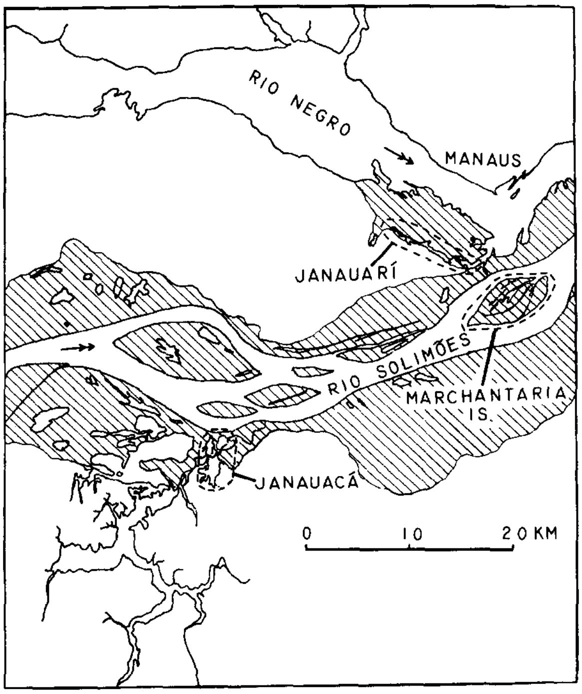

Fig. 1. Central Amazon showing 3 sampled areas. Hatched area indicates maximum area flooded.

When the water level drops, which occurs in about half the time it takes to rise (Fig. 2), vegetation is stranded, and the associated rich invertebrate food supply is lost. Zooplankton densities increase (Brandorff & Andrade 1978), but by this time the surface area is much reduced. Emigration from the forested and deforested floodplain occurs, and rising concentrations of fish in the littoral zone are partly mitigated by emigration of some larger species to the channels and rivers and by predation (Worthmann 1982, Bayley 1983).

Methods

Sampling

Abundance and biomass density estimates for each sample were possible because the efficiency of the

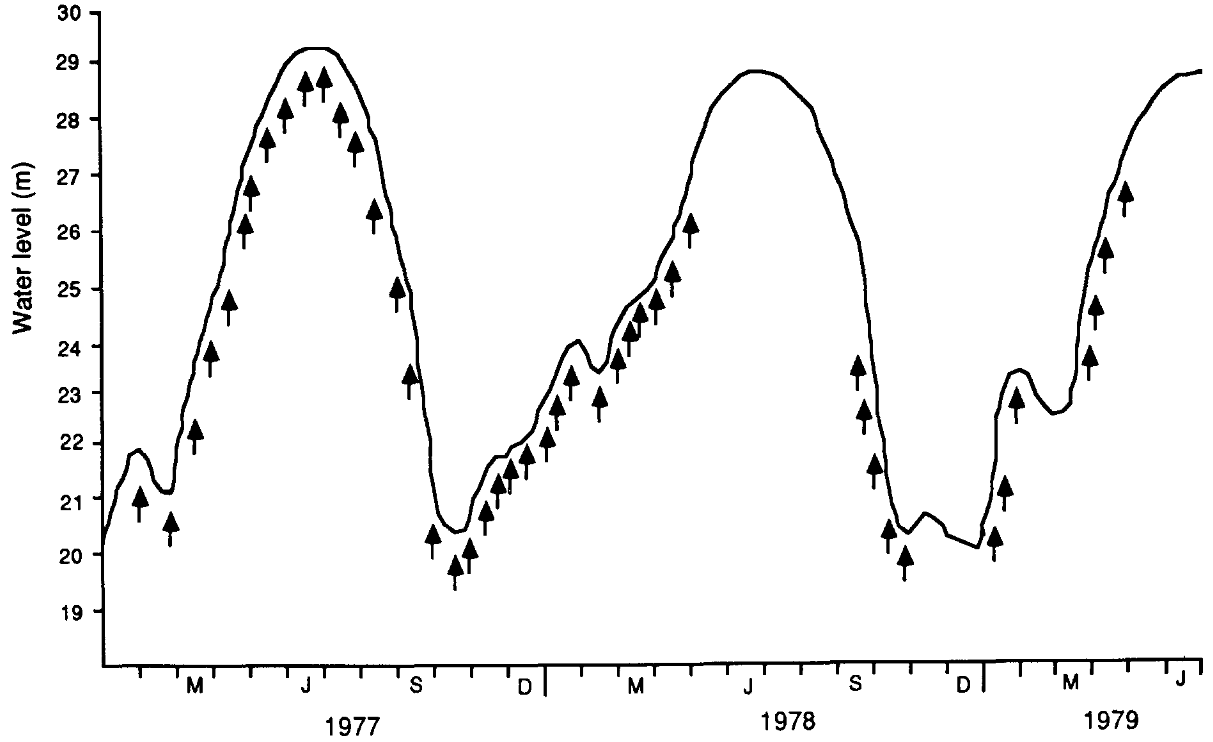

Fig. 2. Daily water levels (solid line). Arrows indicate times of sampling excursions.

sampling gear was determined in a separate study covering the same range of habitats and seasons (Bayley 1983). Twenty-three calibration experiments were conducted in which the standard gear, a 25 m long by 6 m deep seine of 5 mm stretched mesh, was fished within a blocked-off area. The standard seine fished a known area within the 50 m block net, so fish could evade the seine as though it were being fished in isolation. The population enclosed by the block net was estimated from the retrieval of marked fish after beaching the net, and the part of that population vulnerable to the 25 m seine was estimated according to the proportion of the blocked area covered by the seine. Efficiency depended on fish length and species group (Table 1). Therefore, growth rate and biomass estimates presented here are based on size distributions and quantities corrected for the appropriate catchabilities of each species-size group under each sampling condition. Captured fish ranged from 9 mm to 1 m long, although the majority of the growth estimates was for fish between 15 mm and 200 mm long.

Samples were obtained from February 1977 to June 1979 in three areas in the R. Solimões floodplain upstream of Manaus (Fig. 1): Marchantaria Island, Janauacá, and Janauarí. Water from the Rio Solimões influenced sampled areas for varying periods dring the annual hydrologic cycle. Intensive sampling, yielding 588 samples, took place every 2 weeks for 15 months starting in March 1977 (Fig. 2). Samples were taken from the shoreline and up to 4.5 m deep and 300 m offshore.

Fish distribution was restricted during intermediate and high water levels due to a deoxygenated hypolimnion below 3–6 m which contains H_2S (Schmidt 1973). In sheltered areas the deoxygenated zone can begin at 1–2 m depth, and mid-day surface values of only 0.5 m l^{-1} DO were often recorded during intermediate to high water levels (Junk et al. 1983). At low water there is sufficient oxygen for fish throughout the water column in most habitats of the floodplain because the depth is less than that of the epilimnion at higher water and macrophytes are sparse. However, the extent of area flooded is much reduced.

Offshore areas contain a pelagic assemblage with few species being shared with inshore areas. Samples at the edge and within clearings of the flooded forest were obtained, but not within the forest itself. Floodable forest made up about 34% of maximum flooded area in Marchantaria and Janaurarí and about 14% in Janauacá, after discounting permanently inundated areas (Bayley 1983: Chapter 2).

Annual water level amplitudes reached 8.5 m during the study period (Fig. 2). Therefore, the geographic locations of samples varied with each period in concert with the displacement of habitats. During the rising-water season, these habitats consisted of varying quantities of aquatic and terrestrial macrophytes, logs, and branches which were removed after enclosure. During the falling-water season, macrophytes remained stranded and more open-water habitats with softer substrates predominated.

Growth

Weight-length relationships were derived from measurements of recently killed larger specimens, and were supplemented by lengths and weights from smaller, preserved fish whose measurements had been corrected for changes due to the time spent in formalin and alcohol (Bayley 1983).

Twelve common species (Table 2) with temporal series of length frequencies showing clear modal size progressions (Bayley 1983: Fig. 4.1, 4.2) were selected for growth rate analyses, comprising 6.2×10^4 individual fish. Similar, but more limited, data were obtained from two more species (Bayley 1983), which were only included in multispecies comparisons. Each cohort consisted of the pooled distributions from an average of 8 seine samples, corrected for sampling selectivity. There was an average of 119 individual fish per cohort.

Since individual growth is implied from modal progressions, bias may result from size-dependent mortality within cohorts. Worthmann (1982:40) compared modal progressions with otolith daily growth rings of a common species, *Plagioscion montei*, from Janauacá. For a cohort ranging from 20 mm to 100 mm modal standard length, identical growth rates were obtained from the independent methods.

Examples of all the species have been identified and catalogued at the Smithsonian Institution and São Paulo Museum, Brazil. They could be distinguished from congenerics down to the smallest size captured, except for two sibling species groups which contain very closely related forms which could be defined as different species. *Curimata roseni* is externally identical to *C. kneri* and grows to a similar size, but possesses two less vertebrae on average (R. Vari, pers. comm.). *Anchoviella carrikeri* is identical to *A. guianensis* except for a slightly longer jaw (G. Nelson, pers. comm.) but grows to a similar size.

Table 1. Mean percent efficiencies (based on numbers of fish caught divided by the vulnerable population within the area covered by the net) of 25 m seine under different species groups and selected lengths.* (Mean length in mm, from snout to extremity of median caudal ray, given in parentheses.)

Species group:	A	B	C
Max. efficiency:	11% (15) 48% (20) 87% (40) 15% (200)	7% (15) 26% (20) 73% (60) 49% (200)	6% (15) 22% (20) 39% (50) 14% (200)

A: Open water, typically schooling, species; dominated by Characoidei.

B: Territorial, especially when adult; dominated by Cichlidae.

C: Bottom living or eel-like; dominated by Siluriformes.

* Data based on two fishing methods: standard beach seine describing a semi-circle, and an offshore method describing a circle and gathering the lead and float line at one point. The efficiencies of these two methods were indistinguishable. A minority of samples was taken in deep water using the net as a lampara seine from a canoe, and produced lower efficiencies in the range of 2–29%.

The mean individual fresh weight calculated for each cohort from length-weight relationships (Table 2) was plotted against time for each species (Fig. 3). Since weight is on a logarithmic scale, the instantaneous growth rate is represented by the slope, which decreases with increasing age.

The simplest model which described growth in each species without requiring absolute age determinations was selected. The allometric relationship, $dW/dt = kW^x$ (W = weight, k, x = fitted parameters), of Parker & Larkin (1959) provided good empirical fits (Table 3) using the discrete, linearized form of the model, $\ln(\Delta W/\Delta T) = \ln(k) + x\ln(W)$.

The residuals from these regressions and others below were well-behaved statistically: at $p = 0.05$ no skewness, kurtosis, or correlation with the independent variable was observed. Therefore, parametric tests were employed. A total of 295 estimates of growth increments for the 12 species were obtained.

Independence of sampled areas

Factors affecting growth could be tested by using data from each area or by pooling data from all three areas. The former would provide more statistical power, but would be invalid if a single subpopulation of each species occupied two or more areas. Although growth differences were not detected between areas, there were indications that the sub-

Table 2. Biometric and biomass data for 12 species used in growth analyses.

Max. wt. # (g)	a*	b* ± SE	r^2*	% of family biomass	% of total biomass	Feeding guild (when juvenile)
Acarichthys heckeli (Cichlidae)						
145	1.466E-5	3.055 ± 0.006	0.996	17	2.1	omnivore
Colossoma macropomum (Serrasalmidae)						
27000	2.064E-5	3.053 ± 0.016	0.995	9	0.9	omnivore
Triportheus albus (Characidae)						
430	1.808E-5	2.900 ± 0.013	0.992	8	0.8	omnivore
Triportheus angulatus (Characidae)						
460	1.162E-5	3.026 ± 0.009	0.995	14	1.4	omnivore
Triportheus elongatus (Characidae)						
165	1.319E-5	2.927 ± 0.016	0.992	24	2.4	omnivore
Brycon melanopterus (Characidae)						
5200	1.134E-5	3.117 ± 0.029	0.990	6	0.6	omnivore
Anchoviella guianensis (Engraulidae)						
9.7	1.711E-6	3.439 ± 0.031	0.978	60	0.1	omnivore
Semaprochilodus taeniurus (Prochilodontidae)						
540	2.296E-5	2.976 ± 0.018	0.990	19	1.6	detritivore
Semaprochilodus insignis (Prochilodontidae)						
810	2.596E-5	2.976 ± 0.015	0.989	20	1.6	detritivore
Prochilodus nigricans (Prochilodontidae)						
2300	1.768E-5	3.028 ± 0.014	0.994	61	5.0	detritivore
Potamorhina latior (Curimatidae)						
385	7.146E-6	3.160 ± 0.018	0.992	21	0.7	detritivore
Curimata kneri (Curimatidae)						
325	1.001E-5	3.169 ± 0.015	0.998	6	0.2	detritivore
Total					17.5	

Maximum weights were taken from gillnet or market data (unpublished) when they exceeded the maxima from the seine samples.
* Parameters of weight-length relation $W = aL^b$ (W in g, L in mm) using GM regression of Ricker (1973) of the $\log_e$ transformed variables.

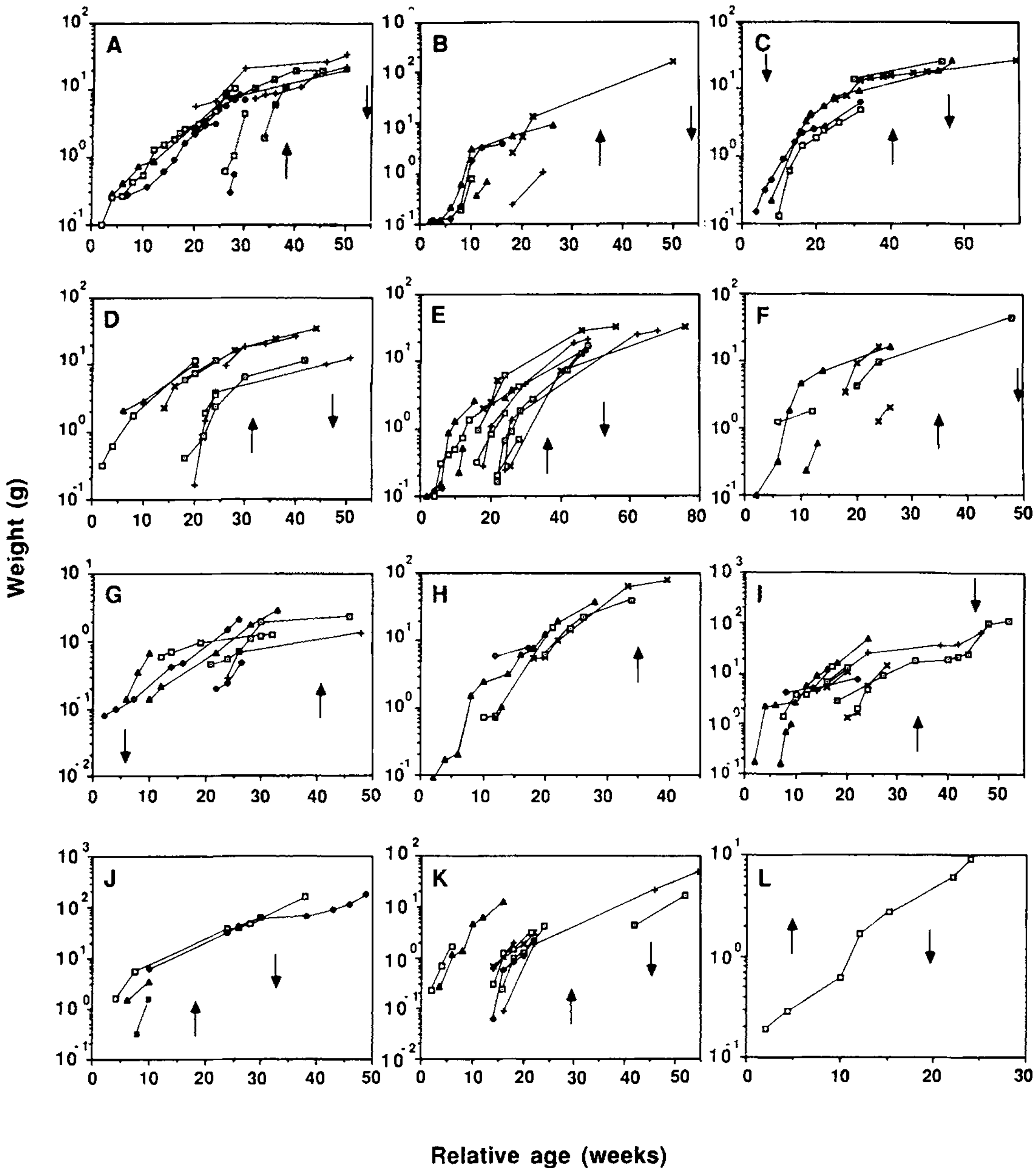

Fig. 3. Mean fresh weight (g) versus relative age (weeks) by species (lines indicate interpretation of cohorts or broods): A. *Acarichthys heckeli;* B. *Colossoma macropomum;* C. *Triportheus albus;* D. *Triportheus angulatus;* E. *Triportheus elongatus;* F. *Brycon melanopterus;* G. *Anchoviella guianensis;* H. *Semaprochilodus taeniurus;* I. *Semaprochilodus insignis;* J. *Prochilodus nigricans;* K. *Potamorhina latior;* L. *Curimata kneri* (species A–G are omnivores when juvenile, H–L are detritivores).

Triangles = Marchantaria area.

Squares = Janauacá area.

Circles = Janaurarí area.

Centered symbols = 1976/77 year class.

Open symbols = 1977/78 year class.

Solid symbols = 1978/79 year class.

Upward and downward arrows indicate times of maximum and minimum water levels, respectively.

populations of juveniles did not mix.

The areas (Fig. 1) are close together when viewed on the scale of the Amazon basin, but differences between cohorts suggest that the main river is an effective barrier for young or small fish once they have been recruited to the floodplain nursery areas. First, a cohort progression of a species in one area does not necessarily appear in one or more of the other areas, or it may appear at a different time (Fig. 3). Second, there are distinct populations in which juveniles are separated geographically but older fish undertake long migrations. Random samples of 32 and 41 specimens of juvenile *Semaprochilodus insignis* from Marchantaria and Janauacá areas, respectively, had lateral line scale counts which were significantly different (X^2 test, $p<0.005$). Transverse scale counts also indicated a similar difference in this well-defined species.

Another commercial-sized characoid, *Hemiodus microlepis*, had significantly different scale counts between samples from the two closest areas, Marchantaria and Janauarí (Johns 1982). Worthmann (1982) found morphological, chemical, and growth differences between stocks of *Plagioscion squamosissimus* and *P. montei* in the lower R. Negro (in 'black' water) and L. Janauacá.

Therefore, it is assumed that transfers of the young fish studied do not occur between areas within the short time periods of early growth increments studied here. Growth increments and densities of potential competitors are consequently estimated within areas.

Diet and potential competitors

The density dependence of growth rate of a species was tested with respect to the density of all species utilizing the same resources. Since guild biomass (including that of the species being tested) was tested against deviations in growth of a single mem-

Table 3. Regression statistics of allometric growth equation (log(weight increment/time) versus log(weight)) by species.

Slope ± SE	Weight range (g)	Intercept	No. points	p
Acarichthys heckeli				
0.702 ± 0.101	0.10–36.2	−1.95	50	<0.001
Colossoma macropomum				
0.947 ± 0.159	0.11–165.4	−1.66	17	<0.01
Triportheus albus				
0.362 ± 0.112	0.13–27.4	−1.77	33	<0.01
Triportheus angulatus				
0.354 ± 0.115	0.16–34.6	−1.01	24	<0.01
Triportheus elongatus				
0.605 ± 0.081	0.08–103.8	−1.71	37	<0.001
Brycon melanopterus				
0.677 ± 0.162	0.10–45.5	−1.29	12	<0.01
Anchoviella guianensis				
0.671 ± 0.215	0.08–3.03	−2.35	24	<0.01
Semaprochilodus taeniurus				
0.914 ± 0.125	0.09–77.0	−1.87	22	<0.001
Semaprochilodus insignis				
0.559 ± 0.152	0.16–98.6	−1.22	31	<0.001
Prochilodus nigricans				
0.582 ± 0.166	0.31–243.6	−0.96	15	<0.01
Potamorhina latior				
0.635 ± 0.105	0.06–52.6	−1.28	25	<0.001
Curimata kneri				
1.244 ± 0.172	0.19–12.1	−1.43	5	<0.01

ber of that guild, the definition of each guild is important.

There is considerable diet overlap within species groups and animals of similar size ranges. I divided young Amazon floodplain fish and *Macrobrachium* spp. into three guilds – detritivores, piscivores, and omnivores (Bayley 1983: Chapter 4) – on the basis of published information (Marlier 1967, 1968; Knöppel 1970; Saul 1975; Carvalho, F.M. 1979; Santos 1979, 1981; Almeida 1980; Paixaõ 1980; Carvalho, M.L. 1981; Barthem 1981) insofar as it pertains to juveniles. This information was supplemented by personal observations.

Detritivores comprise the mud and fine-detritus feeders, often termed iliophagous, and consume particles within the Fine Particulate Organic Matter (FPOM) definition of less than 1 mm diameter. Conversely, the detritus in the diet of many omnivores is typically coarser and mixed with other items. Prochilodontidae and Curimatidae spp. qualify as detritivores from a very small size (18–20 mm long), below which there were no growth estimates. *Macrobrachium* spp. are also included in this guild, since fine plant debris has been observed in their stomach contents (Marlier 1967). Detritivores comprised 36% of the floodplain biomass in the floodplain between Manaus and the R. Purus mouth (Bayley 1983).

A major difference between this guild and the following two is the constant fine particle size of the food, which is independent of the size of the consumer. Therefore, the biomass of potential competitors comprised all sizes of detritivores sympatric with the species concerned.

Piscivores specialize almost entirely on fish, but also consume *Macrobrachium* spp. (Worthmann 1982; personal observations). Common members are *Cichla ocellaris, Hoplias malabaricus, Plagioscion, Raphiodon vulpinis,* and *Acestrorhynchus.* Piscivores comprised 35% of the floodplain biomass (Bayley 1983). Six growth increments estimated from two piscivores (*Plagioscion* spp.) were insufficient for density-dependence analyses.

The remaining guild, 'omnivores', would be inappropriate for the more specialized adults of many of the species included, but there is a trend toward greater omnivory and diet overlap with reducing size. For example, Santos (1981) compared diet overlap (*sensu* Horn 1966) between three Anostomidae species within four size ranges. He noted a general increase in mean overlap with decreasing size, with a maximum mean overlap of 0.91 for the smallest group, 20–100 mm standard length. These species are common members of my omnivore guild.

Diet overlap between common species from two families whose adults contrast in their feeding regimes were compared to illustrate increased omnivory in juveniles. Volumetric stomach content data (Santos 1979, 1981, Almeida 1980), stratified by fish size and season, were used from three Anostomidae species, whose adults were predominantly herbivorous, *Schizodon fasciatus, Rhytiodus microlepis,* and *R. argenteofuscus* and two omnivorous *Triportheus* spp. (Characidae), *T. angulatus* and *T. elongatus.*

Overlaps (Horn's (1966) modification of Morisita (1959)) based on data of seven food categories by volume of these five species (Santos 1979, Almeida 1980) were compared for low or falling-water levels and high or rising water using the *paired-t* test (Table 4A). Mean overlap at low water (0.57) was greater than at high water (0.48) but was not significantly different when comparing species pairs (*paired-t* = 1.56, 9 df, $p>0.05$). The data were then split among size groups corresponding closely to adults and juveniles. The average diet overlaps (Table 4B) of 0.64 for juveniles and 0.45 for adults were significantly different (*paired-t* = 2.43, 10 df, $p<0.05$). With juvenile data there was no significant difference ($p>0.05$) between mean interfamilial and intrafamilial species overlaps, whereas with adults the ranges do not even overlap (Table 4B). Corresponding overlaps were significantly different within both seasons (Table 4A) because the samples were dominated by adults which are more specialized.

Six 'omnivorous' species in this study (see the Characidae, Cichlidae, and Serrasalmidae in Table 2) share resources of aquatic and terrestrial invertebrates, detrital macrophytes, and filamentous algae when juvenile. However, the smallest species, *Anchoviella guianensis,* for which the growth estimates included adults, appears to feed primarily on zooplankton (personal observation). A subset of the omnivore guild, Clupeidae, Engraulidae, *Anodus, Eigenmannia, Triportheus,* and Tetragonopterinae, which mainly consumed zooplankters when small, were regarded as potential competitors to this species.

Biomass densities of guilds were estimated for each of the 295 growth-increment estimates for appropriate size ranges. For each increment, there was a length range which encompassed the distributions used. This was found to be close to ± 50% of the mean length of the pooled distributions. The mean guild biomass density was calculated from (1) fish within this length range (except detritivores for which all sizes were used) and (2) samples taken during the time interval and from the area corresponding to each growth estimate and within the depth and areal distribution of the species concerned.

The mean number of samples corresponding to each biomass estimate was 19 ± 1 SE. Individual guild biomass estimates, as fresh weight, ranged from 1 to 83 g m^{-2}. The mean annual biomass, comprising all species and sizes, was 160 g m^{-2} (Bayley 1983).

Density-dependence tests

Residuals from the separate species regressions (Table 3) based on the Parker & Larkin (1959) growth function were examined in relation to guild biomass densities or their logarithmic transforms. A thorough attempt was made to find density-dependent growth by analysing separate species and their joint effects in guilds. Correlations were tested under these conditions:

(a) All data by species.
(b) During rising water by species.
(c) During falling water by species.
(d) Detritivores and omnivores under conditions (a), (b) or (c), using pooled residuals from respective species.

The results of (a), (b) and (c) are shown in Table 5 by species for log-transformed data; only three significant results were obtained, one of which was

Table 4. Diet overlaps for five species between (A) two hydrological seasons and (B) adults and juveniles (from stomach content data by volume of Almeida (1980) and Santos (1979, 1981)).

A		Falling-low water season				
	Species	1	2	3	4	5
Rising-high water season	1		0.80	0.40	0.35	0.68
	2	0.98		0.41	0.40	0.36
	3	0.42	0.44		0.97	0.66
	4	0.20	0.22	0.93		0.67
	5	0.19	0.22	0.49	0.71	
B		Juveniles				
	Species	1	2	3	4	5
Adults	1		0.73	0.65	0.55	0.33
	2	0.99		0.82	0.56	0.37
	3	0.33	0.25		0.88	0.66
	4	0.21	0.13	0.96		0.86
	5	0.21	0.17	0.56	0.73	

1 = *Triportheus angulatus* (Characidae).
2 = *Triportheus elongatus* (Characidae).
3 = *Schizodon fasciatus* (Anostomidae).
4 = *Rhytiodus microlepis* (Anostomidae).
5 = *Rhytiodus argenteofuscus* (Anostomidae).

a positive relationship. No significant results were obtained for untransformed biomass densities. Sign tests of correlations were not significant in any of the three sets. This indicates that density dependent growth is not a general phenomenon among the species tested.

Two of eight species indicated density-dependent growth at $p<0.05$ during falling water, but one of these indicated a reverse effect during rising water. These two species were omnivores, of which four could be tested during falling water, but pooled residuals from all four potentially competing omnivores during falling water (d) indicated no significant effect at $p<0.1$. A similar result for detritivores was obtained.

Growth and hydrological season

A general effect was investigated by combining data for all species in a two-way analysis of covariance of $\mathrm{Ln}(\Delta W/\Delta t)$ between periods of rising and falling water and between three classes of maximum weight (<300 g, 300–2000 g, >2000 g: Table 2) with Ln(mean weight) as the covariate. There were no significant interactions at $p<0.1$ between maximum weight and season or between either of these and the covariate. A highly significant ($p<0.001$) seasonal difference was observed. Growth, as $\Delta W/\Delta t$, was on average 60% faster during the rising-water period when adjusted for the covariate and maximum weight.

The maximum weight attained was also a significant main effect ($p = 0.003$) in the covariance analysis, with larger species showing more positive deviations. The association of faster growth with

Table 5. Density-dependent growth tests by species. Residuals of log-transformed allometric growth function for each species correlated with log (guild biomass of appropriate time period and size range). Sign of correlation shown with significance in parentheses.

All data	Rising-water season	Falling-water season
Acarichthys heckeli		
− (.22)	− (.20)	+ (.36)
Colossoma macropomum		
+ (.23)	+ (.11)	+ (2 pts. only)
Triportheus albus		
− (.50)	+ (.02)*	− (.03)*
Triportheus angulatus		
− (.27)	+ (.48)	+ (.20)
Triportheus elongatus		
− (.18)	+ (.42)	− (.02)*
Brycon melanopterum		
+ (.15)	+ (.13)	no data
Anchoviella guianensis		
+ (.30)	+ (.41)	− (2 pts. only)
Semaprochilodus taeniurus		
− (.25)	− (.35)	− (2 pts. only)
Semaprochilodus insignis		
+ (.37)	+ (.28)	− (.34)
Prochilodus nigricans		
+ (.38)	− (.31)	+ (.14)
Potamorhina latior		
+ (.26)	+ (.26)	+ (.43)
Curimata kneri		
+ (.07)	no data	+ (.12)

* Tests significant at $p<0.05$.

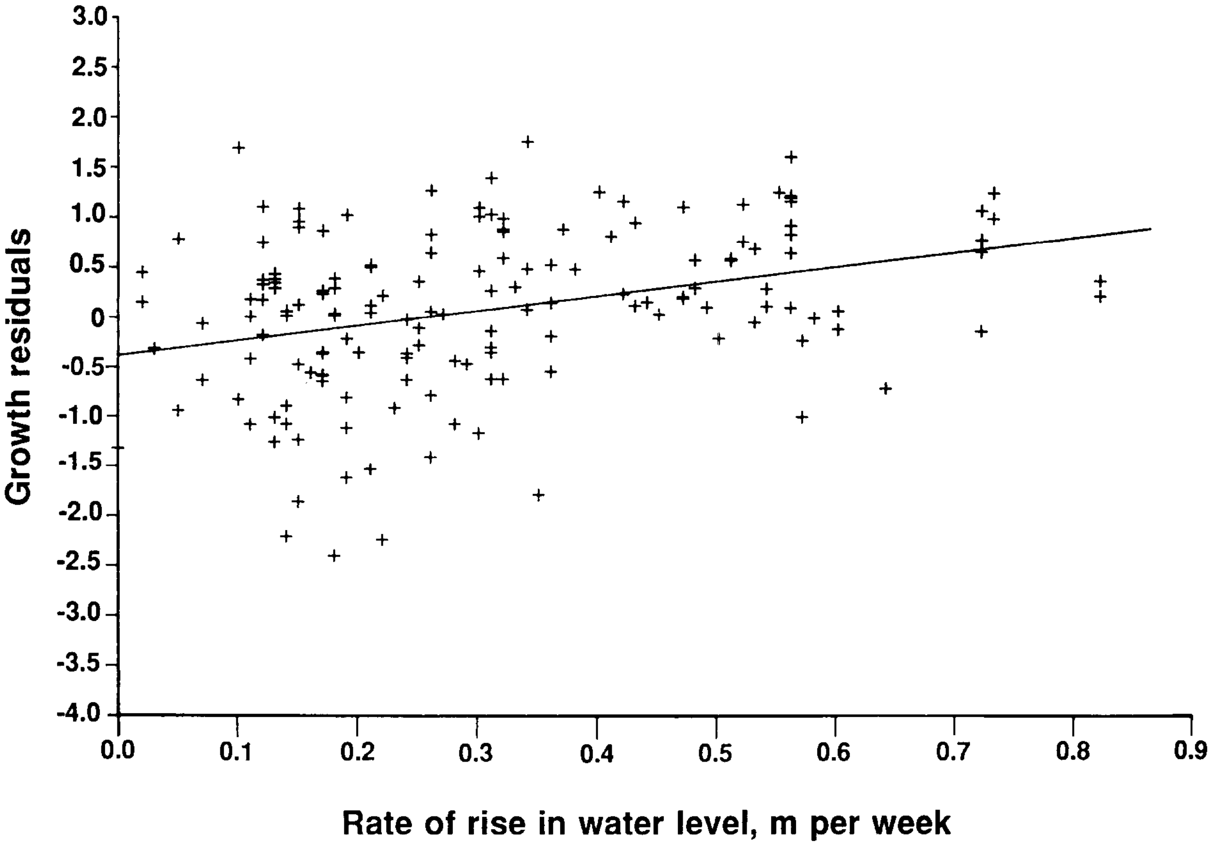

Fig. 4. Growth residuals (from $\log_e$ transformed allometric growth regressions from each species) of 'omnivores' versus rate of flooding.

larger species at younger ages has also been shown for Africa and the Paraná system (cited in Welcomme 1979:139).

Is the strong seasonal effect due to particular subsets of species? Growth increments of young detritivores were not correlated significantly with hydrological season. The main effect was due to omnivores growing faster during rising water.

Another hydrological effect on growth within seasons was indicated. Combined data for individual species residuals from the Parker Larkin model were highly correlated with rate of water level increase during the rising-water season ($p = 0.0002$), whereas during the falling-water period no significant effect was found ($p = 0.13$). However, this effect was again attributable to omnivores, which exhibited a significant correlation at $p<0.00001$ ($r = +0.346$, $df = 155$) (Fig. 4), whereas detritivores indicated no significant relationship.

The growth data and limnological observations suggest that food supply increases with rate of flooding. Assuming that the rate of flooding is positively related to food supply, a more sensitive test for density-dependent growth was to relate growth deviations from the regression in Figure 4 with guild biomass. No significant results at $p<0.05$ were obtained for the guild or for any individual species.

In summary, the statistical tests supported the circumstantial evidence that growth of 'omnivores' was enhanced when the rate of flooding increased. Conversely, a lower growth rate was indicated during falling water, but it was not influenced by the rate of fall. Density-dependent growth for two of four omnivorous species was indicated during this period. The results for juvenile omnivores are consistent with these deductions: (1) seasonally varying factors, presumably dominated by food availability, affect growth rates, (2) resources are sufficient during rising water for competition not to occur, (3) growth is limited, presumably by food, during falling water, and (4) growth during this period may be controlled in some species by interspecific competition. The evidence is weakest for (3) and (4), since not all species indicated density dependent growth, and neither the sign test of correlation coefficients nor a pooled data test were significant during the falling-water season. However, growth increments were significantly smaller ($p<0.001$) during falling water compared with rising water for pooled data. Separate tests on young detritivores indicated neither seasonal nor density-dependent effects.

Discussion

Seasonal effect

Seasonal effects on fish feeding in tropical streams have been reported (Angermeier and Karr 1983; Power 1983, 1984). Seasonal feeding and growth in adult tropical floodplain fishes have been reported (in Welcomme 1979). An a priori division between high and low water seasons has been the norm, whereas evidence reported here suggests a more realistic division between rising and falling water in floodplains.

The highly significant positive relationship between rate of flooding and growth of omnivores may be due to anoxic zones (Junk et al. 1983), which may temporarily limit food availability. One would expect better oxygen conditions over recently flooded land where material would not yet be decomposing rapidly. Conversely, slow flooding produces (1) denser emergent macrophyte stands, restricting water circulation, and (2) more stagnant conditions in which the effects of both aquatic and terrestrial decomposition are accentuated. I have observed fish under stress due to low oxygen during pauses in the flooding process.

Increased feeding by juveniles of Janauacá during the rising-water period has been reported (Santos 1981). The mean stomach fullness of juveniles of all three 'omnivorous' species he investigated was highest during the rising-water period of January to April, which corresponds to the highest growth rate period (Fig. 2). His results for the predominantly herbivorous adults, however, did not indicate such a trend, which he attributed to interruptions due to spawning activity.

In large floodplains, adults of many fishes (Lowe-McConnell 1964; Welcomme 1979; Goulding 1980; Ribeiro 1983; Junk 1985) show more striking seasonal characteristics than are reported here for juveniles. They accumulate large fat reserves during flooding and cease or reduce feeding during falling water, when substantial lotic migrations typically occur. Exceptions to this are floodplain 'piscivores' (e.g., Worthmann 1982), since the contracting environment would be expected to increase or at least maintain their food supply, and the majority does not undergo migrations along the main river.

Power (1984) found growth rates of marked armored catfish in a tropical stream increased most markedly during the first weeks of the rainy season, when periphyton which was previously unsafe to graze became more deeply submerged. Growth rates declined, but were still positive, at high water levels. Although the mechanisms are not necessarily the same in a floodplain, where water moves laterally as well as vertically, the general principle of increased rate of resource availability with increased rate of flooding could apply to both environments.

However, one should be cautious in extrapolating the effect of the rate of flooding on growth to other river systems. Rapid flooding, such as occurs in the upper reaches of the basin (personal observations in Peru and Bolivia), can clearly have no positive effect on growth, since the productive processes described above cannot develop fast enough, even at tropical temperatures. Increased algal growth and reduced deposition of inert mineral particles during low water may produce the reverse effect in areassubject to rapid flooding.

Density dependence and competition

A density-dependent effect on growth rate does not prove that competition has occured, but at least suggests that the fitness of the next generation may be affected. It is more difficult to infer competition from diet overlap studies. Angermeier (1982) showed that diet breadths increased as food levels declined in the summer and fall in a warm-temperate stream, and suggested that competition may occur during that period. Power (1983) found the same in a tropical stream, in which the overlap of grazing substrates of four species of armored catfish increased when resources were more limited at low water. Failures to find evidence of competition with field experiments are probably under-reported in the literature (Connell 1983).

There is little evidence of density-dependent effects on growth in floodplains. Dudley (1974) only reported significant ($p<0.1$) density-dependent growth in one adult age-group of *Tilapia macrochir,* one of three species and various age-groups he studied. Kapetsky (1974) failed to find density-dependent growth for any combination of species and year class he studied in the Kafue floodplain, but found significant effects of seasonal hydrological factors. However, an extended data set from the same floodplain did not indicate a positive effect of degree of flooding between years on growth of two species (Dudley 1979).

The evidence for density-dependent growth in this study is tenuous. Three significant results (including two of the expected negative relationship) from 31 tests were found (Table 5), compared with about 1.5 which would be expected from random data at $p = 0.05$. However, the tests were conducted within sets of different criteria, and the significantly negative results were from two out of four omnivorous species tested during the falling-water period. However, neither pooled data for this guild nor a sign test for all the species during this season were significant. This season lasts for only 3–4 months during which growth is depressed; any general density-dependent effects of juveniles on total production of the species concerned would be small. The hydrograph during this study (Fig. 2) was similar to the record of the previous 70 years (Bayley 1983).

Considering that specialization tends to increase with age and that larger individuals have the capacity to feed much less frequently, there seems little likelihood of interspecific competition among adults, except possibly among some very closely related species. These arguments do not, of course, rule out the 'ghost of competition past' shaping adaptations to their present form.

The lack of density-dependent effects on the growth of young detritivores is not surprising when one considers the abundance of fine detrital matter in the floodplain. Conversely, the lack of seasonal effect is counterintuitive, considering that the flooded land area increases fourfold annually in the study area (Bayley 1983). The increased flooded area is counteracted by the increased area of substrate covered by the deoxygenated hypolimnion (Schmidt 1973), which is associated with H_2S. This would prevent access by the non-air-breathing detritivores to areas where their own food source is more concentrated (Junk et al. 1983). Also, recently flooded land is hard, and personal observations indicate that young detritivores tend to be farther offshore but within the oxygenated epilimnion during the rising-water period. Adult detritivores would be expected to have highly seasonal growth rates, however, because of their extensive migrations and seasonal fat deposits (Bayley 1973, Ribeiro 1983, Junk 1985).

There is insufficient biological information on juvenile omnivores and detritivores to explain the observed difference during the rising-water period. Physiological processes may be controlling detritivore growth during normal hydrological conditions.

In conclusion, there is little empirical evidence here to suggest that interspecific competition for resources plays a major role in the co-evolution of Amazon floodplain fishes. However, it is conceivable that an occasional 'bottleneck' or 'crunch' (sensu Wiens 1977) in the form of a prolonged low water season or mistimed flood affecting reproduction may adjust the community structure via interspecific competition. However, I think it would be very difficult to obtan field evidence in the tropical floodplain environment which could distinguish between this mechanism and an adjustment due to autecological effects.

Predation may control the co-evolution of many species rather than competition. A preliminary analysis (Bayley 1983) indicated that 75–100% of prey productivity was accounted for by predation by the 'piscivore' guild, which averaged 35% of the floodplain biomass, but excluded non-fish piscivores such as avian and reptile species. Junk et al. (1983), sampling in Marchantaria with seines and gillnets, found that only 5% of the total catch were piscivores. However, as they stated, their fish sampling was qualitative. It did not take into account the much lower seine net catchability of the larger fish (Bayley 1983), among which predators were more numerous. Intensive, year-round sampling in five floodplain regions using a gillnet fleet (Barthem 1981) indicated that 35% of the catch comprisedpiscivores.

The threat of predation on juvenile fish must affect their feeding strategies (Werner & Mittelbach 1981). Especially during the falling-water period, the predation threat may temporarily intensify competition and weaken individual prey fish which would subsequently be eaten before the effects of competition on the population could be expressed. The threat of predation near the surface on periphyton grazers in the distinct environment of a small tropical stream was postulated to contribute to seasonal differences in growth rate (Power 1983, 1984). In floodplains the considerable seasonal contraction in the aquatic environment and associated food resources for omnivores cannot easily be distinguished from the contraction of feeding areas due to the concentration of piscivores at low water. Both effects probably contribute to the growth rate differences.

Relating the processes of density-dependent mortality, predation, and food availability, such as attempted for young marine fish by Cushing & Harris (1973) and Cushing (1975:127), may be a useful point of departure for floodplain fishes, providing that seasonal transitions are included. However, quantifying food availability from the numerous sources in the Amazon floodplain would be a major task.

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References cited

Almeida, R.G. 1980. Taxonomic aspects and feeding habits of 3 species of *Triportheus* (Pisces: Characoidei, Characidae), in Lago do Castanho, Amazonas. M.Sc. Thesis, Instituto Nacional de Pesquisas da Amazonia, Manaus. 104 pp. (In Portuguese).

Angermeier, P.L. 1982. Resource seasonality and fish diets in an Illinois stream. Env. Biol. Fish. 7: 251–264.

Angermeier, P.L. & J.R. Karr. 1983. Fish communities along environmental gradients in a system of tropical streams. Env. Biol. Fish. 9: 117–135.

Barthem, R.B. 1981. Experimental fishing with gillnets in Central Amazon lakes. M.Sc. Thesis, Instituto Nacional de Pesquisas da Amazonia, Manaus. 84 pp. (In Portuguese).

Bayley, P.B. 1973. Studies on the migratory characin, *Prochilodus platensis* Holmberg 1889 (Pisces, Characoidei) in the Rio Pilcomayo, S. America. J. Fish Biol 5: 25–40.

Bayley, P.B. 1981. Fish yield from the Amazon in Brazil: comparisons with African river yields and management possibilities. Trans. Amer. Fish. Soc. 110: 351–359.

Bayley, P.B. 1983. Central Amazon fish populations: biomass, production and some dynamic characteristics. Ph.D. Thesis, Dalhousie University, Halifax. 330 pp.

Beckman, W.C. 1941. Increased growth rate of rock bass, *Ambloplites rupestris* (Rafinesque), following reduction in the density of the population. Trans. Amer. Fish. Soc. 70: 143–148.

Bennett, G.W. 1954. Largemouth bass in Ridge Lake, Coles County, Illinois. Illinois Natural History Survey Bulletin 26: 217–276.

Brandorff, G.-O. & E.R. Andrade. 1978. The relationship between the water level in the Amazon River and the fate of the zooplankton population in lago Jacaretinga, a vàrzea lake in the central Amazon. Stud. Neotrop. Fauna & Environ. 13: 63–70.

Carvalho, F.M. 1979. Diet, ovarian development, and chemical composition of *Hypophthalmus edentatus* and *Potamorhina pristigaster* (Pisces: Ostariophysi), in Lago do Castanho, Amazonas, Brazil. M.Sc. Thesis, Instituto Nacional de Pesquisas da Amazonia, Manaus. 96 pp. (In Portuguese).

Carvalho, M.L. 1981. Diet of juvenile tambaquì (*Colossoma macropomum*) and its relationship with the zooplankton community of Lago Grande-Manaquiri, R. Solimões, Amazonas. M.Sc. Thesis, Instituto Nacional de Pesquisas da Amazonia, Manaus. 90 pp. (In Portuguese).

Chapman, D.W., W.H. Miller, R.G. Dudley & R.J. Scully. 1971. Ecology of fishes in the Kafue River. University of Idaho Technical Report FAO, Rome, FI:SF/ZAM 11 Tech. Rep. 2: 66.

Connell, J.H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. Amer. Nat. 122: 661–696.

Cushing, D.H. 1975. Marine ecology and fisheries. Cambridge University Press, London. 278 pp.

Cushing, D.H. & J.G.K. Harris. 1973. Stock and recruitment and the problem of density dependence. Rapp. P-V. Reun. Cons. Int. Explor. Mer. 164: 142–155.

Dudley, R.G. 1974. Growth of tilapia of the Kafue floodplain, Zambia: predicted effects of the Kafue Gorge Dam. Trans. Amer. Fish. Soc. 103: 281–291.

Dudley, R.G. 1979. Changes in growth and size distribution of *Sarotherodon macrochir* and *Sarotherodon andersoni* from the Kafue floodplain, Zambia, since construction of the Kafue Gorge Dam. J. Fish Biol. 14: 205–223.

Goulding, M. 1980. The fishes and the forest. University of California Press, Berkeley. 280 pp.

Grice, F. 1959. Elasticity of growth of yellow perch, chain pickerel and largemouth bass in some reclaimed Massachussetts waters. Trans. Amer. Fish. Soc. 88: 332–335.

Hickling, C.F. 1946. Haddock on the Porcupine Bank, September 1944. J. Mar. Biol. Assoc. UK 26: 398–407.

Hile, R. 1936. Age and growth of the cisco, *Leucichthys artedi* (Le Sueur), in the lakes of the northeastern highlands, Wisconsin. Bulletin of the United States Bureau of Fisheries 48: 211–317.

Hile, R. & H.J. Deason. 1934. Growth of the whitefish, *Coregonus clupeaformis* (Mitchill), in Trout Lake, northeastern highlands, Wisconsin. Trans. Amer. Fish. Soc. 64: 231–237.

Horn, H.S. 1966. Measurement of "overlap" in comparative ecological studies. Amer. Nat. 100: 419–424.

Iles, T.D. 1973. Interaction of environment and parent stock size in determining recruitment in the Pacific sardine as revealed by analysis of density-dependent O-group growth. Rapp. P-V. Reun. Cons. Int. Explor. Mer. 164: 228–240.

Iles, T.D. 1968. Growth studies on North Sea herring. II. O-group growth of East Anglian herring. J. Cons. Int. Explor. Mer. 32: 98–116.

Johns, P.M. 1982. A key and proposed revisions to the characoid fishes of the Family Hemiodontidae from the Central Amazon. Honours Thesis, Department of Biology, Dalhousie University, Halifax. 49 pp.

Junk, W.J. 1973. Investigations on the ecology and production biology of the floating meadows (Paspalo-Echinochloetum) on the Middle Amazon, Part 2: the aquatic fauna in the root zone of floating vegetation. Amazoniana IV: 9–102.

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

Junk, W.J. 1985. Temporary fat storage, an adaptation of some fish species to the waterlevel fluctuations and related environmental changes of the Amazon river. Amazoniana IX: 315–351.

Kapetsky, J.M. 1974. Growth, mortality, and production of five fish species of the Kafue River Floodplain, Zambia. Ph.D. Thesis, University of Michigan, Ann Arbor. 194 pp.

Kawanabe, H. 1958. On the significance of the social structure for the mode of density effect in a salmon-like fish, "Ayu", *Plecoglossus altivelis* Temminck et Schlegel. Mem. Fac. Sc. Kyoto Univ. Series Biol. 25: 171–180.

Knöppel, H.-A. 1970. Food of Central Amazonian Fishes. Amazoniana II: 257–352.

LeCren, E.D. 1958. Observations on the growth of perch (*Perca fluviatilis*) over twenty-two years with special reference to the effects of temperature and changes in population density. J. Anim. Ecol. 27: 287–334.

Leggett, W.C. 1977. Density dependence, density independence, and recruitment in the American shad (*Alosa sapidissima*) population of the Connecticut River. pp. 3–17. *In:* W. Van Winkle (ed.) Assessing the Effects of Power Plant Induced Mortality on Fish Populations. Pergamon Press, New York.

Lowe-McConnell, R.H. 1964. The fishes of the Rupununi savanna district of British Guiana, South America. Part 1. Ecological groupings of fish species and effects of the seasonal cycle on the fish. J. Linn. Soc. Zool. 45: 103.

Marlier, G. 1967. Ecological studies on some lakes of the Amazon valley. Amazoniana 1: 91–115.

Marlier, G. 1968. Etudes sur les lacs de l'amazonie centrale. Cadernos da Amazonia, Instituto Nacional de Pesquisas da Amazonia, Manaus. 57 pp.

Morisita, M. 1959. Measuring of interspecific association and similarity between communities. Mem. Fac. Sc. Kyushu Univer. Series E Biol. 3: 65–80.

Paixão, I.M.P. 1980. Diet and reproduction of *Mylossoma duriventris* Pisces, Characoidei), in Lago Janauacá, Amazonas, Brazil. M.Sc. Thesis, Instituto Nacional de Pesquisas da Amazonia, Manaus. 127 pp. (In Portuguese).

Parker, R.R. & P.A. Larkin. 1959. A concept of growth in fishes. J. Fish. Res. Board Can. 16: 721–745.

Power, M.E. 1983. Grazing responses of tropical freshwater fishes to different scales of variation in their food. Env. Biol. Fish. 9: 103–115.

Power, M.E. 1984. Depth distributions of armored catfish: predator-induced resource avoidance? Ecology 65: 523–528.

Raitt, D.S. 1939. The rate of mortality of the haddock of the North Sea stock 1919–1938. Rapp. P-V. Reun. Cons. Int. Explor. Mer 110: 65.

Ribeiro, M.C.L.B. 1983. Migrations of jaraqui spp. (Pisces, Prochilodontidae) in the Rio Negro, Amazonas, Brazil.

M.Sc. Thesis, Instituto Nacional de Pesquisas da Amazonia, Manaus. 192 pp. (In Portuguese).

Ricker, W.E. 1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30: 409–434.

Santos, G.M. 1979. Diet, reproduction, and systematic aspects of *Schizodon fasciatus* Aggasiz, *Rhytiodus microlepis,* and *Rhytiodus argenteofuscus* in Lago Janauacá, Amazonas, Brazil. M.Sc. Thesis, Instituto Nacional de Pesquisas da Amazonia, Manaus. 91 pp. (In Portuguese).

Santos, G.M. 1981. Diet and feeding habits of *Schizodon fasciatus* Agassiz, 1829, *Rhytiodus microlepis* Kner, 1859, and *Rhytiodus argenteofuscus* Kner, 1859, in Lago Janauacá, Amazonas. (Osteichthyes, Characoidei, Anostomidae). Acta Amazonica 11: 267–283. (In Portuguese).

Saul, W.G. 1975. An ecological study of fishes at a site in Upper Amazonian Ecuador. Proc. Acad. Nat. Sci. Philadelphia 127: 93–134.

Schmidt, G.W. 1973. Primary production of phytoplankton in the three types of Amazonian waters. II. The limnology of a tropical flood-plain lake in Central Amazonia (Lago do Castanho). Amazoniana 4: 139–203.

Starrett, W.C. & A.W. Fritz. 1965. A biological investigation of the fishes of Lake Chautauqua, Illinois Nat. Hist. Survey Bull. 29: 1–104.

Stroud, R.H. 1948. Growth of the basses and black crappie in Norris Reservoir, Tennessee. Tennessee Acad. Sci. J. 23: 31–99.

Viosca, P., Jr. 1943. Phenomenal growth rates of largemouth black bass in Louisiana waters. Trans. Amer. Fish. Soc. 72: 68–71.

Welcomme, R.L. 1979. Fisheries ecology of floodplain rivers. Longman, London. 317 pp.

Werner, E.E. & G.G. Mittelbach. 1981. Optimal foraging: field tests of diet choice and habitat switching. Amer. Zool. 21: 813–829.

Wiens, J.A. 1977. On competition and variable environments. Amer. Sci. 65: 590–597.

Worthmann, H.O. 1982. Aspekte der Biologie zweier Sciaenidenarten, der Pescadas *Plagioscion squamosissimus* (Heckel) und *Plagioscion monti* (Soares) in verschiedenen Gewässertypen Zentralamazoniens. Ph.D. Thesis, University of Kiel. 176 pp.