

# FOOD WEBS

*Integration of Patterns & Dynamics*

Edited by

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## Factors Driving Temporal and Spatial Variation in Aquatic Floodplain Food Webs

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### Introduction

The early literature on food webs makes few distinctions between local and regional ecosystems and processes. Leaving aside other problems (Cohen et al., 1990; Winemiller, 1990; Pimm et al., 1991; Yodzis, 1992), a major shortcoming of food web descriptions until recently was the omission of temporal and spatial variation. Kitching (1987) showed that food web structure varied among relatively simple aquatic communities in pitcher plants. Neotropical aquatic food webs have large seasonal variation in the numbers of species, predator-prey interactions, and numerous food web statistics (Winemiller, 1990). Aquatic food webs in both the tropics (Winemiller, 1990) and temperate latitudes (Warren, 1989) show small-scale spatial variation in food web structure. Recently, ecology has witnessed a greater recognition of temporal variation in ecological patterns and processes, and the interplay between species assemblages with local ecosystems and regional biotas with landscapes (Brown, 1984; Menge and Sutherland, 1987; Collins and Glenn, 1991; Wilson, 1992; Holt, 1993; Polis et al., this volume). In addition to the spatiotemporal dynamics of predator-prey interactions, food web structure and function are influenced by other factors that change species relative abundances and distributions. A basic model of spatiotemporal food web variation must integrate habitat disturbance, succession, and life history strategies in addition to predator-prey interactions (Figure 28.1). This chapter examines spatial and

temporal variation in food webs of lowland rivers and floodplains, and shows that periodic disturbance, geomorphic processes, life histories, and food web dynamics interact to produce a fairly predictable ecosystem succession in floodplains on three continents.

### Floodplain Ecosystems

The floodplains of lowland rivers are highly heterogeneous landscapes, dynamic on temporal scales ranging from days to decades. Given low elevational gradients, bank erosion and sediment deposition cause lateral river meandering. Bank erosion cuts off channel segments (meandering loops) to form lentic oxbows (lagoons), side channels, and sloughs (Welcomme, 1979). Over the long term, oxbow lakes undergo a relatively predictable succession in physiography and biota. Young oxbows are deep and often devoid of rooted aquatic macrophytes. At lake formation, the oxbow community is a sample of the river biota. With time and greater isolation from the active river channel, oxbows become shallower and support more aquatic macrophytes and lentic-adapted organisms and fewer lotic-adapted organisms. Sedimentation leads to formation of a marsh, which is succeeded ultimately by meadow or forest. This gradual succession can be interrupted by periodic flooding that scours and transports sediments and permits a partial exchange of channel and floodplain faunas.

Channel meandering, oxbow formation, sedimentation, flooding, desiccation, and succession all operate on different time-

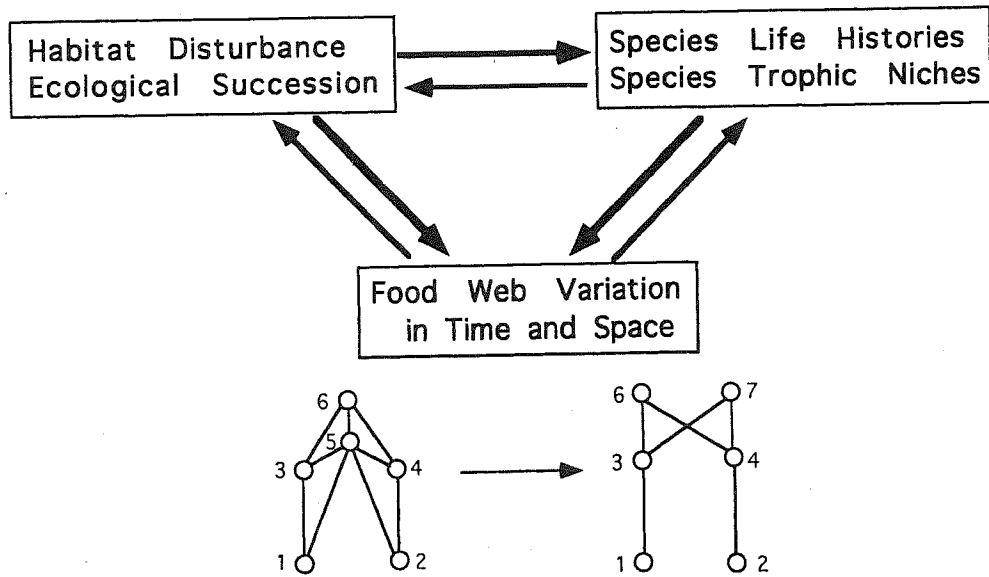


Figure 28.1. Conceptual model of the interrelationships between habitat disturbance, ecological succession, life history strategies, predator-prey interactions, and spatiotemporal variation in food web structure and function.

scales, yet interact to produce a dynamic and highly heterogeneous landscape that supports high biotic diversity. The importance of riparian landscapes for the maintenance of regional biodiversity is becoming increasingly clear (Naiman et al., 1993). Regional biodiversity of floodplains may be explained, at least in part, by the intermediate disturbance hypothesis (Huston, 1979). Local assemblages are periodically disturbed by flooding and erosion, so that the broader landscape contains a diverse array of successional stages and species.

In the tropics, many lowland continental regions show strong wet-dry seasonality (Figure 28.2), with major consequences for the quality, stability, and spatial connectivity of aquatic floodplains (Figure 28.3). The area and timing of annual floods are relatively predictable, and aquatic organisms exploit the relatively benign conditions of flooded plains for reproduction. Juvenile growth/survival are enhanced in the flooded plains which tend to be less turbulent, more productive, and contain fewer predators than permanent channels. Each dry season, floodplains dry out and aquatic organisms must migrate back to permanent water bodies, or cope with harsh conditions in shallow ephemeral pools (e.g., hypoxia, heat stress). Massive dry-sea-

son mortality is a normal occurrence in some aquatic populations, and each wet season their numbers are regained from small numbers of surviving adults.

In many temperate regions, annual precipitation is unpredictable, particularly in expansive lowland regions of continents. In Texas, monthly precipitation is essentially stochastic with high interannual variability (Figure 28.2). Hence, flood frequency and magnitude are highly variable and unpredictable. Temporal changes in the quality and connectivity of temperate floodplains are noncyclic, and faunal interchanges and local aquatic community reorganization occur unpredictably on a scale of years and decades, rather than annual cycles. In old oxbow lakes located great distances from the active channel, interchange with the river fauna may occur only briefly during rare, high-amplitude floods. The timing of annual reproduction by aquatic organisms of temperate floodplains primarily reflects the annual thermal regime, rather than precipitation or flood height.

Because precipitation and flooding are more regular in the tropics, integration of local species assemblages into regional floodplain biotas tends to be much faster than in temperate regions (Figure 28.3). Species diversity is generally higher in tropical low-

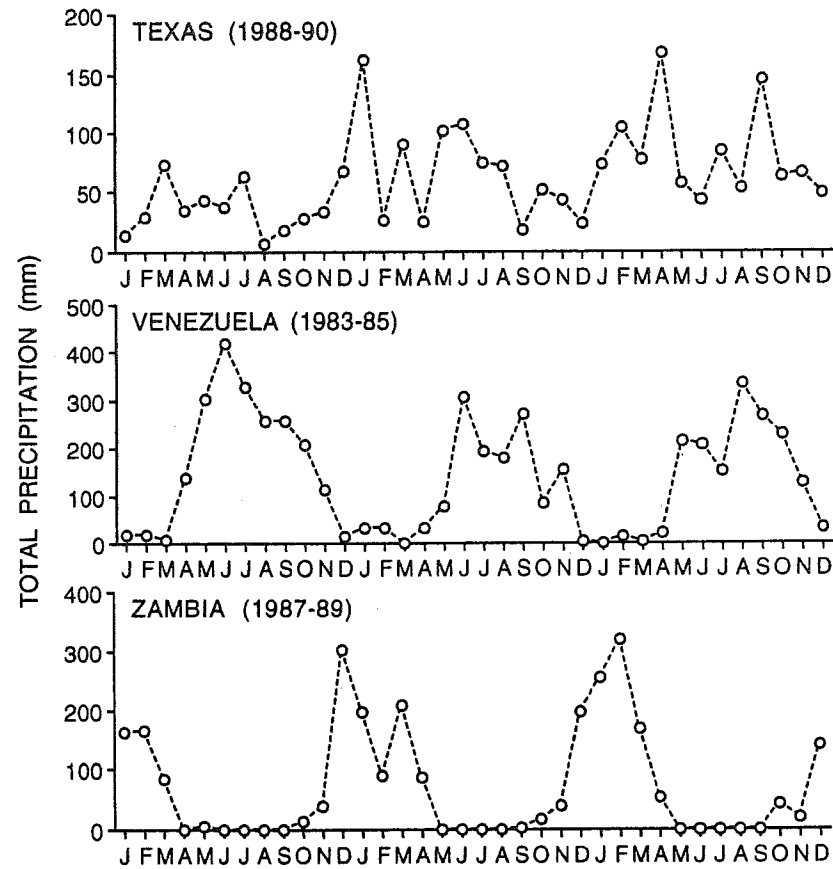


Figure 28.2. Monthly precipitation plotted over three consecutive years for one temperate (Texas) and two tropical (Venezuela, Zambia) regions. The upper plot shows an essentially random distribution of rainfall, whereas rainfall is markedly seasonal in the two bottom plots.

land rivers. Historical factors certainly underlie strong latitudinal differences in species diversity, but it remains an open question whether or not the rapid integration of local community elements into a regional fauna also fosters diversity. Predicting species, food web, and diversity patterns on floodplain landscapes requires understanding how temporal and spatial dynamics of habitats drive ecological succession and food web structure and function. Here, aquatic food webs of floodplains from three different continents are compared in the context of these questions.

### Food Webs of Three Study Systems

#### South America

Caño Marca is a low-gradient stream in the Venezuelan llanos with a large, seasonally

inundated floodplain (for details on the habitat, community, and food web see Winemiller, 1989, 1990). The seasonal distribution of rainfall (Figure 28.2) causes pronounced within-year variation in most all ecosystem components. The detailed seasonal food webs reported earlier (Winemiller, 1990) are aggregated here using diet similarities and shared enemies (predators). Species can be grouped by several aggregation methods, each one yielding a different food web (Yodzis and Winemiller, unpublished manuscript). For our present purpose, species were aggregated into food web nodes based first on large overlap among dominant diet items, and secondly on common enemies. Predator-prey links represented by predator dietary proportions  $> 10\%$  by volume were considered dominant; nodes with relative abundances  $> 1\%$  were considered common.

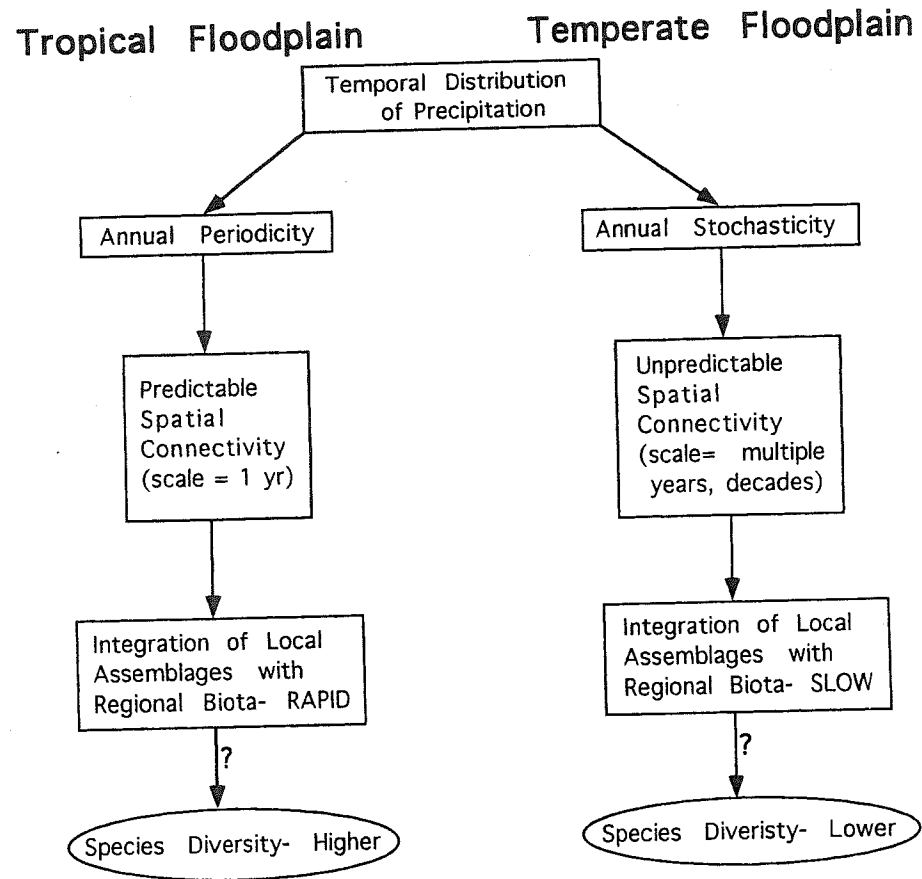


Figure 28.3. The influence of temporal distribution of precipitation on predictability and scale of connectivity of aquatic floodplain habitats and the rate of integration of local communities with the regional biota. The causal relationship between rate of faunal integration and regional species diversity is unknown.

Common fish species were determined from numeric abundances in monthly samples; relative abundances of nonfish nodes were estimated from total volumes consumed by the entire fish community over the specified time period. Sample sizes of stomach content analyses were generally in the hundreds for each consumer species (Winemiller, 1990). The rules of thumb used for aggregating webs are subjective, so the webs (Figure 28.4) should be used cautiously for comparisons of web statistics, such as connectance, in combination with webs constructed from other criteria (Winemiller, 1990).

Great seasonal variation exists in webs from the same location (Figure 28.4). Some species were very common during only one season. Several factors account for seasonal

fluctuations in the upper web components. (1) Some species have seasonal migrations and exit during the onset of harsh dry season conditions. These migrations are mostly local; the organisms return to spawn following inundation. Examples include the piranha (*Pygocentrus cariba*) and glass characin (*Charax gibbosus*). (2) Other species remain throughout the year, but suffer high mortality during the dry season, when aquatic macrophyte cover is reduced and fishes (including predators) are at their highest densities. The small darter characin (*Characidium* sp.) and corydoras catfishes (*Corydoras aeneus*) are among the resident populations reduced during the dry season, but rebounding during the wet season.

Life history strategies greatly influence

seasonal population dynamics. The wet season food web is dominated by species with divergent tactics: (1) those that remain throughout the dry season and survive harsh conditions and predation in fairly large numbers owing to special adaptations like aerial respiration and armor; (2) those that remain during the dry season and are reduced in density by hypoxic conditions or predation, but rebound quickly due to high fecundity and pulsed spawning after the first floods (the periodic strategy of Winemiller, 1992; Winemiller and Rose, 1992; see below) or to early maturation and multiple spawning of small clutches (opportunistic strategists); and (3) those that exit during the dry season but return with the rains to spawn large numbers of eggs.

The annual cycle of flooding and desiccation dramatically affects the lower food web. Many aquatic plants and invertebrates survive in dry sediments in a state of quiescence or in an arrested state of early development (e.g., diatoms, rooted macrophytes, molluscs, entocostostracans, conchostracans). These organisms exhibit an impressive burst of production during the earliest phase of wet season flooding. Even one group of fishes, the annual killifishes (Rivuliidae), has evolved this capability. The killifish, *Rachovia maculipinnis*, is a dominant component of the Caño Maraca web during the wet season, but is virtually eliminated by predators by the beginning of the transition season. Sources of basal production differ markedly between seasons (Figure 28.4 and 28.5). During the wet season, the flooded zone spans a large area and is choked with emergent and aquatic macrophytes. Few invertebrates or fishes feed directly on these plants, but many herbivores consume periphyton (diatoms, filamentous algae) on the submerged macrophyte surfaces. This wet season primary production is rapidly transferred to the upper web via invertebrates and juvenile fishes. During the transition season, the

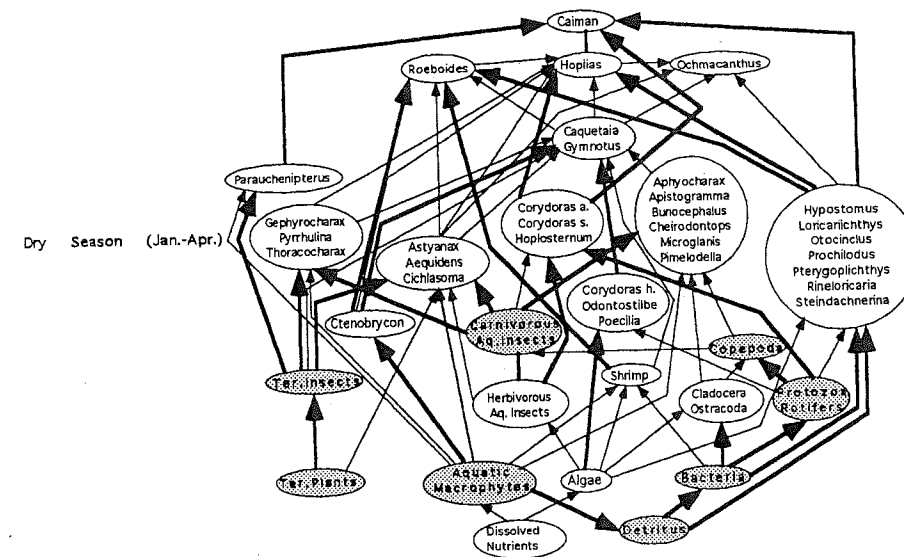
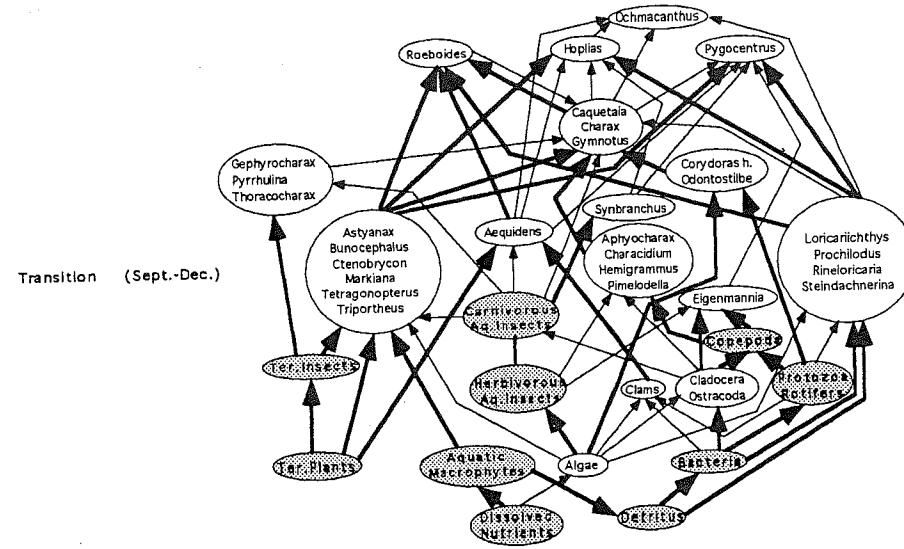
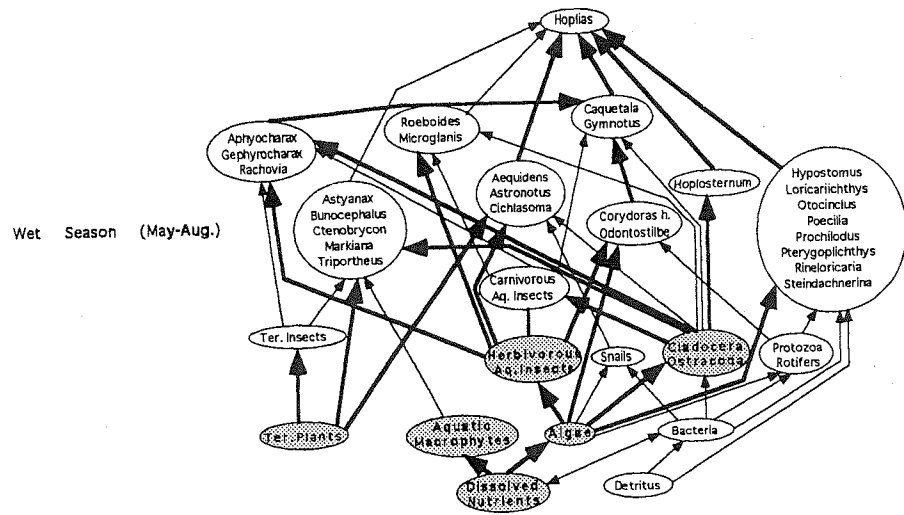
floodplain dries, and the accumulated macrophyte biomass dies and decomposes. The combined effects of macrophyte decomposition and the confinement of water in isolated pools and small channels causes a reduction in dissolved oxygen and higher concentrations of hydrogen sulfide. Many larger resident organisms survive hypoxia by virtue of special respiratory adaptations, and are able to feed and in some cases reproduce. Detritus derived from aquatic macrophytes is the primary source of basal production in the dry season web via consumption by microbes, protozoa, invertebrates, and fishes (Figure 28.4).

#### Africa

With a unimodal annual distribution of rainfall (Figure 28.2), the Upper Zambezi River and its floodplain have a strong seasonal cycle of flooding and desiccation (for details, see Winemiller (1991)). Following the same criteria as above, a composite food web was created using data from locations throughout the Upper Zambezi/Barotse floodplain (Figure 28.6). Fish diets were estimated from stomach content analyses (from ten specimens for rare species to several hundred for common species). Diets of aggregated invertebrate groups were not directly estimated, but based on the sources used for neotropical webs (Winemiller, 1990).

Much of the basal production originates on the marginal floodplain (Figure 28.6). Aquatic macrophytes, periphyton, and much of the detritus from aquatic plants originates on the floodplain during high water (January–April). Basal production transfers upward through the web primarily in the aquatic habitats of the floodplain (lagoons, sloughs, canals), but also in the river channel. A massive movement of floodplain components to the river channel occurs during the period of falling water (May–August). In the low-water period (September–December), top predators

*Figure 28.4.* Major features of food web structure of the Caño Maraca swamp during the three seasons of the annual cycle in the Venezuelan llanos. Only common predator-prey interactions are illustrated (volumetric dietary proportions > 10%), bold arrows represent volumetric dietary proportions > 20%, shaded nodes are dominant biomass elements of the lower food web, and only dominant fish species (relative numeric abundance > 1% of total individuals sampled from fauna) are included within trophic aggregations.



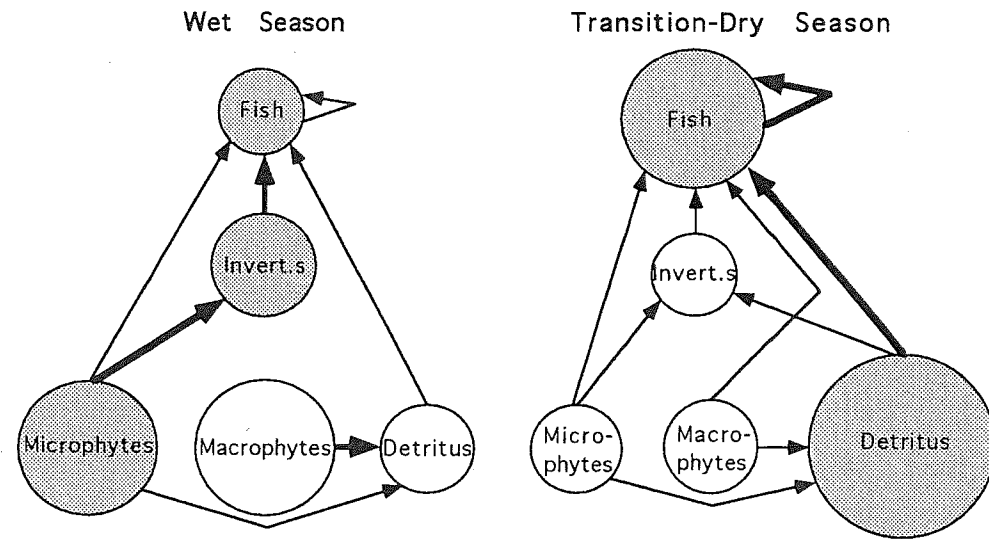


Figure 28.5. Highly aggregated food web for Caño Maraca floodplain showing the major shift in basal input and flows that occurs between the wet and transition-dry seasons.

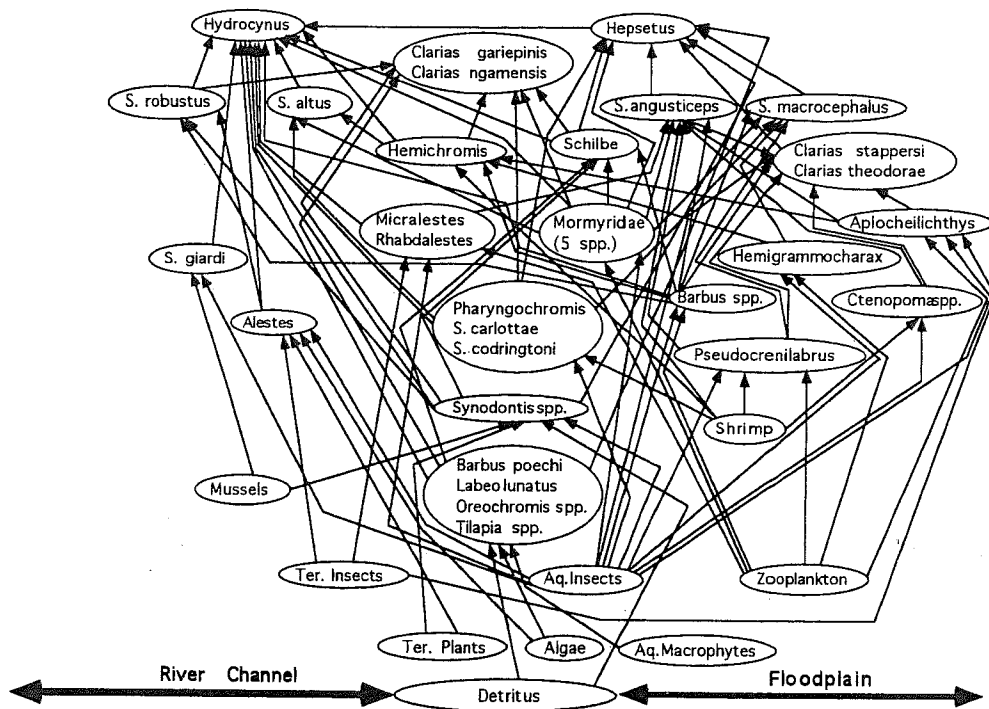


Figure 28.6. Major features of the annual composite food web of the Upper Zambezi River/Barotse Plain of western Zambia. Only common community elements (species-relative numeric abundances > 1%) are depicted in the trophic aggregations, and only common predator-prey interactions are illustrated (dietary proportions > 10%).



(e.g., African pike, *Hepsetus odoe*, and silver catfish, *Schilbe mystus*) either settle into large lagoons where they maintain their top trophic positions, or inhabit edge habitats of the river channel where some fall prey to the African tigerfish, *Hydrocynus forskahlii* (Winemiller and Kelso-Winemiller, 1994). As in the South American llanos, detritus becomes an increasingly important input at the base of aquatic floodplain webs as the abundance of submerged macrophytes decreases with falling water levels.

#### North America

Research initiated in 1993 on the middle Brazos River and associated floodplain habitats also highlights spatial variation in food web structure. Because of the highly variable, random distribution of rainfall in central Texas (Figure 28.2), connections between oxbow lakes and the active river channel are infrequent and unpredictable on a multidecade scale. Intensive standard sampling of all major food web components (plankton nets, benthic samplers, seines, gillnets, electrofishing, etc.) reveals very similar faunal elements in the river and oxbow lakes. Because newly formed lakes tend to be deeper and more frequently flooded than old oxbows, their aquatic communities are actually more mature than those of old oxbows. The Brazos River experienced a 100-year flood in December–January of 1991, reintroducing water and river faunal components into oxbows that had previously dried out. Younger, more stable oxbows closer to the river probably experienced a partial biotic exchange with the river during this century flood. Four local ecosystems will be compared: the river channel, an old shallow oxbow with a young aquatic community (Siegert's), an old deep oxbow with a mature community (Moehlman's slough), and a young, medium-depth oxbow with a mature community (Big Bend).

In each system, a relatively small number of taxa dominate the summer food web, comprising the bulk of standing biomass and production. For example, calanoid copepods (*Diaptomus* spp.), grass shrimp (*Palaemonetes kadiakensis*), gizzard shad (*Dorosoma cepedianum*), threadfin shad (*D. petense*), white crappie (*Pomoxis annularis*), channel catfish (*Ictalurus punctatus*), and gar (*Lepi-*

*sosteus* spp.) were always major biomass components. These species are considered primary (or core) web components. Primary species should be the major pathway for ecosystem nutrient recycling. Species were aggregated to illustrate the core structure of the composite Brazos River web (Figure 28.7). Other species occur, but generally at much lower biomasses than primary species. This latter group is denoted as secondary species (similar to Colwell's (1973) interstitial and hypercontigent species) because they are strongly influenced by the relative abundances of certain primary species and the integrity of primary food web structure, but reciprocal effects are less likely. For example, crappie that feed heavily on abundant shad would not be greatly influenced by low densities of silversides (*Menidia beryllina*). In this case, silversides would be greatly influenced by shad, as competitors for zooplankton prey, and by crappie as predators. The specific factors that cause shad to be dominant planktivores and silversides to be secondary planktivores in a given ecosystem are not well addressed by the holistic food web paradigm. Additional species-specific information and other methods of analysis are required to understand the factors regulating distributions and abundances of secondary species. A third group of tertiary species (similar to Hanski's (1982) satellite species) can be identified. For example, a single pirate perch (*Aphredoderus sayanus*) was collected among the four sites intensively sampled. Pirate perch are more abundant elsewhere, especially in eastern Texas. Tertiary species probably have little impact on the structure and function of primary food webs, or even on secondary web components. The literature on trophic cascades in aquatic webs deals only with primary food webs and largely ignores secondary and tertiary species (e.g., Carpenter et al. (1987)).

Nutrient concentrations were high (total phosphorus range = 0.85 – 1.5 mgL<sup>-1</sup>) and detritus abundant in each of the four webs. Evidence of a trophic cascade (high abundances in alternate trophic levels) in oxbow lakes was obtained when standing stocks of faunal components were standardized across all four localities for species (Figures 28.8 and 28.9) and aggregate trophic groups (Figure 28.10). Slightly different results were ob-

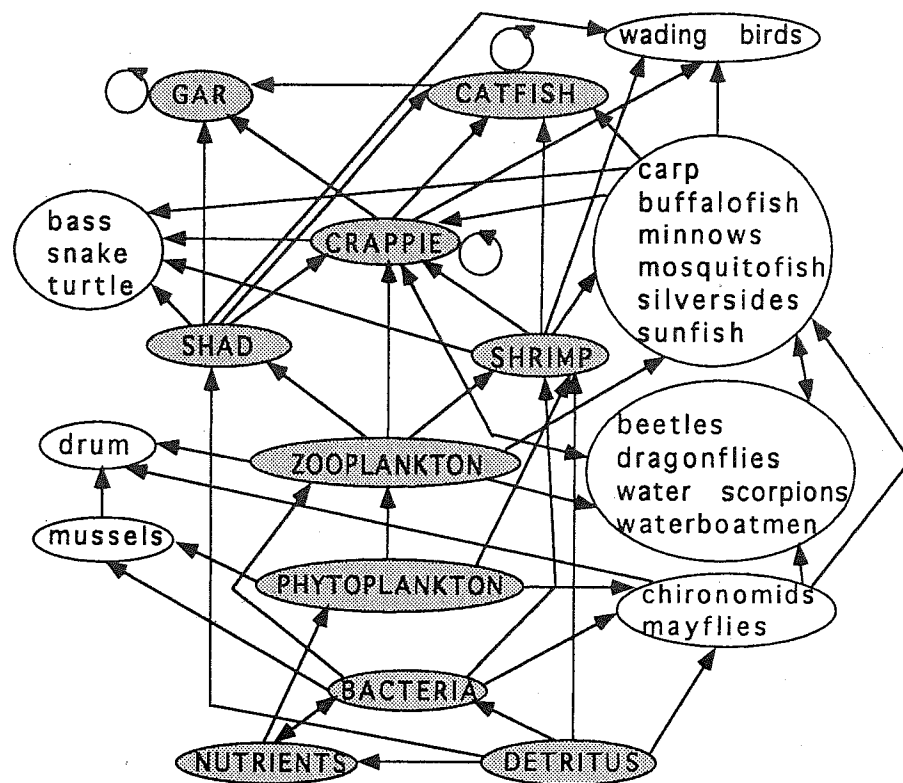


Figure 28.7. Aggregated food web for the Barazos River and associated floodplain aquatic habitats. Only common species and links are illustrated. Shaded nodes represent primary species that comprise the dominant biomass and production elements.

tained for abundance data based on numbers of individuals versus collective biomass for the trophic groups zooplankton—fish. Therefore, both the numerical and biomass data sets were standardized; the arithmetic means for the two standardized data sets are plotted in Figures 28.8 and 28.10. The channel web did not indicate a trophic cascade, and was dominated by nutrients, detritus, predatory gar, and catfishes. Compared with the oxbows, the channel ecosystem is much more frequently disturbed by changes in hydrology and geomorphology, so that at any given moment, it likely is in successional disequilibrium.

#### Life-History Strategies and Ecological Succession

A triangular, two-dimensional continuum predicts the principal life history syndromes in fishes (Winemiller, 1992; Winemiller and

Rose, 1992) and emphasizes demographic trade-offs among age/size of maturation, juvenile survivorship, and fecundity. The end points of the continuum define three unique life history strategies: equilibrium, opportunistic, and periodic. Examples of relative equilibrium species (delayed maturation, brood guarding, or hiding, large eggs, small clutches) include many cichlids, centrarchids, and some catfishes. Relatively opportunistic species (rapid maturation, short life span, frequent spawning, small eggs, small clutches) include small characoids, minnows (Cyprinidae), and killifishes (Rivuliidae). Examples of periodic-type fishes include migratory tropical characids, large cyprinids, and the gizzard shad. Intermediate strategies occupy the central region of the surface defined by a given empirical data set. The model predicts that (1) Seasonal environments or large-scale spatial variation favor late maturation, high fecundity, and pulsed reproductive

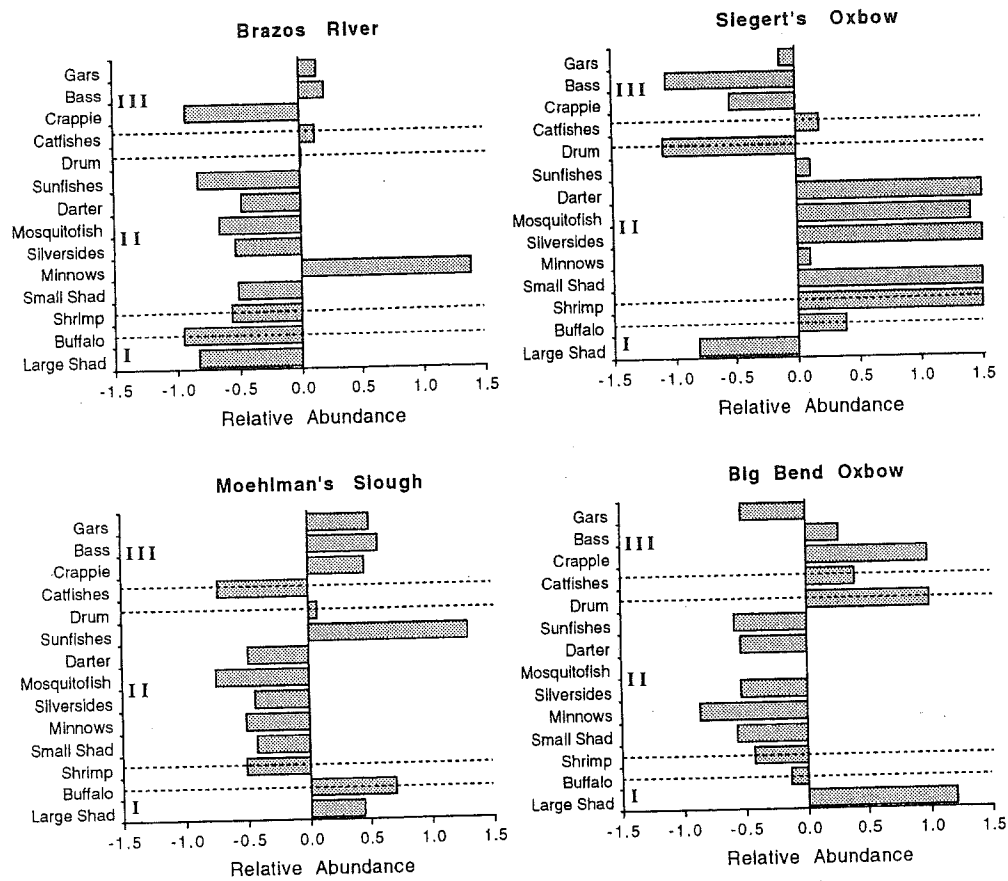


Figure 28.8. The standardized relative abundances (abundances standardized within species across sites) of shrimp and fish groups in four local ecosystems of the middle Brazos River. I = detritivore, II = zooplanktivore/insectivore, III = piscivore.

bouts; (2) crowded habitats with relatively stable resources favor smaller clutches and greater investment per offspring; and (3) stochastically varying and frequently disturbed habitats or intense predation favor early maturation and other traits allowing opportunistic reproduction and rapid recolonization.

This life history model predicts qualitative population responses to different kinds of disturbances, and provides a basis for comparing responses of different species to similar disturbances (Winemiller and Rose, 1992). Recruitment by long-lived periodic strategists, such as the African tigerfish, exploits large-scale temporal variation in the environment. Large losses in the egg/larval stage during unfavorable years are compensated by the production of persistent cohorts in favorable years. The widespread occurrence of dominant year classes in many long-lived, periodic

fish stocks supports this view (e.g., Setzler et al. (1980)). For shorter-lived periodic species, like many mid-sized minnows and characids, some recruitment must be achieved each year; factors influencing within-year (e.g., seasonal) variation are more important relative to between-year variation.

How might this life history model influence interpretation of spatiotemporal variation in food webs? The ultimate driving factor for recruitment by periodic species is large-scale variation in the physical environment, which determines variation in habitat quality for early life stages. A strong cohort of periodic type-species produced in one year could have long-lasting effects on the food web due to the storage effect (Chesson, 1983). Many aspects of food web structure and dynamics cannot be predicted from a deterministic model of species interactions, because domi-

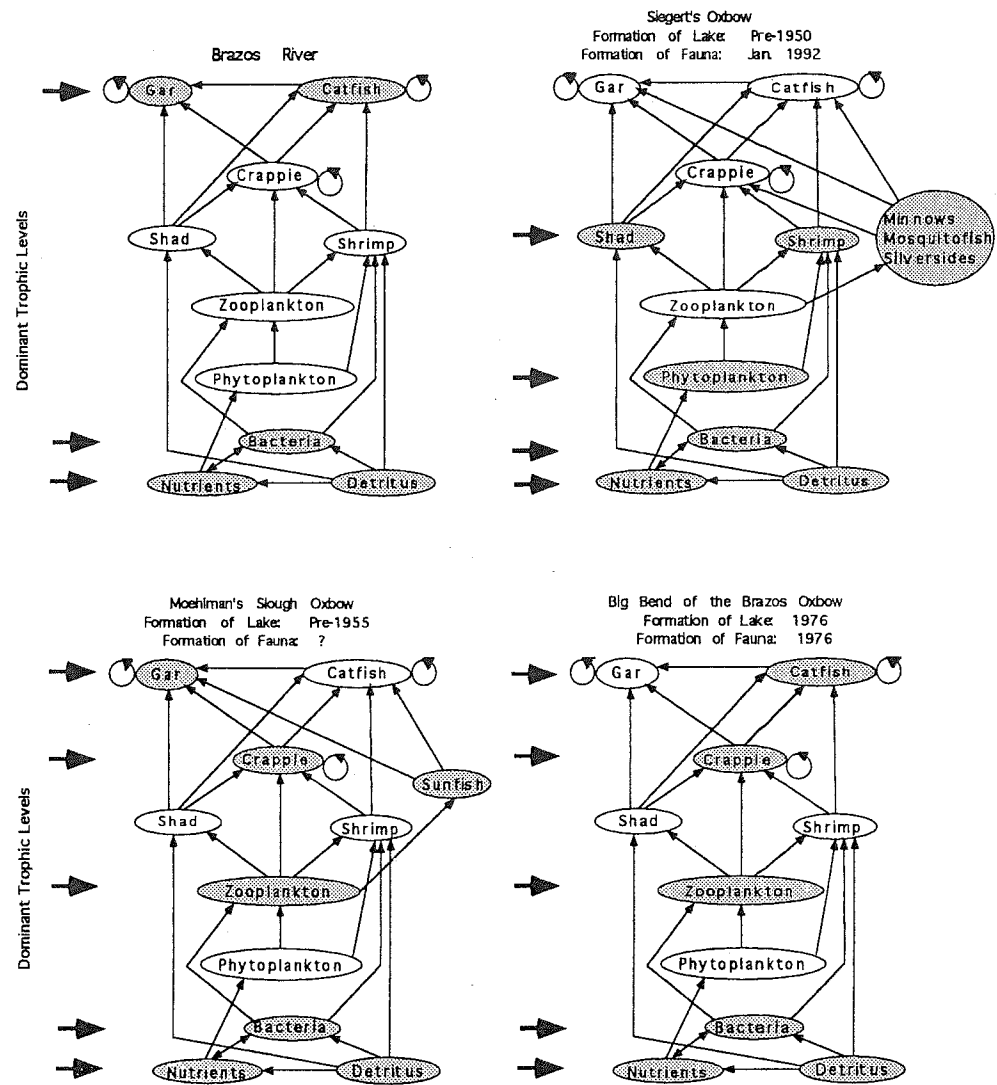


Figure 28.9. Between-locality variation in the primary structure of food webs in the Brazos River floodplain corridor.

nant biomass components reflect extrinsic factors from the distant past, with little or no linkage to recent conditions. Extreme equilibrium-type species should respond more strongly to density-dependent ecological factors, and hence to variation in food web structure (biotic components). Finally, abiotic and biotic factors that vary randomly at small spatiotemporal scales should greatly influence the recruitment of small opportunistic species.

Based on reproductive and demographic data collected in conjunction with the food

web research, fish species in each of the study systems were classified into the above three life history categories (see also Winemiller (1989) and Winemiller and Rose (1992)). Although the model describes a continuum of attributes, species usually could be assigned to just one strategy. For intermediate cases, species were subjectively placed in that category perceived to best describe their full suite of characteristics (usually the periodic strategy). For example if clutch size was intermediate, egg size was relatively large, and parental care present (e.g., *Ictalurus* spp.), the

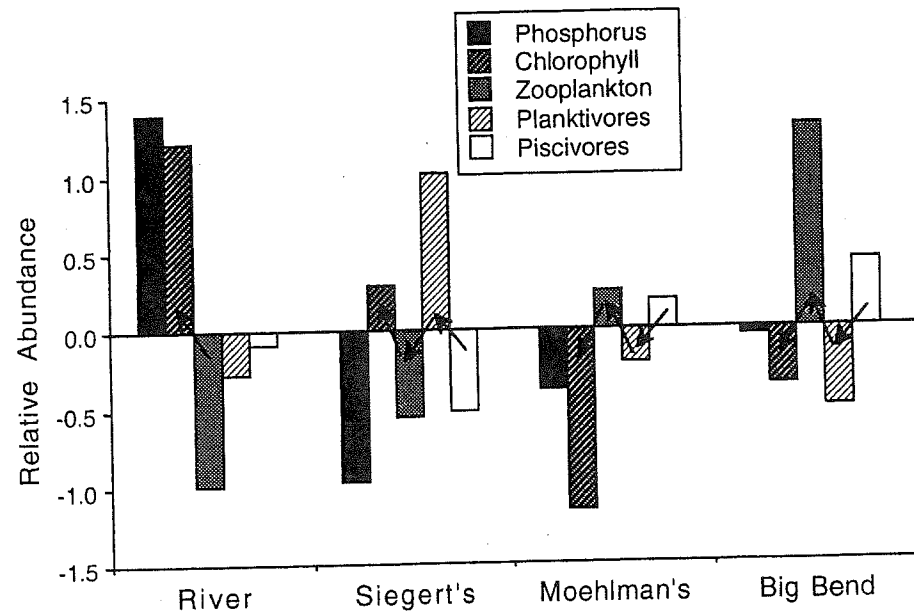


Figure 28.10. Between-trophic level variation in standardized relative abundances (trophic groups standardized across sites) for four local ecosystems of the Brazos River floodplain corridor. Total phosphorus (dissolved + particulate) and chlorophyll *a* were based on concentrations, all other trophic groups were based on numerical abundances.

species was categorized as equilibrium. Fishes were also categorized by trophic group: herbivore/detritivore, omnivore, invertebrate feeder, and piscivore. Relative frequencies of life history strategies and trophic groups were then compared across localities (Brazos, Zambezi) and seasons (Maraca) (Figure 28.11).

Using total numbers of individuals sampled, both life history strategies and trophic groups had significant associations with locality and season (Figure 28.11,  $X^2$ ,  $P < 0.0001$ ). In the Brazos system, the relative proportion of opportunistic-type fishes was greater in more recently (and frequently) disturbed systems; the proportion of equilibrium-type fishes was greatest in deeper oxbows with the oldest faunas (Figure 28.11). There was a strong trend for invertebrate feeders to dominate more disturbed systems, and for piscivores to dominate more mature faunas. The association between life history and trophic group was significant for all four local systems (range  $X^2 = 78-645$ ,  $df = 4$ ,  $P < 0.0001$ ). The Zambezi system had a greater proportion of opportunistic- and periodic-type fishes on the seasonal floodplain, and

more equilibrium species in the channel. The relative proportion of piscivorous fishes was greater in the Zambezi channel; the association between life history, and trophic group was significant in each habitat ( $X^2 = 193-411$ ,  $df = 6$ ,  $P < 0.0001$ ). The wet season web at Caño Maraca contained fairly equal numbers of all three life history types, the transition season a greater proportion of periodic fishes, and the dry season web contained a greater proportion of opportunistic fishes (Figure 28.11). Omnivores dominated all seasons, but herbivores were less common and piscivores more common during the transition season. The association between life history and trophic group was not significant in any season ( $X^2 = 7.95-11.19$ ,  $df = 6$ ,  $P > 0.08$ ).

The general pattern revealed by these analyses is summarized in a graphical model of community succession (Figure 28.12). Recently disturbed habitats are dominated by populations with opportunistic, colonizing life histories, and high intrinsic rates of increase (Winemiller and Rose, 1992). Following the passage of time without major disturbances, periodic strategists, by virtue of their

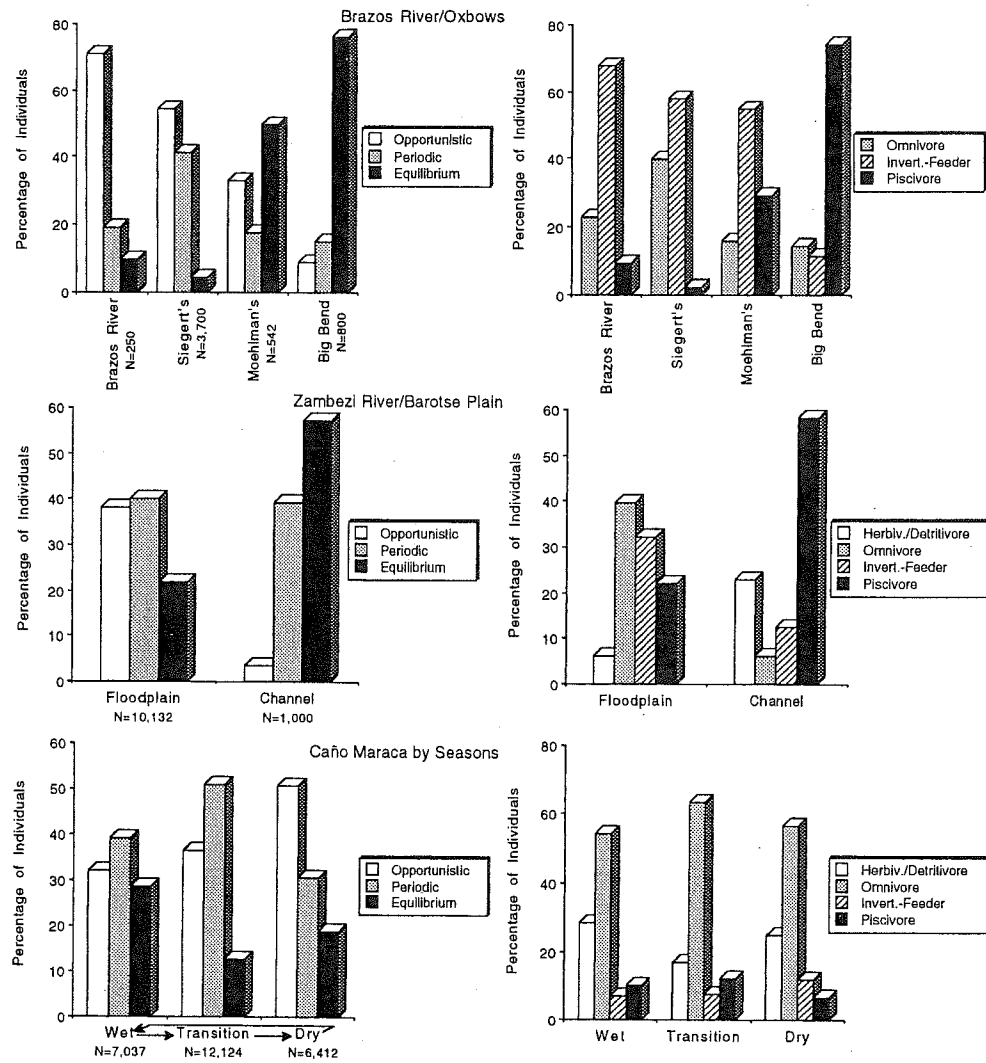


Figure 28.11. Percentages of individual fishes associated with different life history strategies and trophic groups in samples from different locations in the Brazos River and Zambezi River floodplain corridors and in samples from different seasons in the Caño Maraca floodplain.

large fecundities, eventually have episodes of strong recruitment. If long-lived, the storage effect allows them to dominate the community in the absence of major disturbances (e.g., complete desiccation) or crowding and resource limitations that severely reduce subsequent recruitment. When succession proceeds unimpeded by disturbances for a long time, strong density dependence in recruitment may favor domination by equilibrium-type species with traits that enhance early life-stage survival (e.g., parental care). This model suggests that periodic strategists

should dominate aquatic ecosystems that experience intermediate frequencies of major disturbance (i.e., the middle section of the abscissa in Figure 28.12).

### Discussion

A fundamental problem for food web research is linking the different perspectives of demography/biodiversity versus nutrient/energy dynamics. Food web research needs a body of theory that links evolutionary units

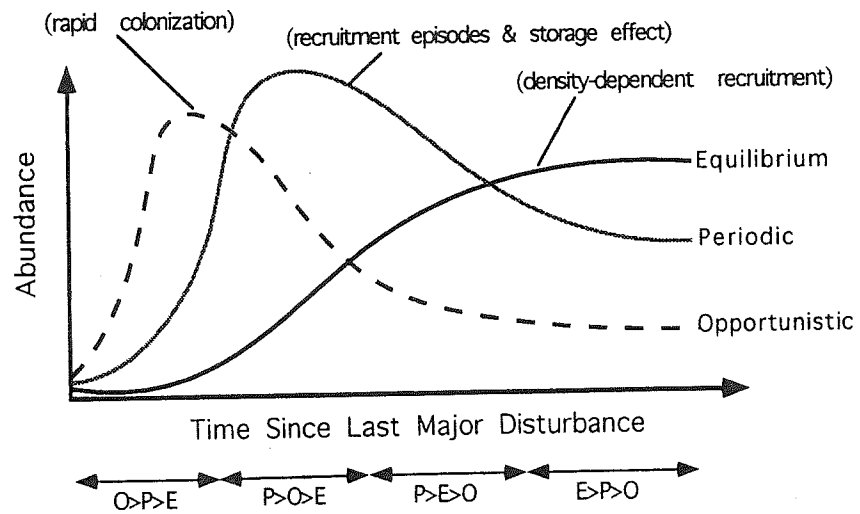


Figure 28.12. Graphical model predicting trends in the relative dominance of alternative life history strategies in communities during the process of ecological succession following major habitat disturbances. In aquatic floodplain ecosystems, periodic desiccation is the principal agent of disturbance.

with ecosystem compartments. Life history is a key factor influencing food web structure and function. When food web analyses are based on number of individuals, species relative abundances and production are skewed toward small opportunistic species and are heavily influenced by population dynamics. When analyses are based on biomass, the webs are dominated by long-lived, periodic-type species and influenced by the storage effect and somatic growth. In addition, spatiotemporal scale influences operational food web units and their dynamics. At very small spatial and temporal scales, the factors driving recruitment dynamics of different life histories may be obscured. Aggregation of units at large spatial and temporal scales may mask habitat heterogeneity and blur important sources of disturbance.

Floodplain food webs can shift quickly between domination by microbial-based and primary production-based inputs without major changes in species composition or in the relative abundance ranks of standing stocks. This appears to be especially true in tropical systems where many invertebrate and fish species can feed efficiently on either attached algae or detritus. Facultative diet shifts and the importance of detritus has not been emphasized in much of the recent literature dealing with aquatic and aboveground food webs.

The rich mosaic of local food webs scat-

tered across regional landscapes is driven by a combination of predictable abiotic and biotic processes, modified by chance events. At present, the food web paradigm has no generally accepted methods for dealing with variation in space and time. The recent modeling efforts by Pahl-Wostl (1993) represent an early step in this direction. Is it logical to speak of an average regional food web or a composite annual web? At any given moment, most local floodplain ecosystems are in a state of transition following disturbances of some kind (desiccation, flooding) that shift them toward earlier successional states. If one were to construct a composite food web, what form should that model take? Future food web theory should encompass both environmental heterogeneity and life history responses to such heterogeneity.

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