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SPATIAL AND TEMPORAL VARIATION IN TROPICAL FISH TROPHIC NETWORKS¹

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Abstract. Observed properties of natural food webs have both important theoretical and important management implications. Four lowland aquatic food webs were investigated over the course of two years: a large swamp and a small stream in Costa Rica, and a similar swamp and stream in the Venezuelan llanos. Each local ecosystem differed from the three others with respect to environmental changes associated with seasonal rainfall. Phylogenetic composition and diversity of biotas also varied among systems. Volumetric proportional utilization coefficients from fish gut contents were used as estimates of the intensity of predator–prey interactions. An annual and two or more seasonal food webs were constructed for each local community. Aquatic communities were defined operationally using common fish species as consumers, and using the sink subweb associated with the top predator of each system. A computer calculated a variety of food-web statistics and plotted food-web diagrams containing either (a) all observed trophic links (predator–prey interactions), or (b) subsets with weak links eliminated at prescribed thresholds.

Individual community food webs contained from 58 (stream, Costa Rica) to 104 (swamp, Venezuela) interactive taxonomic units and from 208 to 1243 total trophic links. Food-web parameters were very sensitive to changes in level of link threshold. Web connectance and related parameters converged near link threshold 0.04 (utilization coefficients <0.04 eliminated) in a variety of inter-web comparisons. Despite large differences in assemblage composition and attributes of the physical environment, distributions of trophic levels calculated according to a trophic continuum algorithm were very similar among study systems. Herbivores, detritivores, and their direct predators formed the largest proportions of fishes in each assemblage, followed by omnivores and secondary carnivores. Fishes that fed at more than one trophic interval were extremely common in all food webs.

Analysis of covariance was used to compare structural features of different webs across a range of link thresholds. Extensive among-site variation in food-web parameters was associated with differences in species richness and environmental differences associated with rainfall patterns, physiography, and gross primary production. Seasons generally influenced food-web parameters less than did site differences. Relative importance of detritus, aquatic primary production, and terrestrial production in aquatic food webs varied seasonally in each system. Detritus, derived primarily from aquatic macrophytes, was an important pathway in both tropical swamp ecosystems. Aquatic primary productivity comprised the largest fraction of fish diets during the wet season in the Venezuelan swamp, but it formed the major component of fish diets during the dry season at all other sites.

Based on comparisons using 13 webs, two-thirds of the pairings among six food-web parameters used (number of nodes, compartmentation, connectance, average number of prey per node, average number of predators per node, ratio of consumer nodes to total nodes) were positively intercorrelated. Several food-web relationships previously described as constant (e.g., connectance \times species richness constancy, species scaling law, link–species scaling law) were not confirmed by my data. These earlier food-web trends are extremely sensitive to methodological biases, especially decisions regarding the degree of taxonomic lumping of species into trophic units. Although food webs have unique emergent properties and spinoff a number of potentially informative macrodescriptors, empirical studies must achieve greater precision and uniformity before analyses can be performed across different systems. Several problems and potential resolutions are discussed.

Key words: *community; compartmentation; complexity; connectance; Costa Rica; detritus; food web structure; link threshold; llanos; predation; primary production; seasonality; species richness; trophic links; Venezuela.*

INTRODUCTION

Properties of food webs have become subjects of great interest over the past decade and a half (Gallopín

1972, Cohen 1978, Paine 1980, 1988, Pimm 1982, DeAngelis et al. 1983, Pimm and Kitching 1988, Lawton 1989). The concept of the food web as a network of local trophic interactions is a fairly simple idea that dates back to the early development of ecology as a scientific discipline (Darwin 1859, Elton 1927). Until

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recently, food webs have served primarily as heuristic devices, useful in depicting complex ecosystems as diagrams comprised of many interactive parts. Much of the recent surge of interest in food webs as ecological macrodescriptors seems to have been provoked by May's theoretical findings, which defined conditions for mathematical stability (local or Lyapunov stability) within randomly constructed interactive networks (May 1972, 1973). Although the generalizability of May's model to natural systems has been debated on the grounds of the nonrandom design of the latter (DeAngelis 1975, Lawlor 1978, Yodzis 1981), his research served to stimulate and redirect research in community ecology. For example, questions addressing the relationship between stability and diversity have become more focused as terms are defined with improved operational precision (Pimm 1979, 1984, Connell and Sousa 1983, King and Pimm 1983).

Much of the dialogue stimulated by May's stability analysis can be attributed to the use of a handful of very basic, operational parameters in his model. For example, the number of species and number of feeding interactions within communities can be measured or estimated in communities. The relative magnitude or strength of interspecific interactions is a much more difficult parameter to estimate. In theory, food webs possess many features required of a good ecological macrodescriptor (Orians 1980). The fundamental units of food webs can be observed or estimated, and yet as units, they have their own emergent properties. Properties of *real* food webs (i.e., descriptive food webs obtained from the ecological literature) have been investigated primarily from a theoretical perspective by contrasting observed systems with randomized model systems (Pimm and Lawton 1980, Yodzis 1981, 1988, Pimm 1982, Auerbach 1984, Cohen et al. 1986). Predominance of this theoretical approach may be due, in part, to a paucity of suitable empirical data for rigorous comparisons. Cohen (1978) observed a fairly constant prey-to-predator ratio among thirteen food web diagrams taken from the literature. Briand (1983) compiled 40 food webs from the literature and concluded that webs associated with physical environments characterized by small fluctuations are more connected than those in more variable environments. Based on 62, and later 113, food webs, Briand and Cohen (1984, 1987, Cohen and Briand 1984) proposed that certain features of food webs are scale-invariant (see *Discussion: Do food webs exhibit scale invariance?*, below). Unfortunately, each of these analyses suffers from a number of potentially confounding sources of variation, including (1) differences in duration and thoroughness of field investigations, (2) variation in original criteria used for determining either presence or absence of individual trophic links, (3) differences in criteria used for assigning membership in communities, and (4) large disparities in criteria used for grouping biological species into "trophic species" (Pimm 1982, Paine 1983, 1988).

The basic questions raised by these and other investigators are of fundamental importance for a fledgling discipline faced with great complexity, evolving terminology, and few unifying models. Comparative tests based on quantitative estimates of predator-prey interactions are needed to evaluate the influence of biological and environmental factors on properties of real food webs (Kitching 1987, Lawton 1989). This report contains several such tests, using neotropical fish assemblages as the principal units for definition and construction of local food webs. Although some methods employed here may not lend themselves easily to studies of other kinds of ecological communities, I attempted to achieve greater uniformity and precision in estimates of food-web parameters than are seen within collections of webs compiled from diverse literature sources.

By dealing directly with tropical freshwater fishes as consumers, a substantial fraction of the total predator-prey interactions can be estimated for an aquatic community. Tropical fishes in diverse assemblages display a particularly wide range of trophic niches (e.g., algivores, detritivores, granivores, omnivores, planktivores, insectivores, and piscivores of various kinds; Fryer 1959, Lowe-McConnell 1975, 1987, Saul 1975, Goulding 1980, Winemiller 1987). In addition, fish diets can be estimated accurately via stomach-content analysis using large numbers of preserved specimens. This investigation compares aquatic food webs at two locations in the Venezuelan llanos and two in the Atlantic lowlands of Costa Rica. In an attempt to reduce error during inter-site comparisons, data were gathered and analyzed in a nearly identical manner for each assemblage. Insights into biological, environmental, and methodological bases of food-web properties are sought through (1) between-site comparisons and (2) within-site comparisons between tropical wet and dry seasons.

STUDY SITES

Throughout 1984 I collected fishes from two locations in the state of Portuguesa, Venezuela. The more faunistically diverse site, Caño Maraca (88 fish species) is a swamp creek of the Río Apure-Orinoco drainage in the western llanos (8°52'30" N, 69°27'40" W; Fig. 1). The region lies within low, flat terrain that experiences extensive sheet flooding during the wettest months (June-August). During this time a large area bordering the creek channel is converted from exposed, sun-baked soil and thorn-scrub habitat into a productive marsh with diverse aquatic vegetation (Fig. 2). These floodplain areas are termed "esteros" in the local Spanish. During the driest months (December-May), the main stream channel is reduced to a network of mud-bottom pools blanketed by *Pistia stratiotes*, *Salvinia* spp., and *Lemna* spp.

The other Venezuelan site, Caño Volcán (8°59'15" N, 69°53'30" W), is a third-order stream of the Río Apure drainage, lying in the lowest tier of the Andean piedmont (Fig. 1). This stream flows through deciduous



FIG. 1. (A) Pool region of the Caño Maraca swamp creek in Venezuela (July 1984); (B) pool region of the Caño Agua Fría Viejo swamp creek in Costa Rica site (October 1985); (C) shallow-run region of Caño Volcán, a small forest stream in Venezuela (July 1984); (D) small pool at Quebrada, a small forest stream in Costa Rica (September 1985).

forest, is narrow, and contains both pool and riffle habitats. Caño Volcán differs from Caño Maraca in having (a) a coarser substrate, (b) a steeper gradient, (c) a more stable dry-season discharge, (d) steeper banks, (e) a more forested watershed, (f) fewer aquatic invertebrate species, and (g) only 20 fish species. The western llanos average ≈ 2.0 m of rainfall annually, with well over half of the total falling during four consecutive months (normally from May to August).

Aquatic feeding interactions were also studied at two sites located in Limón province, Costa Rica, each month between February and December 1985. The first of these sites, Caño Agua Fría Viejo, is a tributary creek of the Río Tortuguero located within Tortuguero National Park ($10^{\circ}30'05''$ N, $83^{\circ}30'05''$ W), and contained 55 fish species (Fig. 1). Sites studied within Caño Agua Fría Viejo were located ≥ 10 km upstream from the ultimate confluence with the Caribbean Sea. The creek's watershed is covered by dense lowland forest, dominated by *Raphia taedigera* in many stretches. Aquatic habitat at Caño Agua Fría is similar to that of Caño Maraca in Venezuela during the wet season. Caño Agua Fría differs from Caño Maraca in having (a) a more forested watershed, (b) a predominantly sandy as opposed to mud/clay substrate, (c) more numerous deep pools, and (d) a much less severe dry season (actually

two brief dry periods at Caño Agua Fría as opposed to one lengthy dry season at Caño Maraca). The Tortuguero region receives ≈ 5.0 m of rainfall annually. Broad floating mats of aquatic sedges (Cyperaceae) and grasses (Gramineae) were frequently encountered along sunlit marginal habitats of Caño Agua Fría. *Eichhornia crassipes* and other rooted aquatic macrophytes grew in the main channel of the stream throughout the year.

The other Costa Rican site is a small unnamed creek lying on the northern border of Tortuguero National Park ($10^{\circ}32'22''$ N, $83^{\circ}30'10''$ W; Fig. 1). The creek (hereafter referred to as Quebrada) drains the forest floor on the barrier island separating the freshwater Laguna Tortuguero from the Caribbean Sea (additional Tortuguero environmental data appear in Gilbert and Kelso [1971]). Only forest pools and the creek beyond a point 30 m above the confluence of the creek with the lagoon were evaluated. Quebrada has a sand and leaf-litter bottom, low gradient, both pool and riffle/run habitats, and 21 fish species. Quebrada is shorter, narrower, and shallower than Caño Volcán in Venezuela, and lacks large-scale, substrate particles in its riffles. Quebrada has a much flatter watershed than Volcán, and is associated with lateral sheetflooding in the adjacent rainforest during the wettest months (June–August, November–December).



FIG. 2. (A) View of the floodplain ("estero") region of Caño Maraca during the early wet season (June 1984); (B) View of the same region at Caño Maraca during the early dry season (January 1984).

METHODS

Sampling procedures

Fishes were collected principally by two sizes of seine (3.2-mm mesh, 2.5 m length; 12.7-mm mesh, 20 m length), but also with dipnets, experimental gillnets, cast nets, and hook and line. On each outing an attempt was made to sample the entire fish assemblage so that the sample for each species reflected its relative abundance and population size structure. Complete descriptions of collecting dates, techniques, and sample sizes for preserved specimens appear in Winemiller (1987) and Winemiller and Pianka (1990). Except for very abundant species, for which a subsample representative of the abundance rank in the collection was retained, all collected individuals were fixed in a 15% formalin solution. The body-cavity wall of large specimens was slashed to allow rapid penetration of formalin and fixation of stomach contents. Collecting efforts did not seriously impact local fish stocks, because only a fraction of total aquatic habitat was sampled at each site each month, and fishes could move freely between study sites and adjacent bodies of water. Following examination, a portion of the fishes collected in Venezuela was deposited in the Museo de Ciencias Naturales, La Universidad de los Llanos Occidentales

Esquiél Zamora, Guanare, Portuguesa, Venezuela, and a portion from Costa Rica was deposited in the Museo de Zoología, Universidad de Costa Rica, San José, Costa Rica. The remainder was deposited in the Natural History Collection of the Texas Memorial Museum, University of Texas, Austin, Texas.

Trophic data

Preserved specimens were identified, counted, and measured for standard length to the nearest 0.1 mm. Species relative abundances were calculated as the number of individuals of each species divided by the total number of fishes collected during the period considered (further details in Winemiller [1987]). Whenever available, 30 specimens of each species from each monthly collection were dissected for stomach content analysis. All available specimens of seasonally abundant piscivores, such as *Hoplias malabaricus* (Erythrinidae) and *Pygocentrus notatus* (Characidae), were dissected for stomach contents. Five Venezuelan and 20 Costa Rican detritivore/algivores were usually dissected from each monthly sample. These fishes typically exhibited comparatively low intraspecific variation in feeding habits and required more time and labor for diet estimates. When a monthly sample contained >30 specimens, individuals were chosen for dissection so that size classes were represented in proportions approximating those in the field sample. The total number of specimens examined for stomach contents was 9950 from Caño Maraca, 4222 from Caño Agua Fría Viejo, 3040 from Caño Volcán, and 2078 from Quebrada.

All food items in the anterior half of the gut were removed, examined under a dissecting microscope, and identified. An explanation of the food categories appears in Appendix 1. Prey items were then sorted, blotted dry, and measured in appropriately sized graduated cylinders by water displacement. The degree of resolution for very small items was 5 μ L. For volumes <5 μ L, a value was estimated by spreading the sample on a glass slide and comparing it to a similarly spread substance of volume equalling 5 μ L. Because their long digestive tracts are normally packed with a blend of fine-grained macroscopic and microscopic particles, detritivores and algivores were treated differently. Entire guts of detritivores and algivores were removed and a small sample of the contents of each was taken from the anterior-most segment. The sample was placed on a glass slide for examination under a light microscope. The volume of the entire gut and its contents were then measured by water displacement. The relative proportion of each identifiable item on the slide was estimated, then multiplied by the gut-plus-contents volume. In nearly all instances, the volume of gut tissue was negligible in relation to its contents. The relative proportions of food items estimated in this manner should closely reflect the consumption of food resources by the local population as a whole. The dif-

ference in methods for estimating the total volume of prey items used by detritivores vs. other forms did not yield major disparities in the community resource matrices, since volumes of prey items were ultimately converted to relative utilization proportions (p_{ij} s).

A unique trophic level was calculated for each fish species using the formula of Adams et al. (1983):

$$T_i = 1.0 + \sum_{j=1}^n T_j(p_{ij}),$$

where T_j is the trophic level of prey species j and p_{ij} is the fraction of the consumed food (proportion by volume) of species i consisting of prey species j . Following this method, plants are coded as $T = 0.0$, herbivores are $T = 1.0$, and a consumer eating exactly half plant and half herbivore tissue would be $T = 1.5$, and T_i s are computed sequentially from bottom to top. The use of this measure implies that ecological pyramids are more accurately represented by a trophic continuum rather than by consumers at discrete levels (Carney et al. 1981, Adams et al. 1983, Cousins 1985, 1987).

Food-web program

A brief description of the computer program used for construction of food webs and computation of food-web statistics follows. Listings of prey items eaten by each fish species, expressed as a proportion of the total volume of food consumed during a given time interval at a site (i.e., the community resource matrix expressed as p_{ij} s), were input for construction of food webs. Non-fish species from the fish prey lists were initially assigned basic prey lists of their own, based on information in Pennak (1978). The non-fish components of each community were run through the program for computation of positional x , y coordinates used later in constructing two-dimensional food-web diagrams. Because the study addresses actual observed variation in natural food webs, only data involving fishes as consumers were used for numerical comparisons. Once computed, the x , y coordinates of all non-fish community components were fixed, and estimated trophic interactions between non-fish species and their prey were eliminated from all subsequent calculations, including food-web statistics. Fish consumers were then merged with their appropriate non-fish community components to form input for the food-web program.

For consumer "nodes," the vertical coordinate was equal to the species' previously calculated trophic level (i.e., $y = T_i$). A consumer's horizontal coordinate was calculated as the geometric mean of the x coordinates of its prey (each weighted by p_{ij}). The program calculated horizontal positions in such a way that fish species consuming no other fishes were assigned coordinates first, fishes eating the previous fishes were second, and so on in a hierarchical fashion, until the spatial coordinate of the top-predator species was determined. Fol-

lowing this algorithm, each consumer was placed in a central position above the distribution of its prey on the horizontal axis. At the basal level, aquatic plants ($T = 0.0$) were assigned fixed x coordinates on the left half of the horizontal axis, and terrestrially based plants (also $T = 0.0$) were positioned horizontally across the right-hand side. Detritus categories ($T = 0.0$) were assumed to be a mixture of both aquatic and terrestrial matter, and were thus assigned fixed x coordinates near the center of the horizontal axis. Consequently, the horizontal position of a given consumer species reflects, to some degree, its relative dependence on pathways derived from autochthonous (algae plus aquatic macrophytes, species listed in Winemiller [1987]) vs. allochthonous (terrestrial plant tissues, fruits and seeds) sources of primary production.

Links that involve the movement of matter and energy from prey to predators positioned at lower trophic levels were identified and counted (termed "up-links"). The program allows production of food-web graphics and statistics either with or without up-links. Up-links were generally represented by small p_{ij} s, and always occurred at much lower frequencies than down-links. A few instances of cannibalism were identified but are not depicted in the food-web diagrams (self-eating loops were usually obscured by dense aggregations of predator-prey links in earlier versions of the program).

Input for the food-web program.—Community resource matrices were manipulated in several ways prior to their use as input to the food-web program. First, all unidentified partially decomposed fishes were divided equally (by volume) among the identified-fish prey categories for piscivores. Since some unidentified fishes were probably rare forms that had not been previously identified in diets, this procedure may overestimate evenness of diet components for generalist piscivores. Unidentified microcrustacea, aquatic insects, and terrestrial insects were retained as separate prey categories in an effort to partially offset lumping of biological species into trophic species (nodes) at lower trophic strata due to my inability to identify these operational taxonomic units (OTUs) at the species level. These categories undoubtedly contained many fragments of common identified insects in addition to unidentified rare forms. Unfortunately, this source of error is unavoidable given the means presently available. Non-fish vertebrate flesh was assigned to one of the following OTUs: turtles (probably *Pseudemys scripta*), mammals (probably Rodentia), or shorebirds (all three eaten by the piranha, *Pygocentrus notatus*, at Caño Maraca).

The trichomycterid catfish, *Ochmacanthus alternus*, consumed only mucous slime (Winemiller and Yan 1989). Aquarium observations revealed that *Ochmacanthus* is a nocturnal ectoparasite of relatively slow-moving, scaled fishes that have a thick, protective coating of mucus. Consequently, diet data were reentered for *Ochmacanthus* as *Hoplias malabaricus* ($p_{ij} = 0.33$),

Astronotus ocellatus (Cichlidae, $p_{ij} = 0.33$), and *Caquetia kraussii*, *Cichlasoma orinocense*, and *Aequidens pulcher* (Cichlidae, each with $p_{ij} = 0.11$) as best estimates based on the thick external slime layer, relatively large body size, slow swimming behavior, and relative abundances of these five species. In the cases of *Roeboides dayi*, *R. guatemalensis* (Characidae), and *Pimelodella* sp. 3 (Pimelodidae), fish scales were reassigned as fish prey categories at the specific level. Scales constituted a significant portion of the diet of these species. Aquarium observations of the behavior of two aggressive scale predators (*Roeboides* spp.), together with recorded information on scale morphology (i.e., size, shape, and ctenoid vs. cycloid morphology) provided a basis for conservative estimates.

In addition, three piranha species (*Serrasalmus irritans*, *S. medini*, and *S. rhombeus*: Characidae) were fin specialists during most of the year at Caño Maraca (Winemiller 1989b). Again, conservative estimates of the specific identity of their prey were possible based on three observations. First, the morphology and color of fin fragments in predator stomachs allowed accurate identification of prey in several instances. Second, shape and frequency of piranha nips on examined fish specimens were recorded and used to approximate the relative extent that prey species were exploited by each piranha species (e.g., Winemiller 1990a). Finally, I observed predatory behavior of immatures of all three species in aquaria. Each species exhibited fairly stereotypical behavioral patterns during prey pursuit and attack. *Serrasalmus irritans* was primarily a stealth predator of open water habitat and, to a lesser extent, of the edges of structures. *Serrasalmus rhombeus* was observed to ambush slower prey from concealed positions near structures, especially near the substrate. *Serrasalmus medini*, a more rotund fish, was more maneuverable and persistent during pursuit in the water column than the other two species.

Output: food-web graphics and statistics.—Trophic links in food-web diagrams were represented as undirected lines between nodes (species). Lines could be printed as a uniform width (line width = 1), or varied to represent the relative magnitude of interaction. For example, line width = 10 produces ten different line thicknesses ranked one to ten. In this case, the thinnest lines would collectively represent the lowest ten percentiles of interaction strengths (ranging from $p_{ij} = 0.0001$ to some value x_1). A width rank of ten represents the highest ten percentiles of observed interaction strengths ($p_{ij} = x_9$ to x_{10}). The actual values of x_1 through x_{10} depend upon the actual distribution of p_{ij} s observed in a given resource matrix. The program also allows one to choose the lower limit of the magnitude of trophic interactions to be included in analyses and graphics (termed “link threshold”). At a link threshold (LT) of zero, all interactions represented by p_{ij} s between 0.0001 and 1.0 are included in the web, whereas at LT = 0.05 only p_{ij} s between 0.05 and 1.0 are included.

Except for the up-link exclusion option, computations and rules involved in calculation of two-dimensional coordinates for food-web graphics do not affect calculations of food-web statistics. The link threshold and up-link exclusion options permit generation of several values for each food-web statistic using a single input file (i.e., resource matrix). An additional option permits weighting of trophic links by standardized relative abundances (mean value = 1.0) of either the predator or prey node. Kitching (1987) discussed reasons for considering the effect of differential species abundances on food-web structure. Consumer relative abundances were based on the monthly field samples, while non-fish relative abundances were calculated using total volumes in community resource matrices (i.e., for each prey node, volumes were summed across all fish consumers). Weighting of trophic links by predator or prey relative abundances had very little or no statistically significant effect on food-web properties (K. O. Winemiller, *unpublished manuscript*). All analyses presented here involved weighting of trophic links by predator standardized relative abundances.

Web connectance was calculated according to the formula given by Pimm (1982):

$$C = \frac{kn}{n(n-1)} = \frac{k}{n-1}, \quad (1)$$

where k is the average number of species with which any given species (in this paper, nodes) interacts, as either predator or prey, and n is the number of species in the food web. The formula is based upon the observation that $n(n-1)$ interactions are possible when the potential for cannibalism is excluded (Pimm 1982).

The program calculates Pimm and Lawton's (1980) compartmentation statistic (\bar{C}_1), a relative measure of the degree to which a web is divided into subunits. Compartmentation was derived from the formula,

$$\bar{C}_1 = \frac{1}{n(n-1)} \sum_{i=1}^n \sum_{j=1}^n S_{ij}, \quad (2)$$

when $j \neq i$. S_{ij} is the number of species with which both i and j interact (either as predator or prey) divided by the number of species with which either i or j interact. Pimm and Lawton cautioned that \bar{C}_1 may not be valid for comparisons of webs having different numbers of nodes or trophic links. \bar{C}_1 can be shown algebraically to be positively correlated with web connectance (C) when the latter is used as an estimate of the average probability of pairwise species interactions (see *Discussion: Food-web tautologies*, below). As a crude test for significant compartmentation in observed webs, \bar{C}_1 was calculated for 25 randomly generated webs. Each web was based on a matrix having the same number of nodes, links, basal nodes, and top predators as its observed prototype (following methods of Pimm and Lawton [1980]). The distribution of \bar{C}_1 values based on randomized webs in relation to ob-

served values constitutes a Monte Carlo test of statistical significance (Pimm and Lawton 1980).

To allow comparative evaluation of the distribution of interaction strengths (as estimated by resource matrix p_{ij} s), the proportion of major to minor trophic links was computed for food webs using ten different criterion levels for definition of major links ($p_{ij} = 0.0, 0.005, 0.01, \dots, 0.045$). In addition to the number of connected nodes and total web links, both the average number of prey and predator links per node were calculated for food webs at different link thresholds.

By definition, ecological communities have boundaries that are poorly defined and rather abstract in space and time (Whittaker 1975, Lane 1986). As a consequence, communities can be delimited in a variety of ways, probably none of which is entirely objective. For the purposes of the present comparisons, local food webs were delimited by fish species and their prey OTUs. Because large samples are required for accurate characterization of diet via stomach content analysis, only common fish species were included in the analyses and graphics presented in this report. Common species were defined as those contributing to 95% of the total number of individual fishes collected during a given sampling period (i.e., the rarest species comprising 5% of the total number of fishes in the sample were excluded from the data set). Several food webs were constructed at each site based on separate seasonal samples plus an annual matrix. Caño Volcán and the two Costa Rican sites were each divided into one wet- and one dry-season food web. Caño Maraca was divided into dry-, wet-, and transition- (September–December) season webs, the latter corresponding to a dynamic period of extremely high fish densities and gradual desiccation of aquatic habitat. Following Pimm (1982), each food web was also analyzed as the top-predator sink subweb. A top-predator sink web consists of all prey consumed by a designated top predator, in this case the piscivore having the highest trophic level value (T) plus all prey consumed by the prey of the top predator, and so on. Since all food webs are actually subwebs of larger interactive ecological networks, sink webs provide additional, and arguably more natural, units for inter-site comparisons of food-web properties relative to those defined by taxonomic or geographic criteria (Cousins 1980).

RESULTS

Composition of food webs

The total number of nodes, the number of fish species, and the number of trophic links for a given threshold showed large variation among 13 common-fish food webs (Table 1). Except for the Caño Maraca wet-season web, more total nodes and fish nodes were obtained for sites when data were combined into an annual resource matrix rather than analyzed separately as a seasonal web. Fish diets were influenced by resource avail-

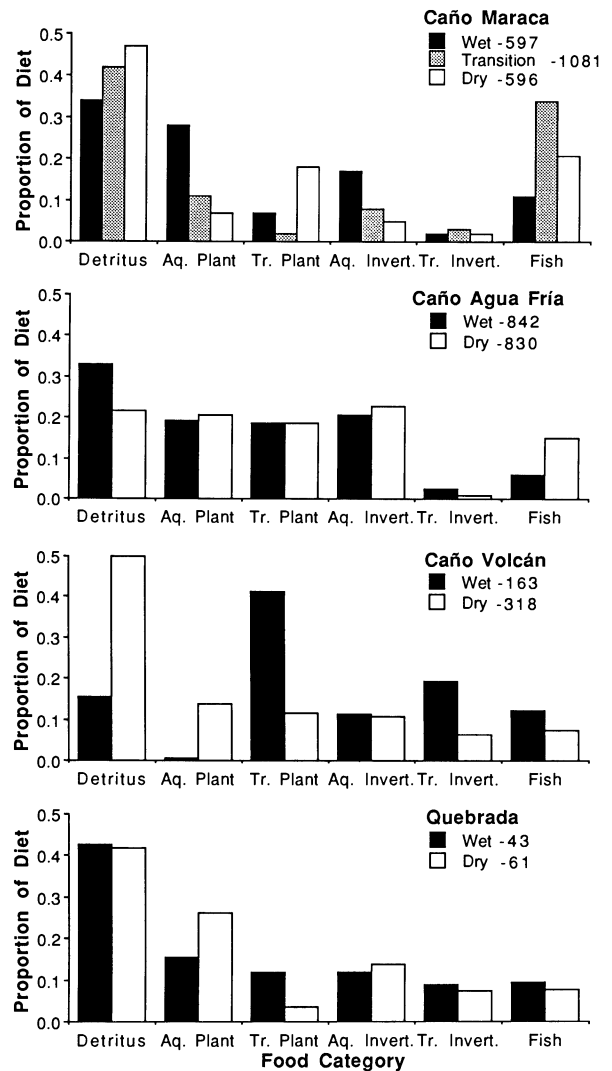


FIG. 3. Seasonal changes in volumetric proportions of six broad resource categories at the four study sites. Data are based on pooled stomach samples from all species collected at each site. Numbers in shading keys are total volume of food removed from stomachs (in millilitres).

abilities that fluctuate as seasons change (Fig. 3). As a result, more links were obtained for combined annual webs than for seasonal webs at each site (Table 1). Based on assemblage-wide resource consumption, seasonal fluctuations in resource availabilities were much greater at the Venezuelan sites (average seasonal differences in resource proportions were 0.11 and 0.16 at Caño Maraca and Caño Volcán, respectively) than in Costa Rica (mean seasonal difference was 0.04 for both sites). Interregional differences in temporal patterns of resource availability were influenced by a host of environmental factors associated with seasonal variation in rainfall (see Discussion: Dominant pathways of production, below).

Thirteen top-predator sink subwebs (derived from 13 common-fish webs) also show more nodes and links

TABLE 1. Parameter values for basic components of food webs defined by common fish species at four tropical sites. LT = link threshold, the lower limit of the magnitude of trophic interactions included in analyses. At LT = 0.0, all observed links are retained in the data set.

Community food web	No. nodes	No. fish nodes	Number of links				
			LT = 0.0		LT = 0.01		LT = 0.045
			Obs.	Ret.	Prop.*	Ret.	Prop.*
Caño Maraca (annual)	101	40	1243	470	0.38	204	0.16
Caño Agua Fría Viejo (annual)	83	25	536	206	0.38	113	0.21
Caño Volcán (annual)	66	11	334	136	0.41	54	0.16
Quebrada (annual)	62	11	288	111	0.38	48	0.16
Caño Maraca (dry season)	89	38	677	329	0.48	158	0.23
Caño Maraca (wet season)	104	44	1012	427	0.42	223	0.22
Caño Maraca (transition)	87	31	863	362	0.42	153	0.18
Caño Agua Fría (dry season)	76	22	449	172	0.38	95	0.21
Caño Agua Fría (wet season)	71	16	316	112	0.35	64	0.20
Caño Volcán (dry season)	64	9	264	114	0.43	48	0.18
Caño Volcán (wet season)	60	10	254	101	0.40	42	0.16
Quebrada (dry season)	58	9	208	91	0.44	41	0.20
Quebrada (wet season)	60	11	244	93	0.38	42	0.17

* Proportion of total observed links (link threshold = 0) retained in web at a link threshold of 0.01 or 0.045.

in combined annual webs than in seasonal food webs (Table 2). The total number of nodes was reduced from 3% (Caño Volcán, annual) to 67% (Quebrada, dry) in top-predator subwebs as compared to webs defined by the common-fish assemblage (mean = 21.9% reduction in total nodes per web). The total number of observed trophic links (LT = 0) ranged from 2% (Volcán, annual) to 91% (Quebrada, dry) less in predator subwebs compared with common-fish webs (mean = 50.5% reduction in links per web).

Between-web variation in the effect of link threshold on total number of trophic links was negligible (Table 2). Webs defined by common fishes retained between 35 and 48% of the total number of observed trophic links at a threshold of 0.01 (mean = 40.4%) and between 16 and 23% of total observed links at a threshold of 0.045 (mean = 18.8%). Top-predator subwebs retained between 36 and 50% of the total observed trophic links at a threshold of 0.01 (mean = 41.0%) and

between 15 and 28% of total observed links at a threshold of 0.045 (mean = 19.0%). Proportions of trophic links retained at the two link thresholds were not significantly different between common-fish webs and top-predator sink webs (Kolmogorov-Smirnov, both tests $P > .05$).

Trophic level

Distribution of fish trophic levels was similar for all four annual common-fish food webs (Fig. 4). Each assemblage was dominated by primary carnivores ($T = 2.0-2.5$) and herbivores ($T = 1.0-1.5$). Omnivores ($T = 1.5-2.0$) were less abundant than herbivores at each site, but always outnumbered secondary and tertiary carnivores ($T > 2.5$). The two most diverse sites, Caño Maraca and Caño Agua Fría, had greater proportions of primary carnivores (comprised mostly of insectivorous fishes) than the smaller stream sites. Seasonal differences in trophic-level frequency distributions

TABLE 2. Parameter values for basic components of top-predator sink subwebs at four tropical sites. Link threshold (LT) is defined in Table 1.

Top-predator sink subweb	No. nodes	No. fish nodes	Number of links				
			LT = 0.0		LT = 0.01		LT = 0.045
			Obs.	Ret.	Prop.*	Ret.	Prop.*
Caño Maraca (annual)	91	30	953	370	0.39	157	0.16
Caño Agua Fría Viejo (annual)	64	12	292	104	0.36	52	0.18
Caño Volcán (annual)	64	9	261	104	0.40	42	0.16
Quebrada (annual)	48	4	93	35	0.38	16	0.17
Caño Maraca (dry season)	62	16	309	128	0.41	65	0.21
Caño Maraca (wet season)	79	22	524	220	0.42	111	0.21
Caño Maraca (transition)	72	15	402	179	0.44	76	0.19
Caño Agua Fría (dry season)	56	6	152	60	0.39	33	0.22
Caño Agua Fría (wet season)	61	7	171	64	0.37	31	0.18
Caño Volcán (dry season)	60	6	182	74	0.41	34	0.19
Caño Volcán (wet season)	57	6	149	62	0.42	25	0.17
Quebrada (dry season)	19	1	18	9	0.50	5	0.28
Quebrada (wet season)	38	3	53	23	0.43	8	0.15

* Proportion of total observed links (LT = 0) at LT = 0.01 and 0.045.

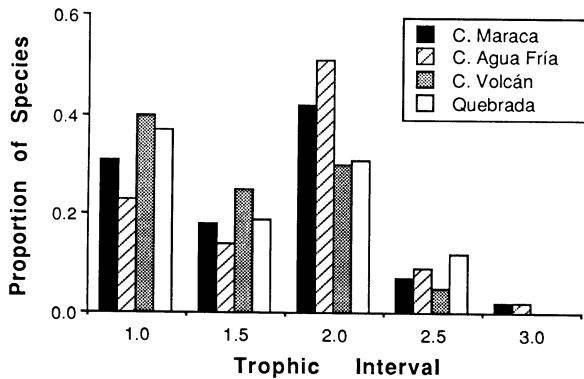


FIG. 4. Relative proportions of species in five trophic-level intervals at each study site. Trophic level is a continuous variable. Individual values were calculated from combined annual data according to the algorithm of Adams et al. (1983). All species collected with $N > 2$ are included in the distributions.

within sites were small (mean between-season difference in trophic-level interval proportions = [number of species in the interval]/[total number of species] = 0.04 [wet/dry] and 0.02 [wet/transition], Maraca; 0.04 [wet/dry], Agua Fría; 0.04 [wet/dry], Volcán; 0.13 [wet/dry], Quebrada) and nonsignificant (χ^2 , $df = 7$, $P > .05$).

Caño Volcán annual food webs exhibited approximately twice as many up-links relative to down-links as webs at the other three sites (Fig. 5). Ratios of up-links to down-links for seasonal common-fish webs were 0.116 (wet), 0.135 (transition), and 0.126 (dry) at Caño Maraca. Caño Agua Fría seasonal webs had up-link/down-link ratios of 0.179 (wet) and 0.175 (dry), and Quebrada webs had ratios of 0.173 (wet) and 0.078 (dry), whereas Caño Volcán seasonal webs had ratios of 0.209 (wet) and 0.228 (dry). A large proportion of up-links appeared to result from omnivorous fishes feeding on predatory terrestrial arthropods trapped in the water's surface tension. Except for Caño Volcán, the lowest up-link ratio occurred during the season of relatively greater aquatic primary production, as evidenced by standing stocks at each site (wet, Maraca; dry, Agua Fría; dry, Quebrada). Fish assemblages consumed larger fractions of allochthonous food resources during the season of low aquatic production at the highly seasonal Venezuelan sites (Fig. 3). Winding through hilly terrain, Caño Volcán had steeper banks and a much narrower floodplain than the other three sites. Caño Volcán fishes exhibited relatively greater consumption of terrestrial sources of primary production than fishes at other sites having broad floodplains (Fig. 3). Most characiform fishes at Caño Volcán (e.g., *Lebiasina erythrinoides*, *Astyanax metae*, *Brycon whitei*, *Bryconamericus beta*, *Corynopoma riisei*) consumed small carnivorous arthropods year-round. Up-links also resulted from consumption of carnivorous aquatic arthropods (e.g., belostomatid hemiptera, odonate nymphs) by omnivorous fishes.

Prey size appeared to be of much greater importance in structuring aquatic food webs than was trophic level per se. For example, species of the characid genus *Brycon* consumed large quantities of plant material. Although these large fishes possess multicuspid teeth that can be used to tear and crush fruits, seeds, flowers, and leaves, they occasionally consume large spiders and beetles stranded at the water's surface. Compared with arthropod prey, fishes consumed by other fishes at lower trophic strata comprised only about 10% of up-links on average.

Food-web diagrams

Annual food-web diagrams were extremely complex, showing high densities of trophic links over most regions of the graphs (Fig. 6). Trophic links commonly spanned > 1 trophic-level interval. Despite the fact that high link densities prohibited careful examination of specific structural details of diagrams, the rules used for assigning node positions permitted evaluation of several basic web features. First, variation in the location of areas with greatest trophic-link densities in complex food webs illustrates dominant regions of transfer of matter and energy through the web. For example, both the common-fish community web and top-predator web for Caño Agua Fría exhibited fairly even input of matter from aquatic, detrital, and terrestrial sources, but showed high link densities (i.e., darkest) in the regions of secondary consumers of animals feeding on aquatic sources of primary production and detritus (Fig. 6). Second, the horizontal position of the top-predator nodes indicates their relative reliance on aquatic (left-hand) vs. terrestrial (right-hand) sources of primary production.

The diverse Caño Maraca and Caño Agua Fría annual diagrams show fairly even utilization of aquatic, terrestrial, and detrital input from the base of the web (Fig. 6). The greater number of trophic links originating

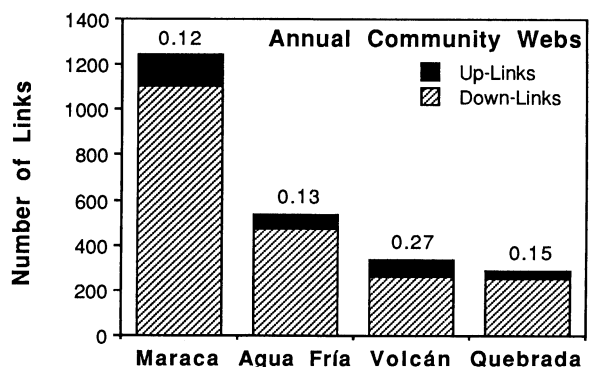


FIG. 5. Number of up-links (predation on a species at a higher trophic level) and down-links (predation on a species at a lower trophic level) in annual community webs at each study site (all links are included, i.e., $LT = 0$; link threshold is defined in Table 1). Numbers above each bar are ratios of up-links to down-links.

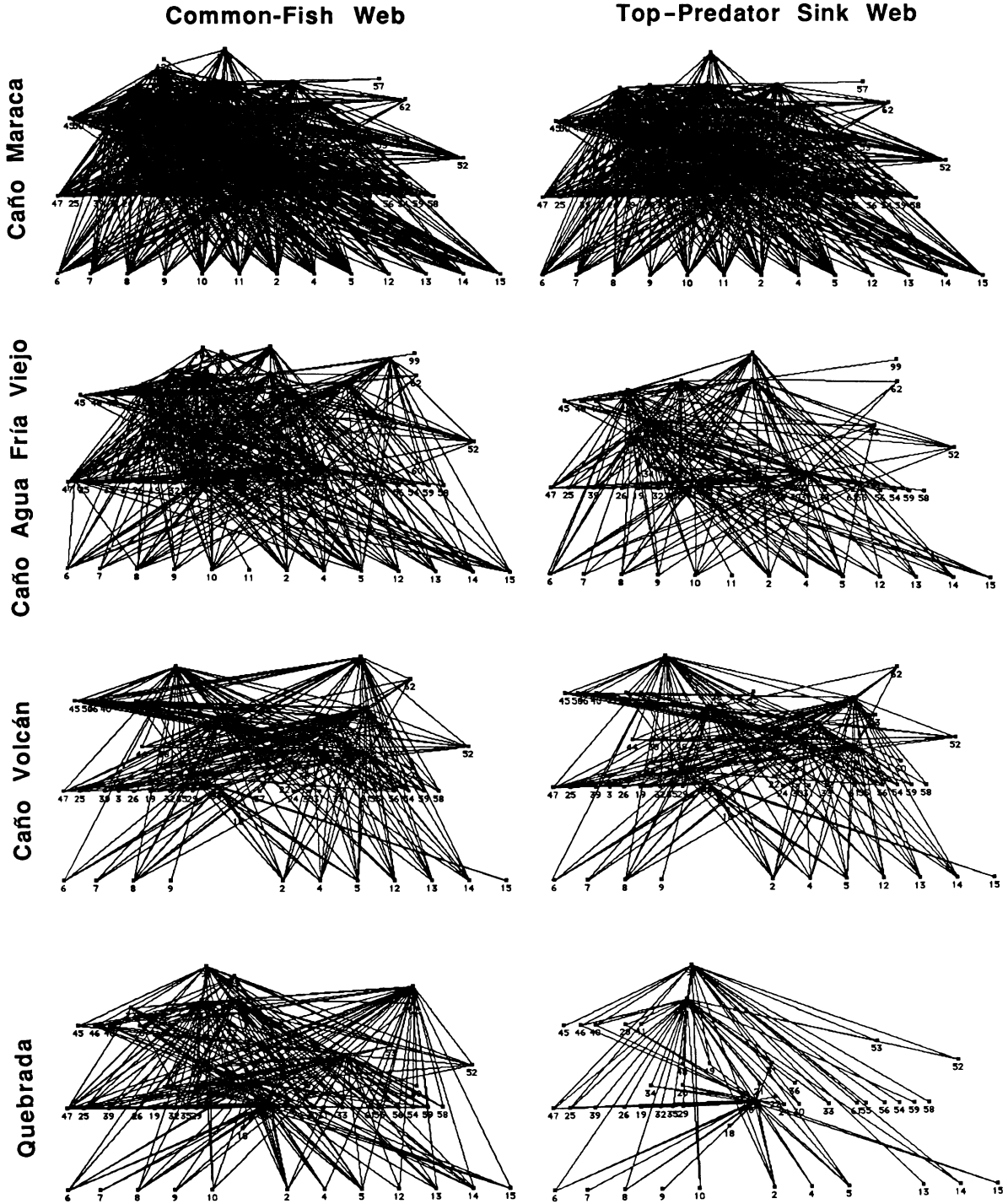


FIG. 6. Computer-illustrated, community food-web diagrams (left) and top-predator sink web diagrams (right) for each site, based on combined annual resource matrices. All observed feeding interactions were drawn ($LT = 0$) as undirected lines of uniform thickness. (Link threshold, LT , is defined in Table 1.) Nodes 2 through 62 (non-fishes) were fixed based on trophic affiliation with either the terrestrial or aquatic environment, and vertical positions were fixed based on the trophic continuum and rough diet estimates. The vertical position of each fish node was equal to its trophic level, and horizontal position was calculated as the mean of the horizontal positions of its prey (weighted by their volumetric proportions in the consumer's diet). Numbers specify nodes, which are identified in the Appendices.

from left-hand and central basal nodes of less speciose Caño Volcán and Quebrada web diagrams indicates a greater community-wide utilization of terrestrial and detrital sources of material in both common-fish and top-predator sink webs (Fig. 6). The top-predator node in the Caño Maraca annual food web (the mucus parasite *Ochmacanthus alternus*, $T = 2.87$) was positioned left of center, indicating dominance of trophic interactions linked to aquatic input at the base of the top-predator sink subweb (Fig. 6). Major piscivores positioned high and far to the left of the Maraca web included *Caquetia kraussii* ($T = 2.48$), *Hoplias malabaricus* ($T = 2.42$), and *Pygocentrus notatus* ($T = 2.41$). The top predator in the Caño Agua Fría top-predator subweb (the scale-predator *Roeboides guatemalensis*) was positioned centrally, indicating almost equal input from aquatic and terrestrial sources of primary production. Two other predators (*Lutjanus jocu*, $T = 2.54$, and *Belonesox belizanus*, $T = 2.50$) were also positioned high and more toward the aquatic production region of the horizontal axis in the Agua Fría web.

Both Caño Volcán and Quebrada top-predator nodes (*Roeboides dayi*, $T = 2.39$, and *Rhamdia guatemalensis*, $T = 2.70$, respectively) were positioned left of center, and thus were largely reliant on aquatic sources of production within their sink subwebs. The highest trophic level at Caño Volcán (2.48) actually corresponded to a non-piscivore, *Corynopoma riisei* ($T = 2.48$). This small, invertebrate-feeding fish was not used for defining the top-predator sink subweb analysis, since, in effect, the sink subweb of *Corynopoma* simply consisted of nodes contained in its diet and nothing else. *Corynopoma* fed heavily upon carnivorous terrestrial insects, whereas *Roeboides* fed on fish scales in addition to a variety of invertebrates at Caño Volcán. The Quebrada annual food web also exhibited a high node above the terrestrial region of the diagram (Fig. 6). As was the case for *Corynopoma* at Caño Volcán, the node representing *Alfaro cultratus* ($T = 2.45$) at Quebrada was not a part of the top-predator sink subweb (Fig. 6). *Alfaro*, a member of the livebearing Poeciliidae (Cyprinodontiformes), exhibited remarkable convergence with the characid *Corynopoma* (Characiformes) in feeding ecology, habitat affinities, and body form (Winemiller 1987). In addition to *Rhamdia*, *Gobiomorus dormitor* ($T = 2.58$) was positioned high above the aquatic production region of the Quebrada annual community food web.

The 60% reduction in trophic links of annual webs associated with $LT = 0.01$ can be viewed graphically by comparing the left column of Fig. 6 with the series of food webs in Fig. 7. These latter diagrams, containing only strong interactions corresponding to $LT = 0.01$ (i.e., all $p_{ij} < 0.01$ eliminated from diagrams), appear superficially to be as structurally complex as the largest webs used by Cohen (1978), Pimm (1982), Briand (1983), and Briand and Cohen (1987) for food-web analysis (e.g., see Fryer 1959: Figs. 89–91). In other

words, tropical fish food webs constructed with less than half of all observed feeding interactions look very similar to diagrams illustrated for other ecological communities from the earlier literature.

Between-site comparisons of food-web properties

Since trophic links exhibit large variation in relative magnitude, descriptive food-web statistics (compartmentation, connectance, mean number of prey per node, mean number of predators per node) were computed at 10 link thresholds ranging from 0.0 to 0.45 for all comparisons. Analysis of covariance was performed for each of the four food-web statistics for the main effect of site, with link threshold as the covariate (F statistic from the Type III ss). Statistical tests of significance using the compartmentation statistic (\bar{C}_1) are offered here only for a very rough preliminary analysis of differences in the degree of web subdivision or "blocking," and should be interpreted with extreme caution. Pimm and Lawton (1980) warned that values of \bar{C}_1 are probably not comparable for webs having different numbers of species, basal species, links, and so on. In addition to the ANCOVA test of between-group differences, compartmentation values calculated from 25 randomly constructed webs were compared with values obtained from each original observed food web at three link thresholds ($LT = 0.0, 0.02, 0.04$) to test for levels of food-web subdivision significantly lower than random expectation. Based on the null-model approach (Pimm and Lawton 1980), none of the annual common-fish webs or annual top-predator subwebs were significantly compartmented. Since none of the \bar{C}_1 values generated from randomized webs was smaller than observed compartmentation of their corresponding annual webs, inter-site and seasonal comparisons of compartmentation are only relative and rather tenuous.

Except for the annual Quebrada top-predator sink web (and to a much lesser extent the Volcán predator sink web), compartmentation declined rapidly between $LT = 0.0$ and 0.01 , followed by a much more horizontal slope between $LT = 0.01$ and 0.045 (Fig. 8). Except for the Quebrada top-predator sink web, slopes for log-transformed compartmentation values regressed against link threshold were not significantly different between sites. Because the probability of Type I error increases during multiple comparisons, statistical significance was inferred at $P < .012$ for tests of inter-site effects on food-web parameters using ANCOVA, and at $P < .025$ for between-season comparisons. Both the annual Maraca community web and top-predator sink webs were less compartmented than annual Volcán and Quebrada webs when variation across link thresholds was taken into account (Table 3, Fig. 8). Likewise, the annual Agua Fría community web and top-predator subweb were less compartmented than were the Volcán and Quebrada webs (Table 3, Fig. 8).

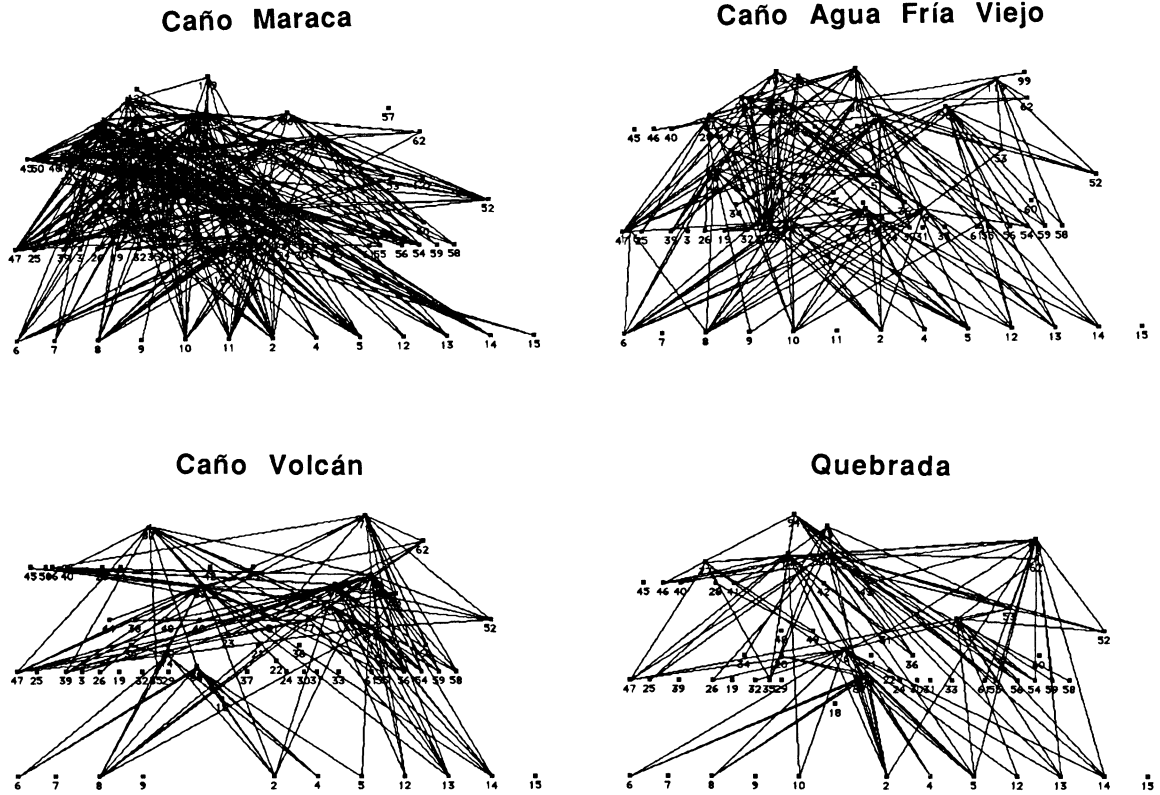


FIG. 7. The same community food webs from the left column of Fig. 6 drawn without weak trophic links corresponding to volumetric proportions of diet < 0.01 (i.e., link threshold = 0.01; link threshold is defined in Table 1).

The annual Caño Maraca community web was more connected than the other three webs (Table 3, Fig. 8). Connectance of Agua Fria, Volcán, and Quebrada annual community webs was not significantly different. Except for the Agua Fria–Volcán pairing, all annual top-predator sink webs had significantly different connectances (Table 3, Fig. 6). Maraca annual top-pred-

ator sink web was most connected, followed by Agua Fria, Volcán, and Quebrada.

For both annual community food webs and top-predator sink webs, Maraca had more predators per node than the other three sites (Table 3, Fig. 6). The annual Agua Fria community web had more predators per node than did the Volcán and Quebrada com-

TABLE 3. Results of ANCOVA (link threshold as covariate; df 1, 17) for tests of inter-site differences among food-web parameters (log-transformed) for annual common-fish webs and top-predator sink subwebs.

Sites compared	Log compartmentation		Log connectance		Log no. prey/node		Log no. predators/node	
	F	P	F	P	F	P	F	P
Common food webs								
Maraca–Agua Fria	2.01	.17	8.81	.008	4.82	.04	24.15	<.0001
Maraca–Volcán	38.01	<.0001	21.42	.0002	0.11	.74	90.59	<.0001
Maraca–Quebrada	18.45	.0005	26.90	<.0001	4.51	.048	100.22	<.0001
Agua Fria–Volcán	25.99	.006	1.55	.23	6.87	.017	14.83	.001
Agua Fria–Quebrada	9.80	<.0001	4.93	.04	0.00	.99	25.71	<.0001
Volcán–Quebrada	1.80	.18	1.50	.23	6.49	.020	3.22	.09
Top-predator sink subwebs								
Maraca–Agua Fria	4.00	.06	49.79	.0004	5.36	.033	65.92	<.0001
Maraca–Volcán	25.88	<.0001	41.31	<.0001	0.32	.58	112.58	<.0001
Maraca–Quebrada	32.23	<.0001	120.66	<.0001	13.86	.002	309.48	<.0001
Agua Fria–Volcán	11.51	.003	1.41	.25	3.62	.07	1.39	.25
Agua Fria–Quebrada	27.86	<.0001	38.63	<.0001	1.88	.18	80.59	<.0001
Volcán–Quebrada	7.33	.015	33.46	<.0001	11.44	.003	79.17	<.0001

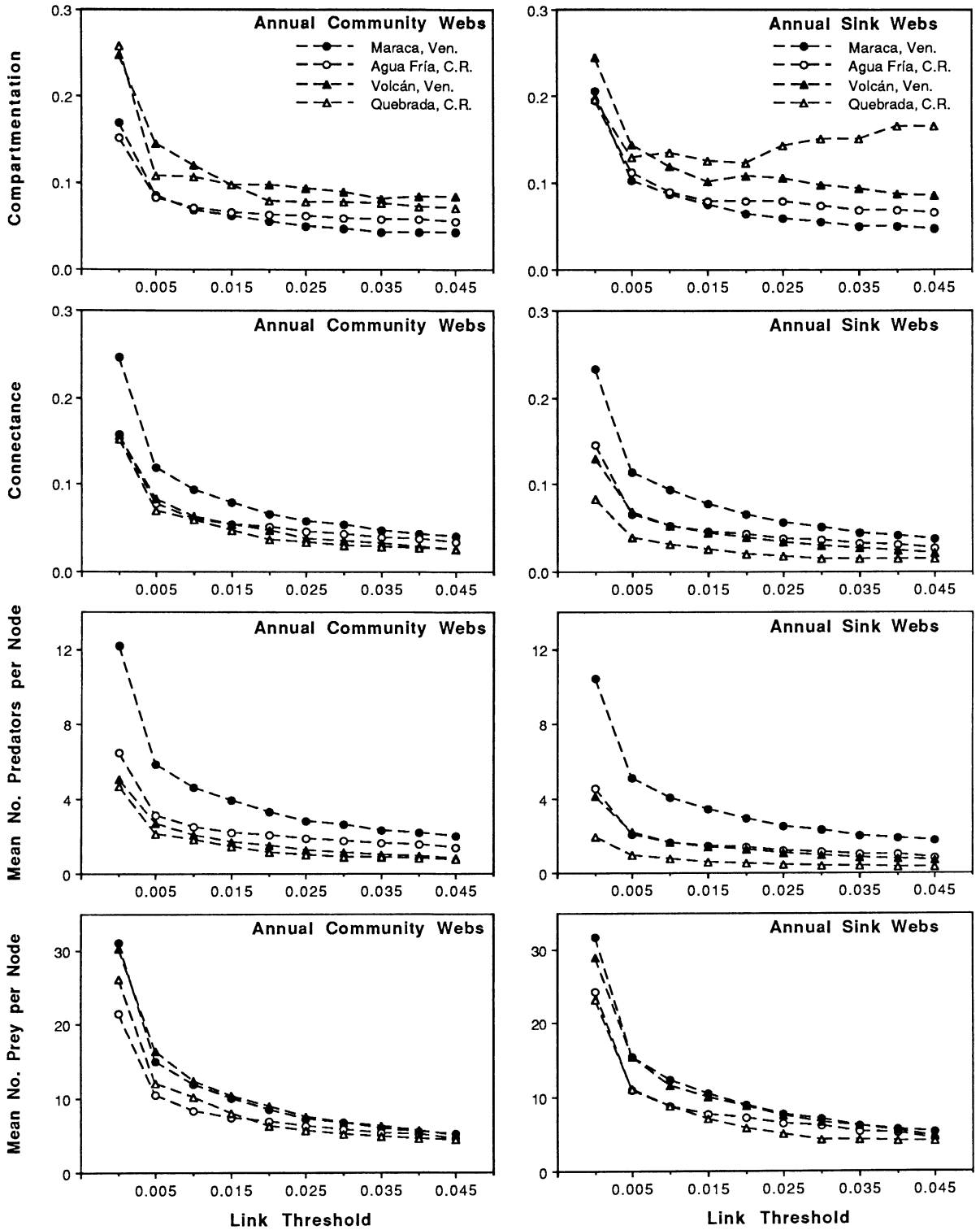


FIG. 8. Between-site comparisons of four food-web parameters at ten link thresholds for annual community webs (left column) and top-predator sink webs (right column). Link threshold is defined in Table 1.

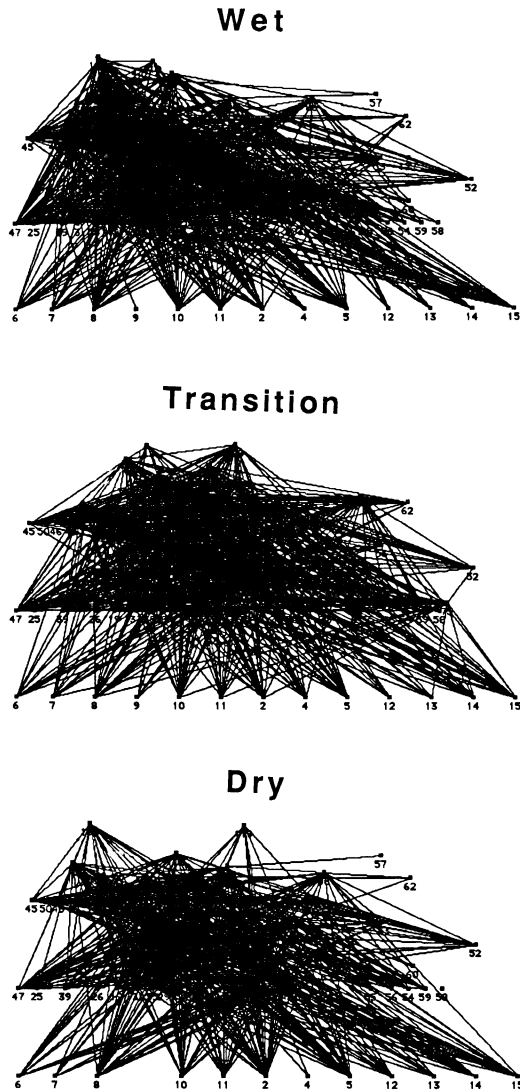


FIG. 9. Community food-web diagrams for Caño Maraca during three seasons (LT = 0; link threshold is defined in Table 1). The top predator during the wet season was the fin-nipping piranha, *Serrasalmus irritans* (Characidae). The top predator during the transition and dry seasons was the mucus-feeding catfish, *Ochmacanthus alternus* (Trichomycteridae).

munity webs, whereas the Volcán web had more prey per consumer node than the Quebrada web. Both Agua Fría and Volcán had more predators per node than Quebrada for top-predator sink webs (Table 3, Fig. 8). The annual Volcán community web averaged more prey per consumer node than Agua Fría and Quebrada (Table 3, Fig. 8). Among annual top-predator sink webs, Maraca and Volcán had on average, more prey per consumer node than Quebrada (Table 3, Fig. 8).

Inter-seasonal comparisons of food-web properties

Seasonal differences in relative positions of top-predator nodes and regions of greatest trophic link densities

can be observed in the Caño Maraca community food-web diagrams (Fig. 9). The piranha *Serrasalmus irritans* was the top predator ($T = 2.93$), positioned over aquatic sources of primary production in the wet-season diagram. *Hoplias malabaricus* ($T = 2.90$) and *Ochmacanthus alternus* ($T = 2.90$) were also positioned high and far left in the wet-season food web. *Ochmacanthus* ($T = 2.89$) was the top predator positioned centrally above aquatic, detrital, and terrestrial sources of production in the transition-season Maraca diagram. *Roeboides dayi* ($T = 2.88$) and *Charax gibbosus* ($T = 2.74$) were positioned much farther toward the aquatic region of the horizontal axis of the transition-season diagram. *Ochmacanthus* ($T = 2.84$) was the top predator in the Caño Maraca dry-season diagram. Again, *Ochmacanthus* was positioned over the center of the horizontal axis, indicating relatively even reliance on aquatic and terrestrial sources of production during the dry season (Fig. 9). The swamp eel, *Synbranchus marmoratus* ($T = 2.83$), was positioned far to the left, above the aquatic production region of the dry-season Maraca diagram (Fig. 9).

Overall, season demonstrated much less effect on food-web parameters than regional differences. Compartmentation and connectance showed no significant seasonal variation at Caño Maraca in either common-fish community webs or top-predator sink webs (Table 4). The transition-season top-predator sink web averaged more prey per node than the dry sink web at Maraca (Table 4, Fig. 10). The wet-season top-predator sink web had, on average, more prey per node than the dry sink web; however, the level of significance was only marginal ($P = .026$). The wet-season top-predator sink web exceeded the dry season one for average number of predators per node (Table 4, Fig. 10). In addition, wet-season predators per node was greater than that for transition-season near the chosen significance level (Table 4, Fig. 10).

For Caño Agua Fría community webs, dry-season connectance and mean number of predators per node were greater during the dry season than the wet season (Table 4, Fig. 11). Only compartmentation showed seasonal influence among Agua Fría top-predator sink webs; however, this main effect was largely diminished by the interaction between link threshold and season (note slope differences in Fig. 11).

Connectance showed no seasonal difference in either community or top-predator Caño Volcán webs. Compartmentation and average number of prey per node were greater during the dry season in Volcán community food webs (Table 4, Fig. 12; note the slope difference for compartmentation). Mean number of prey per node was also greater during the dry season in Volcán top-predator sink webs (Table 4, Fig. 12).

Mean number of prey per node was greater during the dry season at Quebrada in both community and top-predator sink webs (Table 4, Fig. 13). Compartmentation and connectance were greater during the dry

TABLE 4. Results of ANCOVA (link threshold as covariate; df 1, 17) for tests of within-site seasonal differences among food-web parameters (log-transformed) among common-fish webs and top-predator sink subwebs.

Site	Seasons compared	Log compartmentation		Log connectance		Log no. prey/node		Log no. predators/node	
		F	P	F	P	F	P	F	P
Common food webs									
Maraca	Wet vs. Dry	0.15	.70	0.00	.99	4.82	.04	4.26	.054
Maraca	Wet vs. Trans.	1.10	.31	0.97	.33	0.79	.38	1.40	.25
Maraca	Trans. vs. Dry	0.42	.52	1.26	.27	9.94	.006	0.38	.54
Agua Fría	Wet vs. Dry	0.38	.55	8.96	.008	1.64	.21	14.46	.001
Volcán	Wet vs. Dry	8.49	.01	0.01	.93	8.00	.01	0.95	.34
Quebrada	Wet vs. Dry	0.77	.39	0.59	.45	4.97	.04	0.02	.88
Top-predator sink subwebs									
Maraca	Wet vs. Dry	1.01	.06	0.02	.64	5.89	.026	10.90	.004
Maraca	Wet vs. Trans.	0.73	<.0001	1.68	.21	1.16	.29	5.89	.026
Maraca	Trans. vs. Dry	0.05	<.0001	0.06	.43	13.16	.002	1.08	.31
Agua Fría	Wet vs. Dry	4.19	.0011	3.30	.08	2.71	.12	0.95	.34
Volcán	Wet vs. Dry	0.34	.06	2.29	.15	7.49	.014	4.55	.047
Quebrada	Wet vs. Dry	455.0	<.0001	48.61	<.0001	11.72	.003	1.32	.26

season in Quebrada top-predator sink webs (Table 4, Fig. 13).

Intercorrelations among food-web properties

Correlation analysis was performed on six food-web parameters using all 8 annual webs and sink webs and all 18 seasonal webs and sink webs reported earlier. Ten of 15 pairings between food-web parameters were positively correlated at LT = 0.0 (Table 5). High correlations were obtained for (1) connectance with total number of nodes, (2) predators per node with total nodes, (3) proportion of consumer nodes with total nodes, (4) connectance with predators per node, (5) connectance with proportion of consumer nodes, and (6) predators per node with consumer nodes (Table 5).

An almost identical pattern of positive intercorrelations among food-web parameters was obtained for measurements performed at LT = 0.045 (Table 6). Compartmentation was weakly correlated with connectance in both data sets. Number of prey per consumer node, actually a crude measure of diet diversity, was not correlated with any other food-web variable.

Habitat dimensions and compartmentation

Pimm and Lawton (1980) presented a means of comparing the number of community predator-prey interactions listed as occurring between species occupying particular habitat patches with the number of interactions dictated by random expectations. A chi-square analysis is performed on food webs using expected values for between-habitat trophic interactions (\hat{Q}) generated with the algorithm of Pimm and Lawton (1980). The random expectation, \hat{Q} , is a function of the number of species in each habitat and the average number of interactions per species within each habitat. When \hat{Q} significantly exceeds the number of observed between-habitat interactions (Q), more interactions are occurring within habitats than would be expected by chance.

To test for subdivision of food webs in association with characteristics of the aquatic habitat, the algorithm of Pimm and Lawton (1980) was performed on each dry-season, annual community web at LT = 0.0 and 0.01. In addition, the most seasonal site, Caño Maraca, was tested during the wet and transition seasons (LT = 0.01). Habitat was divided along two spatial dimensions: vertical (pelagic vs. benthic) and horizontal (open water vs. vegetation). The two small streams, Caño Volcán and Quebrada, had very few aquatic macrophytes; consequently, only compartmentation in association with the vertical dimension could be tested for these systems. Each node was assigned to one habitat based on where the majority of individuals were collected or observed. Cases in which an operational taxonomic unit (OTU) was entirely restricted to only one habitat were rare. As a result, this analysis is probably biased in favor of within-habitat species interactions.

Since expected between-habitat interactions (\hat{Q}) were never significantly greater than observed values (Q), none of the dry-season food webs exhibited significant compartmentation in association with habitat at either link threshold (Table 7). By contrast, all six dry-season webs had significantly more between-habitat trophic interactions than expected by chance at LT = 0.0 (Table 7), a result that runs counter to the predicted direction of bias from subjective assignment of OTUs to habitats. Caño Maraca food webs were not significantly compartmented during the other two seasons either. Both wet and transition webs at Caño Maraca had more between-habitat interactions along the horizontal dimension than expected by chance (Table 8). This analysis reveals no tendency for food webs to be organized into interactive blocks within major habitat divisions. Moreover, the interface between vegetation and open water seems to be a particularly active area for aquatic predation (discussed below, see *Discussion: Food-web compartmentation*).

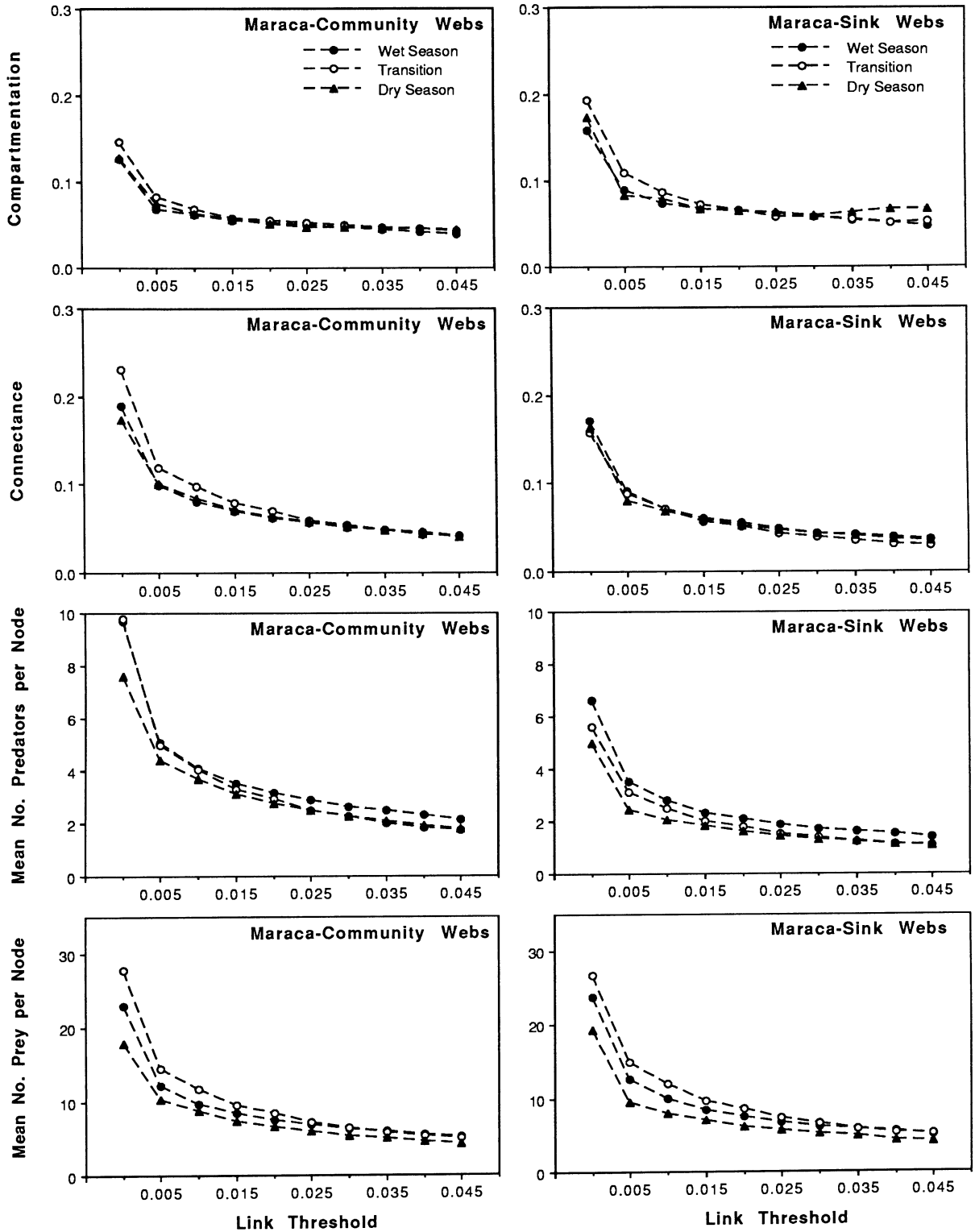


FIG. 10. Between-season comparisons of four food-web parameters at 10 link thresholds for Caño Maraca community (left column) and top-predator sink webs (right column). Link threshold is defined in Table 1.

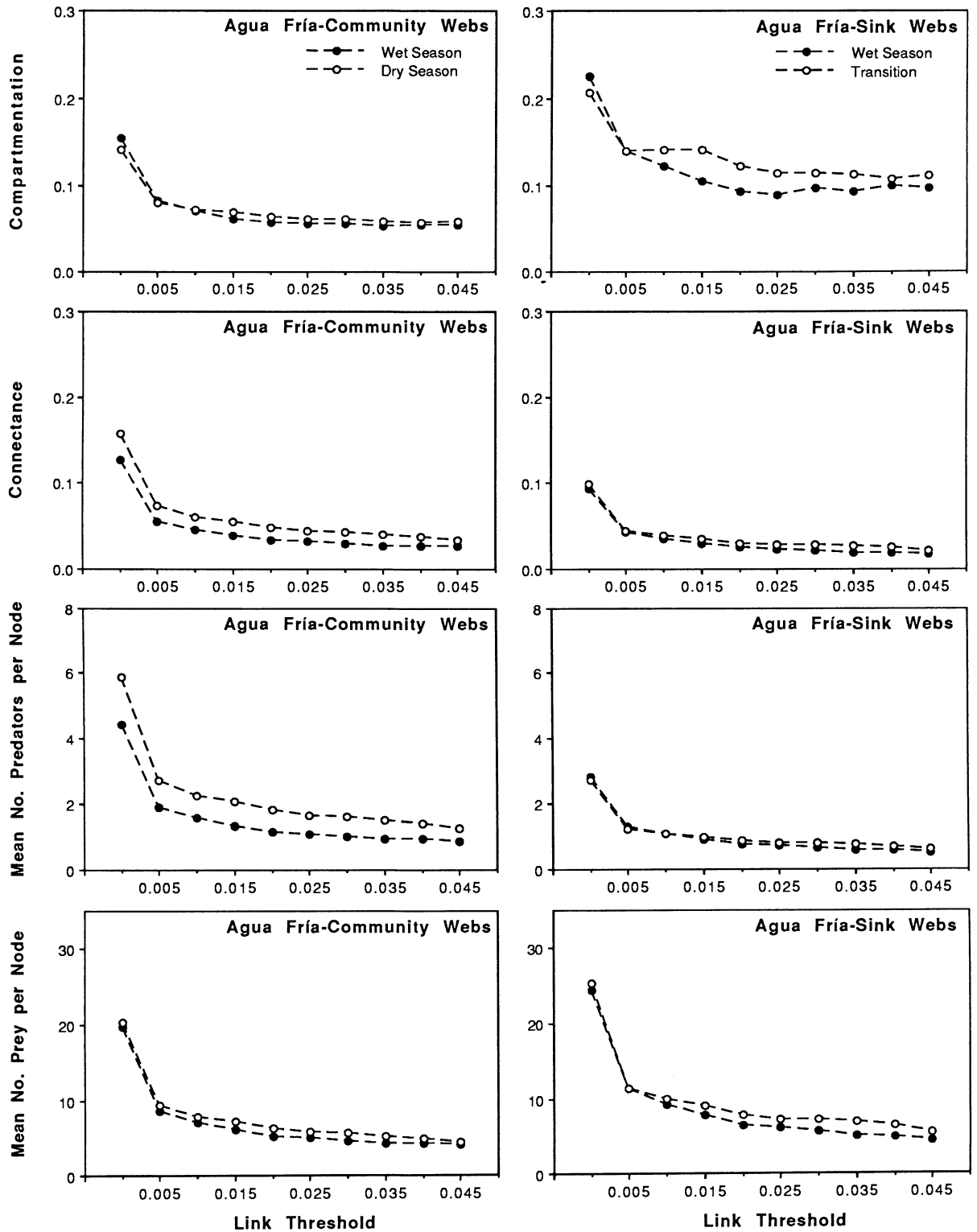


FIG. 11. Between-season comparisons of four food-web parameters at 10 link thresholds for Caño Agua Fria Viejo community (left column) and top-predator sink webs (right). Link threshold is defined in Table 1.

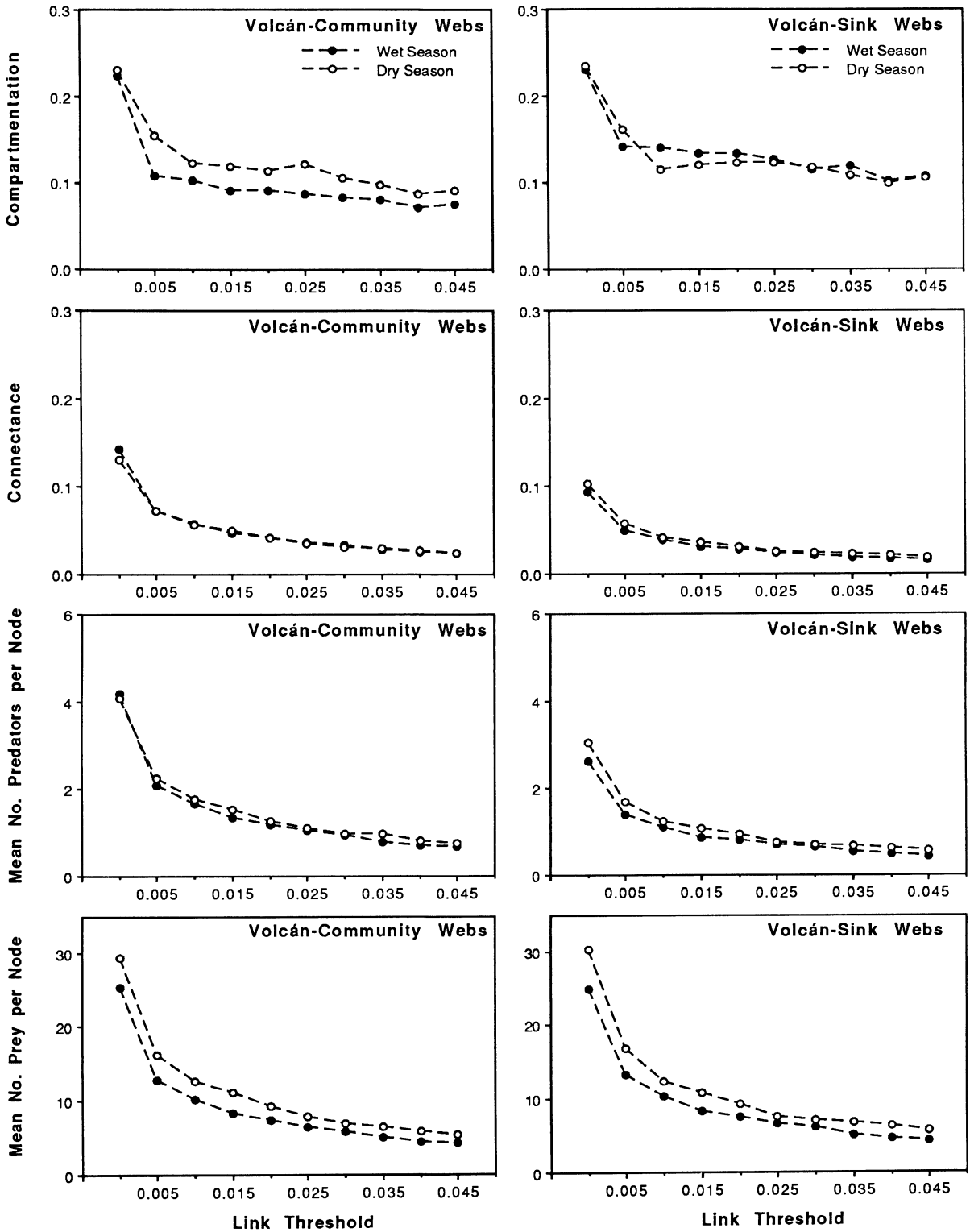


FIG. 12. Between-season comparisons of four food-web parameters at 10 link thresholds for Caño Volcán community (left column) and top-predator sink webs (right). Link threshold is defined in Table 1.

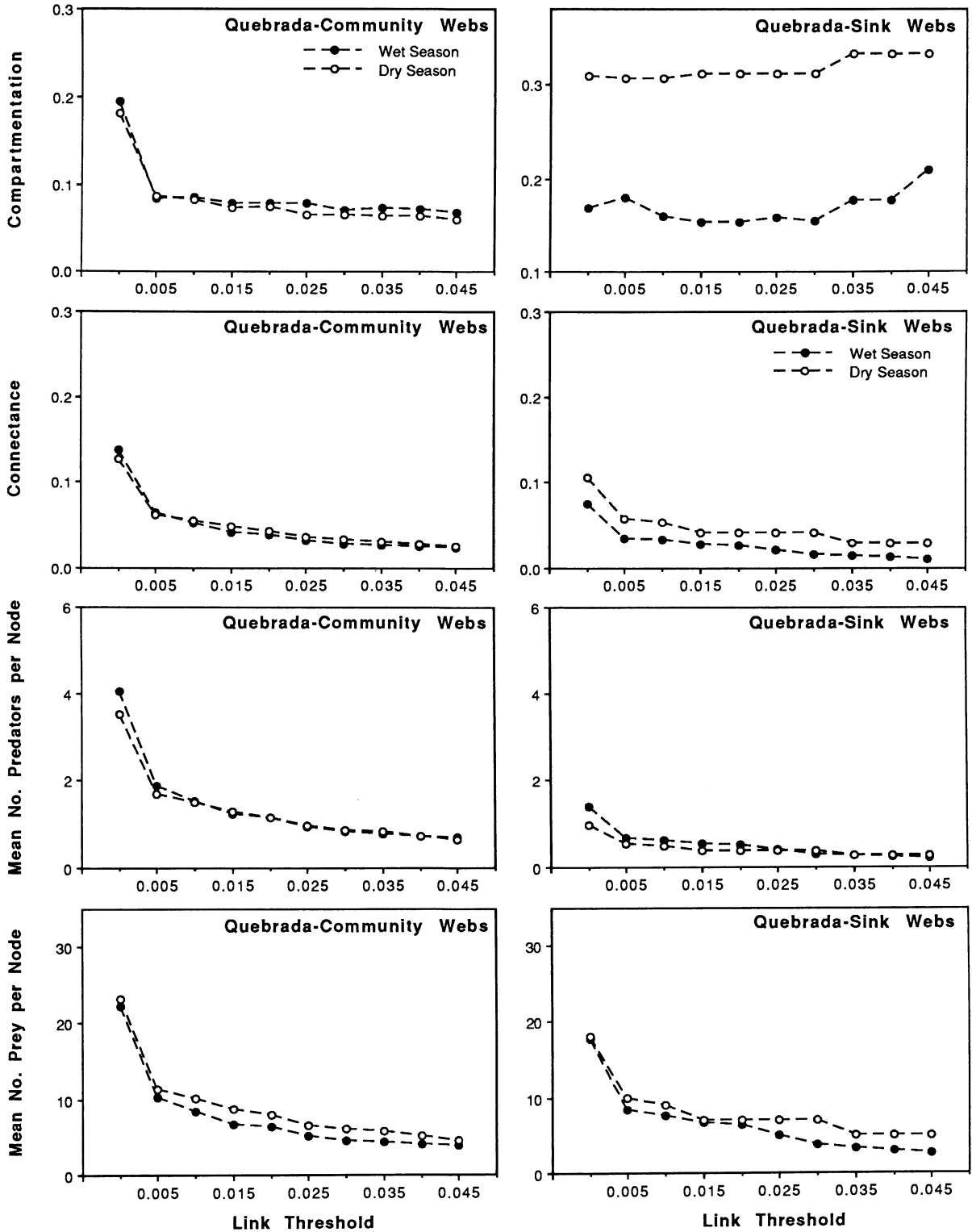


FIG. 13. Between-season comparisons of four food-web parameters at 10 link thresholds for Quebrada community (left column) and top-predator sink webs (right). Link threshold is defined in Table 1.

TABLE 5. Correlations (r^2 ; common-fish and top-predator sink webs, $df = 25$) among six food-web parameters at link threshold = 0.0. Link threshold (LT) = the lower limit of the magnitude of trophic interactions included in analyses. Even the weakest observed links are retained for the analysis at $LT = 0.0$.

	No. nodes	Compartmentation	Connectance	Prey/Node	Pred./Node
Compartmentation	.44*	...			
Connectance	.67****	.18*	...		
Prey/Node	.11	.10	.13	...	
Predators/Node	.85****	.30*	.92****	.13	...
Consumer/Total nodes†	.83****	.53****	.75****	.001	.85****

* $P < .05$, **** $P < .0001$.

† The ratio of fish consumer nodes to total nodes in the connected web.

DISCUSSION

The tropical aquatic food webs analyzed in this report are more species rich than those compiled from the literature and used in earlier studies (e.g., Cohen 1978, Yodzis 1981, Pimm 1982, Briand and Cohen 1984, 1987, Cohen et al. 1985). For example, Briand and Cohen's (1987) 113 food webs have an average of 17 trophic species (range = 2–48) compared with an average of 75 nodes for 13 common-fish community webs (range = 58–104) and an average of 59 nodes for top-predator sink webs (range = 19–91) in this study. Briand and Cohen's 113 webs averaged 34 trophic links (range = 2–138). In the present study, common-fish community webs averaged 514 links at $LT = 0.0$ (range = 208–1248). Even with many observed trophic links eliminated at $LT = 0.045$, the fish community webs had far more links (mean = 99, range = 41–223) than webs listed in Briand and Cohen's compendium. Top-predator sink webs averaged 274 links (range = 18–953) at $LT = 0.0$ and 48 links (range = 5–157) at $LT = 0.045$. In spite of these statistics and the impressive complexity of diagrams associated with each tropical aquatic system (Figs. 6, 7, and 9), the food webs presented here probably represent fairly rough approximations of the true complex network of trophic interactions. For example, only observed feeding links between fishes and their prey were included for analysis. How many more links would have been added to each web if the feeding of molluscs, predaceous insects, and other organisms had been estimated? The total number of trophic links could be increased yet further by splitting nodes comprised of lumped taxa into separate species. In addition, only common fishes were

included in the analyses. Omission of rare species and sampling error are undoubtedly to blame for some species having no apparent predators, an obvious biological absurdity (even top predators are not immune to predation). Analysis of the same systems with rare fishes included did not necessarily eliminate species with no predators, and in some cases magnified gaps in food webs caused by sampling error (K. O. Winemiller, *unpublished manuscript*).

For over a decade, ecology has been challenged to seek out and explain robust universal patterns among natural food webs (Gallopín 1972, Cohen 1978, Pimm 1982, DeAngelis et al. 1983, Briand and Cohen 1984, 1987, Paine 1988, Lawton 1989). The scientific merits of this endeavor are obvious. Apart from the wealth of natural history contained in a complex food-web diagram, recognition of common features and properties of food webs is likely to reveal much about the structure and function of ecosystems. Yet, in practice, completely reliable estimation of the sum total of feeding interactions within a local community, even a very simple one, would be difficult and probably impossible, given the technology and financial resources presently available. Scientists in all disciplines seek general unifying laws of nature. Yet, the immense practical difficulties of dealing simultaneously with temporal, spatial, and intraspecific variation in food webs threaten to foil the best intentions of ecologists once again.

Limitations and suitability of data used for analysis of food webs should be evaluated a priori. In this study, tropical aquatic food webs were estimated, manipulated, and analyzed using the same criteria in an attempt to minimize generalizations based on artifacts of methodology. Although the standard protocol em-

TABLE 6. Correlations (r^2 ; common-fish and top-predator sink webs, $df = 25$) and among six food-web parameters at link threshold = 0.045. Link threshold (LT) is defined in Table 5.

	No. nodes	Compartmentation	Connectance	Prey/Node	Pred./Node
Compartmentation	.49****	...			
Connectance	.79****	.24*	...		
Prey/Node	.10	.03	.14	...	
Predators/Node	.96****	.40*	.85****	.11	...
Consumer/Total nodes†	.74****	.44*	.55****	.01	.75****

* $P < .05$, **** $P < .0001$.

† The ratio of fish consumer nodes to total nodes in the connected web.

TABLE 7. Observed (Q) and expected (\hat{Q}) numbers of trophic interactions (links) between vertical (pelagic vs. benthic) and horizontal (open water vs. vegetation) habitat divisions during the dry season at each site.

Site	Habitat A	Habitat B	Number of nodes		Number of links		Q	\hat{Q}	χ^2
			In A	In B	Within A	Within B			
Link threshold† = 0.0									
Maraca	Pelagic	Benthic	38	51	149	252	276	196.2	45.7***
Maraca	Open	Vegetation	47	42	201	177	299	188.4	89.9***
A. Fría	Pelagic	Benthic	34	44	90	168	191	126.9	45.1***
A. Fría	Open	Benthic	41	37	119	119	211	118.7	97.6***
Volcán	Pelagic	Benthic	31	34	77	69	118	72.9	38.5***
Quebrada	Pelagic	Benthic	29	37	47	76	85	60.6	42.9***
Link threshold† = 0.01									
Maraca	Pelagic	Benthic	38	48	79	143	106	108.6	0.2
Maraca	Open	Vegetation	45	41	105	92	132	98.3	16.5***
A. Fría	Pelagic	Benthic	27	33	39	76	60	56.9	0.2
A. Fría	Open	Vegetation	27	33	53	48	74	50.0	35.7***
Volcán	Pelagic	Benthic	25	24	41	29	44	35.0	3.3
Quebrada	Pelagic	Benthic	23	31	23	43	30	32.3	0.3

*** $P < .001$.

† Defined in Table 5.

ployed for food-web construction and analysis by no means eliminates artifactual trends, it at least facilitates discrimination among alternative factors influencing food-web features. The primary challenge of food-web research now is to discriminate among biological, environmental, mathematical, and methodological (artifactual) influences on characteristics of food webs.

Some basic structural properties of food webs

Several theoretical treatments of food webs have argued against occurrence of so-called biological absurdities, such as a species that preys only upon itself, and loops in which species A eats species B and B eats A, or in which species A eats B, which in turn eats species C, which eats A (Pimm 1982, Cohen and Newman 1985). Obviously, no heterotrophic population can persist without energy and nutrient input from exogenous sources. Yet cannibalism does exist in many food webs. Fifteen of 6688 total trophic links in community food webs were cannibalistic (average $p_{ij} = 0.078$). Most cannibalism was on juvenile piscivores that occurred at high densities in vegetation (e.g., *Hoplías malabaricus* at Caño Maraca and *Eleotris amblyopsis* at Caño Agua Fría Viejo). Several two-species

feeding loops were identified. Feeding loops involving adult size classes of two species were rare. At Caño Maraca, the tiny trichomycterid catfish, *Ochmacanthus alternus*, feeds on the external mucous slime of the large cichlid, *Astronotus ocellatus*, which in turn preys upon *Ochmacanthus*. More commonly, feeding loops involved reciprocal consumption of juveniles by two piscivores, or consumption of a piscivore's offspring by adults of a primarily non-piscivorous prey. For example the cichlid *Cichlasoma dovii* consumed juvenile sleepers, *Gobiomorus dormitor* (Eleotridae), and *Gobiomorus* consumed juvenile *C. dovii* at Caño Agua Fría Viejo. Reciprocal feeding on juveniles was also observed between vegetation dwellers *Eleotris amblyopsis* (Eleotridae) and *Cichlasoma friedrichsthalii* (Cichlidae) at Caño Agua Fría. Feeding loops involving three or more species were not observed in any data set. Omission of invertebrate feeding in aquatic food webs probably underestimated feeding loops to some extent. Conceivably, large belostomatid and nepid Hemiptera could prey upon juvenile piscivores that feed on insectivorous fishes that in turn prey upon the hemipterans. A similar scenario could involve leeches, predaceous aquatic Coleoptera, or even ectoparasitic crustaceans (the latter observed attached to fishes but not encountered in fish stomachs).

TABLE 8. Observed (Q) and expected (\hat{Q}) numbers of trophic interactions (links) between vertical (pelagic vs. benthic) and horizontal (open water vs. vegetation) habitat divisions during the wet and transition seasons at Caño Maraca. (Link threshold† = 0.01.)

Season	Habitat A	Habitat B	Number of nodes		Number of links		Q	\hat{Q}	χ^2
			In A	In B	Within A	Within B			
Wet	Pelagic	Benthic	47	57	170	114	143	140.4	0.1
Wet	Open	Vegetation	55	49	130	127	170	128.2	19.5***
Transition	Pelagic	Benthic	45	46	128	103	131	115.5	3.0
Transition	Open	Vegetation	46	45	123	94	145	108.5	17.5***

*** $P < .001$.

† Defined in Table 5.

Pimm and Lawton (1978) used stability analysis to show that omnivory, in the form of a species feeding on >1 trophic level T , should be rare in natural communities (i.e., momentarily leaving aside the problem of discrete trophic levels). Their results also predict that omnivores should rarely feed on organisms not occupying an adjacent trophic level (either above or below). Yodzis (1984) performed a similar analysis involving randomized model webs which supported a "common-sense" explanation for the apparent rarity of omnivory, namely, that physiology constrains feeding on both plant and animal tissues. In contrast, omnivory was the rule in the detailed description of a fishless aquatic food web of Hildrew et al. (1985), with larvae of an alderfly (Neuroptera, Sialidae) feeding on four trophic levels. Instances of consumers feeding on >1 level (i.e., whole-integer interval within the trophic continuum) were common in all 13 tropical aquatic food webs, even when incidental detritus feeding was eliminated by performing analyses at higher link thresholds. For example, *Rhambdia* in the annual Quebrada community web fed on three different trophic levels (e.g., seeds at $T = 0.0$; prawns at $T = 1.0$; *Eleotris* at $T = 2.3$).

When omnivory is defined as feeding at multiple trophic levels, recognition of the trophic continuum concept invalidates most questions concerning omnivory in food webs. In essence, nearly all consumers would be considered omnivores following this liberal definition. Yet, omnivory was common, even when defined in the classical sense as consumption of both plant and animal tissue. Species that consumed relatively large fractions of both plant and animal material included: *Bryconamericus beta*, *Ctenobrycon spilurus*, *Creagrutus* sp., *Astynax* (5 spp.), *Brycon* (2 spp.), *Loricarichthys typus*, *Aequidens pulcher*, and *Cichlasoma orinocense*. Benthic algivore-detritivores (e.g., *Phallichthys amates*, *Poecilia gilli*, *Curimata argentea*, *Hypostomus argus*) generally consumed small volumetric fractions of microscopic animals (e.g., nematodes, protozoa, rotifers). Even though most of these microfaunal elements were probably grazed incidentally with algae and detritus, and represent only a tiny fraction of total energy consumed (excluding bacterial decomposers), they could have nutritional importance if they contain minor but critical dietary components.

Do food webs exhibit scale invariance?

Recently, Cohen and Newman (1985) introduced a static model of food webs in an attempt to explain three "laws" of food-web structure (i.e., species scaling law, link scaling law, link-species scaling law). Cohen and Newman's cascade model assumes that species are ordered in a hierarchy in such a way that species can only prey upon other species positioned at lower trophic levels. In spite of the cascade model's power for explaining observed variation in food webs obtained from the literature, Cohen et al. (1985) expressed grave

reservations about the reliability of the data that the model seeks to explain. Aside from obvious problems associated with placing consumers at discrete trophic levels in the traditional sense (Cousins 1985, 1987), my analysis indicates that up-links (species feeding on species at higher trophic positions in a continuum) are common in food webs. While the cascade model may have considerable merit for explaining trends observed in relatively simple food webs compiled from the literature, its most basic assumption is clearly violated in tropical aquatic food webs.

Recently, Warren and Lawton (1987) offered an alternative hypothesis to explain the apparent hierarchical arrangement of species in food webs that gives rise to the food-web scale-invariance laws. In accordance with Elton's (1927) earlier contention, Warren and Lawton argued that structural features of food webs might be caused by body size constraints on animal feeding. If animals consume only organisms smaller than themselves, many of the features observed in simple food webs essentially will fall into place. Similar food-web features can be obtained if the entire size hierarchy of feeding is reversed, as seen for example, in systems in which tiny parasitoids prey upon larger herbivorous insects than in turn feed upon plants much larger than themselves.

The scale-invariance food-web laws of Briand and Cohen (1984, 1987) are perhaps explained most parsimoniously as artifacts of variation in the manner of food-web construction. Consider the species scaling law: the proportion of basal species (nodes that do not feed) to total species in food webs is about 0.19, the proportion of intermediate species (nodes that serve both as prey and predators) is about 0.53, and the proportion of top-predators is about 0.29 across a range of 3 to 33 total species. These proportions are actually mean values based on highly aggregated species categories. The original data clearly are not scale-invariant (considerable scatter is apparent in Fig. 2 of Briand and Cohen 1984).

Plots of the proportion of basal, intermediate, and top nodes in tropical aquatic food webs exhibit substantial scatter as well (Fig. 14). Using thirteen community aquatic webs, the proportion of top nodes was considerably lower than 0.29 at both $LT = 0.0$ (mean = 0.11) and $LT = 0.045$ (mean = 0.23). But what is being measured here? Theoretically, species suffering no mortality from predation do not exist in nature. Even the fiercest of predators suffers some level of predation, usually on eggs or juveniles. In addition, the role of parasites in food webs is essentially ignored (Lawton 1989). Piscivorous fishes in freshwater tropical systems actually suffer greater levels of parasitism than fishes feeding lower in the trophic continuum (K. O. Winemiller, *personal observation*). The proportion of top predators in community food webs is influenced entirely by two factors: (a) a priori decisions used for assigning community membership and (b) sampling

error. For example, *Roeboides dayi* is a top node in the Caño Volcán food webs because no other species was observed to consume it in the common-fish communities. Had I chosen to include *Hoplias malabaricus*, a rare species at Caño Volcán, *Roeboides* would not have been a top node. Inclusion of rare species in the analysis does not greatly reduce the number of top predators, because small samples tend to underestimate diet breadth for food generalists, thus leaving gaps in the web. Moreover, predation cuts across major habitat boundaries, so that avian and reptilian predators could be (and theoretically ought to be) considered for a full representation of feeding relationships impinging on fish populations.

The proportion of intermediate species in aquatic webs was higher than Briand and Cohen's 0.53 at $LT = 0.0$ (mean = 0.73) but similar at $LT = 0.045$ (mean = 0.55). This result suggests that food-web diagrams taken from the literature tend to depict only the strongest feeding interactions. Since the proportions of top, intermediate, and basal species in food webs are mathematically interdependent, the proportion of intermediate nodes should also be greatly influenced by sampling error and subjectivity during node assignment. The plot for intermediate nodes vs. total nodes is almost a mirror image of the top nodes plot in Fig. 14. The proportion of basal nodes shows an inverse relationship with total nodes in aquatic food webs (Fig. 14; linear regression slope = -2.3 , $r^2 = 0.89$). The linear regression for proportion of basal species crosses the predicted line of slope zero at total nodes = 67. Again, the proportion of basal nodes is constrained by relative proportions of top and intermediate nodes. The trend for basal species is derived primarily from the positive correlation between proportion of fish consumer nodes and total species in aquatic food webs (Tables 5 and 6).

Briand and Cohen's (1984) link-species scaling law theorizes that the average number of links per species in food webs is approximately constant at 1.86 in food webs. At $LT = 0.0$, the average number of links per node was positively correlated with species richness for community food webs (Fig. 15; $r^2 = 0.87$, $P < .0001$, regression slope = 0.16). The grand mean for thirteen webs was 6.31 links/node at $LT = 0.0$. The grand mean for links per node was 1.81 at $LT = 0.045$, a value very close to Briand and Cohen's (1984) predicted value. Even at $LT = 0.045$, the average number of links per node was not constant, but increased with species richness (Fig. 15; $r^2 = 0.88$, $P < .0001$, regression slope = 0.02). Moreover, the true value for the average number of links per node was underestimated here, because only fish diets were quantified in the analysis. Even excluding weak links from the analysis, inclusion of invertebrate feeding in food webs certainly would raise values well above 1.86 in all of these webs. Comparison of my food webs with earlier data sets supports Paine's (1988) recent hypothesis that personal

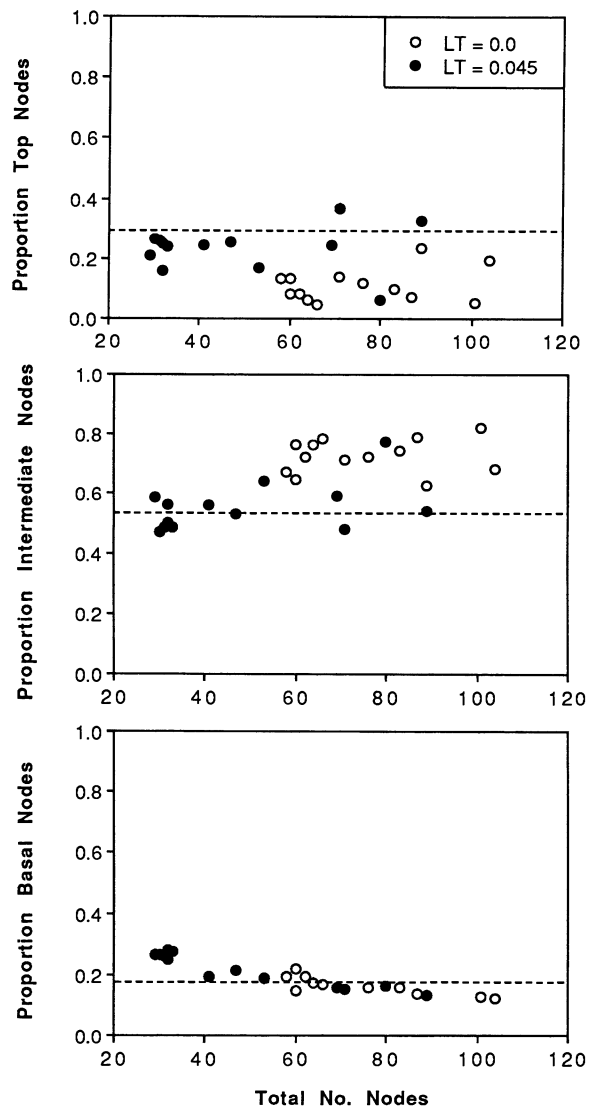


FIG. 14. Relative proportions of basal, intermediate, and top nodes in 13 community food webs at two link thresholds. Link threshold (LT) is defined in Table 5. Basal species were defined as plants and detritus (nodes 2–15). Dashed lines correspond to predictions of Briand and Cohen's (1984) species scaling law.

idiosyncracies in drawing food webs yield artifactual trends in food-web connectance vs. species richness. Like Paine, I hypothesize that many significant trophic links were omitted from earlier published food-web diagrams in the interest of pictorial simplicity (see also Winemiller 1990b). Visual traceability of links in diagrams was not a primary objective during production of computer graphics in this study (Figs. 6, 7, and 9).

Food-web tautologies

A general inverse hyperbolic relationship between food-web connectance (C) and species richness (n) has been uncovered repeatedly (Rejmánek and Stary 1979,

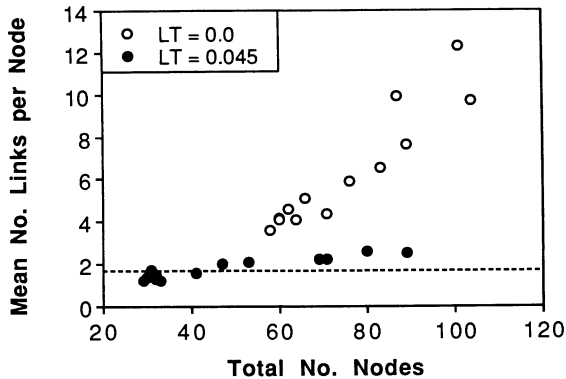


FIG. 15. Plot of the mean number of trophic links per node for 13 community food webs at two link thresholds. The dashed line corresponds to the constant value of 1.86 predicted by Cohen and Briand's (1984) link-species scaling law. Regression slope for $LT = 0.045$ was significantly different from horizontal (slope = 0.02, $t = 8.81$, $P < .0001$). Link threshold (LT) is defined in Table 5.

Yodzis 1980, Pimm 1982, Briand 1983, Auerbach 1984). If the average number of links per node is held constant as prescribed by the species-link scaling law, web connectance has to decline with an increase in species richness. If the average number of links per node of real food webs is 1.86, the numerator, k , in Eq. 1 will remain constant at ≈ 3.7 (1.86 interactions/node in the role of predator plus 1.86 interactions/node as prey) while the denominator increases with increasing n . Thus the inverse hyperbolic trend ($Cn = 3.1$) is precisely what one would expect given Briand and Cohen's (1984) link-species scaling law, because the two analyses are based almost entirely on the same data. Obviously, any artifacts derived from personal idiosyncracies during food-web construction that affect one analysis must affect the other.

Other food-web measures are correlated due to simple mathematical constraints. For example, more connected food webs should exhibit more prey and predators per node when the total number of nodes and the fraction of consumer nodes is kept constant. In my analysis, the mean number of predators per node was highly correlated with connectance, but the mean number of prey per consumer node was not (Tables 5 and 6). Lack of correlation between the average number of prey per consumer node and connectance can be attributed to the fact that both species richness (total nodes) and the proportion of consumer nodes varied greatly among webs. Connectance was positively correlated with both the total number of nodes and the proportion of consumer nodes due, in part, to the manner in which food webs were constructed. Only observed links involving fishes as predators were used to construct food webs. Consequently, C increases with n when fish consumer nodes are added to webs in greater proportions than non-fish prey nodes. This was probably a significant factor in my analysis, as evi-

denced by the positive correlation between the relative proportion of consumer nodes and the total number of food-web nodes. The positive correlation I obtained between C and n stands in stark contrast to the frequently cited generalization that web connectance always decreases as a hyperbolic function of species richness (see also Winemiller 1990b). Given the incongruous and primitive state of most published food-web data, it is far too early to speak of generalizations such as scale invariance and C as a constant function of n (Paine 1983, 1988). Many additional food webs based on quantitative estimates of feeding in different kinds of ecosystems are required before broad generalizations can be made with confidence (Pimm and Kitching 1988, Lawton 1989). Criteria and methods used for construction of food webs should be experimented with and reported in order to factor out ecologically meaningful trends from artifacts (Lawton 1989).

May (1973) hypothesized that compartmentation (blocking) of interactive networks might increase the probability of stability in large complex systems. Several investigators have claimed to observe evidence of May's "amusing corollary" in nature (Gilbert 1977, McNaughton 1978, Moore and Hunt 1988). Pimm (1982) tested May's corollary and found that compartmentation actually reduced the probability of network stability. Compartmentation and connectance were positively correlated in my aquatic food webs as well. D. Haydon (*personal communication*) has corroborated Pimm's finding algebraically. Dynamical reasons for expecting compartmentation in webs appear questionable at best. Moreover, based on random probabilities, connectance (C) and Pimm and Lawton's compartmentation index (\bar{C}_1) should be positively correlated. C is an appropriate estimate of the random probability that any two species in a food web will interact. The average number of nodes with which any two species interact (numerator of S_{ij}) can be estimated as $[C^2(n-2)]$. The number of species with which either of two species interact (denominator of S_{ij}) can be estimated as $[2Cn - (C^2(n-2))]$. As a result compartmentation can be estimated based on average probabilities as

$$\bar{C}_1 = \frac{C^2(n-2)}{2Cn - (C^2(n-2))}. \quad (3)$$

Eq. 2 simplifies to

$$\bar{C}_1 = \frac{C(n-2)}{2n - (C(n-2))} = \frac{C(n-2)}{2n - Cn + 2C}. \quad (4)$$

For webs with large n , \bar{C}_1 is approximated by

$$\frac{C(n-2)}{2n - Cn} \sim \frac{C}{2 - C}. \quad (5)$$

Eqs. 4 and 5 show that as the value of C increases, the value of \bar{C}_1 also increases given random expectation.

For this reason, inter-web comparisons using \bar{C}_1 are probably invalid if connectance values are unequal.

Inter-site variation in food-web structure

Paine (1988) argued against construction of food webs based on feeding data pooled across regions or major habitat boundaries, because regional omissions from pooled lists of potential prey are likely to have important biological meaning (e.g., distinction between the realized vs. the fundamental niche). For example, Paine's data for the sea slug, *Navanax inermis*, show almost no overlap in prey consumed in rocky vs. more protected, soft-sediment sites (Paine 1988). Intraspecific differences in feeding by fish populations at different sites corresponded to a specialist-generalist species gradient. For example, the Central American poeciliid *Alfaro cultratus* exhibited relatively little spatial variation in diet compared with the South American cichlid *Aequidens pulcher* (Table 9). *Alfaro* feeds heavily on ants and minute terrestrial insects. *Aequidens* had a broad diet, both within and between sites, that included algae, aquatic and terrestrial plants, a great variety of aquatic invertebrates, and occasionally juvenile fishes. Diets of most freshwater fishes are broad enough that pooling diet data across large spatial scales or major habitat divisions would likely yield food webs containing predators and prey that seldom co-occur in nature.

Several inter-site differences in food-web properties are probably best explained as resulting from environmental differences rather than demographic/mathematical epiphenomena of the kind commonly sought in food-web analyses (Pimm and Lawton 1977, Cohen 1978, Pimm 1982, Pimm and Rice 1987). The four aquatic ecosystems differed from one another to varying degrees with respect to four basic factors: (a) annual distribution of rainfall, (b) physiography, (c) substrate composition, and (d) biotic composition. Each of these factors is in turn influenced, either presently or historically, by a universal underlying factor: geography. Local ecological conditions result from interactions among these basic factors plus a multitude of secondary and tertiary factors (Pianka 1988). On the one hand, food webs may help us understand how external factors affect interactions among local populations, and perhaps reveal interesting emergent properties born of them (sensu Briand 1983, Briand and Cohen 1987). On the other hand, ecologists may have to carefully sift through lists of potential external factors to uncover the principal agents moulding observed food-web structures (sensu Paine 1966, 1980, 1983). Although I hope that the former scenario might someday become a reality, the present state of the young art of food-web analysis seems to indicate the latter. Comparisons of three observed features of tropical aquatic food webs illustrate this contention: (1) food-web complexity in relation to community composition, (2) dominant pathways of production, and (3) food-web compartmentation.

TABLE 9. Volumetric proportions of the most important prey items consumed by the poeciliid *Alfaro cultratus* at two sites in Costa Rica and the cichlid *Aequidens pulcher* at two sites in Venezuela. Diets are based on combined annual data (description of habitat at each site appears in *Introduction: Study sites*).

<i>Alfaro cultratus</i> (N = 413)		
	Caño Agua Fria Viejo	Quebrada
Diatoms	0.05	0
Filamentous algae	0.05	0
Fruit	0.02	0.02
Unidentified terrestrial insects	0.20	0.08
Hymenoptera	0.36	0.61
Terrestrial Coleoptera	0.04	0.07
Isoptera	0	0.03
<i>Aequidens pulcher</i> (N = 687)		
	Caño Maraca	Caño Volcán
Fine detritus	0.05	0.07
Filamentous algae	0.01	0.07
<i>Chara</i>	0.08	0
Seeds	0.24	0.14
Snails	0.10	0
Clams	0.18	0.02
Ephemeroptera	0.01	0.06
Aquatic Coleoptera	0.08	0.02
Chironomidae	0.07	0.20

Food-web complexity and community composition

Over eighty species of freshwater fish and numerous aquatic invertebrates at Caño Maraca are derived historically from the great species source pools of the Orinoco and Amazon River basins (Mago-Leccia 1970, Roberts 1972). The two basins actually remain connected by the Casiquiare channel in southern Venezuela, and numerous species are currently found in both basins. Whereas the Caño Volcán biota belong to the same biogeographic region as Caño Maraca, the two sites share only 11 species, or about half of the fauna at Volcán (according to criteria used in the present investigation, only 7 of these were defined as common species at Volcán). The inability of most Caño Maraca fishes to invade piedmont aquatic habitats like Caño Volcán is undoubtedly due to major differences in food resources and habitat characteristics, and probably not to particular features or dynamics of the regional food webs. For example, the aquatic vegetation-feeding anostomid, *Schizodon isognathus*, has no food resources at Caño Volcán (reasons discussed below, see *Dominant pathways of production*). A small number of *Curimata argentea* (mud-feeding curimatid), *Gephyrocharax valenciae* (Characidae, surface insectivore), and *Loricarichthys typus* (Loricariidae, omnivore-detrivore) were collected in the extreme downstream segment of Caño Volcán during wet conditions in 1984. Like *Schizodon*, *Curimata* and *Loricarichthys* probably do not encounter suitable environmental conditions for survival in the piedmont. The reasons why *Gephy-*

rocharax is unable to invade Caño Volcán are less clear, because it does occur in some piedmont streams of low elevation. Exploitation competition with *Corynopoma riisei* (the two characids have nearly identical size ranges, basic morphologies, reproductive modes, and feeding ecologies) is the most likely factor preventing *Gephyrocharax* from successfully invading Caño Volcán.

The Caño Agua Fría and Quebrada faunas are associated with two historical source pools: the Caribbean Sea and South American drainages adjacent to the isthmus of Panama. The Costa Rican freshwater fish fauna is dominated by poeciliids, cichlids, and peripheral fishes belonging to a number of marine-allied families. All available biogeographic evidence supports a model in which ancestral stocks of Central American poeciliids and cichlids dispersed north from South to Central America on an early land bridge, perhaps during the late Cretaceous or early Tertiary (Myers 1966, Bussing 1976). Together with invading marine species, these freshwater fishes speciated and diversified to occupy vacant freshwater ecological niches on the Central American land mass. With the establishment of the present-day isthmus of Panama (early Pliocene), the new southern element of freshwater fishes (characiforms and siluriforms) probably invaded Central America (Myers 1966, Bussing 1976). As a result, only the swamp eel, *Synbranchus marmoratus*, was encountered in both Costa Rican and Venezuelan study regions (synbranchids are capable of airbreathing and terrestrial dispersal, and thus exhibit far less conservative distributional patterns than most classical freshwater fishes). All 21 fish species collected at Quebrada also occurred at Caño Agua Fría Viejo. However, most Caño Agua Fría fishes were unable to successfully invade the smaller Quebrada aquatic environment. As was the case for Caño Volcán in Venezuela, a few stray individuals of other fish species were collected near the mouth of Quebrada, but these were never associated with persistent local populations over a 4-yr period of wet-season sampling at the site (K. O. Winemiller, *personal observation*: data for 1983–1986).

Does local food-web structure influence assemblage composition, or does assemblage composition determine features of food webs? While the answer to both questions is probably yes, I see no way to make a clear distinction here. I suspect the latter may more often be the case, for reasons related to methodology of food-web construction. Consider web connectance, a parameter frequently cited as a comprehensive measure of community complexity (Rejmánek and Stary 1979, Pimm 1980, 1982, Yodzis 1980, Briand 1983). The influence of level of OTU identification on the relationship between C and n was discussed previously here and elsewhere (Hastings 1988, Paine 1988). The relative fraction of fishes to non-fish prey influenced connectance to some degree in my webs. Total species richness and the relative fraction of fish consumers in food webs were positively correlated (Tables 1, 2, 5,

and 6). Connectance is dependent on a host of criteria, including: (a) levels of OTU identification, (b) definition of the food-web assemblage, and (c) criteria for trophic link assignment. The biology underlying web connectance becomes fairly illusive in light of these and other methodological considerations.

Simply and precisely, what does food-web connectance measure? Trophic links are drawn between predator and prey by whatever criteria the investigator chooses, until a network is formed. If predators have very broad diets on average, a highly connected web results. We would expect more prey per predator and predators per prey on average as well. If predators are highly specialized in their selection of prey, a very unconnected network is constructed. In a theoretical, minimally connected web, each predator would feed on a single prey, with $C = 2/n$ (Pimm 1980, Auerbach 1984). Simply stated, food-web connectance is essentially a restatement of the ecological generalist vs. specialist problem, an area of inquiry that dates back at least to Darwin's time. The ecological specialist-generalist continuum continues to provoke formulation of new hypotheses and test of old ones, and the issue is by no means fully resolved (Price 1984, Schoener 1987). Unfortunately, methodological problems associated with food-web construction risk introducing new forms of bias into a field of research already faced with challenges wrought by biological diversity and historical constraints. Empirically, the ecological specialization problem and competition theory would seem to be attacked more directly and with greater precision at the guild level, when guilds can be identified fairly objectively.

Dominant pathways of production

The most biotically diverse of the study systems, Caño Maraca, also has the most seasonally variable environment. Large seasonal variation in availability of aquatic habitat from extensive sheet flooding results from the flat topography and uneven distribution of annual precipitation. High primary productivity during the wet season is supported by nutrient-rich alluvial soils derived from erosion of the western slopes of the Andes in Venezuela. The aquatic environment at the other Venezuelan site, Caño Volcán, differed greatly from Caño Maraca due to the effects of topography on hydrology. The fine sand and interspersed cobble substrate at Caño Volcán is replaced by thick mud and rich detritus from aquatic macrophytes in the low-lying, productive Caño Maraca floodplain. Proportionally greater utilization of terrestrial sources of primary production is seen in Caño Volcán food webs relative to Caño Maraca webs (Figs. 3, 6, and 7). A large fraction of wet-season aquatic primary production is channelled through the Caño Maraca food web as detritus during the ensuing 8 mo of transition and dry conditions. Though difficult to estimate quantitatively, detritus pathways appear to be the dominant channels

for the transfer of energy from aquatic primary production to top predators in swamp food webs (see also Darnell 1961, Minshall 1967, Bowen 1983, Odum and Biever 1984).

Due to obvious methodological constraints, the role of the prokaryotic assemblage of food webs was not investigated. Prokaryotes dominate many aspects of detritus pathways in food webs (Rich 1984). Since a significant, if not major, fraction of the energy gained by macroscopic detritivores is derived from prokaryotes and fungi, decomposers could justifiably be inserted into food webs as additional trophic levels in pathways leading from dead matter to top predators. The large characoid *Prochilodus mariae* fed chiefly on fine, silty sediments (mud) throughout the year at Caño Maraca. Curimatids and loricariid catfishes were facultative detritivores at Caño Maraca. Most of these fishes switched from feeding heavily on algae and associated microorganisms during the wet season to nearly exclusive detritivory during the dry season. A very similar scenario was described by Power (1983) for loricariids inhabiting lowland forest streams in Panama.

A partial switch from algivory to detritivory was also observed in two abundant livebearers (*Poecilia sphenops*, *Phallichthys amates*) and two cichlids (*Cichlasoma maculicauda*, *C. nigrofasciatum*) at Caño Agua Fría in Costa Rica. Increased consumption of detritus occurred during wet rather than dry periods at Caño Agua Fría (Fig. 1). Again, this fundamental difference can be attributed to geographical differences underlying ecosystem variation. Although dry periods occur at Tortuguero twice each year (March–May, September–October), they are much less distinct than the llanos dry season, and rainfall is more evenly distributed throughout the year. Felt-like layers of diatoms and filamentous algae covered submerged substrates at Caño Agua Fría during dry periods. Extremely slow rates of water discharge from the swamp/forest creeks during the dry season also resulted in accumulation of both floating and rooted aquatic macrophytes. Nordlie and Kelso (1975) estimated planktonic primary production in Laguna Tortuguero (downstream from Agua Fría) to be approximately seven times as great during the dry season as during the wet season. Lower discharge rates are probably associated with increased accumulation of dissolved nutrients in swamp creeks. I am aware of no direct measurements on aquatic nutrient levels of tributary creeks in the Tortuguero area. Heavy rains of the wet period caused a significant increase in current velocities in the channel of Caño Agua Fría (increasing from near 0 m/s in April to >0.4 m/s in June). Faster wet-season currents scoured attached algae, and transported a large fraction of accumulated aquatic macrophytes downstream to the Laguna Tortuguero and ultimately to the sea. Large floating islands of *Hydrocotyl* and *Eichhornia* were frequently observed floating past the barrier island during the rainy

seasons at Tortuguero. Detritus accumulated during dry periods was also transported downstream by swift wet-season currents, but a substantial fraction remained packed along the margins of swamp/forest creeks. While the central channel was composed primarily of shifting sand, large deposits of macroscopic detritus particles >1 m deep were common beneath mats of floating sedges along sunlit margins of Caño Agua Fría during the wettest months. In addition, swift current compacts and kills many aquatic macrophytes during the wet season. The eleotrid, *Dormitator maculatus*, dwells within these compacted plant mats and was observed to feed heavily on a mixture of living and dead aquatic plant tissues.

Terrestrial primary production entered aquatic food webs in pulses of varying duration and magnitude. Caño Maraca fishes consumed a greater fraction of terrestrial plant tissues during the dry season (primarily in the form of flowers and leaves from deciduous trees and seeds of Cyperaceae and Gramineae). A very small fraction of terrestrial primary production was consumed by fishes during the transition season at Caño Maraca, when fishes, detritus, and aquatic plant tissues formed major diet components. Fishes at the swampy Costa Rican site consumed a virtually identical fraction of terrestrial plant products during wet and dry periods. Lack of seasonal variation in consumption of terrestrial primary production by the Caño Agua Fría community can be attributed to more continuous rainfall and greater year-round availability of allochthonous input. In addition to being essentially evergreen, the watershed is much more forested at Caño Agua Fría than at Caño Maraca.

Greater utilization of terrestrial primary production at Caño Volcán during the wet season (Fig. 3) was associated with increased fruit and seed production by forest trees and with reduced availability of attached algae from stream scouring during brief but frequent flash floods. At the Quebrada site in Costa Rica, lateral sheet flooding into the rainforest made terrestrial sources of primary production more available to the aquatic ecosystem during wet seasons. Again, the two Costa Rican ecosystems exhibited less seasonal variation in the fraction of allochthonous input than the Venezuelan sites, the difference resulting primarily from geographical variation in annual distribution of precipitation.

Food-web compartmentation

Not only were trophic interactions not organized into blocks within the major habitat compartments tested, but they tended to occur across habitat boundaries at frequencies greater than predicted by chance alone (Tables 7 and 8). One could attempt to explain this finding primarily with respect to its implications for stability analysis (*sensu* Pimm and Lawton 1978, Sprules and Bowerman 1988), or in terms of behavioral interactions between predator and prey (Werner et al. 1983,

Power et al. 1985, Fraser et al. 1987, Kerfoot and Sih 1987). The difficulties associated with measures of compartmentation and their relation to network connectance weaken the foundations for exploring the mathematical implications of absence of blocking in my food webs. However, the high frequencies of feeding interactions between major habitat divisions in aquatic webs appear to have a strong basis in behavioral ecology. A certain fraction of estimated between-habitat interactions undoubtedly resulted from error associated with subjective placement of prey into broad habitat categories. For example, all seeds were classified as a surface resource in the vertical dimension, because most seeds are taken by midwater and surface-dwelling fishes at the surface or as they fall through the water column. Yet a number of primarily benthic fishes take small heavy seeds after they have fallen to substrate (e.g., *Aequidens pulcher* and *Creagrutus* sp.). Likewise, chironomid larvae and many other aquatic invertebrates inhabit both open and vegetation habitats.

Assuming error from categorization is random with respect to bias in favor of or against within-habitat trophic interactions, the use of aquatic vegetation and other submerged substrates as refugia by prey probably accounts for large proportions of between-habitat interactions in food webs. A number of essentially open-water-dwelling fishes were captured along edges of dense mats of aquatic vegetation (e.g., *Cichlasoma dovii* and *Gobiomorus dormitor* at Caño Agua Fría, *Hoplias malabaricus* and *Caquetia kraussii* at Caño Maraca). Because dense mats of aquatic plants are used almost universally by small prey organisms as refugia, the interface between vegetation and the open water environment forms an important region for predator-prey interactions. Adult size classes of the characids *Charax gibbosus*, *Roebooides dayi* (Maraca), and *Roebooides guatemalensis* (Agua Fría) were almost always captured at the edge of dense aquatic vegetation with cast nets or small seines. *Charax* fed on small midwater fishes and aquatic insects, whereas both *Roebooides* species fed on a combination of fish scales and aquatic insects. Ephemeroptera were the dominant aquatic insects in the diets of all three characids. Aquarium-housed specimens of all three species were observed to hover lazily in midwater until prey fishes appeared within appropriate striking distances. Presumably, the interface between aquatic vegetation and open-water habitats provides these species with both (a) cover for ambush of passing open-water fishes, and (b) a substrate for gleaning Ephemeroptera nymphs. Although juveniles of the cichlid *Caquetia kraussii* were captured and presumably fed within aquatic vegetation, adult size classes used the vegetation-open water interface in a manner similar to *Charax*.

A few nocturnal fishes used vegetation as a day refuge and foraged in open water at night (e.g., *Rhamdia* sp. 1, *Gymnotus carapo*). As a result, these species were

vulnerable to vegetation-dwelling predators by day and a different suite of open-water predators by night. Both *Gymnotus* and *Rhamdia* (especially smaller size classes) preyed upon vegetation-dwelling invertebrates in addition to open-water fishes. Again, none of the aquatic food webs showed evidence of blocking in association with major habitat divisions. Three behavioral observations contributed to lack of habitat compartments in food webs: (1) prey refuging, (2) use of edges of habitats with structural complexity as foraging arenas, and (3) frequent movement between habitats by either predators or prey.

Temporal variation in food-web structure

Seasonal and ontogenetic diet shifts are common in freshwater fishes (Werner 1984, Werner and Gilliam 1984). For example, at Caño Maraca nine dominant piscivores shifted from zooplankton to aquatic invertebrates and later to fishes with increasing body size (Winemiller 1989a). Ontogenetic shifts were also evident in diet data for fishes in other trophic guilds and from other sites (K. O. Winemiller, *personal observation*). Although fish species were not divided into separate age classes in food webs, ontogenetic diet shifts greatly influenced temporal variation in webs, especially at the highly seasonal site, Caño Maraca. A large fraction of the fishes at Caño Maraca exhibited peak reproduction during the early wet season (Winemiller 1989a). Proportionally greater consumption of aquatic invertebrates by fishes during the Caño Maraca wet season (Fig. 3) was due to a combination of greater availability of microcrustacea (including ephemeral forms like eubranchipods) and immature insects with an abundance of juvenile fishes in the greatly expanded aquatic environment. During the gradual transition to dry conditions, fish, macroscopic invertebrates, and detritus gained increasing importance in the diets of local populations comprised of predominantly sub-adult and adult fishes. Because a larger fraction of fish species exhibited more continuous reproduction at less seasonal sites, ontogenetic diet shifts were less synchronous.

Other major causes for temporal variation in food webs were shifting availabilities and qualities of aquatic habitat and food resources. The general lack of significant seasonal variation in food-web parameters was somewhat surprising, given the extent of seasonal variation observed among both physical and biotic environmental parameters at each site. Degree of seasonal variation in the quality and amount of food and space can be ranked from high to low, with Maraca > Volcán > Agua Fría > Quebrada. If we eliminate the compartmentation statistic from consideration (all \bar{C}_1 values were nonsignificant based on comparisons with null randomizations), Caño Maraca showed one seasonal effect among nine comparisons using community webs, and four of nine using top-predator sink webs (Table 4). The average number of prey per node was greater

during the transition than the dry season at Caño Maraca. As harsh dry-season conditions advanced at Caño Maraca, large generalist piscivores, such as *Pygocentrus*, migrated downstream to more benign habitats (Winemiller 1989b). The fish assemblage that remained throughout the peak dry season exploited larger fractions of detritus. Interestingly, web connectance at Caño Maraca was not significantly affected by season, despite major changes in assemblage composition and in the quality and availability of aquatic habitat and resources. This result seems to support Paine's (1983, 1988) contention that connectance is too coarse a measure to serve as a sensitive macrodescriptor for dynamic community-level phenomena. The least seasonal site (albeit a seasonal environment nonetheless), Quebrada, showed no significant seasonal changes among community web comparisons; however top-predator sink webs showed seasonal effects for two of three measures (Table 4). The average number of prey per node and connectance were highest in the dry top-predator sink web. During this period, young-of-the-year fishes produced in the flooded forest were left crowded together in the small creek channel following desiccation of the surrounding terrain. Many aquatic organisms in these small food webs fell prey to the pimeleodid catfish, *Rhamdia guatemalensis*, and eleotrid, *Eleotris amblyopsis*.

CONCLUSIONS

The food-web approach clearly has potential to enhance our understanding of pathways of energy and material transfer and the structure of the hierarchy of species trophic interactions in aquatic ecosystems. This largely qualitative aspect of food-web analysis has a long tradition (Summerhayes and Elton 1923, Caddy and Sharp 1986), and overlaps to a large extent with systems ecology (Lindemann 1942, Odum 1983). Application of strict assembly rules for computer illustration of food-web diagrams facilitated qualitative assessment of relative reliance on aquatic vs. terrestrial production by individual nodes. The same graphics program also obliterates visual traceability of trophic links (or "walks" following Cohen et al. [1985]) in most complex webs. In general, swamp ecosystems in both South and Central America were dominated by detritus pathways, whereas channels fueled by allochthonous input dominated substantial portions of small forest-stream assemblages. Tremendous dry-season standing stocks of red-belly piranhas, *Pygocentrus notatus*, in llanos creeks (Mago-Leccia 1970, Taphorn and Lilyestrom 1985, Winemiller 1987, 1989b) are supported, in large part, by very short web tracks running from detritus to abundant detritivores (e.g., *Curimata*, *Prochilodus*) to piranhas.

Each of the four study sites experienced some degree of seasonal variation in rainfall, availability and quality of aquatic habitat, sources of primary production, and assemblage composition. Statistical analysis of food-

web metrics demonstrated low sensitivity for detecting community response to environmental variation related to seasons. Assemblage diversity at each site was clearly influenced by both historical/biogeographical and contemporary ecological components, and, again, food webs were largely uninformative with respect to the relative importance of each component. Distributions of fishes in a trophic continuum revealed consistent pattern for all four systems. Fishes occupying trophic interval $T = 1-1.5$ (herbivores and detritivores) dominated swamp communities, followed by $T = 2-2.5$ (primarily herbivore predators), $T = 1.5-2.0$ (omnivores), and $T = 2.5$ (secondary and tertiary carnivores) and above. Forest-stream fishes had very similar trophic-interval distributions, except that fishes occupying the interval 2-2.5 were most dominant. Feeding links between fishes and organisms at higher trophic levels constituted from 12 to 27% of all trophic links.

The results of this study prompt me to comment briefly on the current state of empirical food-web research. I will not attempt a comprehensive overview; rather I refer the reader to recent critical reviews of the field in DeAngelis et al. (1983), Paine (1988), Cohen and Newman (1988), Hastings (1988), Peters (1988), Pimm and Kitching (1988), Lawton (1989), and Yodzis (1989). While disagreements persist, and will continue to do so as in any healthy field of science, a general consensus seems to be emerging with respect to two basic problems of food-web theory; (1) the stability-complexity model and (2) the lack of recognition of temporal and spatial variation in species interactions. Too much emphasis has been placed on food-web complexity (i.e., connectance) and its relation to May's (1972) model of community stability. Published food-web diagrams provided convenient raw material for intellectually stimulating analyses of a very timely and appropriate question: do natural communities possess special structures or properties that enhance system stability? If they do, we are compelled to learn more about them.

There are a number of serious problems associated with stability analyses based on structures observed in published food webs. If an observed web property fails to meet the criteria for Lyapunov stability, how does one interpret its apparent existence? There are at least four possibilities here. First, the basic criterion for either stability or complexity is conceptually wrong. Pimm (1984) listed five stability and three complexity measures, each having a large degree of ecological relevance. Second, it is probably risky to assume that even a complete and accurate listing of predator-prey interactions represents the sum total of interactions impinging on local population densities (Menge and Sutherland 1987). Some very critical mutualists (e.g., pollinators, seed dispersers) will actually appear as predators in certain instances. Alternatively, to assume that all observed predator-prey interactions have co-evolutionary significance may be equally invalid. Third,

the analysis was carried out assuming that May's parameter i , average interaction strength, was constant (Paine 1980, 1983, Peters 1988). All interactions depicted by the original author were assumed equal or average, when in fact the opposite was the case. Fourth, the original data set was inappropriate for the analysis, perhaps because organisms were misidentified, certain elements were not chosen for study, or data were omitted for convenience. Subjective disparities, and even some kinds of subjective similarities, in methods employed for food-web construction can introduce bias into empirical analyses (e.g., taxonomic lumping). Because the analysis is usually performed by someone unacquainted with the original field investigator and his or her study system, this latter point is difficult to evaluate (see also Paine 1988).

Paine (1988) and Peters (1988) argued against a static view of food webs, because in reality species interactions vary through time and space. Recognition of this fact is sobering for the field investigator attempting detailed descriptions of even a simple community. Obviously, a certain amount of data must be combined and averaged (as with seasonal and annual resource matrices here) to have any chance for completeness. In addition to nature's changing spectrum of linkage presence and absence, the relative magnitude of feeding interactions varies. Paine (1988) and Pimm and Kitching (1988) expressed a certain degree of optimism that food-web studies could be improved with greater consideration and more precise estimation of natural variation in interaction strengths. Hastings (1988) recognized the importance of variation in the magnitude of species interactions, but expressed a more pessimistic view of its potential role in strengthening future food-web work. For a crude beginning, I chose to estimate the relative strengths of predator-prey interactions from consumer utilization coefficients (volumetric) in community resource matrices. Figs. 8, and 10-13 clearly illustrate the effect of variable interaction strength on the calculation of food-web parameters. Very little interesting variation is observed at $LT = 0.045$ (Figs. 8, and 10-13). Although the appropriate level of analysis is unclear, if even there should be one (ANCOVA provides perhaps only one of several possible options here), I am certain that variable magnitude of interspecific interactions cannot be overlooked.

In light of the serious problems discussed here and in recent critical reviews of food webs, is there a future for the food-web research paradigm? I join others who contend that it is far too early to abandon the endeavor. Several authors have pleaded for new and improved field data, including experimental work (Cohen et al. 1986, Pimm and Kitching 1988, Lawton 1989). The need for additional, detailed investigations of natural communities can hardly be debated. However, the need for an improved field research protocol for empirical food-web studies has been largely overlooked. Future field studies should strive for greater objectivity, and, when possible, greater uniformity in methods of data

gathering and presentation. Alternative methods should be explored and critically evaluated. Minimally, food-web studies should report sample sizes, spatial and temporal scales, rules for defining assemblages, and variation among operational taxonomic units. If food-web data are to have demographic implications, analyses should use local populations as OTUs, and variation in strength of interspecific interactions should be estimated.

Food webs provide a suite of potential community-level macrodescriptors for ecological comparisons. Theoretical work that sorts out tautological relationships (rather than creates new ones) is badly needed. Broad generalizations, such as the C_n constancy (Briand 1983) and link-scaling laws (Briand and Cohen 1984), are premature given the data presently at hand (Paine 1983, 1988, Winemiller 1990b). Food webs will continue to aid our understanding of relationships within complex interactive networks, particularly those aligned in the vertical dimension (e.g., Carpenter and Kitchell 1987). Food webs also may provide a powerful means of dealing with indirect effects (Pianka 1987). Utility of food webs for understanding competitive interactions (e.g., the interval graph approach of Cohen 1978) appears somewhat less promising in light of confounding methodological and tautological problems.

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APPENDIX 1

Diet categories used in the fish stomach content analyses.

Numeric code	Web node
2	Fine detritus (organic mud component)
3	Larval anurans (Amphibia)
4	Coarse detritus
5	Vegetative detritus
6	Diatoms
7	Desmids and unicellular green algae
8	Filamentous algae
9	<i>Chara</i> sp. (macroscopic filamentous algae)
10	Aquatic macrophytes
11	<i>Wolffia</i> spp. and <i>Lemna</i> spp.
12	Terrestrial vegetation
13	Fruits (soft tissues) and flowers
14	Seeds and nuts
18	Other Protozoa
19	Diffugiid Protozoa
20	Rotifera
21	Nematoda (non-parasitic forms)
22	Hydracarina (water mites)
23	Nematophora (horsehair worms)
24	Annelida (earthworms)
25	Gastropoda (snails, Mollusca)
26	Bivalvia (clams, Mollusca)
27	Thoracica (shipworms, Mollusca)
28	Copepoda (microcrustacea)
29	Cladocera (microcrustacea)
30	Amphipoda (Crustacea)
31	Eubranchiopoda (Crustacea)
32	Ostracoda (microcrustacea)
33	Isopoda (Crustacea)
34	Unidentified microcrustacea
35	Palaemonid shrimp (<i>Macrobrachium</i> spp.)
36	Crabs (<i>Dilocarcinus</i> and <i>Callinectes</i> spp.)
37	Collembola (springtails)
38	Plecoptera (stonefly nymphs)
39	Ephemeroptera (mayfly nymphs)
40	Odonata nymphs
41	Other aquatic Hemiptera
42	Corixidae (aquatic Hemiptera)
43	Gerridae (aquatic Hemiptera)
44	Trichoptera larvae
45	Aquatic Coleoptera, larval forms
46	Adult aquatic Coleoptera
47	Chironomid larvae (Diptera)
48	Other aquatic Diptera larvae
49	Mosquito larvae (Diptera)
50	Aquatic Neuroptera larvae
51	Unidentified aquatic insects
52	Unidentified terrestrial insects
53	Hymenoptera
54	Orthoptera
55	Terrestrial Coleoptera
56	Lepidoptera larval forms
57	Hirudinea (leeches)
58	Lepidoptera adults
59	Terrestrial Diptera
60	Terrestrial Hemiptera
61	Isoptera (termites)
62	Arachnida (spiders)
77	Adult anurans (Amphibia) (only eaten at C. Volcán, dry season)
99	Lizard (Gekkonidae) (only eaten at C. Agua Fría, wet season)
122	Turtle flesh (<i>Trachemys scripta</i>) (only at C. Maraca, wet season)
123	Bird flesh (only eaten at C. Maraca, wet season)
124	Mammal flesh (only eaten at C. Maraca, wet season)

APPENDIX 2
Fish censuses at two study sites in Venezuela.

Fish species	Caño Maraca		Caño Volcán	
	Node	Total no. collected	Node	Total no. collected
Erythrinidae				
<i>Hoplias malabaricus</i>	88	521		152
<i>Hoplerythrinus unitaeniatus*</i>		14		
Lebiasinidae				
<i>Characidium</i> sp. 1	105	237		
<i>Characidium</i> sp. 2*		32		
<i>Lebiasina erythrinoides</i>			88	473
<i>Pyrrhulina</i> cf. <i>lugubris</i>	97	363		
Anostomidae				
<i>Leporinus frederici*</i>		72		
<i>Schizodon isognathus*</i>		92		
Curimatidae				
<i>Curimata argentea</i>	85	2496		
<i>Curimata cerasina*</i>		22		
Prochilodontidae				
<i>Prochilodus mariae</i>	83	623		12
Characidae				
<i>Acestrorhynchus microlepis*</i>		2		
<i>Aphyocharax alburnus</i>	104	757		
<i>Astyanax bimaculatus</i>	89	1299	85	191
<i>Astyanax integer*</i>				30
<i>Astyanax metae</i>			92	271
<i>Astyanax superbus*</i>				10
<i>Brycon whitei*</i>				18
<i>Bryconamericus beta</i>	130	51	76	2667
<i>Bryconamericus deuterodonoides*</i>				8
<i>Charax gibbosus</i>	122	331		
<i>Cheirodontops geayi</i>	107	112		
<i>Colossoma macropomum*</i>		1		
<i>Corynopoma riisei</i>			73	344
<i>Creagrutus</i> sp.			77	993
<i>Ctenobrycon spilurus</i>	75	2390		
<i>Gephyrocharax valenciae</i>	77	1249		
<i>Gymnocorymbus thayeri*</i>		3		
<i>Hemigrammus</i> sp.	79	231		
<i>Hemigrammus marginatus*</i>		1		
<i>Markiana geayi</i>	92	1068		
<i>Mylossoma duriventris*</i>		8		
<i>Odontostilbe pulcher</i>	73	3182		
<i>Poptella orbicularis*</i>		22		
<i>Piaractus brachypoma*</i>		1		
<i>Pygocentrus notatus</i>	106	238		
<i>Roebooides dayi</i>	108	1154	82	280
<i>Serrasalmus irritans</i>	129	76		
<i>Serrasalmus medini</i>	128	68		
<i>Serrasalmus rhombeus*</i>		50		
<i>Tetragonopterus argentea</i>	117	200		
<i>Triportheus</i> sp.	94	744		
<i>Triportheus angulatus*</i>		56		
<i>Xenogoniates bondi*</i>		16		
Gasteropelecidae				
<i>Thoracocharax stellatus</i>	86	412		
Gymnotidae				
<i>Gymnotus carapo</i>	98	372		
Sternopygidae				
<i>Eigenmannia virescens</i>	132	276		
<i>Sternopygus macrurus*</i>		5		
Hypopomidae				
<i>Hypopomus</i> sp. 1	133	67		
<i>Hypopomus</i> sp. 2		3		

APPENDIX 2 Continued.

Fish species	Caño Maraca		Caño Volcán	
	Node	Total no. collected	Node	Total no. collected
Apterontidae				
<i>Apterontus alburnus</i> *		2		
<i>Adontosternarchus devananzi</i> *		59		
Rhamphichthyidae				
<i>Rhamphichthys marmoratus</i> *		23		
Ageneiosidae				
<i>Ageneiosus vittata</i> *		19		
Pimelodidae				
<i>Microglanis iheringi</i>	135	324		
<i>Pimelodus blochii</i> *		8		
<i>Pimelodella</i> sp. 1*		9		
<i>Pimelodella</i> sp. 2	101	332		
<i>Pimelodella</i> sp. 3	78	217		
<i>Pseudoplatystoma fasciatus</i> *		5		
<i>Rhamdia</i> sp. 1	111	124		
<i>Rhamdia</i> sp. 2*				34
Auchenipteridae				
<i>Entomocorus gameroi</i> *		56		
<i>Parauchenipterus galeatus</i>	112	223		
Trichomycteridae				
<i>Ochmacanthus alternus</i>	119	545		
Aspredinidae				
<i>Bunocephalus</i> sp.	109	902		
Callichthyidae				
<i>Callichthys callichthys</i> *		1		
<i>Corydoras aeneus</i>	87	412		
<i>Corydoras habrosus</i>	81	647		
<i>Corydoras septentrionalis</i>	121	248		
<i>Hoplosternum littorale</i>	82	232		
Loricariidae				
<i>Ancistrus</i> sp.	134	62	78	243
<i>Cochlodon plecostomoides</i> *		6		
<i>Farlowella</i> sp.*		1		
<i>Hypostomus argus</i>	110	379	83	337
<i>Hypoptopoma</i> sp.	136	52		
<i>Loricichthys typus</i>	91	501		
<i>Otocinclus</i> sp.	74	686		
<i>Pterygoplichthys multiradiatus</i>	124	479		
<i>Rineloricaria caracasensis</i>	84	628		
<i>Sturisoma</i> sp.*		1		
Cyprinodontidae				
<i>Pterolebias hoignei</i> *		2		
<i>Rachovia maculipinnis</i>	90	131		
Poeciliidae				
<i>Poecilia reticulata</i>	80	313	74	2400
Synbranchidae				
<i>Synbranchus marmoratus</i>	102	95		6
Cichlidae				
<i>Apistogramma hoignei</i>	103	219		
<i>Astronotus ocellatus</i>	93	176		
<i>Aequidens pulcher</i>	76	755	89	651
<i>Caquetia kraussii</i>	96	795		
<i>Cichlasoma orinocense</i>	95	365		
<i>Crenicichla geayi</i> *		1		174
<i>Crenicichla saxatilis</i> *		23		
Total number of individuals		29324		9294
Total number of species		83		20

* Not included in common-fish community.

APPENDIX 3
Fish censuses at two study sites in Costa Rica.

Fish species	Caño Agua Fría Viejo		Quebrada	
	Node	Total no. collected	Node	Total no. collected
Lepisosteidae				
<i>Atractosteus tropicus</i> *		11		
Engraulidae				
<i>Anchoiella elongata</i> *		2		
<i>Anchoa lamprotaenia</i> *		1		
Anguillidae				
<i>Anguilla rostrata</i> *		11		
Characidae				
<i>Astyanax fasciatus</i>	79	1798	79	402
<i>Astyanax nasutus</i> *		1		
<i>Bramocharax bransfordi</i> *		1		
<i>Brycon guatemalensis</i>	91	116		
<i>Carlana eigenmanna</i> *		9		4
<i>Hypphessobrycon tortuguerae</i> *		2		
<i>Roeboides guatemalensis</i>	93	123		
Gymnotidae				
<i>Gymnotus cylindricus</i> *		3		18
Pimelodidae				
<i>Rhamdia guatemalensis</i>		1	94	466
Belonidae				
<i>Strongylura timucu</i> *		7		
Cyprinodontidae				
<i>Rivulus isthmensis</i> †		270		52
Poeciliidae				
<i>Alfaro cultratus</i>	98	240	98	917
<i>Belonesox belizanus</i>	89	221		3
<i>Brachyrhaphis parismina</i>	114	60		
<i>Phallichthys amates</i>	81	1343	81	776
<i>Poecilia gilli</i>	75	1213	75	518
Atherinidae				
<i>Melaniris hubbsi</i>	101	478		
Syngnathidae				
<i>Oostethus lineatus</i>	77	379	77	34
<i>Pseudophallus mindii</i> *		1		
Synbranchidae				
<i>Synbranchus marmoratus</i> *		7		3
Centropomidae				
<i>Centropomus ensiferus</i> *		1		
<i>Centropomus parraleus</i> *		5		
<i>Centropomus pectinatus</i> *		18		
<i>Centropomus undecimalis</i> *		4		
Mugilidae				
<i>Agonostomus monticola</i> *		3		
<i>Mugil curema</i> *		1		
Lutjanidae				
<i>Lutjanus griseus</i> *		1		
<i>Lutjanus jocu</i>	104	48		
Gerreidae				
<i>Diapterus plumieri</i> *		3		
<i>Diapterus rhombeus</i> *		4		
<i>Eucinostomus melanopterus</i> *		3		
Pomadasyidae				
<i>Pomadasyis crocro</i>	86	122		

APPENDIX 3 Continued.

Fish species	Caño Agua Fria Viejo		Quebrada	
	Node	Total no. collected	Node	Total no. collected
Cichlidae				
<i>Cichlasoma alfaroi</i>	109	34		24
<i>Cichlasoma centrarchus</i>	82	345		
<i>Cichlasoma citrinellum</i>	87	84		
<i>Cichlasoma dovii</i>	88	159		
<i>Cichlasoma cf. friedrichsthali</i>	80	944	80	162
<i>Cichlasoma maculicauda</i>	83	451		7
<i>Cichlasoma managuense*</i>		1		
<i>Cichlasoma nigrofasciatum</i>	76	133	76	179
<i>Cichlasoma rostratum*</i>		11		
<i>Cichlasoma septemfasciatum*</i>		7		
<i>Herotilapia multispinosum*</i>		4		20
Eleotridae				
<i>Dormitator maculatus</i>	84	251	84	83
<i>Eleotris amblyopsis</i>	74	1692	74	934
<i>Eleotris pisonis</i>	90	278		10
<i>Gobiomorus dormitor</i>	73	16873	73	
Gobiidae				
<i>Evorthodus lyricus</i>	116	84		48
<i>Gobionellus fasciatus</i>	78	142		
<i>Gobionellus pseudofasciatus*</i>		2		
<i>Gobiosoma spes*</i>		10		2
Bothidae				
<i>Citharichthys spilopterus</i>		22		
Soleidae				
<i>Achirus lineatus</i>	113	100		
<i>Trinectes paulistanus</i>	108	117		
Tetraodontidae				
<i>Sphoeroides testudineus*</i>		1		2
Total number of individuals		11537		7719
Total number of species		59		22

* Not included in common-fish community.

† *Rivulus* were commonly collected from forest pools that were normally isolated from the creek, and thus largely non-interactive with its food web.