
Notes and Comments

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IMPROVING FOOD WEBS¹

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A food web is the pattern of flows of energy and materials among organisms that results when some organisms eat or consume other living organisms or their parts. A food web sometimes incorporates flows between organisms and the abiotic or dead biotic environment, including decomposers and detritus. Based on analyses of existing webs, experience constructing webs, the needs of prospective theories about food webs, and the requirements of practical managers of ecological systems, this paper offers some recommendations to improve future reports of food webs.

Improved webs are important because they can help answer basic scientific questions about biotic community organization and can help solve practical environmental problems. The availability of food to eat and the risk of being eaten are among the major factors that influence the population dynamics and the evolution of most species. Treating species in isolation or in relation to principal predators or prey species neglects the possibility of more complex evolutionary and ecological interactions via the food web and other pathways (Pianka 1987).

Many practical problems could benefit from a better understanding of food webs. For example, biological concentration of toxins and pollutants could be better predicted if food webs were known better. Strategies for integrated pest management, control of disease vectors, industrial waste-water treatment, and wildlife conservation could be developed better if the consequences of modifying webs by adding or deleting species could be foreseen.

A step toward understanding the dynamics of com-

munities is to describe the pathways along which feeding interactions occur. That largely descriptive task is the topic of this note. Food web studies do not replace experimental studies of the mechanisms by which populations interact, but complement such studies, because it is risky to extrapolate from the operation of an experimentally demonstrated mechanism to the effect of an intervention in a real community.

Need for standardization.—A major obstacle to further progress in understanding food webs is the weakness of the available data base (Paine 1988 and many others). This weakness is more severe than a matter of not having enough reports of webs. A bigger problem is the lack of methodological standards for defining, observing, and reporting webs (Closs 1991). Because many published webs are by-products of research with other aims, webs per se and their comparability across studies often received little attention. Recent studies show that food webs would reward more careful treatment.

A historical example suggests that a constructive consensus on how to improve food webs can be developed. During the International Biological Programme, >100 woodland sites were described using standard forms developed during workshops (DeAngelis et al. 1980). The data were useful in cross-site comparisons.

Tentative nature of these recommendations.—Because food webs are constructed for many different habitats, involve enormously diverse organisms, and are constructed by individuals or groups with varying philosophies, the following recommendations are general. They mainly concern goals rather than detailed means and methods. The recommendations should be viewed as proposals for standards, rather than as apodictic revelations of the right way to do things. The tone of voice is tentative. Offering recommendations should stimulate discussion on how food webs can be improved.

Many of these recommendations have been made elsewhere. It seems useful to collect, amplify, and clarify these recommendations in a single place. Though many of our observations may seem obvious, we had difficulty finding published reports that conform to some of the most essential recommendations. The rarity of exemplary webs suggests that few ecologists have followed procedures that, when stated here, may seem to be common sense.

Drafts of this note circulated among students of food webs in November 1990, March, April, and December 1991. All co-authors and commentators made written contributions.

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Recommendations

The recommendations call for two broad categories of improvements: more *explicitness* and more *exhaustiveness*. Explicitness should be achievable in a study of any scope, large or small. Exhaustiveness may be difficult with limited resources but is a worthwhile goal.

Priorities.—Field workers with different special interests and goals will establish differing priorities among the recommendations proposed here. Nevertheless, a shared guide to establishing priorities ought to be that another investigator could repeat the work and have a substantial probability of obtaining compatible results. This guide entails explicitness at each step in planning, executing, and reporting field work. Explicitness entails the costs of systematic documentation and reporting, but increases the objectivity, accuracy, and cumulative usefulness of the data. If a study follows our strong recommendation that yield–effort curves be reported for observed species and links, readers can judge the study's usefulness for their own purposes.

What constitutes a minimum viable food web data set depends on the purpose of the study. To illustrate, one investigator may include the most abundant species (as measured, e.g., by biomass) that constitute two thirds of the total biomass in the habitat, and the trophic relations among these species; another may study the species with an annual energy flux (or carbon flux, etc.) above a certain level, and the trophic relations among these species. These studies have different goals, but both make clear how the components of the web were selected, what was omitted, and how to go about replication in another habitat if desired.

As more comprehensive, more detailed, more explicit webs become available, smaller, highly aggregated, incompletely described webs may progressively be dropped from analyses of web structure (though such webs may remain useful for other purposes, such as pedagogy). Consequently, any boundary between “good” webs and “bad” webs is neither sharp nor stationary.

The setting.—The setting of a food web study should be delimited with precision, including the longitude, latitude, and altitude (or depth of trawl or net) of the study area (for biogeographical comparisons), the objective means of defining the boundaries of the study area, the precise dimensions of the physical volume included if the volume is fixed, a description of the extent to which the study area may shift in time, the time interval over which observations were made, and the number of hours of direct observation or other quantitative measures of sampling effort. Where appropriate, the observer should report how sampling effort was allocated to different organisms or different

portions of the community. Observations should be logged with place and time for investigations of spatial and temporal heterogeneity in webs.

The setting should be characterized objectively. The goal of a particular study may influence the choice of a characterization. Among the possibilities are means and variabilities (over specified time intervals) of energy inputs, of total primary productivity (allocated, if possible, among primary producers), of physical parameters such as temperature, humidity, precipitation, salinity, and depths of the thermocline and euphotic zone, and of measures of habitat structure and heterogeneity. Estimates of the abiotic resources (or stocks) within and flows across the boundaries of the setting could be combined with food web data to give full biogeochemical cycles. Such data make it possible to relate web structure to environmental features.

Information about the surroundings of the immediate study site is valuable, and sometimes essential. For example, a hectare of isolated woodlands should be distinguished from a hectare that belongs to a vast tract of forest; the amphibians or dragonflies in the food web of a temporary pond depend on the surrounding terrestrial environment. The history of the site may be important, e.g., the timing and the nature of past disturbances and, in some aquatic systems, previous weather.

Explicit reports of sampling design and effort would make it possible to develop spatial and temporal hierarchies of food webs. For example, the web of a large terrestrial or marine predator may span an area of tens to hundreds of square kilometres, while many different webs (connected only by top predators, which would appear locally as transient species) could be reported from different habitats ranging in size from square metres to hectares within the same large area. In the temporal dimension, time-specific webs observed over successive brief intervals in a given region could characterize the dynamics of a cumulative web observed in the same region over months or years.

Units of reporting. Organisms.—The kinds of organisms in a food web should be reported by using units of observation that are as refined as possible. Aggregating units of observation for subsequent analysis is easy, whereas disaggregating them is often impossible. An appropriate level of aggregation depends on whether the strength of feeding links is reported qualitatively or quantitatively. When feeding links are reported qualitatively (present or absent), no information is lost by aggregating organisms into trophic species while retaining the taxonomic identifiers of the organisms belonging to each trophic species. A trophic species is defined as a largest set of organisms with identical sets of predators (if any) and identical sets of prey (if any). When quantitative information about the

strength of feeding links is collected, as is recommended below, lumping organisms into trophic species may obliterate differences in the strengths of connections between different kinds of organisms that have identical sets of predators and prey. In this case, lumping organisms into trophic species in a primary report is not desirable.

Organisms should be grouped into individual biological species unless more refined units of reporting are required to display significant differences in strengths of feeding links. For example, where metapopulation (a change in diet with increasing size or life-cycle stage of the consumer; Hutchinson 1959: 148) occurs, the unit of reporting should be the size classes or life-cycle stages of the consumer (Werner and Gilliam 1984). If genetically differentiated subgroups or different size- or stage- or sex- or age-subgroups of a given taxonomic species have different strengths of feeding links to predators or prey, then these subgroups should be the unit of reporting. When different consumers specialize on a prey's different parts, such as a plant's sap, phloem, leaves, stems, or roots, the different parts should be reported as distinct units (e.g., plant A sap, plant A leaves, plant A roots, plant B sap, and so on); similarly when parasites specialize on different tissues or materials in a host.

Where the diet and predators are uniform throughout life and for all parts of the organism but differ among taxonomic species, the unit of reporting will be the taxonomic species. It is highly desirable to key species identifications to an international standard list of taxonomic names, such as the BIOSIS (1991) standardized on-line data base list. Where multiple biological species have the same predators and the same prey, with matching strengths of linkage, or where it is practically impossible to identify organisms to taxonomic species, the unit of reporting may be a guild or taxonomic unit higher than a biological species. When organisms cannot be identified to species, the most precise identification possible should be given (i.e., if not species, then genus; if not genus, then family, and so on). In any event, the taxonomic level of classification used should be explicitly reported.

The report should be unambiguous about the level of taxonomic refinement used. For example, if predators eat several species of barnacles, and these prey are reported as a single unit, "barnacles," it is important to know whether the barnacle species are lumped because the investigator did not distinguish among them, or because all barnacles had the same strengths of links to the same predators and prey species and were trophically identical. Explicitness is possible even if exhaustiveness is not.

To assess the completeness of observations, a yield-effort curve should accompany a reported food web.

A yield-effort curve plots the hours of observation or other sampling effort on the abscissa and the cumulative number of species observed on the ordinate (e.g., Orians 1969: 786). If the curve plateaus toward an asymptote, the observer has probably covered most of the species in the domain being sampled; if the curve does not level off, the sampling of species is probably incomplete.

A yield-effort curve should be accompanied by an explicit report of the temporal and spatial sampling frame, the sampling plan, the sampling gear, and methods for preserving samples in the field. Repeated day-time sampling may miss nocturnal species altogether; sampling at ground level may miss arboreal and flying species. The size of the mesh of a zooplankton net will determine if rotifers are included among the zooplankton. Since it is impossible to sample everything everywhere at all times, a solution is to be self-conscious and explicit in the planning and the reporting of sampling.

To allow the observer and other users of the data to adjust for the presence of transient or tourist species, each species should be accompanied by a quantitative measure of its abundance per unit of time and space, possibly stratified by heterogeneous subcategories of the habitat. These data would reduce inter-observer subjective differences in which species are reported.

Certain groups of organisms that are commonly neglected in food webs deserve attention equal to that devoted to more familiar groups. Microbes (decomposers, parasites, and autotrophs) are often neglected by macroscopically oriented ecologists, with some notable exceptions.

Ideally, *all* species (or other units) observed within the chosen volume should be reported, whether or not the observer considers them to be transient or tourist or opportunist species, whether or not their interactions with other species in the web seem especially significant. This call for exhaustiveness may have to be tempered by the practicalities of the particular study.

It is just as important to specify clearly what has been excluded as what has been included. An investigator should state, for example, when avian or amphibian predators have been excluded from an insect-dominated web, or when parasites, parasitoids, decomposers, and microflora are omitted.

Information about the mobility of any species would make it possible to determine how much of its life cycle the species spends within the study site. Quantitative measurements of immigration and emigration would make it possible to measure flows across the boundaries of the study site.

Links. — It is crucial to give the sample sizes on which links are based. There is a systematic bias toward apparent increasing specialization with decreasing sample

size of a predator, simply because fewer prey species are likely to be observed in smaller samples. Comparisons across webs require sample sizes to correct for such artifacts. The time frame of sampling should be reported because sampling across seasons may reveal temporal heterogeneity in feeding that could be misinterpreted as a failure to sample links exhaustively in any given season.

A yield-effort curve for links as a function of cumulative sampling effort should be reported. The completeness of observations of links relative to the observations of species may be assessed roughly by noting how many species are reported as having no links, since a total absence of trophic relations would be exceptional even among primary producers. Rare and transient species are especially likely to be among those identified as present but without documented feeding relations. If abundance is indicated for each species, as already recommended, the web can be analyzed either with or without the species that may lack documented feeding relations because of their rarity.

Ideally, *all* observed links within the study volume should be reported, whether or not the observer considers them to be accidental or insignificant, along with a quantitative measure (or the best available estimate) of the frequency of occurrence of, or flow along, such links during the study interval. Cannibalism and facultative scavenging should be included. These data would reduce inter-observer subjective differences in which links are reported.

Ecologists should eventually decide what conventions are to be used to specify links when it is impossible to observe all links present. Agreement on such conventions may ultimately simplify field work, and thereby make it possible to study more than a few localities in comparable detail.

Direct observations of feeding links in nature are preferable to inferences. Direct observations include behavioral observations, quantitative analyses of crop and stomach contents and feces, and chemical (e.g., Blumer et al. 1969), immunological, or isotopic techniques (e.g., Fry 1991) for identifying food sources of consumers captured in the field. Immunological assays of antigens specific to prey species can identify the stomach contents of certain consumers. Such assays can be quantified by the titer of antigen and by the fraction of predators in whose stomachs the antigens are found.

Links based on direct observation should be distinguished from links based on inference. Inferences may be based on indirect evidence (e.g., specific marks on plants of browsing or grazing by certain animals, debris around consumers' nests, holes or chips in mollusc shells), experiments, and prior publications.

When animals are taken from the field and given

choices of food to eat in the laboratory, such experiments impose constraints that may be absent in the field (e.g., the prey may not be able to find a refuge in a fish tank, or the predator may be hungry or sick, or fish pellets may represent food not available in the field). Laboratory experiments do not permit positive conclusions about what and how much the predator consumes in the field unless the observer directly calibrates experimental results against field observations. However, experiments can demonstrate potential links between rare species, and can quantify consumption rates, both of which may be difficult to measure in the field.

Publications sometimes report that when two species occur together one feeds on the other. Such assertions implicitly assume a specific abiotic and biotic setting, including a particular distribution of food availability, which may differ from the setting of the observer's study. It is often difficult to know from past publications exactly what a report of feeding is based on. Inferences based on prior publications should be used only if necessary, with great caution, and with clear labeling. As an example of the potential dangers of cumulating prior publications, Fox and Morrow (1981) argue that many insect herbivores that seem to be generalists, based on literature surveys, are actually specialists in local communities.

Where the strength of a link can be measured quantitatively, it is preferable to assign some absolute measure of importance (e.g., kilograms per square metre per year of dry mass or of carbon, or number of individuals per unit time per unit area or volume) rather than some derivative measure, such as the fraction of a predator's total ingestion. The reason is that a given flow may be a small fraction of a predator's ingestion while simultaneously a large fraction of a prey's loss to predation, or vice versa. It is easier to convert from absolute measurements to normalized measurements than the reverse.

Where the strength of a link cannot be measured quantitatively, it would be useful to classify links qualitatively or to use expert judgment to estimate their strength. An example of a qualitative classification of the strength of links would be: (A) observed to be common, (B) observed to be rare, (C) inferred to be common, (D) inferred to be rare, and (E) known to be absent. Qualitative classifications of links should not be a diversion from the real goal of measuring links quantitatively.

By reporting species and links in fine (and preferably quantitative) detail, field ecologists make possible many alternative analyses, including but not limited to those based on biological species, trophic species, guilds, other taxonomic groupings, and concepts yet to be invented.

Data structures.—Future reports of food webs should use graphical representations of webs only as a psychologically desirable, but optional, adjunct to precise numerical reports in matrix or list form. Food web-directed graphs where the density of links is too great to permit the tracing of individual links should be omitted.

Where the number of species is small enough, webs should be reported in feeding matrix form, with rows corresponding to species eaten, columns corresponding to consumer species, and matrix elements representing quantities of food consumed or frequencies of feeding interactions. Feeding matrices represent metaphoetesis by assigning different size classes or life-cycle stages within a biological species to separate columns (or rows). This format has been used at least since 1880 (Forbes 1880). Separately, each row number and column number of the feeding matrix is identified with the name and measured characteristics of a group of organisms, such as abundance and body size.

Where the number of species is large or the density of links is low, the feeding matrix may be replaced by a list of species, each followed by a sublist of its prey species if any. The list starts with an arbitrary punctuation marker, such as the number -1 (or $*$, or a parenthesis, if the computer language Lisp is used), followed by the identifying number of the first species (or other group of organisms), the identifying number of, and the strength of feeding on, each of its prey (if any), and then another marker. Next comes the identifier of the second species, followed by its prey's identifying numbers (if any) and the strength of its links, then another marker; and so on. Each set of data contained between successive markers could be used to construct one column of a feeding matrix, and vice versa.

The advantage of a feeding matrix over a list of consumers and their prey is that the consumers of a given prey can be read immediately from the matrix row representing that prey, whereas the list requires a search. Apart from this difference in ease of access, the matrix and the list are equivalent.

Food webs are incomplete representations of interspecific interactions in a community because they intentionally omit competitive and mutualistic links (except for the indirect ones arising through trophic links). Direct competitive and mutualistic links should eventually be integrated with food webs. Community interactions could be described by a triplet of matrices, one for feeding, one for direct competition, and one for direct mutualism. Other interactions could be added similarly.

Publication in journals and data bases. There is a gap, real or perceived, between the detail of data that some editors and reviewers will tolerate in reports for

archival journals and the detailed data that the above recommendations would lead observers to report and analysts to desire. Agreement on standards for reporting might lessen the difficulty. Wherever possible, in addition to journal publication, detailed data should be made available in machine-readable form (in a format currently common among ecologists, such as a personal computer diskette or an ASCII file over Internet). ECOWeB (Cohen 1989) is an example of a machine-readable collection of food webs. Deposition of detailed data in machine-readable form, with appropriate documentation, might help relieve the space crunch in standard journals while preserving the data. Because machine-readable formats evolve rapidly, it is prudent to keep and deposit somewhere a full printed copy of all data. Museums might be natural repositories for data as well as for specimens.

Analysts who use webs collected by others should cite the original sources or, where the number of sources is large, should cite a prior publication with references to the original sources. Where individual webs are given special attention in a secondary analysis, the original source should be cited.

Some field investigators are reluctant to make their food web data publicly available because of their large investment of time and effort in gathering them. Such authors, if they are willing, could offer publicly to analyze their data collaboratively, and should consider depositing their data in some public data base several (perhaps 5–10) years after collecting them. Some of the best webs available now were collected and published decades ago by authors no longer alive. It would be a shame not to make the webs now being collected available to future ecologists.

Collaboration.—Because it is rare for an individual to have competence in all organisms from bacteria to birds, food web studies benefit from collaborative efforts among experts in different taxa and subhabitats (e.g., soil, canopy, benthos). Useful food webs rest on competent systematics. Beyond identifying organisms, some taxonomists and museums keep data on the consumers and prey of the species they study. As an incentive for participation in food web studies, ecologists should give generous recognition and support to taxonomists and museum workers who aid them.

Examples

Some beginnings have been made recently in describing food webs in detail as recommended here. Warren (1989), Winemiller (1990), and Martinez (1991) demonstrate varying combinations (though in no case all) of these desirable features: explicit sampling methods; yield-effort curves; consistency of taxonomic identifications within a specific taxonomic domain;

prolonged collaborative research involving multiple specialists; recognition of spatial and temporal variability; large numbers of reported species and links; explicit reporting of data in a form usable by others; estimates of interaction strengths. Future efforts might build on these and similar examples under way, or on data at the Long-Term Ecological Research sites.

Resources

Reaching all the goals described may be nearly impossible with the limited resources typically available to a single investigator or small group of investigators and students. It seems necessary to increase the resources available for empirical studies of food webs. Recommending how to obtain more resources for food web studies is beyond the scope of this note. Cooperation will be required to persuade funding agencies of the possible benefits of more resources for food web studies. Since ecology depends on systematics, ecologists should encourage support for taxonomy as well as for ecology.

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BIOLUMINESCENCE IN DINOFLAGELLATES: A TEST OF THE BURGLAR ALARM HYPOTHESIS

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Bioluminescence in dinoflagellates, unicellular aquatic organisms, has attracted considerable attention, primarily due to the striking nature of this phenomenon—during blooms, disturbances in the water (e.g., breaking waves, the wakes of boats, etc.) can be intensely phosphorescent. Despite a number of hypotheses regarding the function of bioluminescence in dinoflagellates, it is not clear why dinoflagellates bioluminesce (see Morin [1983] for a review). Dinoflagellates are stimulated to bioluminesce by a deformation of their cell membrane generated by shear forces (Hamman and Seliger 1972). These shear forces are often generated by strong stirring of water, such as breaking waves, or the rapid swimming of fish or invertebrates (Sweeney 1987). Sweeney (1987) noted that the light emitted from dinoflagellates is blue-green in color, with the maximum emission being at 474–476 nm. These wavelengths have a low extinction coefficient in water, allowing the light to be visible over relatively long distances. For this reason many researchers have assumed that bioluminescence serves some communication function.

Schantz (1971) suggested that bioluminescence is a form of aposematic coloration, warning potential grazers of noxious substances contained by the prey. Indeed, many of the species of dinoflagellate that bioluminesce also contain toxins. There are also many nontoxic bioluminescent dinoflagellates, perhaps sug-

gesting the existence of a model/mimic system. However, organisms that consume dinoflagellates are often resistant to their toxins, with toxic effects being realized at trophic levels beyond that of the direct grazer of the dinoflagellate (Schantz 1971).

Bioluminescence has also been hypothesized to serve an antipredator function. Esaias and Curl (1972) demonstrated that grazing rates by copepods on dinoflagellates are increased when the bioluminescent capacity of the dinoflagellate is decreased. They hypothesized that the sudden flash of bright light startles the predator, allowing the prey to escape. Although the startle response appears to benefit the dinoflagellate, it is difficult to explain why copepods would continue to respond to the flashes of light generated by dinoflagellates. Buskey et al. (1986) demonstrated that freshwater copepods do not respond to these flashes of light. Therefore maintenance of this startle response must provide some benefit to the copepod. Buskey et al. (1986, 1987) proposed that copepods respond to rapid decreases in light (e.g., shadows) in order to escape predation by ctenophores (which are not present in freshwater), and concluded that the adaptive value of this response physiologically constrains copepods to respond to light flashes generated by dinoflagellates.

Burkenroad (1943) proposed that bioluminescence in dinoflagellates may serve a different function. He suggested that bioluminescence generated by dinoflagellates serves to attract the predators of the dinoflagellate's grazer. This "burglar alarm" hypothesis argues that dinoflagellates render themselves dangerous as prey upon attack because they generate a signal identifying the location of food to individuals two trophic levels up the food chain. If the risk of predation associated with consuming bioluminescent dinoflagellates results in an additional and significant increase to the cost of foraging, this would reduce the net benefit of consumption to a grazer. A significant reduction in the net benefit may cause these dinoflagellates to be eliminated from the grazers' diet. To date, no experiments have determined whether bioluminescence can exert a multi-trophic layer effect necessary to support the burglar alarm hypothesis. Here, we test one prediction of the burglar alarm hypothesis: that bioluminescence serves

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