chain lengths were all terrestrial (webs 24, 25, 27, and 40), three of which appear incomplete, followed by relatively complete aquatic habitats with longer chains. For the two-dimensional webs, seven out of eight webs are incomplete (terrestrial habitats, marshes, and the rocky intertidal). We suggest that the three-dimensional food web descriptions, particularly those of webs in open seas, more completely reflect real food webs, while the two-dimensional and terrestrial three-dimensional webs are descriptions of habitat compartments of real food webs. This is consistent with the resource compartmentation hypothesis and niche theory (6, 8) and the notion of mobile predators linking habitat compartments (9). This analysis also illustrates that relations between environment and chain length cannot be established until the parameters that are sufficient to describe real food webs are identified and used.

**References and Notes**


10. We thank Martin Fowler for writing the program to calculate mean food web length and A. T. Carpenter, M. Coughenour, B. A. Menge, J. Ward and J. A. Wiers for their helpful comments or reviews of the manuscript, and E. J. Rykiel for support. Funded in part by grants from the Department of Energy and the National Science Foundation.

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Response: We welcome further analyses of the data we have assembled on community food webs (1). We also welcome further refinements of the concepts on which those data are based. The conclusion of our paper was an open invitation to ecologists to provide explanations for the difference in mean food chain length observed between two-dimensional (2-D) and three-dimensional (3-D) habitats.

Analyzing the data already published on the first 40 webs in our collection (2, 3), Moore et al. propose that the difference is largely an artifact of differences in how completely food webs are described. They suggest that descriptions are more thorough in 3-D than in 2-D habitats. They offer two arguments.

Their first argument is that the webs from 2-D habitats lump together all plankton and thus appear to have shorter chains than the webs from 3-D habitats, which differentiate between phytoplankton and zooplankton. We have tested this interesting possibility for the whole collection of 113 webs, and find that it has some validity. Out of 40 2-D webs, there are 14 (mostly intertidal) communities that lump phytoplankton and zooplankton grazers as one unit, whereas only one out of 28 3-D webs does so. Thus there appears to be a systematic bias in web description: intertidal ecologists generally do not report the phytoplankton-zooplankton linkage.

We point out, however, that this “cultural bias” would account for only part of the difference in mean chain length observed between 2-D and 3-D habitats in our web collection. Further, the omission of a phytoplankton compartment is justifiable in many aquatic 2-D habitats, such as streams, where algae are not planktonic but are attached, and where zooplankters depend essentially on allochthonous detritus for feeding. Caution must be exercised therefore before “completing” webs that may appear “incomplete” at first glance.

Next, to account for the remaining difference in chain length between 2-D and 3-D webs, Moore et al. suggest that top predators are reported more often in 3-D homogeneous aquatic habitats, where they reside along with their prey, than in 2-D and 3-D terrestrial habitats, which are more compartmentalized. In terrestrial habitats, top pred-

<table>
<thead>
<tr>
<th>Percentile</th>
<th>Two dimensional</th>
<th>Three dimensional</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Original No.</td>
<td>Adjusted</td>
</tr>
<tr>
<td></td>
<td>113</td>
<td>40</td>
</tr>
<tr>
<td>Q3</td>
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<td>2.2</td>
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<td>n</td>
<td>40</td>
<td>8</td>
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Thus well-known debate between Edwards et al. (5) and Menge (6). To our knowledge, this issue has yet to be resolved satisfactorily. Whether occasional predators are omitted relatively less often in 3-D aquatic habitats than in other habitats, as argued by Moore et al., is conjectural at this time and in any event is a difficult hypothesis to test rigorously. Altering original web descriptions, as they do, by the addition here and there—and particularly in 2-D habitats—of so-called "missing top predators" does not constitute a credible test. We could argue on the contrary that there is equally compelling "evidence" that occasional top predators are often missing from 3-D webs. Thus most 3-D aquatic webs could be lengthened by adding one more obvious link: man, the fisherman, as an occasional top predator. In any event, tampering retroactively from original food web versions will probably not provide the answer.

Finally, in discussing the issue of "dimension" raised by Moore et al., we would distinguish a concept that "lacks sufficient rigor," as they say, from a term with different clear definitions in different contexts, as we believe "dimension" to be. Thus the referent of "dimension" in (1) differs from that in some earlier works by Schoener (7) and one of us (J.E.C.) (2). Schoener (7) considered all dimensions of the niche. In (2), only the dimensions of the trophic, or feeding, niche were considered. We (1) considered the apparent flatness or solidity of the physical setting of the food web, at the scale of the human observer. The demonstrable payoff from this phenomenological concept of dimension is a clear, and evidently provocative, association of this "dimension" with the mean and the maximal chain lengths of food webs.

The main purpose of our paper (1) was to compare the influence of three environmental factors (primary productivity, variability, and dimension) on chain length, rather than to confirm the exclusive dominance of any one of these factors and the irrelevance of the others. We found dimension to be far more influential than primary productivity. By contrast, in a study which we previously overlooked, Yodzis (8) found that energy flow explains variation in food chain length better than do limitations resulting from dynamical stability or the body size of predators (he did not consider dimension). His data were the 34 webs among the first 40 of our collection (1-3) that do not include man; his measure of chain length was an index called "trophic height." The influence of energy versus that of other factors on food chain length must be further analyzed.

In conclusion, we hope and expect that the many imperfections of the data we have assembled and the likely imperfections of theory based on those data will provoke field ecologists to render the data obsolete by replacing them with more food webs more systematically observed and more carefully reported.

Frederic Briand
World Conservation Center, International Union for the Conservation of Nature, CH-1196 Gland, Switzerland

Joel E. Cohen
Rockefeller University, 1230 York Avenue, Box 20, New York, NY 10021-6399

REFERENCES

6. B. A. Menge, ibid., p. 1180.
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AAAS–Newcomb Cleveland Prize
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The AAAS–Newcomb Cleveland Prize is awarded to the author of an outstanding paper published in Science. The value of the prize is $5000; the winner also receives a bronze medal. The current competition period began with the 3 June 1988 issue and ends with the issue of 26 May 1989.

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The award will be presented at the 1990 AAAS annual meeting. In cases of multiple authorship, the prize will be divided equally between or among the authors.
Response: Habitat Compartmentation and Environmental Correlates of Food Chain Length
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