

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.

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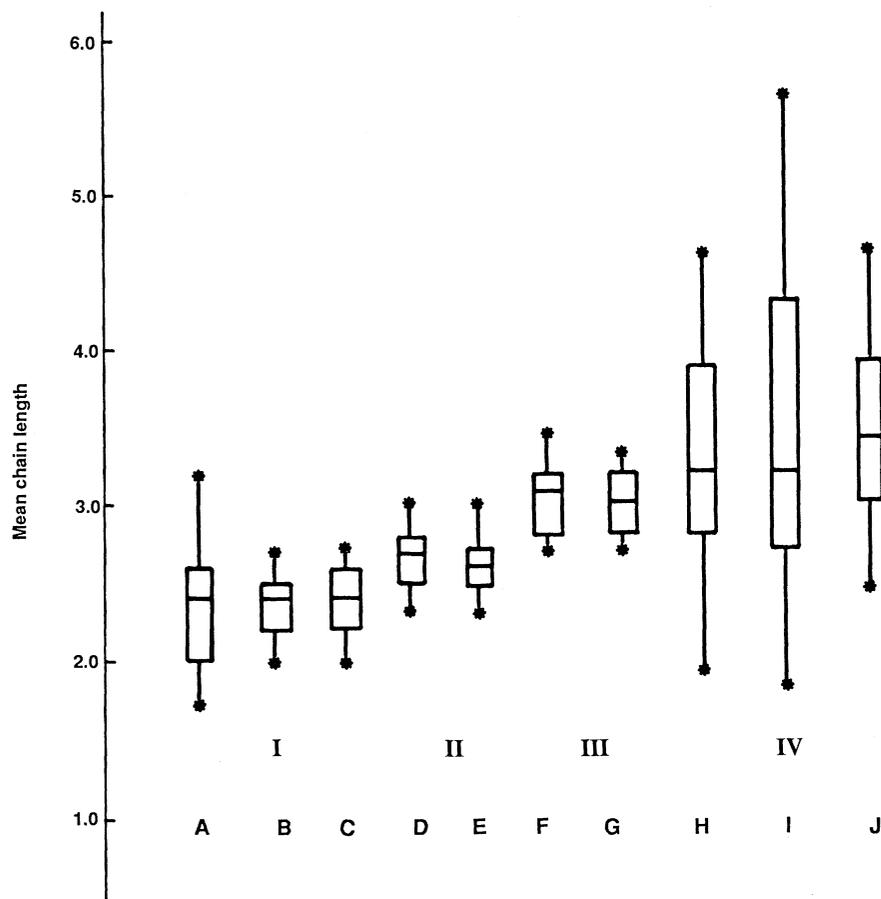
Response: We welcome further analyses of the data we have assembled on community food webs (1). We also welcome further refinements of the concepts on which those data are based. The conclusion of our paper was an open invitation to ecologists to provide explanations for the difference in mean food chain 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 their 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-



Percentile	Two dimensional						Three dimensional			
	Original No.		Adjusted				Original No.		Adjusted	
	113	40	40c	Plankton	Predators	40	113	Predators		
Q3	2.6	2.5	2.6	2.8	2.7	3.2	3.2	3.9	4.3	3.9
Q2	2.4	2.4	2.4	2.7	2.6	3.1	3.0	3.2	3.2	3.4
Q1	2.0	2.1	2.2	2.5	2.5	2.8	2.8	2.8	2.7	3.0
n	40	8	8	8	8	8	8	12	28	12

ators may be only occasional visitors and are thus less susceptible to being recorded.

In general, the original food web investigators omit from their description predators that are occasional. The question of whether links involving "tourist predators" should be depicted or not in web diagrams has been raised many times in the past, by Paine in particular (4). It was also the subject of a 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 with 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.

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