known that neither hypothesis should be given preference. A considerable amount of work by oceanographers and fishery scientists must be done before the role of krill in the Georges Bank food chain can be fully appreciated.

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Habitat Compartmentation and Environmental Correlates of Food Chain Length

Briand and Cohen (*1*) conclude that "the dimensionality of the environment influences mean or maximal [food] chain length more than environmental variability" but do not offer an explanation. After examining the first 40 food webs that Briand and Cohen present (*1*), we find that most of the difference in chain length between habitats of different dimensions appears to be an artifact of the completeness of the web descriptions. Our calculations indicate that the first 40 webs are an adequate sample, as the range and median chain lengths of webs 1 through 40 are similar to those of webs 1 through 113 (Fig. 1).

Many of the webs presented by Briand and Cohen are truncated. In the first 40 webs, 17% of the 138 "producers" are actually consumers. For example, the Aspen parkland community food web (*2*) producers include primary producers, but also consumers, for example, coots, ducks, mice, and ants. Because in all cases these consumers have no resource identified below them and only a single link above them, the mean and maximum food chain lengths are underestimated. Moreover, the intermediate and top predators of many web descriptions are missing. In the New Zealand salt-meadow (*3*) the low mean chain length (1.96) results from single-link chains that portray organisms such as weevil larvae, Hemiptera, harpacticoids, staphylinids, dipterous larvae, haplotaxid worms, oribatid mites, bumblebees, adult Hymenoptera, and redpolls as top predators. Jones (*4*) described a web for the River Clydach that included predatory fish, but Briand and Cohen and others (*5, 6*) use a simplified web for this system, in which predatory fish and some intermediate consumers are deleted. Numerous webs are missing predatory birds and insects and

primary decomposers (bacteria and saprophytic fungi) or do not have phytoplankton distinguished from zooplankton.

We find that the concept of habitat dimensionality lacks sufficient rigor to be used in a standardized manner. In the study by Briand and Cohen, three-dimensional (solid) habitats include lakes, oceans, and forests (including kelp beds), whereas two dimensional (flat) habitats include creeks, rivers, intertidal zones, marshes, grasslands, deserts and tundra. Habitats with both two- and three-dimensional aspects are considered to have mixed dimensions. Habitats may appear to us as solid or flat; however, we question whether organisms within the habitats make this distinction. For example, the Long Island salt-marsh (estuary) includes an air column for birds, a water column large enough to support pelagic organisms and plankton, and a flat bottom for molluscs and water plants; yet this is classified by Briand and Cohen as a two-dimensional habitat. The Marshall Island coral reef is considered a three-dimensional habitat even though it contains only two of the three strata of the Long Island salt-marsh (no air column).

We do not mean to criticize the original food web studies, since their objectives did not include having the webs subjected to structural analyses; however, the completeness of Briand and Cohen's descriptions of the food webs is confounded with the webs' dimensions. In the three-dimensional habitats of Briand and Cohen, phytoplankton are differentiated from zooplankton and generally include top predators [see webs 17, 19–21, 24, 25, 27, 29–32, and 40 (*1, 5*)], whereas the two-dimensional habitats [webs 3, 10–13, 23, 34, and 35 (*1, 5*)] do not have plankton differentiated and lack top predators (birds, fish, and mammals).

We consulted some of the investigators of the original studies, outside experts on the habitats included in the studies, or the original publications and corrected biases in the descriptions by differentiating plankton, conservatively adding top predators where they were obviously missing [for example, gulls and other predators feed on shellfish in the rocky intertidal—webs 10–13 (*6, 7*)]. We then recalculated the mean chain lengths. Differentiating plankton accounted for 20 to 30% of the difference in the median chain length between two-dimensional and three-dimensional webs reported by Briand and Cohen (*1*), while 60 to 70% could be explained by the differentiating plankton and missing top predators (Fig. 1).

The difference in mean chain length between the two-dimensional and three-dimensional webs appears to be a function of how closely their descriptions depict the real food web. If the top predator(s) resided in the same habitat or medium as their prey, the original investigator(s) included them in the description (for example, large mammals, sharks, and boney fish for food web descriptions of open seas). If the top predator(s) of a web spent much time in a habitat or medium other than their prey, however, the investigator(s) did not generally include them (for example, birds and mammals for food web descriptions of the rocky intertidal, streams, and some terrestrial habitats). Of the 12 three-dimensional webs included in our analysis, the four with the lowest mean

Fig. 1 (facing page). Box plots of the frequency distributions of mean chain lengths calculated after Briand and Cohen (*1*). In Group I (A) represents the two-dimensional webs presented by Briand and Cohen (*1*), (B) the subset of two-dimensional webs from the first 40 webs (*1*), and (C) the subset of two-dimensional webs with web 12 corrected to reflect the mean chain length of the food web presented by Briand (*5*) [mean chain length was 2.25 (*1*); it is now 2.32] and small frogs separated from large frogs in web 23. Group II (D, E) are the two-dimensional webs (3 and 10–13) with phtyoplankton and zooplankton separated. Method D assumes that phytoplankton are only consumed by zooplankton, while Method E additionally assumes that phytoplankton are consumed by predators of zooplankton. Group III (F, G) consists of the two-dimensional webs (3, 10–13, 23, and 34) with predators added. Method F adds missing top predators to the Method D webs, and Method G adds top predators to the Method E webs. In Group IV Method H represents the subset of three-dimensional webs from the first 40 webs, (I) the complete set of three-dimensional webs presented by Briand and Cohen, and (J) the subset of three-dimensional webs with predators added (24, 25, and 40) (*1*). Q1 is the 25th percentile, Q2 the 50th percentile, and Q3 the 75th percentile. For each box plot, the upper asterisk represents the largest observation less than Q3 + (Q3 − Q1), and the lower asterisk represents the smallest observation greater than Q1 − (Q3 − Q1).

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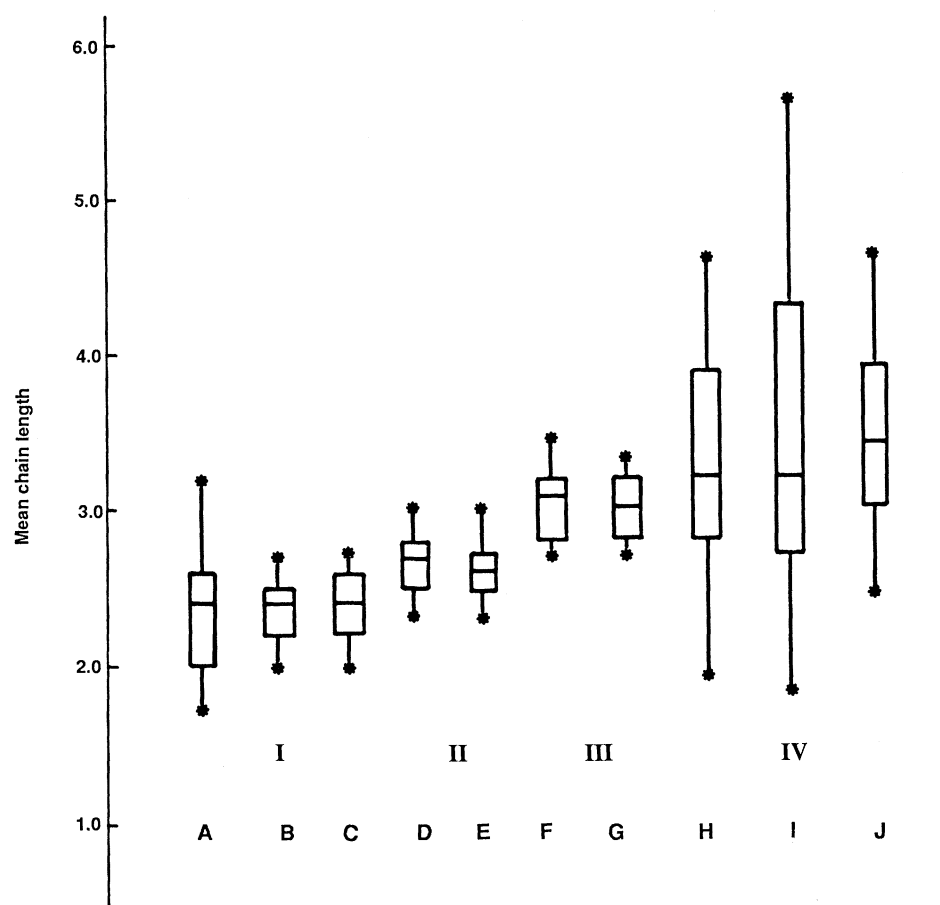
Percentile	Two dimensional							Three dimensional		
	Original No.			Adjusted				Original No.		Adjusted
	113	40	40c	Plankton		Predators		40	113	Predators
Q3	2.6	2.5	2.6	2.8	2.7	3.2	3.2	3.9	4.3	3.9
Q2	2.4	2.4	2.4	2.7	2.6	3.1	3.0	3.2	3.2	3.4
Q1	2.0	2.1	2.2	2.5	2.5	2.8	2.8	2.8	2.7	3.0
n	40	8	8	8	8	8	8	12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