The Role of Discharge Variation in Scaling of Drainage Area and Food Chain Length in Rivers

John L. Sabo, 1,2 Jacques C. Finlay, 2 Theodore Kennedy, 3 David M. Post 4

Food chain length (FCL) is a fundamental component of food web structure. Studies in a variety of ecosystems suggest that FCL is determined by energy supply, environmental stability, and/or ecosystem size, but the nature of the relationship between environmental stability and FCL, and the mechanism linking ecosystem size to FCL, remain unclear. Here we show that FCL increases with drainage area and decreases with hydrologic variability and intermittency across 36 North American rivers. Our analysis further suggests that hydrologic variability is the mechanism underlying the correlation between ecosystem size and FCL in rivers. Ecosystem size lengthens river food chains by integrating and attenuating discharge variation through stream networks, thereby enhancing environmental stability in larger river systems.

In river ecosystems, climate change and human appropriation of fresh water are altering discharge variability and the frequency of intermittency across the globe (15). These hydrologic alterations have implications for the structure of river food webs. FCL in rivers may vary with the stability of the environment [for example, \( \tau \sim 1/(\text{flow variation}) \)], ecosystem size (such as drainage area), and energy supply. All three are correlated because the magnitude of high flows, channel geometry, and the relative supply of aquatic and terrestrial energy sources (such as algae and leaf litter from riparian trees, respectively) vary with drainage area (16–18). Thus, flow variation and other putative controls of FCL may scale with drainage area and mechanically link ecosystem size to FCL. To date, no single study has addressed the simultaneous effects of energy supply, environmental variation, and ecosystem size—and correlations among these drivers—on the length of food chains in rivers or any other ecosystem.

We tested the role of ecosystem size, environmental stability, and energy supply on FCL in 36 rivers in North America. We define FCL as the maximum trophic position of stream-dwelling consumers measured via a stable isotope approach, which can accommodate omnivory and non-integer values of FCL (19). Our analysis expands on previous work on FCL in three ways. First, our study sites include a comprehensive range of values for all putative controls of FCL: (20); a variation of \( >6 \) orders of magnitude in ecosystem size (drainage area, \( A_d = 0.35 \) to \( 10^6 \) km²), a variation of \( >3 \) orders of magnitude in energy supply [gross primary production (GPP) = 0.06 to 18.9 g of O₂ m⁻² day⁻¹], and high-flow variation \( \sigma_{HF} (21) = 0.03 \) to 12.9. Our study sites also include both perennial and intermittent rivers, providing us with an opportunity to quantify how river drying affects riverine food web structure. Second, we used a hybrid of spectral and extreme event statistics to quantify environmental variation (\( \sigma_{HF} \)), which provides a quantitative measure of discharge variation with reference to long-term discharge patterns (21). Third, we used path analysis to quantify and compare the path coefficients of drainage area→FCL and drainage area→flow variation→FCL relationships. In doing this, we asked whether ecosystem size has direct effects on FCL, or whether these effects are indirect and mediated via scaling between drainage area and flow variability (22).

We found that FCL increased with ecosystem size and decreased with \( \sigma_{HF} \) but was unrelated to energy supply (Fig. 1), which is consistent with previous findings (23–25). Ecosystem size had similar effects on FCL when measured as drainage area or cross-sectional area (fig. S1). Food chain length ranged from \( \sim 3 \) (predator) to nearly \( 5 \) (trophic predator), matching the largest range of variation in FCL of any ecosystem (10, 11). Top predators in 32 streams were fish, and these taxa were sufficiently large to be piscivorous in 29 sites (table S1). In intermittent streams, the top predator was consistently an invertebrate or an insectivorous fish. Our results suggest that the strong effect of ecosystem size on FCL arises in part from a relationship between drainage area and flow variation and strong control of FCL by high- and low-flow events. \( \sigma_{HF} \) scaled with drainage area (Fig. 2A), but the power of the scaling relationship was significantly less steep and the mean \( \sigma_{HF} \) value was significantly higher in intermittent than in perennial rivers. Significant negative powers in both cases indicate that flow variation declines with drainage area. Attenuation of discharge variation results from spatial averaging in larger basins of asynchronous precipitation and high flows occurring in upstream portions of the drainage network. FCL increased

1Faculty of Ecology, Evolution, and Environmental Sciences, School of Life Sciences, Arizona State University, Post Office Box 871450, Tempe, AZ 85287–4501, USA. 2Department of Ecology, Evolution and Behavior, Yale University, Post Office Box 208106, 165 Prospect Street, New Haven, CT 06520–8106, USA.

2Department of Ecology and Evolutionary Biology, Yale University, Post Office Box 208106, 165 Prospect Street, New Haven, CT 06520–8106, USA.

3To whom correspondence should be addressed. E-mail: John.L.Sabo@asu.edu

www.sciencemag.org SCIENCE VOL 330 12 NOVEMBER 2010 965
with increasing return times of anomalous high flows (Fig. 2B), and this effect was independent of ecosystem size (Fig. 2C). The relationship between return times and FCL was asymptotic: significantly lower in systems with recent high flows (in the same year) than in systems with events occurring 1 to 5 years before FCL estimation. The shape of the relationship between high-flow return time and FCL did not differ significantly between perennial and intermittent streams, suggesting a similar effect on FCL in spite of significantly lower FCL overall in intermittent rivers. Low-flow events also constitute a form of environmental variation in rivers. Zero flows reduced FCL regardless of ecosystem size (Fig. 2D). For the full data set, path coefficients for the effects of $A_d$ on $\sigma_{HF}$ and $\sigma_{HF}$ on FCL were both significant and negative (Fig. 3A). For the perennial subset, the path coefficient for the effect of $A_d$ on $\sigma_{HF}$ was larger and less variable than in the full data set (Fig. 3B), but the effect of $\sigma_{HF}$ on FCL was not significant. Path coefficients for the direct effect of $A_d$ on FCL were not significant for either data set; however, the total (direct and indirect) effects of $A_d$ were significant in both analyses. The indirect path...
The diagram shows the relationship between drainage area and food chain length. The formula for flow variability is given as $\sigma_{HF}$, and the path coefficients are indicated for different pathways. The diagram illustrates how changes in drainage area can affect food chain length, with a focus on intermittent rivers.

The text discusses the impact of high flows on food chain length, particularly in intermittent rivers, and how this relates to hydrologic variability. It mentions previous work suggesting that high flows can have significant effects on food chains and community structure. The text also highlights the importance of drainage area in predicting how river food webs will respond to human- and climate-related changes in hydrology.

The references include a variety of sources, such as scientific journals and books, covering topics from animal ecology to climate change. The authors thank various contributors for their assistance in conducting the research.

The diagram is labeled with the following text:

**A**
- Path 1: $P_1 + P_2 + P_3 = 0.18$
- Path 2: $-0.55 (-0.95 - 0.15)$
- Path 3: $-0.48 (-0.78 - 0.14)$

**B**
- Path 1: $P_1 + P_2 + P_3 = 0.32$
- Path 2: $-0.9 (-0.99 - 0.81)$
- Path 3: $-0.2 (-0.99 - 0.76)$

The diagram is labeled as "Fig. 3. Path analysis of relationships between ecosystem size (or drainage area), dynamic stability [$= 1/\text{flow variability}$], and FCL."