Research

Global patterns of aquatic food chain length

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Food chain length is a fundamental ecosystem property, and plays a central role in determining ecosystem functioning. Recent advances in the field of stable isotope ecology allow the estimation of food chain length (FCL) from stable nitrogen isotope (δ^{15}N) data. We conducted a global literature synthesis and estimated FCL for 219 lake, stream, and marine ecosystems. Streams had shorter food chains (∼3.5 trophic levels) than marine and lake ecosystems (∼4.0 trophic levels). In marine systems, inclusion of marine mammals increased FCL by 2/3 of a trophic level. For each ecosystem type, estimates of FCL were normally distributed and spanned two full trophic levels. Comparison with published connectance food webs revealed similar mean FCL values, though stable isotope-derived FCL estimates were less variable. At the global scale, FCL showed weak or no relationships with ecosystem size, mean annual air temperature, or latitude. Our study highlights the utility of stable isotopes for quantifying among-system food web variability, and the application of this approach for assessing global-scale patterns of food chain length.

Food chain length (FCL) is a measure of the number of energy transfers or trophic links between primary producers and the top predator in an ecosystem. FCL has long been recognized as a fundamental ecosystem attribute (Elton 1927, Lindeman 1942, Hutchinson 1959, Pimm 1982), and the importance of FCL for ecosystems and their functioning has been widely documented. For example, the number of trophic levels is a central consideration to the study of food chain dynamics (Oksanen et al. 1981, Fretwell 1987), and the structuring of ecosystems via trophic cascades (Carpenter et al. 1985, Pace et al. 1999), as well as mediating the relationship between species diversity and ecosystem function (Worm et al. 2002, Schmitz 2003, Duffy et al. 2005). FCL also plays a role in regulating biogeochemical fluxes (Schindler et al. 1997), fisheries productivity (Pauly and Christensen 1995), and contaminant bioaccumulation in top predators (Kidd et al. 1995).

Despite the central importance of FCL for ecosystems, our understanding of variability in FCL, both within- and among- ecosystem types, remains limited (Post 2002a). In perhaps the earliest consideration of

food chain lengths, Elton (1927) speculated that available energy ultimately limits the number of trophic levels in ecosystems. A clear prediction is that more productive ecosystems should have longer food chains. This 'productivity hypothesis' has found support in some studies (Yodzis 1984, Jenkins et al. 1992, Persson et al. 1992, Kaunzinger and Morin 1998, Thompson and Townsend 2005), but not others (Briand and Cohen 1987). Since then, variants of the productivity hypothesis have been forwarded, most notably the productive space hypothesis, which argues that total ecosystem production (productivity × ecosystem size) should best reflect the capacity of an ecosystem to support additional trophic levels (Schoener 1989), and the hypothesis that food chain length should increase with increasing ecosystem size (Schoener 1989, Vander Zanden et al. 1999, Post et al. 2000). Pimm and Lawton (1977) took a very different approach by examining the stability of mathematical food chain models, and found that long food chains tend to be dynamically unstable, though subsequent work found model stability to be sensitive to assumptions concerning self-dampening terms (Sterner et al. 1997).

A dominant approach for testing theories about food webs has been analysis of catalogues of binary 'community food webs', also known as connectance food webs (Briand and Cohen 1987, Pimm and Kitching 1987, Schoener 1989, Cohen et al. 1990). Over 100 connectance food webs from diverse ecosystem types were culled from the published literature, providing an impressive dataset for comparative food web studies (Briand and Cohen 1987, Cohen et al. 1990). This dataset has been valuable for testing hypotheses about factors affecting food chain length. For example, Briand and Cohen (1987) found that 'three-dimensional' ecosystems such as the pelagic zone or the forest canopy supported longer food chains than 'two-dimensional' ecosystems such as lake bottoms or grasslands. Using an edited version of this data set, Schoener (1989) reported substantial variation in FCL within an ecosystem type. This study also described broad-scale patterns, specifically that marine pelagic ecosystems have the longest food chains, and that stream food chains are short relative to lake and marine systems. This is the only study to have examined variability in food chain length within- and among- ecosystem types, and surprisingly little theory addresses variability in food chain length at this level.

Soon after the publication of these early connectance food web studies, the approach was severely criticized, with the bulk of the criticism focused on the poor quality of the primary data (Paine 1988, Polis 1991). The original food webs were created by diverse ecologists with equally diverse interests and biases. Taxonomic resolution varied widely among studies, and there were no consistent criteria for which species to include, or how important a trophic link must be to be counted. Several authors published highly resolved webs which were found to have food web properties vastly different than the original collection of webs (Martinez 1991, Polis 1991).

These challenges to the connectance approach to the study of food webs has dampened ecologist's ability to conduct comparative food web studies. In recent years, stable carbon and nitrogen isotopes have emerged as a tool for describing energy flow pathways in food webs (Peterson and Fry 1987). Carbon isotope ratios are used as a tracer of food 'source' (Hecky and Hesslein 1995), while nitrogen isotopes are indicative of consumer trophic position (Cabana and Rasmussen 1996, Vander Zanden and Rasmussen 2001). Over the past two decades, a large number of individual studies have used stable isotopes to describe food web structure for one or a small number of ecosystems. Comparing stable isotope data from different sites or ecosystems has been problematic because nitrogen isotope ratios at the base of the food web can differ dramatically among-sites due to differences in nitrogen sources and biogeochemical processes (Cabana and Rasmussen 1996). To address this, isotopic 'baseline' correction methods

have been developed, making stable isotope food web data comparable across-systems (Cabana and Rasmussen 1996, Vander Zanden and Rasmussen 1999, Post 2002b). The ability to estimate food chain length for lake ecosystems has rekindled interest examining factors that determine the number of trophic levels in ecosystems (Vander Zanden et al. 1999, Post et al. 2000). In this study, we conduct an exhaustive literature search to compile stable isotope food web data and estimate FCL from lake, stream, and marine ecosystems. In doing so, we expand upon the comparative food web approach to examine global-scale patterns of food chain length within- and among- aquatic ecosystem types.

Methods

Our goal was to obtain stable isotope data from the published literature that could be used to estimate FCL for lake, stream and marine systems. Data sources were obtained by conducting an exhaustive literature search using ISI Web of Knowledge, followed by examination of the citations included in the original studies. For each ecosystem, FCL is defined as the trophic position of the top predator, estimated as the species or taxon with the highest $\delta^{15}N$ value. For the majority of studies, a fish was identified as the top predator. For the small number of stream and lake systems where a bird or mammal species was included in the study and was found to be the top predator, they were not included, in order to maintain consistency and avoid bias related to whether the study collected terrestrial and transient consumers. Eleven of the 47 marine food webs included $\delta^{15}N$ values for at least one marine mammal taxa. For these food webs, we provide separate FCL estimates for fish and marine mammal top predators, and use this to examine how inclusion of marine mammals in food webs affects FCL estimates.

For each food web, food chain length was estimated as:

$$FCL = \left(\delta^{15}N_{top\ predator} - \delta^{15}N_{baseline} \right)/3.4 + \lambda \qquad (1)$$

Where 3.4 is the trophic level fractionation of $\delta^{15}N$, and λ is the trophic level of the baseline indicator, set at 2 because we used a primary consumer baseline (primary producers = trophic level 1, primary consumers = trophic level 2, and so on). Several recent studies have synthesized trophic level fractionation values from the literature.

Vander Zanden and Rasmussen (2001) and Post (2002b) focused on aquatic consumers and report mean trophic fractionation for non-herbivorous aquatic consumers of 3.3‰ and 3.4‰, respectively, while two other literature syntheses produced lower estimates of

mean $\delta^{15}N$ trophic fractionation (McCutchan et al. 2003, Vanderklift and Ponsard 2003). We assumed a trophic fractionation value of 3.4‰ (Vander Zanden and Rasmussen 2001, Post 2002b), consistent with assumptions in previous comparative food web studies (Vander Zanden et al. 1999, Post et al. 2000). Primary consumers not identified as such by the authors were confirmed using internet or outside literature sources (Barnes 1994, Merritt and Cummins 1996, Thorp and Covich 2001). Several of our FCL estimates differ from estimates reported by the original studies because we used a universal trophic fractionation value to ensure consistent methodologies across studies. $\delta^{15}N$ values for top predators and primary consumers were obtained either directly from tables in the original publications, or estimated from published figures using the free computer software, DataThief (www.datathief.org).

Estimating FCL for a system requires the designation of a site-specific nitrogen isotope baseline (Cabana and Rasmussen 1996, Vander Zanden and Rasmussen 1999, Post 2002b). There is general agreement that primary consumers provide the most appropriate baseline indicator because they exhibit lower temporal variability than primary producers, and are sampled in a wide range of ecosystem types (Cabana and Rasmussen 1996, Vander Zanden and Rasmussen 1999, Post 2002b). Recent studies in north-temperate lake have also reported variation in $\delta^{15}N$ among habitats within an ecosystem, more specifically, a negative relationship between $\delta^{15}N$ and $\delta^{13}C$ among habitats within a lake (Vander Zanden and Rasmussen 1999). This negative $\delta^{15}N$-$\delta^{13}C$ relationship is likely not applicable to other types of lakes or ecosystem types (Fry et al. 1999, Post 2002b). Due to uncertainty associated with within-site baseline variation, we estimated the site-specific baseline as the mean $\delta^{15}N$ of all primary consumer taxa. The number of primary consumer taxa reported ranged from 1 to 29, and was usually >5 taxa for a given site. To assess error associated with using the mean primary consumer $\delta^{15}N$ value as a baseline, we employ a parametric bootstrap procedure. At sites for which $\delta^{15}N$ values were reported for multiple primary consumer taxa, we computed the mean and the associated standard deviation (SD). We randomly drew a value from this distribution, calculated FCL using Eq. 1, and repeated this procedure 1000 times, thereby generating a frequency distribution of FCL values for each site. Error variance in FCL associated with baseline variation was expressed as 1 SD of the mean FCL.

From site location and site descriptions, marine food webs were further classified into the following categories: estuarine, coastal shelf, and pelagic/open ocean. To compare our isotope-based FCL patterns with results from connectance food web studies, we used mean path length, defined as the mean length of all chains leading to the top predator (Briand and Cohen 1987). A number of studies have used variants of Briand and Cohen's ECOWeb (1987) dataset: we included only the webs analyzed by Schoener (1989), which eliminated unrealistic and grossly incomplete food webs. Because there were few stream food webs, we included the connectance webs of Thompson and Townsend (2005). The FCL values of Briand and Cohen (1987) and Thompson and Townsend (2005) approximate the number of links leading to a top predator, not the number of levels, and were thus adjusted (FCL + 1) to allow direct comparison of stable isotope and connectance FCL estimates.

Because our data were taken from the literature, estimates of ecosystem productivity were not available for the vast majority of food webs. At the global scale, primary productivity in lakes and streams tends to decrease as a function of latitude (Kalff 2002). For stream and lake ecosystems, we also estimated mean annual air temperature from a recent global synthesis of air temperature records (Kalnay et al. 1996). Latitude was tightly correlated with mean annual air temperature in our data set ($R^2 = 0.84$, $F_{1,147} = 783.9$, $p < 0.0001$), and is used as a very coarse proxy for potential ecosystem productivity in lakes and streams.

Estimates of ecosystem size for lakes and streams were collected directly from the original papers or from outside sources. Surface area was used as a measure of ecosystem size for lakes. No single measure of ecosystem size was available for stream ecosystems included in our study. Annual average discharge was generally either high (>100 m^3 s^{-1}) or low (<5 m^3 s^{-1}), we thus chose a cutoff of 20 m^3 s^{-1}. Stream order for what we classified as small streams was generally 4th order or less, thus we classified streams as small if ≤4, large if ≥5. Discharge values not provided in the published papers were obtained by calculating mean annual discharge from United States Geological Survey (USGS) stream gauges. It was not possible to define ecosystem size for marine systems.

Results

FCL was estimated using stable isotopes for 219 lake, stream, and marine ecosystems (Fig. 1, Appendix 1). For food webs that reported multiple primary consumer taxa, the parametric bootstrap procedure indicated a mean error variance in FCL (expressed as 1 SD) associated with the baseline to be 0.29 for marine systems, 0.34 for lakes, and 0.38 for streams (Table 1).

For each ecosystem type, FCL as estimated using stable isotopes was approximated by a normal distribution, and spanned at least two trophic levels (Fig. 2A–C). FCL varied significantly as a function of ecosystem type (ANOVA; $F_{2,216} = 19.23$, $p < 0.0001$). Tukey–Kramer multiple comparisons tests indicated significant
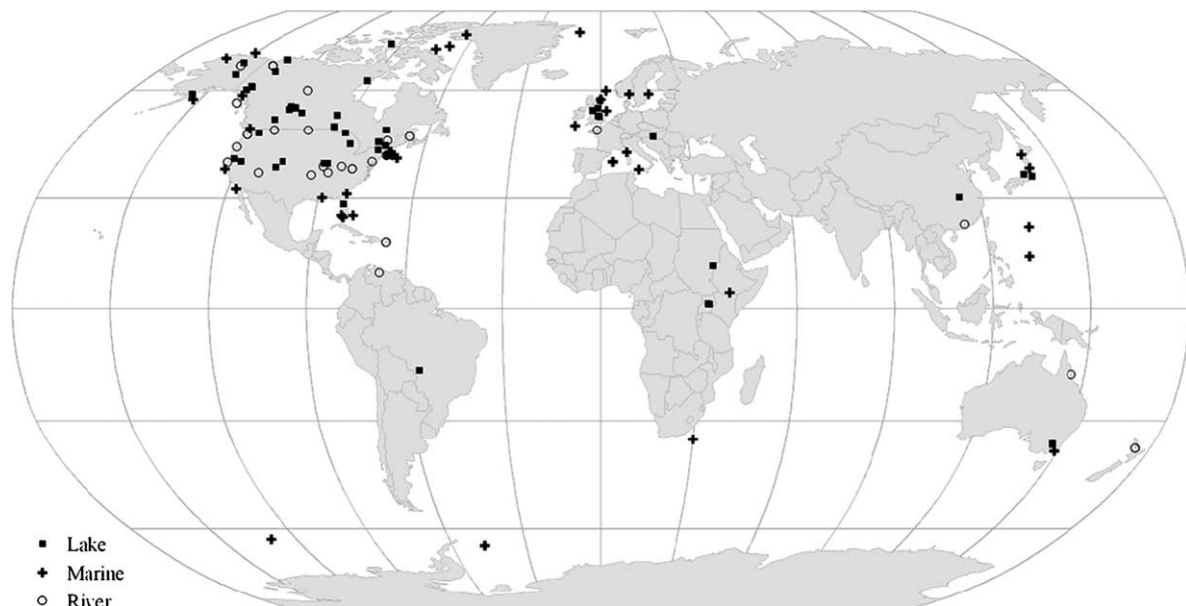
Fig. 1. Location of the stream, lake, and marine food webs included in this study. Lake (solid square), stream (open circle), and marine (+).

differences between streams and lakes ($p < 0.05$), and streams are marine systems ($p < 0.05$). There was no significant difference in FCL between lakes and marine systems ($p > 0.05$). Among marine food webs, there was no significant difference in FCL among estuarine, coastal, and pelagic marine systems (ANOVA; $F_{2,45} = 0.097$, $p > 0.05$). FCL estimates for marine systems are undoubtedly underestimates because we excluded marine mammals, which are often top predators in marine systems. Stable isotope values for marine mammals were included in eleven of the 47 marine food web studies. For this subset of food webs, FCL estimates using the marine mammal top predator averaged 0.64 trophic levels more than FCL estimates using the fish top predator (paired t-test; $t_{10} = -4.05$, $p < 0.001$).

Mean FCL (± 1 SD) for connectance webs (Briand and Cohen 1987, Schoener 1989, Thompson and Townsend 2005) were 3.79 (± 0.69), 3.43 (± 0.89) and 3.91 (± 0.90) for lake, stream and marine systems, respectively (Fig. 2D–F). Connectance FCL values did not vary significantly as a function of ecosystem type (ANOVA; $F_{2,76} = 2.33$, $p > 0.05$). T-tests indicated no

significant differences between connectance and stable isotope FCL estimates for any ecosystem type (lake, $t_{16} = -0.85$, $p = 0.41$; stream, $t_{30} = -0.16$, $p = 0.88$; marine, $t_{51} = -0.35$, $p = 0.73$).

There was a trend of increasing food chain length for streams and lakes towards the poles (Fig. 3), though there was a high degree of variation in FCL at a given latitude, and the relationship was not statistically significant (lake, $R^2 = 0.03$, $F_{1,122} = 3.48$, $p = 0.06$; stream, $R^2 = 0.06$, $F_{1,44} = 2.63$, $p = 0.11$; marine, $R^2 < 0.01$, $F_{1,43} = 0.20$, $p = 0.66$). Finally, there was a weak, but significant positive relationship between ecosystem size and FCL for lakes (linear regression, $R^2 = 0.08$, $F_{1,121} = 10.07$, $p \leq 0.01$; Fig. 4A) but not streams (t-test comparison of large and small streams, $t_{16} = -0.07$, $p = 0.95$; Fig. 4B, C).

Discussion

Over the past two decades, a growing number of studies have used stable isotopes to describe the food web

Table 1. Result of a parametric bootstrap simulation to estimate the effect of site-level baseline (primary consumer) nitrogen isotope variation on error variance associated with estimates of food chain length. Error variance is expressed as 1 standard deviation (SD) of the food chain length value. Also reported are the range and 1 SD of error variance values for each ecosystem type.

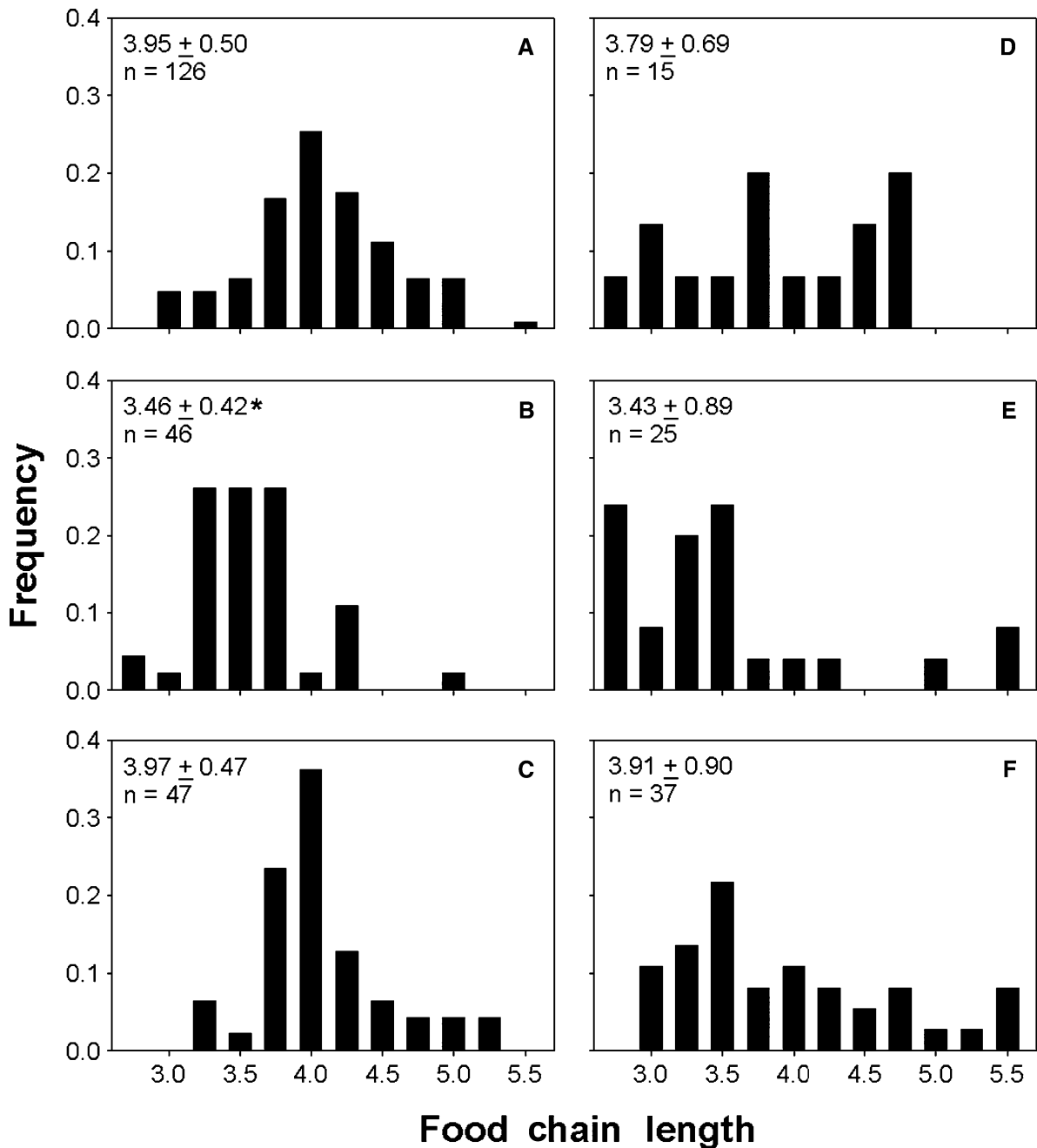| Ecosystem type	Sample size (no. of systems)	Mean baseline variation (1 SD)	Mean error variance (1 SD) for FCL estimates (range in parentheses)	SD
Marine	26	1.16‰	0.29 (0.04–0.65)	0.14
Stream	14	1.28‰	0.38 (0.03–0.78)	0.23
Lake	29	0.97‰	0.34 (0.07–1.06)	0.20

Fig. 2. Patterns of aquatic FCL. (A–C) Frequency distributions of FCL measured using stable nitrogen isotopes for lake (A), stream (B), and marine (C) ecosystems. (D–F) Frequency distributions of connectance FCL estimates for lake (D), stream (E), and marine (F) ecosystems. Mean (± 1 SD) and sample size for each system type are presented in the upper left corner of each panel. * indicates values are significantly different at $p < 0.05$.

structure of individual ecosystems. To date, no efforts have been made to synthesize this widely dispersed literature, and to capitalize on the potential of this approach to examine broad scale food web patterns. This study presents a synthesis of published stable isotope food web data, and offers several new perspectives on broad-scale patterns of food chain length for aquatic ecosystems. Within a given habitat type, FCL spanned two full trophic levels. There were also significant differences among habitat types, with stream
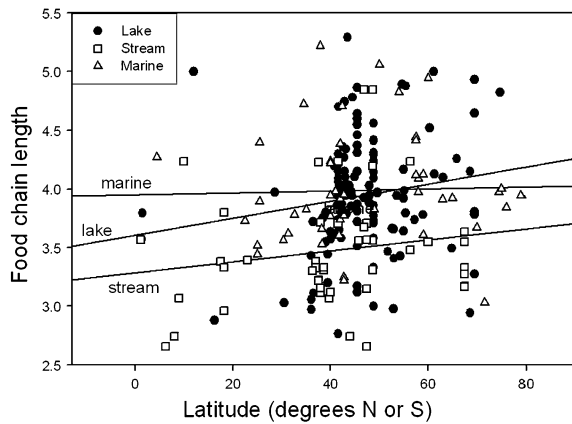
Fig. 3. Food chain length versus latitude (north or south plotted as equivalent) for stream, lake and marine ecosystems. Though there was a trend of increasing FCL with latitude for streams and lakes, relationships were not statistically significant.

food webs being shorter than lakes, and marine systems exhibiting the longest food chains if the typically unsampled marine mammals are included. Past comparative food web studies have used connectance webs – an approach that has been the subject of criticism due to the poor quality of the original data (Paine 1988, Polis 1991, Polis and Strong 1996). Stable isotopes provide an alternative and potentially powerful tool for tracing the pathways of energy/mass flow through ecosystems, and we were able to find a large number of sites from around the world for which FCL could be estimated through the application of baseline correction techniques (Cabana and Rasmussen 1996, Vander Zanden and Rasmussen 1999).

Testing hypotheses of food chain length

The earliest explanation for what constrains the number of trophic levels was forwarded by Elton (1927). His productivity hypothesis posited that due to the inherent inefficiency of trophic transfers, available energy becomes insufficient to support more than a small number of trophic levels (Elton 1927, Pimm 1982). A testable prediction of this hypothesis is that more productive ecosystems should have longer food chains. We were unable to consistently obtain primary productivity data for our food webs. Latitude is a coarse indicator of potential ecosystem productivity for stream and lake ecosystems (Kalff 2002), and undoubtedly there is a high degree of among-site variation in primary productivity at a given latitude. We found no significant relationship between FCL and latitude, though there was a trend for lake and stream food chains to be longer at high latitudes compared to the tropics, which
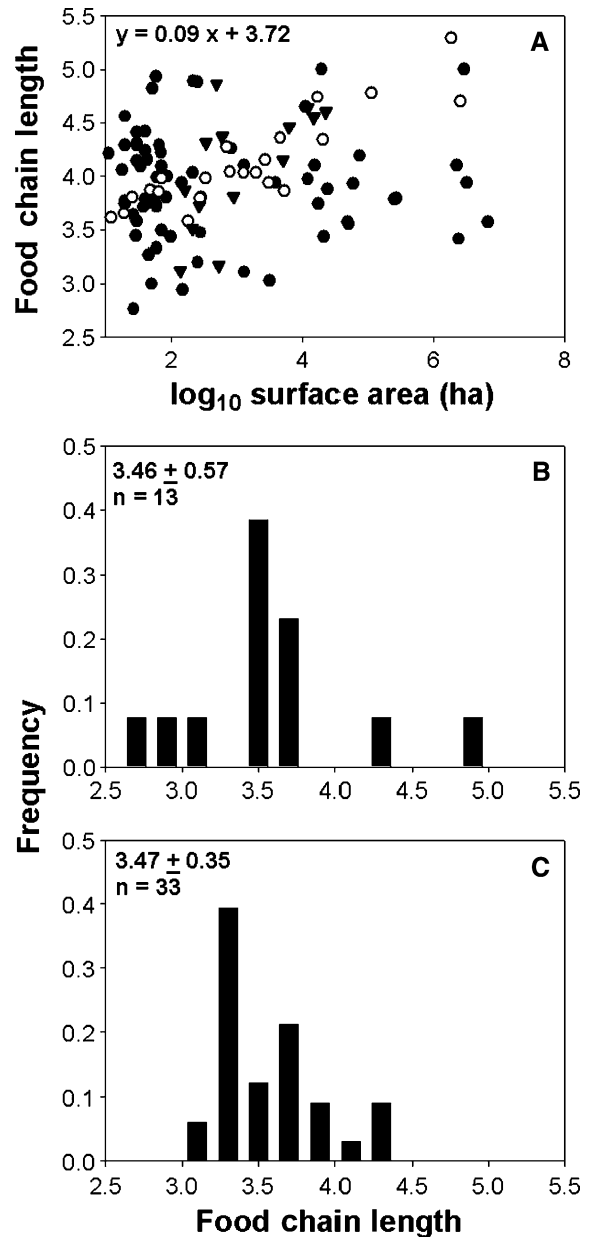

Fig. 4. Relationships between ecosystem size and FCL. (A) Lake surface area vs FCL. Data from Vander Zanden et al. (1999) (triangles) and Post et al. (2000) (open circles) indicated separately. (B, C) Frequency distributions of large (B) and small (C) stream systems (no significant difference at $p < 0.05$).

is the opposite trend of what is predicted from the energy hypothesis.

Are per-unit-area measures of ecosystem productivity even appropriate for testing Elton's productivity hypothesis? This question was raised by Schoener (1989), which noted that per-unit-area productivity

(i.e. $g\ m^{-2}\ yr^{-1}$) is only one factor affecting the energy available for supporting higher trophic levels when considering enclosed or semi-enclosed ecosystems such as lakes or islands. Schoener (1989) proposed that total ecosystem production (the product of ecosystem size and per-unit-area productivity) is the appropriate measure of energy availability for testing whether available energy limits FCL. This point is relevant to comparative lake food web studies (Vander Zanden et al. 1999, Post et al. 2000), in which variation in whole-ecosystem production (productivity × area) was overwhelmingly a function of variation in ecosystem size. This is the result of limited among-lake variation in productivity (1−2 orders of magnitude), and tremendous variation in ecosystem size (∼7 orders of magnitude). Using data in Vander Zanden et al. (1999), total ecosystem production and lake area were closely correlated ($R^2 = 0.94$). The logical extension of this is that ecosystem size is a measure of ecosystem production, and highlights the inherent difficulty in separating the effects of these variables.

Lakes are self-contained ecosystems, and are used as model systems for testing the role of productivity and ecosystems size as potential determinants of food chain length. Vander Zanden et al. (1999) and Post et al. (2000) both reported positive relationships between FLC and ecosystem size in lakes. In the present study, there remains a significant relationship between FCL and lake area for lakes, though at the global scale, the relationship is relatively weak (Vander Zanden et al. 1999, $R^2 = 0.41$; Post et al. 2000, $R^2 = 0.76$; present study $R^2 = 0.08$). Interestingly, if FCL estimates from these two previously published studies are excluded, there is no statistically significant relationship between lake size and FCL ($R^2 = 0.008$, $F_{1,84} = 0.63$, $p = 0.43$). For lakes, the importance of ecosystem size as a determinant of FCL appears to diminish when scaled-up beyond a regional analysis.

Several recent studies have used streams to test hypotheses about the determinants of FCL (Townsend et al. 1998, Thompson and Townsend 2005). In contrast with lakes, streams are open ecosystems, making it more difficult to define ecosystem boundaries or quantify ecosystem size. We found no difference in FCL between large and small riverine systems, indicating a limited role of ecosystem size in determining stream FCL, though recent comparative food web studies reported effects of both productivity and ecosystem size on stream FCL (Townsend et al. 1998, Thompson and Townsend 2005).

Comparison of FCL among ecosystem types

There is notably little theory addressing differences in FCL among ecosystem types, and only one empirical

study (Schoener 1989) explicitly compared food chain length across different ecosystem types. Nevertheless, stream, lake and marine ecosystems differ in profound ways that could result in differences in food chain length, thereby providing an opportunity to test whether the observed patterns are consistent with current hypotheses of FCL. Though FCL varied widely for a given ecosystem type, food chain length in streams averaged 1/2 trophic level shorter than lakes. Marine food chains are longer than both streams and lakes if marine mammals are included, which added an average of an additional 0.6 trophic level. These differences in FCL among ecosystem types provide an opportunity to take a novel approach to examining the factors that determine FCL. Rather than compare FCL among individual ecosystems of the same type (Vander Zanden et al. 1999, Post 2002a, Thompson and Townsend 2005), we examine whether broad-scale food web differences among lakes, rivers, and marine systems are consistent with current hypotheses of FCL.

Might the observed food web differences result from differences in productivity among lakes, streams and marine ecosystems? This is difficult to assess because there is a tremendous degree of among-system variability in primary production for a given ecosystem type. The range of primary productivities ($g\ C\ m^{-2}\ d^{-1}$) for lakes and stream overlap remarkably, ranging from 0.01−20 $g\ C\ m^{-2}\ d^{-1}$ for streams and 0.02 − 30 $g\ C\ m^{-2}\ d^{-1}$ for lakes (Allan 1995, Kalff 2002). Primary production can be notably higher in marine systems, with average rates ranging from 0.01 to 400 $g\ C\ m^{-2}\ d^{-1}$ (Schoener 1989). Nevertheless, marine primary production shows a high degree of overlap with values for lake and stream systems. At the global scale, primary productivity for lakes, streams, or oceans spans 3−4 orders of magnitude. With so much overlap and among-site variability, it is unlikely that among-system differences in FCL are the result of productivity differences.

Lakes, streams, and marine systems do differ in terms of ecosystem size. Streams are generally small in areas and volume compared to lakes, though streams also tend to be 'open' systems, such that mobile consumers (fishes) could effectively serve to enlarge ecosystem boundaries. Coastal and pelagic marine ecosystems also tend to be open, and are undoubtedly the 'largest' ecosystems. Defining ecosystem boundaries for both streams and marine systems is highly subjective, thus making assessment of the role of ecosystem size in determining FCL problematic.

Pimm and Lawton (1977) examined model food chains and concluded that long food chains tend to be dynamically fragile, and less able to recover from environmental perturbation. A resulting prediction was that food chains should be shorter in ecosystems subject to environmental fluctuation and disturbance

(Pimm 1982). Of the aquatic ecosystem types examined here, streams and estuaries are subject to the greatest degree of disturbance, while lakes and open ocean systems tend to be more environmentally stable. There was no difference in FCL between estuarine and coastal/pelagic systems, though our finding of short food chains in streams is consistent with the dynamic stability hypothesis. Overall, our finding that stream food chains are short is consistent with ecosystem size and dynamic stability arguments, and highlights the difficulty in separating potential determinant of FCL from analysis of comparative food web data.

Comparisons with connectance food webs

Using stable isotope methods, we found that stream, lake, and marine ecosystems are generally comprised of three to five trophic levels. Several studies have used direct diet data to reconstruct food webs so as to weight food web linkages according to their energetic importance, similar to what is accomplished with stable isotope techniques. Winemiller (1990) reports an average of 3.6 trophic levels for tropical stream food webs. Food webs in Canadian lakes ranged from three to five levels (Vander Zanden and Rasmussen 1996). Network analysis of estuarine systems reveal approximately 4.5 trophic levels (Baird and Ulanowicz 1989, Christian and Luczkovich 1999). These estimates, derived from weighting trophic links according to their energetic importance, are consistent with the stable isotope-derived FCL estimates reported herein.

Interestingly, stable isotope-derived patterns of FCL did not differ substantially from ECOWeb webs, the widely-used compilation of connectance food webs (Briand and Cohen 1987, Schoener 1989), though connectance food webs tended to be more variable for a given ecosystem type. In light of the many well-known shortcomings of connectance food webs (Paine 1988, Polis 1991, Polis and Strong 1996), a number of highly resolved webs have been constructed to test whether previously described food web attributes are an artifact of poor data. Polis (1991) and Martinez (1991) reported FCL (mean length of all paths leading to the top predator) of approximately 8 trophic levels. Other studies of 'highly resolved' webs indicate 5–6 trophic levels (Hall and Raffaelli 1991, Goldwasser and Roughgarden 1993). It appears that food chains for highly resolved webs are notably longer than those derived from either stable isotopes or the original collection of connectance food webs.

Our interpretation of the above finding is that these highly resolved webs include the many food web links that are energetically unimportant. In fact, the majority of trophic linkages are of minor energetic importance, such that weighting all links equally in a highly resolved

web overinflates mean path length. Alternatively, the ECOWeb webs are taxonomically poorly resolved, and overlook many links. Yet our comparison (Fig. 2) indicates that they manage to capture the broad-scale patterns of energy-weighted FCL, as revealed through stable isotope techniques and the handful of traditional food web studies that have weighted links according to energetic importance (Baird and Ulanowicz 1989, Winemiller 1990, Vander Zanden and Rasmussen 1996, Christian and Luczkovich 1999). While it appears that connectance food webs capture broad-scale patterns of energy-weighted FCL, we caution that FCL estimates for a poorly-resolved web may severely over- or under-estimate FCL for a given ecosystem. Our results correspond with that of Williams and Martinez (2004), which compared different food web measures (i.e. shortest path, longest path, mean path length) for a series of well-resolved webs. They found that mean path length overestimated consumer trophic position relative to flow-weighted webs. This is consistent with the assertion that most trophic linkages are energetically weak, and that shorter trophic pathways tend to be energetically more important.

Use of stable isotopes to estimate food chain length

Stable isotopes provide a relatively new approach for estimating FCL, and it is essential to explicitly consider sources of error, as well as some of the conceptual issues involved in using stable isotopes to measure FCL. Estimating FCL using stable nitrogen isotopes involves designating a nitrogen isotope baseline. Earlier studies in north-temperate lakes used pelagic long-lived primary consumers such as unionid mussels to define a system-specific nitrogen baseline (Cabana and Rasmussen 1996, Vander Zanden et al. 1997). Further work revealed significant C and N isotopic differences among lake habitats (littoral, pelagic, profundal), as well as relationships between primary consumer $\delta^{15}N$ and $\delta^{13}C$ within lakes (Vander Zanden and Rasmussen 1999). Since $\delta^{13}C$ reflects a consumer's carbon source, the within-lake baseline relationship and consumer $\delta^{13}C$ value can be used to approximate a lake- and consumer-specific nitrogen baseline (Vander Zanden and Rasmussen 1999, Post 2002b).

In this study, we considered a much broader range of ecosystem types, many of which do not show the within-system baseline patterns observed for north-temperate lakes. In addition, our use of literature data limits our ability to detect or account for within-system baseline variation. We defined the system-specific baseline as the mean $\delta^{15}N$ of all taxa classified as primary consumers (Cabana and Rasmussen 1996, Lake et al. 2001), and used a parametric bootstrap to

simulate error in FCL associated with baseline variation for the food webs that included multiple primary consumer taxa. The resulting average error variance (expressed as 1 standard deviation) in FCL ranged from 0.29 (marine) to 0.38 (streams). Though not trivial, this analysis indicates that baseline variation is not a major source of error in our FCL estimates.

The stable isotope method provides a continuous measure of consumer trophic position that represents the multiple trophic pathways leading to a consumer, weighted according to the relative importance of the pathway. In order to account for the isotopic baseline, the approach identifies primary consumers and designates them as trophic level 2.0. This raises concern about the accuracy of this designation, as detailed diet studies of many of these taxa have not been conducted, and some species classified as primary consumers may actually be omnivorous and feed on bacteria, protozoans, and detritus. Though we used our best judgment in primary consumer classification, the process undoubtedly involves subjectivities. A final source of error is variation in per-trophic level fractionation. Two recent reviews estimated average trophic fractionation for non-herbivorous aquatic consumers to be 3.3‰ and 3.4‰ (Vander Zanden and Rasmussen 2001, Post 2002b). It is important to note that there is variability associated with these trophic fractionation estimates. Vander Zanden and Rasmussen (2001) summarized the published trophic fractionation values for aquatic consumers, and used a simulation approach to assess how much variation in consumer trophic position results from variation in trophic fractionation. They estimated an error variance (expressed as 1 SD) of 0.11 trophic level resulting from the observed variation in trophic fractionation. Though this is an additional source of error in our FCL estimates, the magnitude of error is small relative to the variation associated with isotopic baseline estimates, and is unlikely to affect our results.

Though stable isotopes offer a useful tool for measuring food chain length, difficulties in defining food web and ecosystem boundaries remains a vexing issue. Lakes are relatively self-contained ecosystems and their boundaries can be easily defined (Vander Zanden et al. 1999, Post et al. 2000). But even in lakes, defining food web boundaries can be problematic: for example, terrestrial carbon is an important contributor to pelagic food webs in lakes (Pace et al. 2004), and birds and mammals may be overlooked as top predators in stream, lake, and marine food webs (Steinmetz et al. 2003). Stream and marine systems are more open, such that top predators may be transient, and range beyond conventionally-defined ecosystem boundaries. Inclusion of marine mammals increased FCL by >0.6 trophic levels relative to estimates that use marine fish as top predator. Less than 25% (11/47) of the marine food webs reported isotope values for a marine mammal, indicating that our FCL estimates are underestimates. Apex predators such as killer whales are unlikely to be sampled in a stable isotope food web study for logistic reasons, and it is unlikely that the true top predators were sampled for these published studies. Inclusion of unsampled trophic levels could lengthen some of our FCL estimates, particularly for marine systems where it could a full trophic level or more to FCL estimates reported here. The same concern applies to river and lake ecosystems, where piscivorous birds and mammals (for example, river otters) are rarely sampled in stable isotope food web studies. We did not include bird or mammalian consumers in our FCL estimates so that FCL estimates would be comparable across studies, and estimated FCL as the fish consumer with the highest trophic position included in the published study. This highlights the fundamental difficulty in defining ecosystem and food web boundaries for open systems, and underscores the importance of finding innovative ways to define ecosystem boundaries in these situations.

Summary

Understanding the factors that structure food webs remains an important challenge of ecology. Ecologist's understanding of variability in FCL, and why food chains tend to be short (Elton 1927, Hutchinson 1959, Pimm 1982) has been limited by the difficulty in even measuring this food web attribute. Furthermore, patterns of FCL may ultimately result from multiple interacting factors, making it difficult to identify a single determinant of FCL (Post 2002a). Nevertheless, an analysis of stable isotope food webs reveals that food webs tend to have three to five trophic levels, which corresponds nicely with the number of trophic levels assumed in studies of food chain dynamics (Hairston et al. 1960, Carpenter et al. 1985, Hairston and Hairston 1993), as well as food chain lengths derived from the ECOWeb compilation (Briand and Cohen 1987, Schoener 1989).

Almost twenty years ago, Paine (1988) argued that food web theory was highly advanced relative to the quality of the food web data, and that further advances in food web ecology would be limited by the poor quality of the data. The next generation of webs were more detailed, and indicated that food chains were longer than previously thought, yet failed to resolve basic questions about the length of food chains. Paine's argument holds true today (Winemiller and Layman 2005). We argue that recent advances with stable isotopes and flow-weighted webs suggest that perhaps empirical food web descriptions are catching up with conceptual and theoretical constructs.

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Appendix 1

Summary information and literature citations for the 219 stable isotope food webs. (Available online as Appendix O16036 at www.oikos.ekol.lu.se)