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PERSPECTIVES

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Temperature affects food-chain length and macroinvertebrate species richness in spring ecosystems

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Abstract. I assessed effects of the widest range of temperatures ever examined on maximal food-chain length (*L*) and macroinvertebrate species richness (*S*) by a worldwide comparison of spring ecosystems with mean water temperatures (*T*) ranging from 4.5 to 93°C. Eukaryotic *L* averaged ~3.2 and varied independently of *T* between 4.5 and 31°C. However, over the relatively narrow *T* range of 35 to 50°C, *L* dropped abruptly to 0 and remained so up to 91°C. The negatively nonlinear relationships of *L* vs *T* and macroinvertebrate *S* vs *T* both deviated from predictions based upon metabolic theory, and the negative effect of *T* on *S* contrasted with positive relationships observed at larger regional scales. Thermal tolerance limits apparently play a major role in causing these relationships, but other factors also may be involved (e.g., availability of colonists adapted to different temperatures and temperature-dependent rates of resource use and species interactions that affect population establishment and persistence).

Key words: bioenergetics, eukaryotes, food-chain length, macroinvertebrates, metabolic theory, species richness, springs, temperature, thermal tolerance.

The length of food chains in ecosystems is limited, usually reaching 3 to 4 levels, and rarely >6 levels. This limit has been attributed to the low efficiency of energy transfer between trophic levels resulting in insufficient energy supplies to support viable populations of high-level predators (Lindemann 1942, Hutchinson 1959). However, although energy availability must set an upper limit to food-chain length, the length that is actually observed in nature may be affected by several other factors. These factors may include environmental stability, ecosystem size or dimensions, predator–prey body-size ratios, colonization history, metacommunity dynamics, and various morphological and behavioral constraints (reviewed in Pimm 1982, Post 2002, Arim et al. 2007b, Sabo et al. 2009, Calcagno et al. 2011). During the last 3 decades, recognition of these potential effects has led to numerous insightful comparative and experimental analyses of foodweb structure (e.g., Pimm 1982, Briand and Cohen 1987, Schoener 1989, Spencer and Warren 1996, Post 2002, Jennings and Warr 2003, Thompson and Townsend 2005, Arim et al. 2007b, Post and Takimoto 2007, Vander Zanden and Fetzer 2007, Sabo et al. 2010). However, a synthetic theory of food-chain length has yet to be achieved.

Variation in food-chain length among ecosystems is not always directly related to energy limitation (cf. Pimm 1982, Yodzis 1984, Spencer and Warren 1996, Thompson and Townsend 2005, Arim et al. 2007b, Sabo et al. 2009), but Arim et al. (2007a) have reformulated the *energy limitation hypothesis* to show how body size and ambient temperature might affect food-chain length in quantifiable ways. Their model is based on the *metabolic theory of ecology* (MTE; Brown et al. 2004). It predicts that the trophic position of species in a community should show a humped relationship with body size and that food-chain length should be negatively correlated with environmental temperature.

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The purpose of my study is to test the metabolic model of Arim et al. (2007a), concerning how temperature should affect food-chain length, by using literature data on spring ecosystems. Springs are especially useful for making such a test because their physicochemical stability, typically small size, and relatively discrete boundaries make them highly amenable to studies of foodweb structure and energy flow at the ecosystem level. As a result, some of these studies have become well known classics that are often featured in ecology and biology textbooks or anthologies (e.g., Odum 1957, Teal 1957, Tilly 1968). In addition, springs exhibit both low variation in temperature within sites and high variation in temperature among sites. The near thermal constancy of springs allows the biota to become precisely adapted to specific temperature levels, and the extreme variation in temperature among springs (from near freezing to boiling temperatures) provides an excellent opportunity to study the effects of a wide range of temperatures on biological systems at many hierarchical levels (Glazier 2009). My study is the first attempt to examine the effects of a large range of temperatures (nearly 90°C) on foodweb structure in natural ecosystems. Authors of previous related studies have examined a relatively narrow range of temperatures (ranges of only 7–12°C) in artificial micro- or mesocosms (Beisner et al. 1997, Petchey et al. 1999).

The *metabolic hypothesis* of Arim et al. (2007a) predicts that food-chain length should show a negatively linear relationship with temperature (Fig. 1A) because higher temperatures increase metabolic costs, thereby increasing the amount of energy that populations need from lower trophic levels to maintain a minimal viable size, while also reducing the amount of energy that species populations can transfer to higher trophic levels. Consequently, as temperature increases, the ratio of energy supply to demand decreases successively at each higher trophic level, and thus, increases the relative extinction probability of species populations at the upper vs lower ends of a food chain.

This hypothesis can be contrasted with an alternative hypothesis, the *thermal tolerance hypothesis*, which predicts that food-chain length should show a negative, stepped relationship with temperature (Fig. 1B). This hypothesis is based on the assumption that the biochemical similarity of all organisms in a given ecological community causes them to have similar thermal tolerance limits. Therefore, below a certain temperature limit, food-chain length should be independent of temperature, but near and beyond this limit, food-chain length should decline abruptly to 0. This hypothesis was inspired by Brock's (1985) review of thermal tolerance limits in various organisms (also see Discussion).

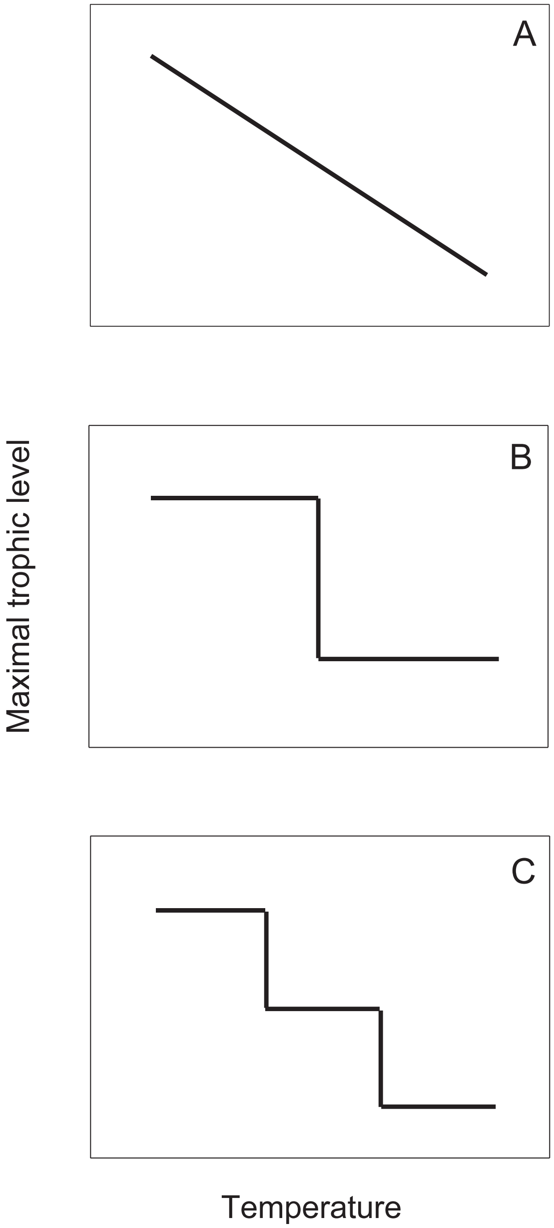

FIG. 1. Alternative hypotheses predicting a decrease in maximal trophic level with increasing ambient temperature. A.—A negatively linear relationship resulting from gradually increasing metabolic costs (after Arim et al. 2007a). B.—A negatively stepped relationship resulting from the abrupt loss of all trophic levels simultaneously as thermal tolerance limits are exceeded. C.—A negatively stepped relationship resulting from the abrupt loss of successive trophic levels as metabolic costs become too great or thermal tolerance limits are exceeded. For more details see the text.

A 3rd possibility is that increased temperature causes trophic levels to drop out abruptly in a successive, stepwise pattern (Fig. 1C). This pattern may be explained by either of the above hypotheses (mechanisms) or both in combination. The metabolic hypothesis may explain this multiple stepped pattern if one relaxes its assumption that consumers are more or less omnivorous (i.e., feed at >1 trophic level), and thus differ continuously in *trophic position* (Arim et al. 2007a). Increased temperature and associated metabolic costs may cause abrupt reductions in food-chain length if consumers do not follow this assumption and instead occupy distinct trophic levels (F. Bozinovic, Pontifícia Universidad Católica de Chile, personal communication). For example, consumers at any one trophic level may abruptly go extinct as temperature increases because their increased metabolic costs cannot be met by switching to prey at trophic levels other than the one to which they are exclusively adapted. Furthermore, even if increasing temperature were to cause the elimination of consumer species in a gradual way, entire trophic levels would drop out abruptly each time the last consumer species at each level disappears.

The thermal tolerance hypothesis also may explain the multiple stepped pattern (Fig. 1C) if one assumes that organisms at high trophic levels are not as tolerant biochemically and physiologically to high temperatures as are those at lower trophic levels. Therefore, as temperature increases, trophic levels should drop out abruptly, one by one, as thermal-tolerance limits are exceeded.

A 4th possibility is that both metabolic costs and thermal tolerance limits affect food-chain length, either independently or synergistically (e.g., because thermal tolerance is metabolically costly). Both of these factors acting together may cause relationships between food-chain length and temperature to follow intermediate patterns between the types shown in Fig. 1 (e.g., a gradual stepwise decrease in food-chain length).

In short, at least 4 major patterns between food-chain length and temperature are possible based upon the effects of 2 major hypothetical mechanisms acting either singly or in combination—the effects of increased metabolic costs or thermal tolerance limits. Other ecologically mediated effects of temperature that may operate through their effect on species richness are also briefly considered (see Discussion).

Methods

Data sources

Literature data on the species composition, trophic structure, and feeding habits of the eukaryotic organisms in 43 spring systems from several regions of the world were used to relate food-chain length to water temperature (Table S1; available online from: http://dx.doi.org/10.1899/11-058.1.s1). All of these springs were alkaline or mildly acidic (pH range = 5.6–9.4 and unrelated to food-chain length). The present analysis focused on maximal food-chain length (i.e., the maximal number of links between the basal and top levels in a food web; sensu Cohen 1978, Schoener 1989). Maximal trophic levels were designated as 1 (only the basal level [producers] present), 2 (primary consumers [herbivores] present), 3 (secondary consumers [primary predators] present), 4 (tertiary consumers [secondary predators] present), or as intermediate fractions (e.g., if a species at the highest trophic level fed at 2 different levels, e.g., 3 and 4, the maximal food-chain length was designated as being midway between these 2 levels, e.g., 3.5). This analysis included detritivores in the primary consumer level and omitted parasites, for which there were insufficient data. Zero values for food-chain length in the very hot springs refer only to eukaryotes because ≥1 levels may still exist in the prokaryotic communities that are present. Insufficient trophic-level information prevented me from including prokaryotes in the analyses.

Additional literature data on macroinvertebrate species richness (Table S2; available online from: http://dx.doi.org/10.1899/11-058.1.s1), and on annual standing crops of producers, primary consumers (herbivores and detritivores), and secondary consumers (predators) (Table S3; available online from: http://dx.doi.org/10.1899/11-058.1.s1) in springs with different water temperatures and from several regions of the world were used to provide insight into the temperature dependence of food-chain length.

Statistical analyses

To evaluate the hypothetical patterns featured in Fig. 1, relationships between maximal trophic level and water temperature were examined by least-squares linear regression, segmented linear regression, and nonlinear sigmoidal regression. Relationships between macroinvertebrate species richness and water temperature also were analyzed by segmented linear regression and an exponential decay function. Residual analyses and the coefficient of determination (r^2) were used to assess the relative goodness of fit of these various statistical models. All statistical analyses were done with SYSTAT 10 (Systat Software, Inc., Chicago, Illinois).

Results

Maximal trophic level (L) decreased significantly with increasing mean water temperature (T) among the 43 spring ecosystems surveyed (Fig. 2A–C). This negative relationship was better described by a segmented linear regression (Fig. 2B) or a nonlinear sigmoidal regression (Fig. 2C) than by a simple linear regression (Fig. 2A). This claim was supported by simple visual inspection and by the significantly lower mean of the residual values for the segmented linear regression (0.345 ± 0.319 SD) vs that for the simple linear regression (0.579 ± 0.379; $t = -3.361$; $p = 0.001$). The better fit of the sigmoidal regression also was indicated by its higher coefficient of determination ($r^2 = 0.861$; Fig. 2C) compared to that of the simple linear regression model ($r^2 = 0.718$; Fig. 2A).

Maximal trophic level (*L*) averaged 3.18 and showed no significant change over a mean *T* range of 4.5 to 30.6°C (Fig. 2B). However, over the *T* range of 35 to 49.1°C, *L* averaged 1.77 and decreased abruptly toward 0 (Fig. 2B). *L* was 0 throughout the range of 50 to 91°C (Fig. 2B). In addition, variation in *L* was highest in the relatively narrow intermediate *T* range (CV = 46.9%), as compared to the wider low and high *T* ranges (CV = 13.5% and 0%, respectively). The difference in variance of *L* between the intermediate and low *T* ranges is significant ($F_{16,24} = 3.73$, $p < 0.005$). This difference remained significant even after the effect of *T* was controlled (i.e., the variances of the residuals for *L* vs *T* are 0.422 and 0.184 for the intermediate and low *T* ranges, respectively; $F_{16,24} = 2.29$, $p < 0.05$).

The number of macroinvertebrate species (S) also showed a nonlinear decrease with increasing temperature among the 53 spring ecosystems surveyed (Fig. 3A, B). Decreases in *S* were seen over each of 3 *T* ranges, though only the decrease in the lowest *T* range (4.5 to 31°C) was significant (Fig. 3A). No macroinvertebrates were present at $T > 52$°C. The overall relationship between *S* and *T* was well represented by an exponential decay function (Fig. 3B).

Discussion

The decline in maximal trophic level (*L*) with increasing temperature (*T*) in spring ecosystems was nonlinear and single-stepped and, thus, appears to be more consistent with the thermal tolerance hypothesis than the metabolic hypothesis proposed by Arim et al. (2007a) (cf. Fig. 2B, C with Fig. 1B). The metabolic hypothesis predicts a gradual linear or multiple-stepped decrease in *L* with increasing temperature (Fig. 1A, C), neither of which was observed. *L*

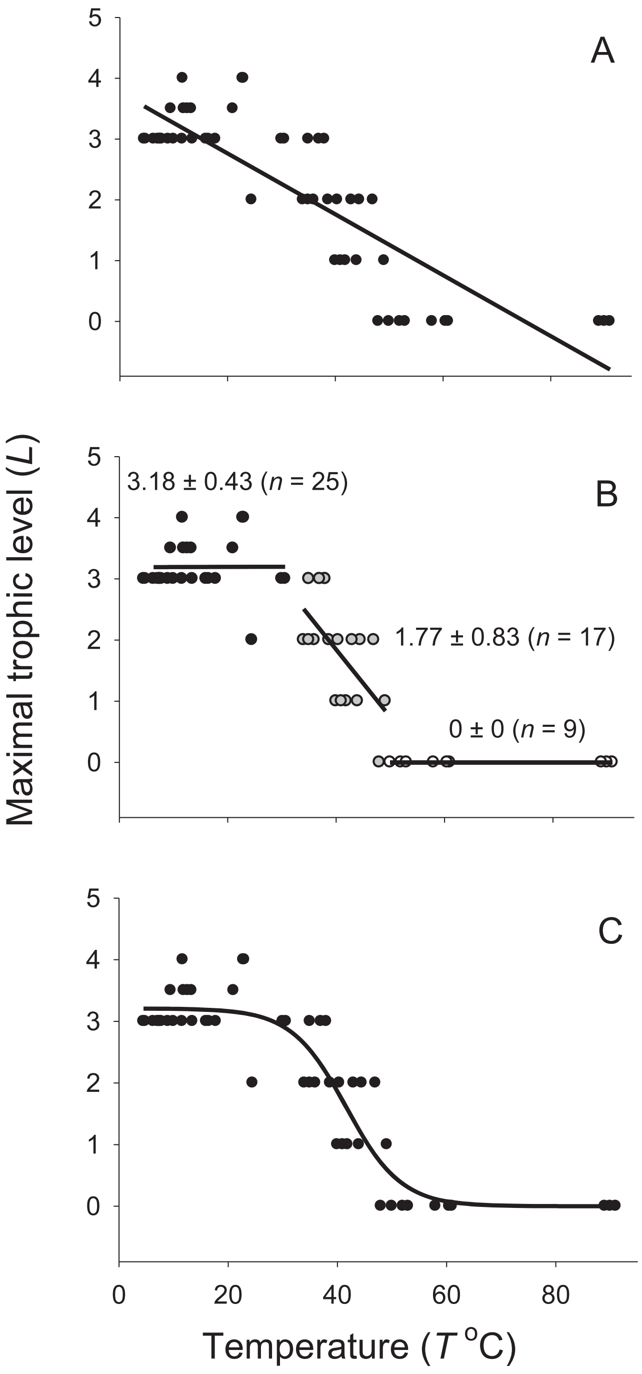

FIG. 2. Maximal trophic level (*L*) in relationship to water temperature (*T*) in 43 spring systems (including data for a source and 1 or 2 downstream sites at each of 7 hot springs; data from Table S1). A.—Linear regression of maximal trophic level (*L*) vs mean water temperature (*T*) ($L = 3.77 - 0.05T$; $r^2 = 0.718$; $p < 0.001$). B.—Segmented linear regression analysis of *L* vs *T*. Data, linear regressions, and correlation coefficients are for 3 temperature ranges: $T =$ 4.5–30.6°C ($L = 3.14 + 0.0003T$, $r^2 = 0.003$, $p = 0.806$); $T =$ 35–49.1°C ($L = 6.27 - 0.11T$, $r^2 = 0.390$, $p = 0.007$); and $T =$ 50–91°C ($L = 0$). Mean *L* values (±1 SD) are indicated for each temperature range. C.—Sigmoidal regression of *L* vs *T* ($L = 3.21/[1 + e^{-((T - 41.63)/-5.03)}]$, $r^2 = 0.861$, $p < 0.001$).

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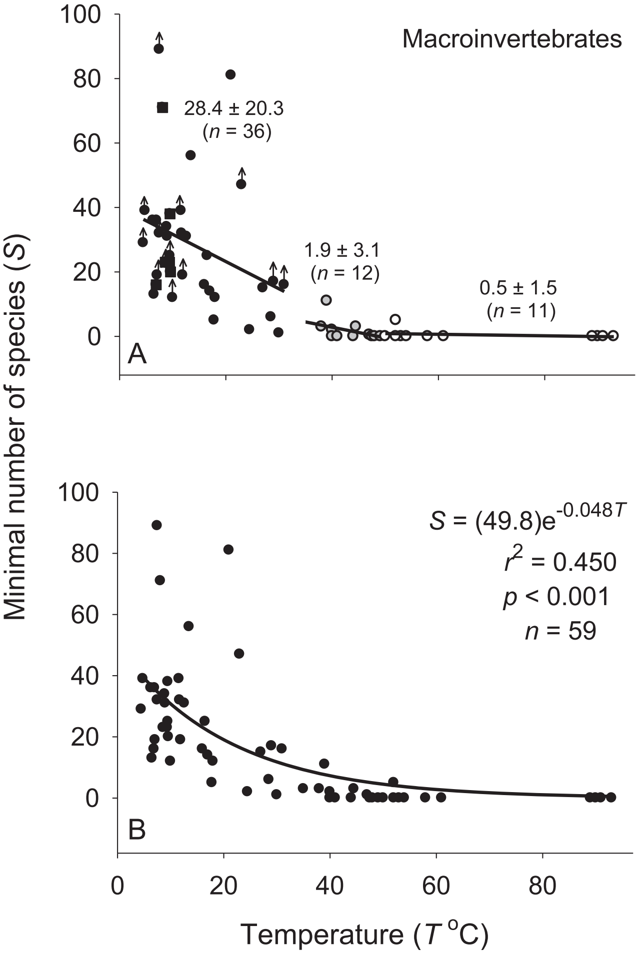

FIG. 3. Macroinvertebrate species richness (S) in relation to mean water temperature (T) in 53 spring systems (including data for a source and a downstream site at each of 6 hot springs (data from Table S2). A.—Data, linear regressions, and correlation coefficients for 3 temperature ranges: $T = 4.5$–31.0°C ($S = 40.10 - 0.84T$, $r^2 = 0.108$, $p = 0.050$); $T = 35$–49.1°C ($S = 15.97 - 0.33T$; $r^2 = 0.226$, $p = 0.118$); and $T = 50$–93.0°C ($S = 1.96 - 0.02T$, $r^2 = 0.076$, $p = 0.411$). Mean S values (±1 SD) are indicated for each temperature range. Upward arrows indicate values of species richness that are minimal estimates. Square symbols denote mean values for several springs in a local region. B.—Fit of all data over the entire temperature range to an exponential decay function.

unexpectedly changed very little over most of the temperature range examined and showed a significant, abrupt decline from ~3.2 to 0 over a relatively narrow range of intermediate temperatures (14.1°C) that constituted only 16.3% of the entire range examined (86.5°C). Furthermore, this sharp drop in L cannot be explained as being the simple result of L having discrete, noncontinuous values because the observed cliff-like decline involved the simultaneous loss of multiple trophic levels.

The observed nonlinear effect of T on L does not appear to be a statistical artifact possibly resulting from a disproportionate influence of the somewhat isolated cluster of 3 points at the highest temperatures depicted in Fig. 2A–C. First, the 3 highest temperature points are not outliers (in the sense of being unusual values) because they continue the trend of L being 0 that is seen at all temperatures >50°C. This continuity can even be seen within single hot spring systems along their temperature-varying lengths from source to downstream sites—e.g., along the continuous temperature gradients of 50 to 91°C in the Octopus hot spring system in Wyoming (Blank et al. 2002) and 53 to 90°C in the Hunter's hot spring system in Oregon (Castenholz 1973) (also see Table S1). Second, even if the 3 points at the highest temperatures are omitted from the statistical analyses, 2- and 3-segmented regressions still give significantly better fits than a simple linear regression. Regressions with 2 linear segments (temperature intervals = 4.5–30.6 and 35–61°C) and 3 linear segments (temperature intervals = 4.5–30.6, 35–49.1, and 50–61°C) both yield significantly less residual variation (means = 0.421 ± 0.292 and 0.369 ± 0.317 SD, respectively) than does simple linear regression (0.558 ± 0.365; $t = -2.023$ and $p = 0.046$; $t = -2.741$ and $p = 0.007$; respectively).

Nevertheless, one could still argue that the metabolic hypothesis plays a role in the observed nonlinear relationship between L and T. For example, increased resolution of the rapid decrease in L over the short T range of 35 to 49.1°C might reveal a multistepped pattern. This possibility requires further research, but even if this multistepped pattern were found, it would be more consistent with the thermal tolerance hypothesis than with the metabolic hypothesis. First, the metabolic hypothesis cannot explain why a multistepped (or linear) decrease in L was not seen over the entire T range, or at least over the part of that range that is physiologically tolerable to most organisms. If L is a function of metabolic costs, as hypothesized by Arim et al. (2007a), why does it not decrease at all over the substantial, typically biologically tolerable T range of 4.5 to 30.6°C? Assuming a temperature coefficient (Q_{10}) of 2 to 3 (Downs et al. 2008) (Q_{10} = the multiplicative effect of a 10°C increase on the rate of a process), a 26.1°C increase in T should cause a 6.1- to 17.6-fold increase in metabolic costs, which should, in turn, have a marked effect on L. However, this pattern was not seen. Second, trophic levels are not always distinct in spring ecosystems (i.e., some consumers may feed at >1 trophic level; Odum 1957, Minckley 1963, Minshall 1967, Tilly 1968). Thus, the original version of the metabolic hypothesis involving a continuous linear effect of temperature on *L* (Fig. 1A) should apply at least in part. This pattern was not observed in my study (Fig. 2B, C). However, DNA and stable-isotope analyses, which can give continuous estimates of trophic position (Coat et al. 2009, Carreon-Martinez and Heath 2010), might help detect more subtle effects of *T* on *L* in spring ecosystems than were observed in my study.

The metabolic hypothesis also is inconsistent with other temperature-related patterns of trophic structure seen in spring ecosystems. According to this hypothesis, the ratio of energy at a high trophic level relative to that at a lower level should decrease with increasing temperature because proportionately more energy should be lost as metabolically generated heat. However, no such decrease was observed for the ratio of energy in the annual standing crop of primary consumers relative to that of primary producers over a temperature range of 9 to 38.7°C, nor for the ratio of energy in the annual standing crop of secondary consumers to that of primary consumers over a temperature range of 7.5 to 23°C (Fig. 4). However, the above patterns are based on small sample sizes ($n = 4$–5), so more data clearly are needed to better evaluate the metabolic hypothesis.

Furthermore, the metabolic hypothesis has difficulty explaining why *L* decreases abruptly between 35 and 50°C because, within this temperature range, primary productivity generally reaches relatively high levels in spring ecosystems (Brock 1970, Glazier 2009). This increased energy availability should at least partially offset any increase in metabolic costs associated with increasing temperature, thus allowing higher trophic levels to persist. Increased primary productivity may help explain why *L* does not decrease between 4.5 and 30.6°C (see below), but the abrupt decrease at higher temperatures is more likely to be the result of exceeding the thermal tolerance limits of consumer species rather than of an increase in metabolic costs, although both may be involved.

Of course, one might reasonably argue that the metabolic hypothesis is intended to explain effects of *T* on *L* only within a biologically tolerable range, and therefore, the abrupt decline in *L* at relatively high temperatures is irrelevant to the hypothesis. After all, the metabolic hypothesis is based on the MTE, which is explicitly limited to a temperature range (0–40°C) that allows most organisms to be normally active (see Brown et al. 2004). However, the metabolic hypothesis still fails to explain why *L* does not decrease at all with increasing *T* within the extensive, tolerable range of 4.5 to 30.6°C (Fig. 2A–C).

All in all, the thermal tolerance hypothesis seems to explain the cliff-like pattern of *L* vs *T* in spring ecosystems better than does the metabolic hypothesis, although temperature-related metabolic costs may influence the thermal tolerance limits that are implicated by my results. However, the single-stepped decrease in *L* with increasing *T* probably applies only to multicellular eukaryotes (especially plants and animals) that have fairly similar upper lethal temperatures (typically 40–55°C; Brock 1985, Glazier 2009). Prokaryotes, which were not examined in my study, may have much higher upper temperature limits (70 to >100°C; Brock 1985, Glazier 2009). Therefore, had prokaryotes been included in my study, a multistepped decrease in *L* with increasing *T* might have been observed (as in Fig. 1C), but only at relatively high temperatures near and beyond the maximum tolerated by most eukaryotes (>40°C). The addition of free-living prokaryotes to the analysis probably would have increased *L* only to 1 or 2 at $T > 50$°C (given that they are mostly producers and decomposers), without totally obliterating the abrupt decline of *L* (from 3–4) that has been observed at high temperatures. However, this conjecture is in need of testing.

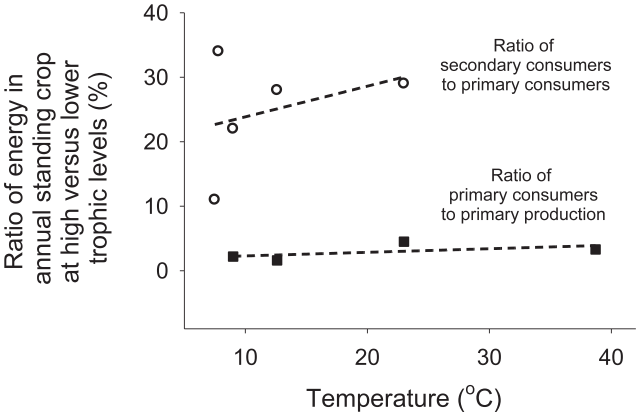

FIG. 4. Percent ratio of energy in the annual standing crop (kcal m^{-2} y^{-1}) of high vs lower trophic levels in 6 spring ecosystems with different water temperatures (data from Table S3). Dashed lines are nonsignificant linear regressions for standing crop ratios of primary consumers to primary producers, and of secondary consumers to primary consumers.

Data in my study are consistent with results of previous work showing that animal consumers rarely exist in springs warmer than 50°C (e.g., Brues 1932, Brock 1970, Langworthy et al. 1979). Above 50°C only algae and microbes are present, and thus, as Brock (1970) remarked, "we have a truncated food pyramid". This truncation cannot be attributed to a lack of resources for consumers. Primary production of the algal/microbial mats in hot springs is very high at the temperatures (50–55°C) at which metazoans tend to disappear (Brock 1970, Mitchell 1974). Clearly, energy limitation is not primarily responsible for the temperature dependence of food-chain length in spring ecosystems (though changes in resource quality may be involved; cf. Beisner et al. 1997).

The decline in *L* with increasing *T* appears to be abrupt, but the number of animal species (*S*) in spring ecosystems decreases relatively gradually with increasing *T*, as illustrated here with macroinvertebrates, the most diverse, visible animals in springs. The effect of *T* on *S* is well portrayed by an exponential decay function (Fig. 3B). Therefore, although the relationship between *S* and *T* is more continuous than that of *L* vs *T*, both relationships are nonlinear and both show a critical *T* of ~50°C at which eukaryotic *L* and macroinvertebrate *S* decline to 0. Furthermore, the decrease in macroinvertebrate *S* with increasing *T* reported here for springs from many regions of the world is consistent with that observed in other local or regional studies (e.g., Tuxen 1944, Lamberti and Resh 1985, Duggan et al. 2007).

The *S* vs *T* relationship suggests that the stepped decrease in *L* with increasing *T* is the result of a gradual decrease in species numbers until no species are present in a trophic level, causing a sharp drop in food-chain length. Increased metabolic costs, as hypothesized by Arim et al. (2007a), may play a role in this temperature-dependent decrease in *S*, but other factors probably are involved as well. The exponential (multiplicative) increase in S with decreasing temperature suggests that multiple, synergistic factors may be operating, including limits on temperature tolerance, availability of colonists adapted to a specific temperature, and rates of dispersal, resource use, and species interactions that affect population establishment and persistence.

Thermal tolerance limits probably are involved in determining why both eukaryotic *L* and macroinvertebrate *S* drop to 0 above a temperature of ~50°C. However, the mechanisms underlying these limits are not well understood. Various processes, including denaturation of enzymes, malfunctioning of cellular membranes, and nuclear and mitochondrial damage can cause heat death (Brues 1932, 1938, Winterbourn 1968, Langworthy et al. 1979, Brock 1985). Neuromuscular systems in animals are especially sensitive to thermal stress (Johnston and Ball 1996, Hochachka and Somero 2002). If animals cannot move, they cannot forage for food or escape from harmful environmental factors.

The average surface temperature of the earth is ~12 to 14°C, and most species should be adapted to live at or near these temperatures (Brock 1970, Hansen et al. 2010). Therefore, more kinds of species should be available to colonize springs with temperatures near 12 to 14°C than those with other temperatures. That the mean temperature of the 4 springs with the highest macroinvertebrate *S* (56–>89 species) is 12.5°C (5–21°C; Fig. 3A, B, Table S2) may not be simply coincidental. Friberg et al. (2009) reported peak macroinvertebrate *S* at 14.8°C for a sample of 10 Icelandic streams with mean temperatures ranging from 6.8 to 23.5°C (for a similar pattern in Icelandic springs, see Tuxen 1944, Glazier 2009). In addition, a species-pool effect may play a role in the positive relationships between temperature and zooplankton species richness observed in Norwegian lakes over the temperature range of 4.5 to 16.5°C (Hessen et al. 2007) and between temperature and faunal and floral species richness observed in Swiss ponds over a temperature range of <2.5 to >8°C (Rosset et al. 2010) (see below).

The rates of various ecological processes that affect population establishment and persistence also may be affected by temperature. As temperature decreases, rates of foraging, population increase, and interspecific interactions may decline, thus allowing more species to coexist on a given amount of resources. In support, authors of several experimental studies have shown that lower temperatures decrease rates of food intake, predation, parasitism, and competitive replacement (reviewed in Brown et al. 2004; also see Dreisig 1981, Bailey 1989, Shipp et al. 1996, Sanford 2002, Soares et al. 2003, Coelho and Bezerra 2006, Rall et al. 2010) and stabilize predator–prey interactions (Beisner et al. 1997, but see Rall et al. 2010). As a result, lower temperatures should reduce competitive exclusion and predatory and parasitic mortality, thereby potentially increasing the number of species populations that can survive in a community (cf. Stegen et al. 2012). These ecological effects may help account for the negative covariation of *S* and *T* even within the biologically tolerable *T* range of 4.5 to 31°C (Fig. 3A). An Arrhenius plot, commonly used to portray associations between temperature and species richness (Brown et al. 2004, Allen et al. 2006, Stegen et al. 2012), also clearly shows the negative effect of *T* on *S* over the *T* range of 4.5 to 39°C (Fig. S1; available online from: http://dx.doi.org/10.1899/11-058.1.s2).

Temperature also may affect dispersal rates, but mixed effects have been reported. Positive relationships were observed by Roff (1977) and Ozawa et al. (2005), whereas a negative relationship was inferred by O'Connor et al. (2006). Furthermore, the temperature of the outside environment where dispersal occurs is often different from that within the spring ecosystem itself. Therefore, the role, if any, that dispersal rates may play in the temperature dependence of L and S observed in my study is difficult to assess.

In any case, the following hypothetical scenario is offered to illustrate how several of the factors postulated above may exert their effects, depending on the temperature range under consideration. At relatively low, above-freezing temperatures (especially near 12–14°C), macroinvertebrate S is high in springs because of the availability of many species colonists adapted to these temperatures and because of weak (slow) species interactions that allow many of these species to coexist. At higher temperatures, rapid resource use allows fewer competitively superior species to persist in the community. At still higher temperatures, thermal tolerance limits are reached, thus limiting further the number of species that can survive. Above 50°C only a few eukaryotic species, if any at all, remain.

The negative relationship between S and T observed here among macroinvertebrate communities in springs contrasts with the positive associations predicted by the MTE (Allen et al. 2002, 2006, Brown et al. 2004). This unexpected finding may be interpreted in 2 major ways. First, spring ecosystems may be considered to be rare or even trivial exceptions because the MTE applies only to the biologically tolerable T range of 0 to 40°C, whereas springs include habitats with much higher temperatures that are lethal to most eukaryotic organisms. However, most of the decline in S with increasing T in springs occurs within the biologically tolerable T range (Fig. 3A) and, thus, cannot be considered a trivial exception to the MTE.

Second, the effects of T on S may be scale-dependent. The kinds and relative magnitude of processes that cause thermal effects on S may be different in small-scale local habitats, such as springs, than in the large-scale geographical regions that have been the major focus of the MTE. After all, a major mechanistic link between S and T invoked by the MTE involves changes in speciation rate (as mediated by thermally sensitive mutation rates) that occur over large geographical areas. Accordingly, the MTE predicts positive associations between S and T that are typically seen at relatively large regional scales (Allen et al. 2002, 2006, Brown et al. 2004, Rombouts et al. 2011; but see Hawkins et al. 2007). However, other mechanisms, as considered in my paper, may be more important at the local habitat scale. In support of this possibility, the recent multivariate model of Stegen et al. (2012) showed that one of these hypothetical mechanisms—the effects of temperature-mediated changes in rates of resource consumption and species interactions on species coexistence—may cause negative associations between S and T in ectothermic animal communities. These effects should be especially strong in small, stable, relatively isolated, resource-limited habitats like springs.

However, other factors may be important at the local-habitat scale, e.g., thermal tolerance limits, temperature-dependent resource abundance, and the availability of more species colonists that are adapted to intermediate vs extremely low or high temperatures. Direct lethal effects may cause S to decline to very low levels at relatively high temperatures, as observed in springs. Sanford (2002) has remarked that temperature may influence the structure of ecological communities through both lethal effects on physiological functioning and sublethal effects on physiological rates. Šímová et al. (2011) also argued that species climatic tolerances may strongly influence latitudinal gradients of S. In addition, positive associations between S and T may arise in local habitats if resource abundance increases significantly with increasing T (cf. Stegen et al. 2012). Perhaps temperature-dependent resource abundance helps account for the positive associations between S and T seen in local ponds and lakes (Hessen et al. 2007, Rosset et al. 2010), but why not also in springs? Differences in S vs T associations reported among these and other aquatic systems may depend, at least in part, on the temperature range examined relative to the temperature at which most colonizing species are adapted (i.e., $T_a \approx$ 10–20°C; see above), i.e., positive if T_a is near the upper end (as observed in the ponds and lakes studied by Hessen et al. 2007, Rosset et al. 2010), negative if T_a is near the lower end (as observed in springs in my study), and humped if T_a is near the middle of the examined T range (as observed in Icelandic springs and streams; Tuxen 1944, Friberg et al. 2009, Glazier 2009). The model of Stegen et al. (2012) also shows that humped relationships between S and T may arise via the effects of T on rates of both resource production and exploitation.

Consideration of the above mechanisms may help elucidate relationships between L and T, a major focus of my paper. Theoretical models of these relationships (e.g., Arim et al. 2007a) should consider the effects of temperature not only on metabolic costs, but also on rates of resource supply, species interactions, and species turnover (colonization and extinction of local populations). For example, increasing resource abundance (primary productivity) with increasing T, as observed in springs up to ~40°C (Glazier 2009), may offset the increased metabolic costs predicted by the model of Arim et al. (2007a), thus weakening or even negating a relationship between L and T over the biologically tolerable T range of 0 to 40°C, a hypothesis requiring testing. In addition, temperature-dependent rates of resource consumption and species interactions may affect rates of colonization and extinction of local populations, which in turn can affect L, as predicted by the metacommunity dynamics model of Calcagno et al. (2011).

However, not all of the patterns and hypotheses regarding the effects of T on S and L discussed here for springs may be generally applicable to other local ecosystems. For example, the importance of direct lethal causes may be limited largely to hot springs and other extreme habitats (e.g., hot deserts, submarine hydrothermal vents, and polar environments) that have unusually high or low temperatures. By contrast, nonlethal or indirect temperature effects operating in springs with a range of biologically tolerable T (0–40°C) may be relevant to a wide variety of local ecosystems.

In any case, their unique twin features of intrasite thermal constancy and intersite thermal diversity make springs highly useful natural experiments for studying a wide variety of problems in thermal biology (Glazier 2009). Springs are available for study in great numbers in many regions of the world. Glazier (2009) has estimated that there are probably $\geq$50 million terrestrial springs worldwide (averaging $>4/\text{km}^2$). In addition, the extreme environmental conditions of many springs, along with their specially adapted denizens, provide excellent opportunities for gaining new insights into how biological systems work. Unusual organisms and extreme conditions have been exploited repeatedly with great success to advance our understanding of the physiology, ecology, and evolution of life (e.g., Bartholomew 1987, Schmidt-Nielsen 1998).

In conclusion, the data presented here strongly suggest that thermal tolerance limits play an important role in reducing the faunal diversity and food-chain length of spring ecosystems with high water temperatures. These biochemical and physiological limits, along with various ecological factors, may help explain why the temperature-dependent patterns of S and food-chain length observed in small-scale spring habitats deviate substantially from predictions of models based on the large-scale MTE. My study also demonstrates that a wide range of temperatures should be examined to appreciate fully the effects of temperature on ecological systems.

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