



Thermal niche diversity and trophic redundancy drive neutral effects of warming on energy flux through a stream food web

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Abstract. Climate warming is predicted to alter routing and flows of energy through food webs because of the critical and varied effects of temperature on physiological rates, community structure, and trophic dynamics. Few studies, however, have experimentally assessed the net effect of warming on energy flux and food web dynamics in natural intact communities. Here, we test how warming affects energy flux and the trophic basis of production in a natural invertebrate food web by experimentally heating a stream reach in southwest Iceland by ~4°C for 2 yr and comparing its response to an unheated reference stream. Previous results from this experiment showed that warming led to shifts in the structure of the invertebrate assemblage, with estimated increases in total metabolic demand but no change in annual secondary production. We hypothesized that elevated metabolic demand and invariant secondary production would combine to increase total consumption of organic matter in the food web, if diet composition did not change appreciably with warming. Dietary composition of primary consumers indeed varied little between streams and among years, with gut contents primarily consisting of diatoms (72.9%) and amorphous detritus (19.5%). Diatoms dominated the trophic basis of production of primary consumers in both study streams, contributing 79–86% to secondary production. Although warming increased the flux of filamentous algae within the food web, total resource consumption did not increase as predicted. The neutral net effect of warming on total energy flow through the food web was a result of taxon-level variation in responses to warming, a neutral effect on total invertebrate production, and strong trophic redundancy within the invertebrate assemblage. Thus, food webs characterized by a high degree of trophic redundancy may be more resistant to the effects of climate warming than those with more diverse and specialized consumers.

Key words: climate change; energy flow; experimental warming; food webs; rivers; streams; trophic basis of production; trophic redundancy.

INTRODUCTION

The effects of climate warming on plants and animals are already being observed as changes in the timing of seasonal activities of many species, as well as shifts in their geographic distribution (Walther et al. 2002, Parmesan 2006). Ultimately, warming is expected to result in significant shifts in community structure through immigration, emigration, local extinction, and species turnover (Gilman et al. 2010, Jackson and Sax 2010, Nelson et al. 2017a). Even small shifts in

temperature can change the relative abundances of species within communities (Nelson et al. 2017a), as each species has its own physiological thermal optimum (Huey and Stevenson 1979, Pörtner and Farrell 2008), on either side of which fecundity and population size decline (Vannote and Sweeney 1980). Consequently, rising temperatures will result in both “losers” (i.e., species whose abundance or biomass decrease as a result of warming) and “winners” (i.e., species whose abundance or biomass increase). Moreover, formerly unrepresented species from the regional species pool may colonize new habitats as these become thermally suitable (Nelson et al. 2017a). Thus, climate warming will inevitably lead to shifting community structure and biotic interactions

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because of novel species combinations, with potentially complex consequences for higher levels of ecological organization, including food webs (Walther et al. 2002, Poular and Blanchard 2005).

Understanding the effects of relatively subtle or inconspicuous changes in community structure, as opposed to more conspicuous changes (e.g., species additions or deletions), on food webs may be particularly important, as climate-related stressors such as warming may primarily affect the relative abundances of species within many communities (Nelson et al. 2017a). With regard to warming-induced changes in community structure, a decrease in energy flux to one species in a food web may be counterbalanced by an increase in energy flux to another species, resulting in a neutral net effect on total energy flux through the food web. Both theory and empirical evidence suggest that there is a high degree of functional or trophic redundancy within most food webs (Williams and Martinez 2000, Woodward et al. 2005). The core concept of functional redundancy is that some species perform similar roles in communities or food webs, and thus may be substitutable with little impact on ecosystem function (Lawton and Brown 1993, Rosenfeld 2002). Consequently, changes in the relative abundance of species within food webs may not strongly influence total energy or material flux if there is a high degree of trophic redundancy among species and community production remains constant. However, relatively few studies have examined relationships among temperature, community assembly, and food web dynamics (Montoya and Solé 2003). Hence, little is known about how warming-induced changes in community structure may influence the flow of energy and materials through entire food webs.

The flux of energy through food webs may not only be affected by temperature-induced changes in community structure. Many aspects of consumer foraging (e.g., handling time, ingestion rates, encounter rates) and physiology (e.g., respiration rates) are strongly influenced by temperature (Rall et al. 2010, Lemoine and Burkepile 2012, Iles 2014, Archer et al., *in press*). Higher temperatures result in greater metabolic demands for ectotherms, driving other biological rates such as consumption and growth (Gillooly et al. 2002, Brown et al. 2004, Archer et al., *in press*). Temperature-driven changes in metabolic demand could result in less energy available for growth if ingestion rates remain constant or increase at a slower pace than metabolism. Consequently, organisms may increase ingestion to maintain similar growth rates at higher temperatures. There is also evidence that resource availability and dietary preferences may change as a result of increasing temperatures (O'Connor et al. 2009, Lemoine et al. 2013, Boersma et al. 2015, Nelson et al. 2017a, Hood et al. 2018). Any changes in diet can affect energy flux as different foods have different concentrations of carbon and nutrients and so different assimilation efficiencies (Sterner and Elser 2002). Thus, the effect of temperature on energy flow through food webs

will likely be influenced by a combination of temperature-induced changes in community structure, organism physiology, resource availability, and diet.

Here, we present results from a 2-yr ecosystem-level experiment in which we warmed a 35-m stream reach by 3.8°C using a geothermal heat exchanger. Our primary goal was to examine how warming-induced changes in community structure altered the flow of energy through the food web of the experimental stream. We used a before–after, control-impact design (Stewart-Oaten et al. 1986) in which one prewarming year (YR1) was followed by 2 yr of warming (YR2 and YR3) in an experimental stream (the warmed stream), with a nearby reference stream acting as a control. We compared the trophic basis of taxon-specific production (i.e., the relative or absolute amount of secondary production attributable to a particular food resource) and quantified fluxes of energy through the two invertebrate food webs using gut contents analysis and invertebrate production estimates.

Previous results from this experiment revealed that warming reduced total invertebrate abundance and significantly altered invertebrate assemblage structure, but led to neutral effects of warming on total biomass and community production due to taxon-specific responses characterized by shifts towards larger-bodied taxa (Nelson et al. 2017a, 2017b). The higher mean temperature also increased the estimated total energy demand from invertebrate consumers in the food web, despite lower total abundance (Nelson et al. 2017a). In addition, warming had large positive effects on primary producers, including a doubling of annual net primary production (Hood et al. 2018) and a 20-fold increase in the biomass of the filamentous green alga *Ulva* during the summer growing season (Nelson et al. 2017a). Here, we examine how these warming-induced effects on ecosystem structure and function influenced energy flux through the food web of the experimental stream. Given that the two study streams receive very low inputs of allochthonous detritus, we hypothesized that in situ primary producers such as diatoms and filamentous algae would be the most important resources for primary consumers regardless of temperature. We expected an increase in the flux of *Ulva* to primary consumers because of its dramatic increase in summer biomass during experimental warming (Hood et al. 2018). In addition, we explored the potential for an increase in consumption of organic matter (i.e., energy flux through the food web) by the invertebrate assemblage, necessitated by the larger energetic demands driven by increased respiration rates at higher temperatures. Finally, we investigated the potential for changes in energy flow driven by changes in assemblage structure or dietary shifts between years. Alternatively, if a high degree of trophic redundancy existed within the food web of the experimental stream, we expected a more muted effect of warming on organic matter consumption, driven by losses and gains of trophically analogous species that differed in thermal preference.

METHODS

Study sites and experimental warming

We conducted this study in two first-order, groundwater-fed streams in the Hengill geothermal region of southwest Iceland. Both streams have comparable physical and chemical characteristics (Appendix S1: Table S1) and similar invertebrate communities (Nelson et al. 2017a). We sampled each stream during a 12-month pre-warming period (YR1) beginning in October 2010 and began warming a 35-m reach of the experimental stream using a gravity-fed heat exchanger (see Nelson et al. 2017a) in October 2011. Importantly, the design of our whole-stream warming experiment allowed for local dispersal processes and the natural reassembly of the invertebrate community (Nelson et al. 2017a). We warmed the experimental stream by an average of 3.8°C over 2 yr (Nelson et al. 2017a, Appendix S1: Table S1), an increase consistent with many current climate models for the next century (IPCC 2013).

Gut contents analysis

To quantify the proportion of food resources consumed by invertebrates, we analyzed the gut contents of common macroinvertebrate taxa from each stream during all 3 yr of the experiment. Each of these common taxa constituted >1% of total invertebrate production (86–94% of total annual invertebrate production was included in the food webs). We used individuals collected in Surber samples primarily during the summer months (May–August; Appendix S1: Table S2) when invertebrate and algal biomass were highest and most growth and production occurred (Nelson et al. 2017a; Appendix S1: Table S3, Fig. S1). However, some taxa (e.g., the caddisfly *Potamophylax cingulatus*, the black fly *Simulium vernum*, and the snail *Radix balthica*) were more abundant and larger during the autumn. Thus, some individuals of these taxa were collected between September and November for gut contents analysis. Five individuals of each taxon per year were analyzed from each stream. When possible, we used individuals of different size classes to characterize potential ontogenetic shifts in diet (Appendix S1: Table S2). We used met2006hods from Parker and Huryn () to remove gut tracts and prepare gut-contents slides. Briefly, we removed the foregut from each individual, suspended gut contents in deionized water, and sonicated them for 30 s. The suspensions were then filtered onto gridded nitrocellulose membrane filters (Metricel® GN-6, 25-mm, 0.45-µm pore size; Gelman Sciences, Ann Arbor, Michigan, USA), the filters dried at 60°C for 15 min, placed onto microscope slides, cleared with Type A immersion oil, and covered with a cover slip. Depending on the density of particles, we photographed 5–10 randomly selected fields of view on each filter at 400× magnification using a digital camera (Spot RT digital

camera; Spot Imaging, Sterling Heights, Michigan, USA). From the photographs, we identified all particles within each field of view and measured the area of particles (µm²) using image analysis software (Image J; Schneider et al. 2012). We classified particles as diatoms, filamentous algae, cyanobacteria, amorphous detritus, bryophytes, or animal material. Filamentous algae were further classified into two categories, *Ulua* and non-*Ulua* filamentous algae. For each slide, we calculated the proportion of each food category in the gut by dividing the area of each category by the total area of all particles measured and used the mean values for each taxon in trophic basis of production calculations. To calculate the trophic basis of production for all strict predators, we used 100% animal material. It was difficult to determine predator gut contents because most predator guts were empty or contained excessively macerated prey, or because of suctorial feeding strategies in the dominant predator taxa (e.g., the dipterans *Limnophora riparia* and *Clinocera stagnalis*). We examined differences in dietary proportions of each food resource between years for each stream using paired Wilcoxon signed-rank tests on logit-transformed proportions with taxa as replicates.

To estimate trophic redundancy in the food web, we calculated proportional similarities (Whittaker 1952, Kohn and Riggs 1982) for each species combination within each stream using dietary proportions (means from all 3 yr). Proportional similarities were calculated as

$$PS = 1 - 0.5 \sum_{j=1}^S |p_{x,i} - p_{y,i}| \quad (1)$$

where *PS* is the proportional similarity index between the diets of two taxa, $p_{x,i}$ is the proportion of food resource *i* in taxon *x*, $p_{y,i}$ is the proportion of food resource *i* in taxon *y*, and there are *S* food resource categories. Equation 1 produces a taxon × taxon matrix of proportional similarity values for each stream. When *PS* is 1.0, the gut contents from both taxa contain identical proportions of resources. We also calculated proportional similarities for each taxon across all years in both streams to evaluate interannual differences in gut contents.

Trophic basis of production and flow food webs

We used annual secondary production estimates from Nelson et al. (2017b; Appendix S1: Table S4), the mean (±95% confidence intervals) proportions of food resources consumed that we obtained from gut contents analysis, assumed distributions of assimilation efficiencies, and modeled net production efficiencies to estimate the trophic basis of production for each taxon and construct organic matter flow food webs, as in Benke and Wallace (1980, 1997) and Cross et al. (2011). We estimated the trophic basis of production and organic matter flows for each stream (experimental and reference) during each year of the study (YR1, YR2, YR3). A

detailed explanation of the methods and calculations for the trophic basis of production and flow food webs can be found in the Electronic Supporting Information (Appendix S2: Methods; Appendix S2: Table S1). Assimilation efficiency is the proportion of ingested food that is not lost as feces (Welch 1968). We used the following assimilation efficiencies: diatoms, 0.3 (95% CI: 0.24–0.36); filamentous algae including *Ulva*, 0.3 (95% CI: 0.24–0.36); cyanobacteria, 0.1 (95% CI: 0.08–0.12); bryophytes, 0.1 (95% CI: 0.08–0.12); amorphous detritus, 0.1 (95% CI: 0.08–0.12); and animal material, 0.7 (95% CI: 0.56–0.84; Benke and Wallace 1980, 1997, Cross et al. 2007, 2011). We did not temperature-correct assimilation efficiencies because of the large variation in the response of assimilation efficiencies to temperature found across published laboratory studies for invertebrates. For example, several studies report an increase in assimilation efficiency with temperature (Schindler 1968, Heiman and Knight 1975), while others report an inverse relationship between assimilation and temperature (Mathavan and Pandian 1975, Bobka et al. 1981) or no relationship at all (Lawton 1970, Giguere 1981, Lawrence et al. 2009). Other studies demonstrate that assimilation efficiency has a unimodal response to temperature, but the temperature at which maximum assimilation efficiency occurs does not always correspond to the temperature at which the highest rates of metabolism occur (Kukul and Dawson 1989), making it very challenging to predict how warming will affect assimilation in specific taxa. Consequently, in order to include potential uncertainty around assimilation efficiencies in our calculations, we resampled with replacement from a normal distribution (μ = mean assimilation efficiency, σ = 10% of the mean).

Net production efficiency (NPE) is the proportion of assimilated material available for new tissue production; the remainder (i.e., $1 - \text{NPE}$) meets other energetic demands, of which respiration is the most significant component. During YR1, we set NPE at 0.5 for all taxa (Humphreys 1979, Benke and Wallace 1980, Cross et al. 2011). To account for increased respiratory costs during the warming manipulation (Nelson et al. 2017a), we calculated NPEs for YR2 and YR3 of the study based on estimated relative changes in respiratory costs from Nelson et al. (2017a). Briefly, we estimated the percent change in respiration rates from YR1 to Years 2 and 3 for both streams using metabolic scaling predictions based on daily temperatures and body-size distributions (Brown et al. 2004, Nelson et al. 2017a). For example, estimated whole-community respiratory costs increased by 41% from YR1 to YR2 in the experimental stream (Nelson et al. 2017a). To correct for this difference, we first multiplied the percentage of assimilated material lost to respiration (i.e., $1 - \text{NPE} = 50\%$) by the estimated percent change in respiration rate (e.g., $50\% \times 141\% = 71\%$). This led to an elevated total energy demand that was equal to the temperature-corrected respiratory costs (i.e., $1 - \text{NPE} = 71\%$) plus the energetic

demand for new tissue production (i.e., $\text{NPE} = 50\%$; $71 + 50 = 121\%$). We then calculated an adjusted NPE as 50% (energy demand for production) \div 121% (the total energy demand for production and respiration) = 41% . For a given amount of secondary production, the adjusted NPE therefore accounted for the higher consumption necessary to support increased respiration rates at higher temperatures. A table with detailed calculations for adjusted NPEs can be found in the Electronic Supporting Information (Appendix S2: Table S2). Uncertainty around NPEs was also incorporated into our calculations by resampling with replacement from a normal distribution (μ = new NPE, σ = 10% of the mean). Gross production efficiencies (GPE) were calculated as the product of assimilation efficiency and NPE.

Data analysis

Error in annual estimates of the trophic basis of production and organic matter flows was incorporated through bootstrapping secondary production estimates (Nelson et al. 2017b), assimilation efficiencies and NPEs (see above), which resulted in 1,000 estimates of annual flows. To determine if there were differences among years in the trophic basis of production and organic matter flows, we used the 95% confidence intervals (i.e., overlapping confidence intervals were interpreted as nonsignificant differences). We examined differences in the proportions that each food resource contributed to production between years using paired Wilcoxon signed-rank tests on logit-transformed proportions with taxa as replicates. Because previous results from this experiment showed that changes in taxon abundance were positively related to thermal preferences (T_{pref} ; Nelson et al. 2017a), we explored if taxon-specific changes in secondary production and organic matter consumption were also related to estimates of T_{pref} . Briefly, T_{pref} was calculated from macroinvertebrate abundance data from 54 sites across Iceland that ranged in average temperature from 6 to 46°C (Ólafsson et al. 2010). We fit Gaussian curves to the $\log_{10}(x + 1)$ abundance vs. temperature for each taxon and T_{pref} for each taxon was estimated as the mean temperature at the center of the distribution. If the amplitude of the distribution was beyond the range in temperature data, we estimated T_{pref} as the temperature at which the highest abundance occurred. A list of T_{pref} values used for each taxon can be found in the Electronic Supporting Information (Appendix S1: Table S5). To explore if taxon-specific changes in secondary production and organic matter consumption were related to estimates of T_{pref} , we first calculated the magnitude of change in production or organic matter flows for each taxon as a response ratio (RR):

$$\text{RR} = \log_{10}(X_A/X_B) \quad (2)$$

where RR is the log(proportional change) in production or organic matter flows from before warming (X_B , YR1)

to after warming was initiated (X_A , YR2 or YR3). We then plotted RR vs. T_{pref} and used least-squares regression to fit linear models to the plot. Throughout this paper we use the terms “consumption” and “flow” synonymously.

RESULTS

Macroinvertebrate diets

Dietary composition of primary consumers varied little between streams or among years (Fig. 1, Appendix S1: Table S6). On average, primary consumer gut contents were comprised of diatoms (72.9%, 95% CI: 70.1–76.0%), amorphous detritus (19.5%, 95% CI: 17.3–21.9%), bryophytes (4.2%, 95% CI: 2.7–5.9%), *Ulva* (1.3%, 95% CI: 0.4–2.4%), other filamentous algae (0.4%, 95% CI: 0.1–0.9%), cyanobacteria (<0.1%), and animal fragments (1.6%, 95% CI: 0.6–2.7%). In the experimental stream, primary consumer gut contents were composed mostly of diatoms (76.0%, 95% CI: 72.0–80.1%), followed by amorphous detritus (12.7%, 95% CI: 10.3–15.2%), bryophytes (5.2%, 95% CI: 3.0–7.6%), animal prey (3.0%, 95% CI: 1.3–5.2%), *Ulva* (2.4%, 95% CI: 0.8–4.3%), and non-*Ulva* filamentous algae (0.7%, 95% CI: 0.1–1.7%). In the reference stream, gut contents were composed of diatoms (69.3%, 95% CI: 65.0–73.3%), amorphous detritus (27.5%, 95% CI: 23.7–31.3%), bryophytes (3.0%, 95% CI: 1.0–5.1%), non-*Ulva* filamentous algae (0.1%, 95% CI: 0.1–0.4%) and cyanobacteria (<0.1%). The mean proportion of diatoms in consumer guts increased marginally from YR2 (0.73) to YR3 (0.84) in the experimental stream (Wilcoxon signed-rank test, $P = 0.05$). The proportions of other compartments (excluding animal prey) in primary consumer guts did not differ among years in either stream (all other Wilcoxon signed-rank tests had $P > 0.05$). In the experimental stream, *Ulva* was found in the guts of only five taxa (the midge *Orthocladius frigidus*, the black flies *Prosimulium ursinum* and *Simulium vittatum*, the snail *Galba truncatula*, and the caddisfly *Potamophylax cingulatus*), and all in relatively low proportions (range = 0.08–0.18; Appendix S1: Table S3). Non-*Ulva* filamentous algae were found in guts of several taxa and also in relatively low proportions (range = 0.01–0.12; Appendix S1: Table S7). Gut contents of invertebrates rarely included bryophytes or cyanobacteria (Appendix S1: Table S7). Although usually not expected to be predacious, some individuals of the black fly *Prosimulium ursinum* contained significant amounts of prey (early-instar chironomids and black flies) in their guts, but only during YR1 and YR2 of the study (proportion of animal material: YR1 = 0.41, YR2 = 0.55, YR3 = 0.00).

Diets were similar among years for most taxa (Appendix S1: Table S8). Proportional similarities of gut contents among years for primary consumers in the reference stream were high, ranging from 0.52 to 0.99 (Appendix S1: Table S8). In the experimental stream, proportional similarities of gut contents among years

were generally high but were more variable than in the reference stream, ranging from 0.17 to 0.99, signaling some differences in diet among years in some taxa (Appendix S1: Table S8). The largest differences in dietary proportions (proportional similarity index values <0.50) among years were observed in the experimental stream for the black fly *P. ursinum* (YR1 vs. YR3 = 0.48; YR2 vs. YR3 = 0.17) and the caddisfly *P. cingulatus* (YR1 vs. YR3 = 0.48; Appendix S1: Table S8). We did not find any animal material in the guts of *P. ursinum* during YR3 and the proportions of *Ulva* and non-*Ulva* filamentous algae increased in the guts of *P. cingulatus* from YR1 to YR3 (Appendix S1: Table S8).

There was also evidence of a high degree of trophic redundancy (i.e., similarities in diets among taxa) in the food webs of both streams. In the reference stream, proportional similarity values between taxa were high, ranging from 0.51 to 0.99 (Appendix S1: Fig. S2). In the experimental stream, proportional similarity values between taxa were more variable, ranging from 0.08 to 0.91 (Appendix S1: Fig. S2). However, all of the lower proportional similarity values (<0.50) could be attributed to pairwise comparisons including one of two taxa, *P. cingulatus* and *P. ursinum* (Appendix S1: Fig. S2). These two taxa had very different diets than the other taxa included in the food web (Appendix S1: Fig. S2). On average, in the experimental stream guts of *P. cingulatus* contained higher amounts of bryophytes (32.0%) and *Ulva* (9.0%) than other taxa. *Prosimulium ursinum* was the only “nonpredator” to have animal fragments in its guts, as well as higher amounts of bryophytes (13.0%) and *Ulva* (4.7%) than many other taxa.

Trophic basis of production

Total annual production of invertebrate taxa used in food web construction did not differ significantly among years in either stream and was higher in the experimental stream than in the reference stream during all 3 yr of the study (Appendix S1: Table S4). Although warming had little effect on total production, it was associated with significant changes in the production of several taxa included in the food web of the experimental stream (Appendix S1: Table S4). Specifically, the production of five taxa decreased from YR1 to YR3 (*Orthocladius*, *P. ursinum*, *S. vernum*, *N. communis*, and *Dicranota*) in the experimental stream, and the production of three taxa increased (*S. vittatum*, *R. balthica*, and *L. riparia*; Appendix S1: Table S4). There were also significant changes between years in the production of several taxa in the reference stream (Appendix S1: Table S4). In the experimental stream, taxon-specific changes in production were related to thermal preferences (T_{pref}), with large positive changes being associated with taxa for which thermal preferences are higher (Fig. 2a, Appendix S1: Table S9).

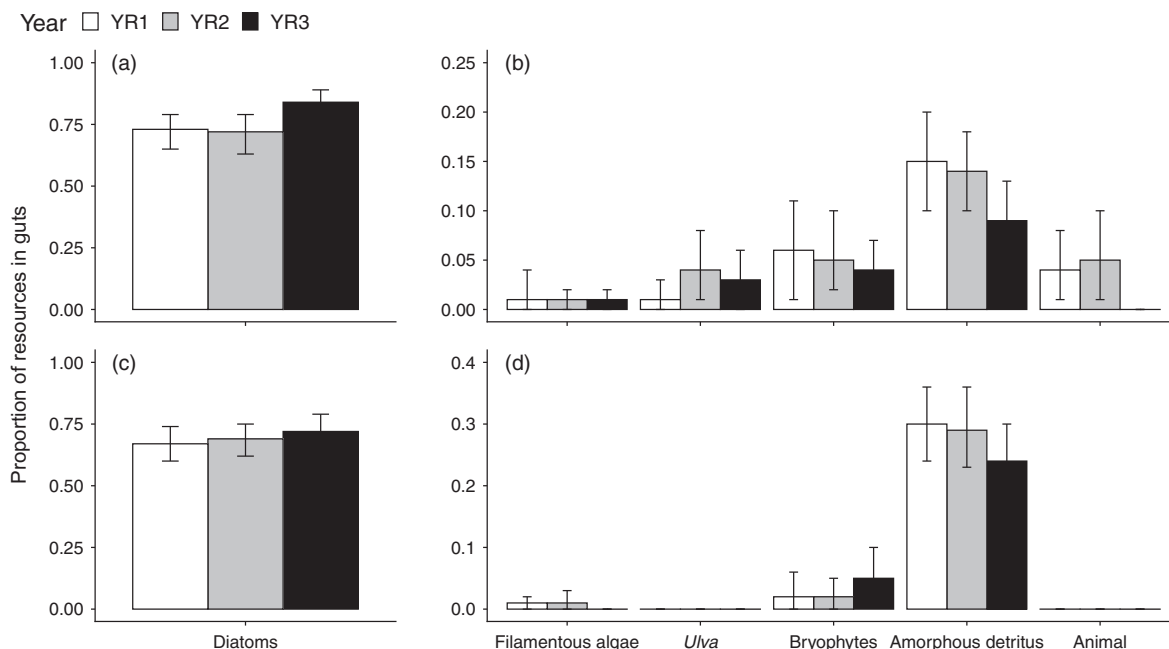


FIG. 1. The mean (\pm 95% confidence intervals) proportion of food resources consumed by primary consumers in the experimental (a, b) and reference stream (c, d) during YR1 (pre-warming; October 2010–September 2011), YR2 (warming; October 2011–September 2012) and YR3 (warming; October 2012–September 2013) of the study. Proportions are means for all common primary consumer taxa.

Secondary production of primary consumers in both streams was primarily supported by diatoms (mean = 85.2%, range = 12–100%; Fig. 3, Appendix S1: Table S10). On average, amorphous detritus contributed approximately 8.9% to the production of primary consumers, and the remaining 5.9% of production was attributed to green algae (1.7%), bryophytes (1.9%), cyanobacteria (<0.1%), and animal material (2.3%). The proportion of production attributed to diatoms increased between YR1 and YR3 in the experimental stream (Wilcoxon signed-rank test, $P = 0.04$). The proportions of production attributable to the other resource categories were not different among years within each stream (all other Wilcoxon signed-rank tests, $P > 0.05$).

The absolute amount of production attributed to diatoms did not differ among years in either stream (i.e., overlapping confidence intervals; Appendix S1: Table S11). In the reference stream, production attributed to diatoms ranged from 3,150 mg DM·m⁻²·yr⁻¹ in YR3 to 4,394 mg DM·m⁻²·yr⁻¹ in YR2 (Fig. 4c, Appendix S1: Table S7). In the experimental stream, production attributed to diatoms ranged from 6,093 mg DM·m⁻²·yr⁻¹ in YR2 to 8,887 mg DM·m⁻²·yr⁻¹ in YR1 (Fig. 4a, Appendix S1: Table S11). However, the absolute amount of production supported by some other food resources did change in the experimental stream (Appendix S1: Table S11). The amount of production attributable to both non-*Ulva* filamentous algae and *Ulva* increased during warming in the experimental stream as predicted. Production attributed to non-*Ulva*

filamentous algae increased over 10-fold, from 3 mg DM·m⁻²·yr⁻¹ (95% CI: 1–8) in YR1 to 45 mg DM·m⁻²·yr⁻¹ (95% CI: 13–106) in YR2 and 31 mg DM·m⁻²·yr⁻¹ (95% CI: 8–89) in YR3 (Appendix S1: Table S11). Invertebrate production attributed to *Ulva* increased dramatically from YR1 (6 mg DM·m⁻²·yr⁻¹; 95% CI: 1–14) to YR2 (405 mg DM·m⁻²·yr⁻¹; 95% CI: 120–777) and from YR1 to YR3 (69 mg DM·m⁻²·yr⁻¹; 95% CI: 9–220). The amount of production attributable to animal prey did not differ among years in either stream (Appendix S1: Table S11).

Organic matter flow food webs.

Total flows of organic matter to consumers were similar among years in both the experimental and reference streams (Table 1, Fig. 5, Appendix S1: Tables S12, S13). In the experimental stream, organic matter flows ranged from 73.73 to 87.36 g DM·m⁻²·yr⁻¹ (Table 1, Fig. 5, Appendix S1: Tables S12, S13). Organic matter flows were smaller in the reference stream than in the experimental stream, ranging from 30.77 to 48.12 g DM·m⁻²·yr⁻¹ (Table 1, Fig. 5, Appendix S1: Tables S12, S13). Diatoms and amorphous detritus dominated organic matter flows in both streams, and flows of bryophytes, cyanobacteria, filamentous algae, and *Ulva* to consumers comprised a small percentage (<10%) of total flows (Fig. 5, Appendix S1: Table S12, S14). In addition, flows of invertebrate prey to predators represented a small percentage (~5–10%) of total flows in both streams (Fig. 5, Appendix S1: Table S12). However, predators consumed 34–58% of total prey production in the

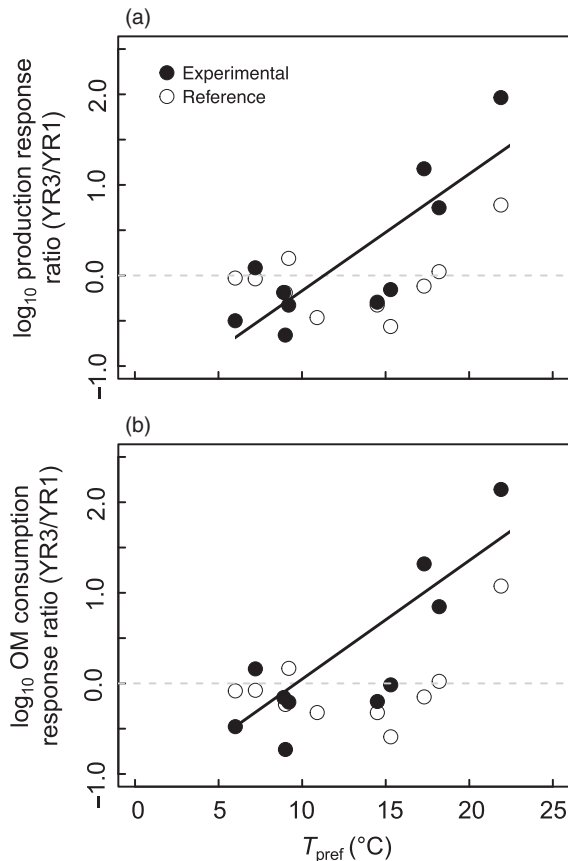


FIG. 2. Relationship between the response ratio measured as RR of (a) secondary production and (b) organic matter (OM) consumption and the temperature preference (T_{pref}) of taxa in the experimental and reference streams. Response ratios were calculated as $RR = \log_{10}(YR3/YR1)$ where RR is the \log_{10} (ratio change) in organic matter consumption from pre (YR1) to post (YR3) warming. T_{pref} values were taken from Nelson et al. (2017a) and presented in Appendix S1: Table S5. The regression line was fit using ordinary least-squares regression and statistics are presented in Appendix S1: Table S9.

experimental stream and 42–61% of prey production in the reference stream. Flows of *Ulva* to consumers increased significantly from $0.04 \text{ g DM}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ (95% CI: 0.01–0.09) in YR1 to $3.77 \text{ g DM}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ (95% CI: 0.99–6.48) in YR2 and $0.58 \text{ g DM}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ (95% CI: 0.09–1.79) in YR3. Flows of non-*Ulva* filamentous algae also increased ~20-fold from YR1 to YR2 and YR3 in the experimental stream (Fig. 5, Appendix S1: Table S12).

Changes in total organic matter flows varied among taxa (Fig. 6). The total amount of organic matter consumed decreased significantly (i.e., nonoverlapping 95% confidence intervals) for several taxa in the experimental stream (Appendix S1: Table S13). Between YR1 and YR3, consumption decreased significantly for three taxa (the midge *Orthocladius frigidus*, the black fly *P. ursinum*, and the oligochaete *Nais communis*). In the reference

stream, consumption decreased significantly for two taxa between YR1 and YR3 (the midge *Micropsectra* and *N. communis*). In contrast, consumption by some other taxa increased during the experiment (Appendix S1: Table S13). For example, consumption increased significantly for three taxa (*Simulium vittatum*, *Radix balthica*, and *Linnophora riparia*) in the experimental stream. Consumption also increased significantly for *R. balthica* in the reference stream, although to a smaller degree (Appendix S1: Table S13). Taxon-specific changes in organic matter consumption between YR1 and YR3 increased with thermal preference in the experimental stream, but not the reference stream (Fig. 2b, Appendix S1: Table S9). Taxa with higher thermal preferences exhibited larger positive changes in organic matter consumption than those with lower thermal preferences (Fig. 2b). In fact, several taxa with lower thermal preferences showed negative changes in total organic matter consumption (Fig. 2b).

DISCUSSION

We quantified effects of experimental warming on the trophic basis of production and flows of organic matter through an intact stream food web that was open to local dispersal and natural assembly processes. Higher temperatures resulted in little change in estimated total organic matter consumption in the experimentally warmed stream, even after correction of NPEs for higher respiratory demand and despite significant changes in invertebrate assemblage structure. Warming did, however, increase the flux of filamentous algae through the food web of the experimental stream. The lack of any significant increase in total energy flux resulted from a neutral effect of warming on total community production, differences in taxon-level responses to warming, and the high degree of trophic redundancy within this algae-based food web. Our results demonstrate that energy flux through stream food webs may be relatively resistant to warming if redundancy of trophic traits and species replacement in food webs are high.

As predicted, in situ primary producers were the most important resource for primary consumers in both streams, regardless of temperature. Diatoms were the most common food item found in gut contents of invertebrates and were also the dominant basis of production for consumers in both streams during all three years of the study. It is possible that certain invertebrate taxa could have changed their selectivity towards more energetically valuable diatom species to offset the increase in metabolic demand at warmer temperatures. Such responses have been documented (e.g., Gordon et al. 2018), but investigating diatom consumption at the genus level was beyond the scope of our study. Regardless, at the relatively coarse scale used to identify resources in this study, dietary proportions of diatoms in guts of consumers remained relatively constant within each stream at the community level. However, dietary

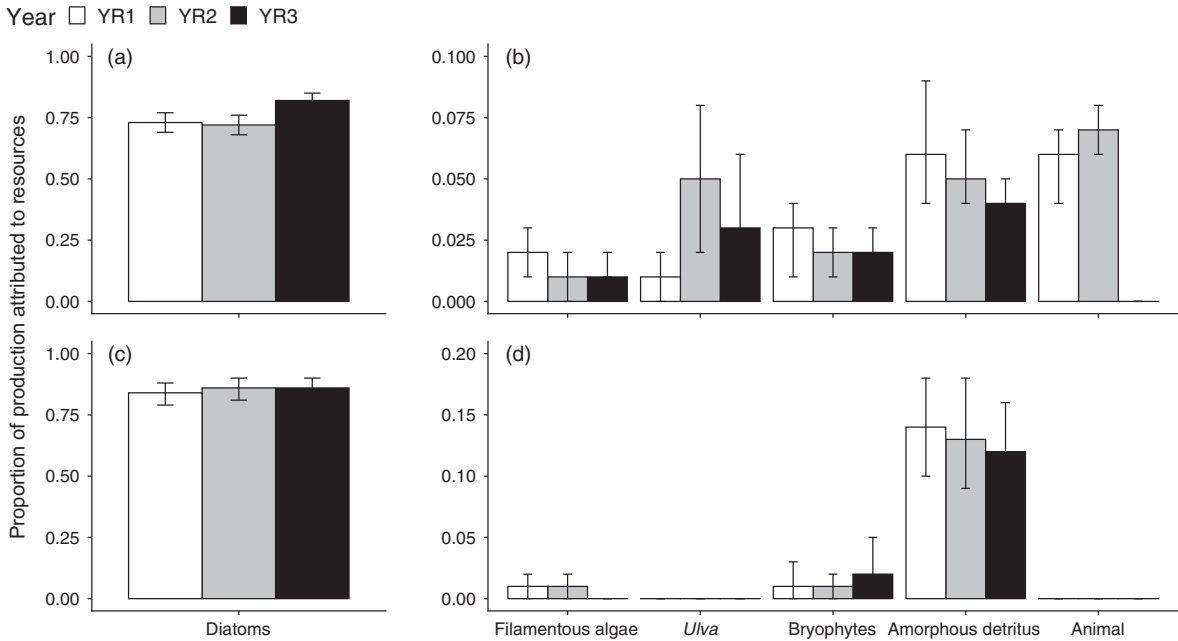


FIG. 3. Proportion of production attributed to different food resources in the experimental stream (a, b) and the reference stream (c, d) during YR1, YR2, and YR3 of the study. Proportions are means for all primary consumer taxa.

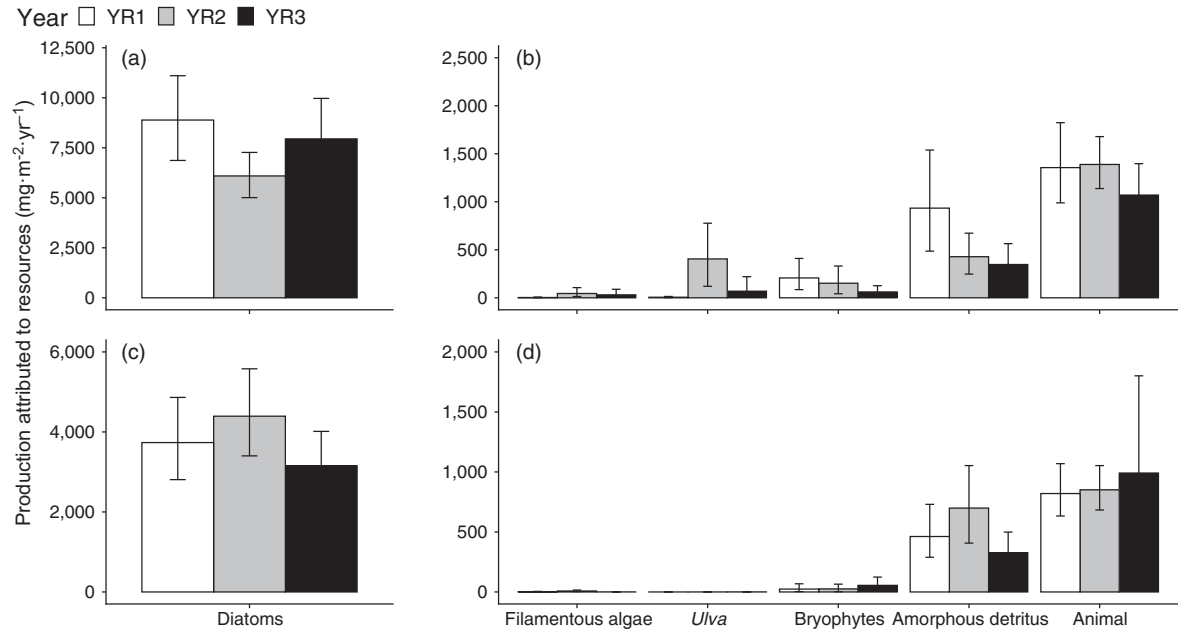


FIG. 4. The absolute amount of production of primary consumers and predators attributed to different food resources in the experimental stream (a, b) and the reference stream (c, d) during YR1, YR2, and YR3 of the study.

proportions differed among years for several taxa. For example, nonbiting midges in the genus *Orthocladius* switched from a mixed diet of diatoms and amorphous detritus to a diet of primarily diatoms, potentially a higher-quality food source (Wotton 1994, Hart and Lovvorn 2003). Diatoms also made up a larger proportion

of the diets of the black fly *S. vernum* and the chironomid *Diamesa* during warming, resulting in lower proportions of amorphous detritus in the guts of these two taxa. Although not significant, the consumption of amorphous detritus declined approximately 63% from YR1 to YR3 in the experimental stream. In food web

TABLE 1. Total organic matter (OM) flows ($\text{g dry mass}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) for the reference and experimental streams during all 3 yr of the study. Numbers in parentheses are 95% confidence intervals.

	Total OM flows ($\text{g dry mass}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$)		
	YR1	YR2	YR3
Reference	37.49 (26.50–52.70)	48.12 (33.39–67.14)	30.77 (22.10–42.82)
Experimental	87.36 (60.73–122.30)	73.73 (53.47–99.47)	82.15 (59.38–113.37)

studies, amorphous detritus is typically defined as organic particles with no recognizable cellular structure (e.g., exopolymer secretions from algae, microbes, plants; Decho 1990, Hart and Lovvorn 2003). Although of uncertain origin, amorphous detritus can represent the dominant trophic support of production in many aquatic ecosystems, including streams (Hall and Meyer 1998, Rosi-Marshall and Wallace 2002, Benke and Wallace 2015). The taxa most responsible for the decline in amorphous detritus consumption were those that exhibited large decreases in production during warming and thus large decreases in overall consumption rates, including of amorphous detritus (e.g., *Diamesa*, *Orthocladius*, *P. cingulatus*, and *N. communis*).

While consumption of amorphous detritus decreased in the experimental stream during warming, consumption of green algae increased. Experimental warming increased gross primary production by 175% (Hood et al. 2018) and led to significantly higher biomass of *Ulva* (20-fold increase; Nelson et al. 2017a), which paralleled an increase in consumption of *Ulva*. Consumption of *Ulva*, however, did decline from YR2 to YR3 ($3.34\text{--}0.58\text{ g DM}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$), despite higher biomass of *Ulva* in YR3. *Ulva* is often considered a palatable and high-quality food resource for many macroinvertebrates (Gianotti and McGlathery 2001, Kamermans et al. 2002, Guidone et al. 2010). Its long filaments and tough cell walls, however, may make it difficult for many smaller-bodied taxa to handle and ingest (Brown 1960, Moore 1975). It is important to note that the production of two taxa that consumed the greatest amount of *Ulva* during YR2 (~99% of total *Ulva* consumed during YR2), the large caddisfly *P. cingulatus* and the chironomid *Orthocladius*, declined significantly from YR2 to YR3. The markedly lower production of these two taxa had the resulting negative effect on community-level *Ulva* consumption during YR3. Hence, one effect of warming was the rerouting of organic matter flows through the food web of the experimental stream because of changes in invertebrate assemblage structure. This result illustrates how food web flows can change both through shifts in resource availability (i.e., “supply”) and through changes in consumer production (i.e., “demand”), and that these two mechanisms can interact and may be challenging to tease apart. Such interactions between resource availability and consumer population dynamics are important considerations for predicting how food webs will respond to future warming.

Although experimental warming had a positive effect on primary production and the biomass of the filamentous green alga *Ulva*, it had little influence on epilithic biofilm biomass (Nelson et al. 2017a). Previous studies have shown that the epilithic biofilm in the experimental stream is dominated in terms of biovolume by cyanobacteria (Guðmundsdóttir et al. 2011, P.C. Furey, St. Catherine University, *personal communication*). However, cyanobacteria were rarely detected in the gut contents of invertebrates from the reference stream and were not detected at all in guts of invertebrates from the experimental stream. These results support the hypothesis that some cyanobacteria may represent a trophic dead-end because of (1) their potential toxicity, (2) their morphology and mucilaginous sheaths, and (3) their deficiency in essential fatty acids (Perga et al. 2013). Thus, while cyanobacteria dominated the epilithic biofilm in the experimental stream, primary consumers selectively ingested epilithic diatoms, effectively rendering cyanobacterial production an energetic dead-end in the stream food web.

In addition to having effects on herbivory, experimental warming also affected predator–prey interactions within the food web. Prior to experimental warming, the percentage of animal material (i.e., early-instar chironomids and black flies) in the guts of *P. ursinum* was ~40%. In YR3, no animal material was found in the guts of *P. ursinum* larvae, suggesting a shift away from prey consumption. Increased carbon demand through elevated respiration rates at higher temperatures has been shown to influence dietary preference. Boersma et al. (2015) offered omnivorous copepods a mixed diet of the autotrophic cryptophyte *Rhodomonas salina* and the heterotrophic dinoflagellate *Oxyrrhis marina* as prey. Copepods preferred *R. salina*, which had a higher relative carbon content than *O. marina*, at higher temperatures, while preferring *O. marina* at lower temperatures. Therefore, demand for nutrients may have been higher at lower temperatures, and the demand for carbon greater at higher temperatures. The changes we observed in the dietary preference of *P. ursinum* may be rooted in a similar mechanism.

Changes in organic matter consumption in response to warming varied greatly among taxa, with decreases in consumption of organic matter by some taxa counterbalanced by increases in consumption by others, resulting in a neutral net effect of warming on total organic matter flux to consumers despite the estimated increase

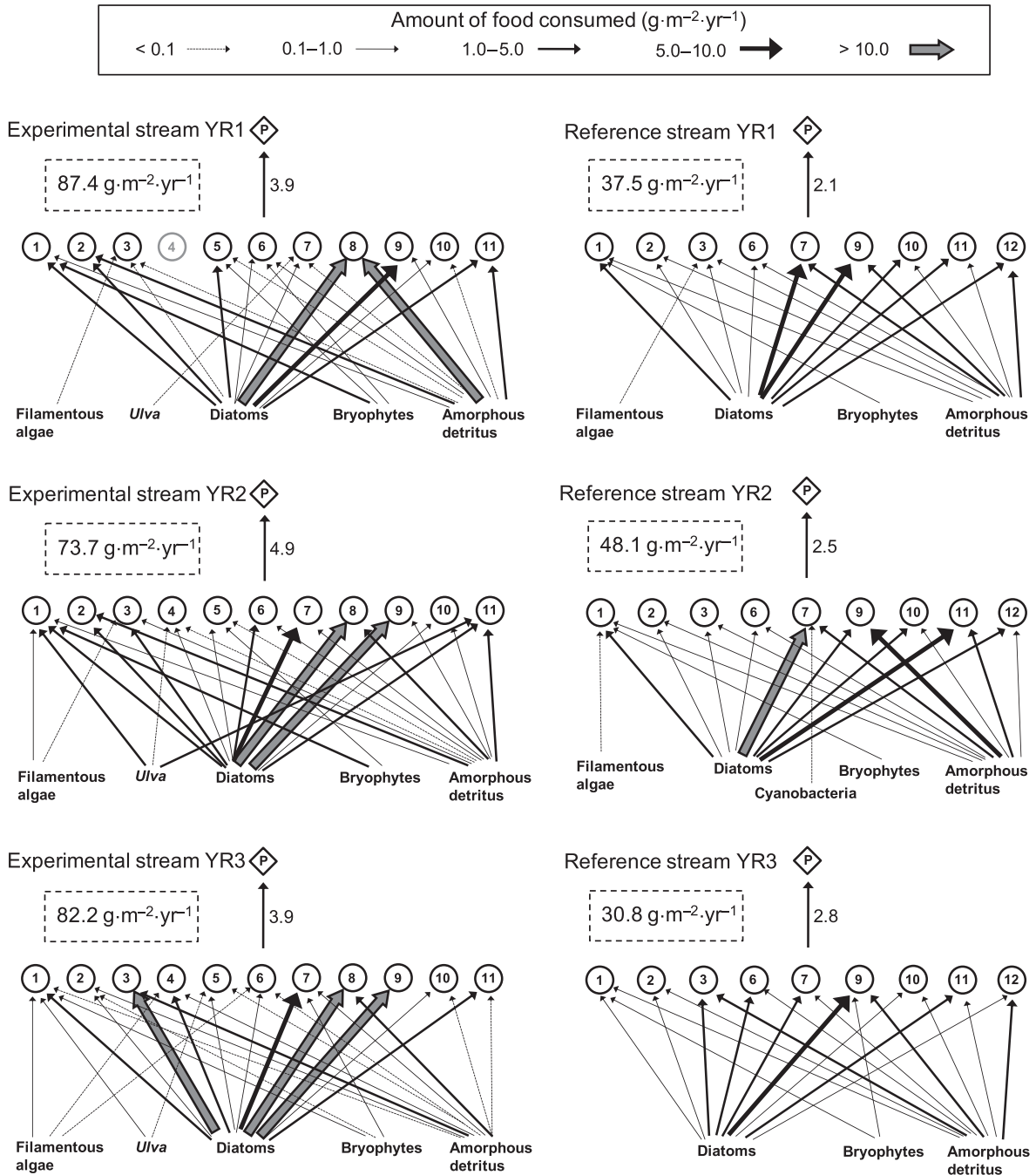


FIG. 5. Organic matter flow food webs for common invertebrates in the reference and experimental streams during YR1, YR2, and YR3. Circles represent primary consumers: 1, *Potamophylax cingulatus*; 2, *Nais communis*; 3, *Radix balthica*; 4, *Galba truncatula*; 5, *Prosimulium ursinum*; 6, *Simulium vernum*; 7, *Simulium vittatum*; 8, *Diamesa*; 9, *Eukiefferiella*; 10, *Micropsectra*; 11, *Orthocladius*; 12, *Rheocricotopus*. The diamond represents all predators: *Limnophora riparia*, *Clinocera stagnalis*, *Dicranota*, *Chaetogaster diaphanous*, *Prosimulium ursinum*. The value by the arrow from primary consumers to predators represents the total amount of organic matter flowing from invertebrate prey to predators in each annual web. Values within the dashed boxes represent mean annual organic matter flows to all taxa in each annual web.

in total metabolic demand driven by higher temperatures that we incorporated into our analysis. Taxon-specific changes in organic matter consumption in the experimental stream correlated with changes in production

and were strongly related to temperature preferences. Ectotherm performance (e.g., growth, metabolism, ingestion rate, reproduction) typically follows a unimodal response with temperature, often described as a

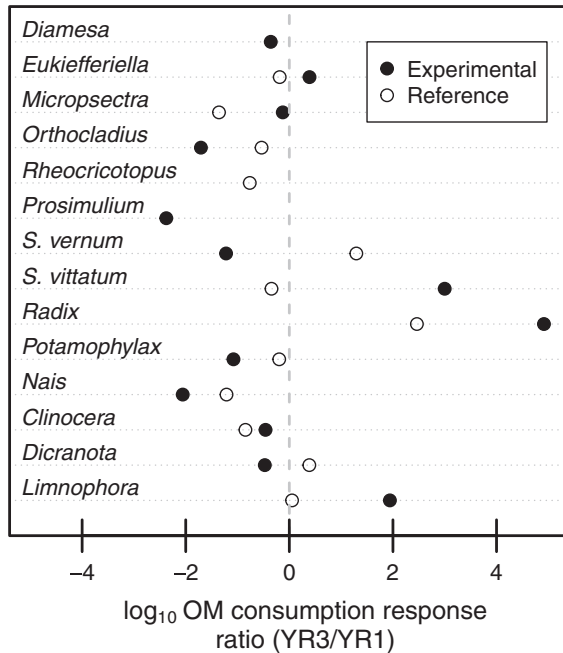


FIG. 6. Response ratios of organic matter (OM) consumption for each taxon in the experimental and reference streams. The response ratio was calculated as $RR = \log_{10}(YR3/YR1)$ where RR is the \log_{10} (ratio change) in total organic matter consumption from pre- (YR1) to post- (YR3) warming. The vertical grey dashed line indicates no change in consumption.

thermal window and visualized using a thermal performance curve (Pörtner and Farrell 2008, Pörtner and Peck 2010). At temperatures near the critical minimum or maximum, energy use becomes increasingly inefficient, resulting in lowered growth, development, and reproductive rates, which together lead to reduced fecundity and population abundance (Vannote and Sweeney 1980). Thus, population abundance should be maximized near the organism's optimum temperature. Based on growth rate and population abundance data from streams in the Hengill region that vary in mean annual temperature (temperature range: 5–21°C), taxa in the Hengill region are highly variable in their thermal preferences (Woodward et al. 2010, Hannesdóttir et al. 2013). In our study, taxa with higher temperature preferences showed greater positive changes in production and consumption than those with lower temperature preferences. This suggests that taxon-level changes in organic matter consumption in response to warming are likely a function of thermal preference and should therefore correlate with changes in abundance, biomass, and production.

Although the neutral net effect of warming on total energy flux may be partially explained by the diversity of responses by different taxa, it is also likely a result of a redundancy of functional or trophic traits. There was a high degree of trophic redundancy among consumers in the two streams studied. Overall, mean dietary proportions were similar among years and between streams for

most taxa. Furthermore, proportional similarities between taxa were generally high. Most gut contents were primarily composed of diatoms, indicating a heavy reliance on this resource for most primary consumers in the food web of both streams. The high degree of trophic redundancy among consumers may be in part due to the simple resource base present in both streams. Both streams have open canopies and receive very few allochthonous inputs (e.g., leaves, grass, wood). Furthermore, macrophyte biomass in the two study streams is low. As a result, consumers in the two study streams have a relatively limited resource base compared to consumers in streams with greater amounts of allochthonous inputs or macrophyte biomass. Trophic redundancy is generally thought to be more prevalent at lower trophic levels (Loreau et al. 2001) and may provide food webs with a level of insurance against the loss of function that accompanies declines in species abundances or extinctions (Petchey et al. 2007). Thus, warming may have a more pronounced effect on the routing and relative or absolute magnitude of organic matter flows in ecosystems with a broader resource base because of the resulting potential for a lower degree of trophic redundancy among consumers. In our study, decreases in consumption by some taxa were compensated for by increases in consumption in others; the high degree of trophic redundancy we observed helps explain the relatively resistant response of the experimental stream food web to warming.

Our main objective was to investigate the effects of increasing temperatures on the flux of energy through stream food webs; however, we acknowledge that factors other than temperature can be important in regulating energy flux through food webs and could have affected the results of our experiment. Although changes in the production and organic matter consumption of taxa were expected in the experimental stream, we also observed interannual differences in the production and consumption of some taxa in the reference stream. For example, the production of *R. balthica* and *S. vernalis* increased in the reference stream from YR1 to YR3 (Appendix S1: Table S4). It is possible that factors not measured or that were beyond the scope of this study (e.g., food quality, food supply, competitive interactions, other climatic factors) contributed to “natural” interannual differences in either of our study streams. Nevertheless, changes in the production and consumption of taxa in the experimental stream were generally much greater than those in the reference stream. Furthermore, these changes were positively related to their thermal preferences, indicating that changes in production and consumption could be attributed to experimental warming with relatively high confidence.

As temperatures continue to rise globally, it is increasingly important to understand and predict the effects of warming on the complex food-web interactions that are responsible for driving ecosystem function. Our study showed that medium-term experimental warming of a

high-latitude stream ecosystem with relatively low allochthonous inputs led to shifts in the routing of basal resources, but a neutral net effect on total organic matter consumption and energy flow, despite significant changes in assemblage structure and higher estimated energetic demands. These patterns were largely driven by the neutral or negative effect of warming on secondary production, variability in taxon-specific responses to warming, and a high degree of trophic redundancy within the food web. Thus, the ecosystem-level function of communities containing species with varying thermal preferences and a high degree of functional redundancy may be relatively robust to the effects of shifts in temperature regimes associated with climate change. Conversely, food webs that contrast in trophic support and topology with those we studied (e.g., more diverse basal resources, higher species richness, higher trophic height, and predator diversity) may demonstrate markedly different responses to warming given a higher likelihood of complex interactions and rerouting of energy fluxes. This potential for strong (and potentially feedback) relationships between food web structure and relative impact of warming underscores the urgency of a comprehensive research agenda focused on climate–food web interactions.

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