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Changes in Feeding Selectivity of Freshwater Invertebrates Across a Natural Thermal Gradient

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Abstract

Environmental warming places physiological constraints on organisms, which may be mitigated by their feeding behavior. Theory predicts that consumers should increase their feeding selectivity for more energetically valuable resources in warmer environments to offset the disproportionate increase in metabolic demand relative to ingestion rate. This may also result in a change in feeding strategy or a shift towards a more specialist diet. This study used a natural warming experiment to investigate temperature effects on the feeding selectivity of three freshwater invertebrate grazers: the snail *Radix balthica*, the blackfly larva *Simulium aureum*, and the midgefly larva *Eukiefferiella minor*. Chesson's Selectivity Index was used to compare the proportional abundance of diatom species in the guts of each invertebrate species with corresponding rock biofilms sampled from streams of different temperature. The snails became more selective in warmer streams, choosing high profile epilithic diatoms over other guilds and feeding on a lower diversity of diatom species. The blackfly larvae appeared to switch from active collector gathering of sessile high profile diatoms to more passive filter feeding of motile diatoms in warmer streams. No changes in selectivity were observed for the midgefly larvae, whose diet was representative of resource availability in the environment. These results suggest that key primary consumers in freshwater streams, which constitute a major portion of invertebrate biomass, can change their feeding behavior in warmer waters in a range of different ways. These patterns could potentially lead to fundamental changes in the flow of energy through freshwater food webs.

Key words: climate change, global warming, diet, *Lymnaea peregra*, Simuliidae, Chironomidae

Anthropogenic climate change has caused global surface temperatures to rise dramatically over the last century. Warming projections forecast a minimum increase of 1.5–2°C by 2100, with the Arctic region likely to experience the highest levels of warming (IPCC 2014). Environmental warming alters the physiology, phenology, and geographic range of species in different ways, according to their thermal tolerances (Parmesan 2006; Chen et al. 2011; Ohlberger 2013). This can lead to the extinction of some species and the introduction of others, altering community structure through changes to the identity, metabolic demand, and activity levels of interacting species (Walther et al. 2002; Root et al. 2003; Urban et al. 2013).

Warming-induced changes to trophic interactions are particularly important because they can dramatically affect whole communities. The highly connected nature of food webs facilitates widespread effects via trophic cascades, where a direct effect on one species also has indirect effects on its consumers and resources (Polis et al. 1996; Pace et al. 1999). For example, temperature-regulated vernal blooms of freshwater diatoms in a large, temperate North

American lake advanced by up to 3 weeks in the past 50 years in response to warming, causing a temporal mismatch with the photoperiod-regulated annual emergence of diapausing zooplankton eggs (Winder and Schindler 2004). This resulted in a long-term decline in zooplankton populations, which depend on the diatoms for food during the crucial development phase; in turn, energy flow to higher trophic levels was reduced. Similarly, experimental warming of ponds has been shown to alter the degree to which both bottom-up and top-down control determine community structure, causing widespread impacts on multiple species throughout the food web (Shurin et al. 2012).

Freshwater communities are thought to be especially vulnerable to such changes for several reasons (Woodward et al. 2010a). First, many freshwater organisms are limited in their dispersal ability by both physiological constraints and a lack of connectivity between freshwater habitats (Finn et al. 2006; Evans et al. 2009), meaning that it is difficult to respond to warming by migrating to areas with more favorable climates. Further, many freshwater ecosystems are simultaneously threatened by other anthropogenic stressors, which can interact with and exacerbate the impacts of warming (Kundzewicz et al. 2008; Arthington et al. 2010). Additionally, it has been suggested that trophic cascades can be particularly strong in freshwater ecosystems compared to other biomes (Halaj and Wise 2001; Shurin et al. 2002), although this idea is controversial and not universally accepted (Schmitz et al. 2000).

Methods used to study the effects of warming on freshwater food webs include theoretical modelling (Petchey et al. 2010; Binzer et al. 2015), mesocosm-based experiments (Petchey et al. 1999; Shurin et al. 2012), whole-ecosystem manipulations (Hogg and Williams 1996), and natural thermal gradients (O'Gorman et al. 2014). Such studies are increasingly focused on general responses across species and changes in the topological structure of the food web (Petchey et al. 2010; O'Gorman et al. 2012; Shurin et al. 2012). However, individual-based responses are also important in this area as they reveal patterns that are not described by species-averaged data (Woodward et al. 2010b).

Individual foraging-related behavioral responses play important roles in determining food web dynamics (Ings et al. 2009), with models based on foraging characteristics such as dietary niche width accurately predicting food web structure (Beckerman et al. 2006; Petchey et al. 2008). Feeding selectivity represents one such example of an individual-based response that impacts community-level dynamics. Changes in consumer selectivity have been shown to affect the selection pressures they exert on different resource species (Lankau 2007; Castillo et al. 2014), the transfer of material through food chains (Zhang et al. 2013), and community structure as a whole (Drenner 1982; Drenner et al. 1984). Indeed, the feeding selectivity of an individual species can be used as a predictor of its likely impacts on the dynamics of ecosystems to which it is newly introduced (Dodd et al. 2014).

Many invertebrate consumer species alter their feeding selectivity in response to a variety of selection pressures. For example, grasshoppers exposed to predation risk switch to a diet with higher carbohydrate content relative to unstressed individuals (Hawlena and Schmitz 2010), and pathogen-infected caterpillars increase their dietary protein intake relative to healthy individuals (Lee et al. 2006). A consumer's feeding selectivity can be thought of in terms of either its overall strategy (i.e. whether it is a generalist or a specialist), or its preference for a particular resource group or species. Empirically, the latter is commonly tested through comparisons of the proportional representation of a resource species in a consumer's

diet and in the environment (e.g., Berumen & Pratchett 2008; O'Gorman et al. 2016). The former can be tested either by analyzing the average value of such calculations for all resource species in the diet (e.g. Blackwood et al. 2001) or by using alternative methods such as comparisons of dietary composition and diversity (e.g. Jonsen and Fahrig 1997) or stable isotope analysis of dietary niche width (e.g. O'Gorman et al. 2016).

Theoretical work has suggested that both of these aspects of feeding selectivity may be affected by warming. The rate at which metabolic demand increases with temperature is thought to outpace the accompanying increase in ingestion rate, resulting in a decreased ingestion efficiency (defined as the ratio of ingestion, i.e., energy intake, to metabolism, i.e., energy demand) in warmer environments (Rall et al. 2010). This may lead to consumers increasing their selectivity for higher quality food items to offset temperature-associated ingestion inefficiency. For example, laboratory choice tests on a herbivorous beetle revealed that increased feeding on nitrogen-rich plant species at higher temperatures resulted in a more specialised diet overall (Lemoine et al. 2013), and brown trout have been shown to choose prey with a higher energetic value as part of a more selective diet at higher stream temperatures (O'Gorman et al. 2016).

This study examines the effects of stream temperature on the feeding selectivity of three freshwater invertebrates as primary consumers in a natural warming experiment, testing two main hypotheses:

1. Freshwater invertebrates will have a more specialist feeding strategy in warmer environments. Logic: feeding on a smaller, higher quality subset of the available resource species at higher temperatures may help consumers to mitigate the effects of decreasing ingestion efficiency (Rall et al. 2010).
2. Freshwater invertebrates will have different preferences for resource taxa in warmer environments. Logic: diatoms differ in their nutritional content and ease of acquisition, thus a switch in resource preference or feeding mode may be more efficient at higher temperatures as resource availability or other selection pressures change.

Materials and Methods

Study site

Samples were collected in August 2008 from the Hengill geothermal system in southwest Iceland (64°03′ N, 021°18′ W). This system contains numerous spring-fed tributaries of the river Hengladalsá, which are differentially warmed by indirect geothermal heating of the bedrock that the groundwater flows over (Arnason et al. 1969). All of the streams are connected via the main stem and are within 2 km of each other, meaning that biotic dispersal constraints are low and the physical and chemical characteristics of the streams are very similar (Friberg et al. 2009; Adams et al. 2013). This lack of other sources of environmental variation makes Hengill an ideal natural experiment for studying the effects of stream temperature on aquatic communities *in situ*. Eight streams spanning a temperature range of 19.5°C were chosen for this study (Figure 1).

Invertebrates were collected in benthic Surber samples (25 × 20 cm quadrat; 200 µm mesh; five samples per stream) and preserved in 70% ethanol. Surveys of the benthos were performed during the same time period to quantify epilithic algal assemblages, consisting of three stone scrapes per stream. Diatom frustules from the stone scrapes were cleared of organic matter with nitric acid, dried, and mounted on slides with naphrax. Relative abundances were estimated by counting the number of individuals of each
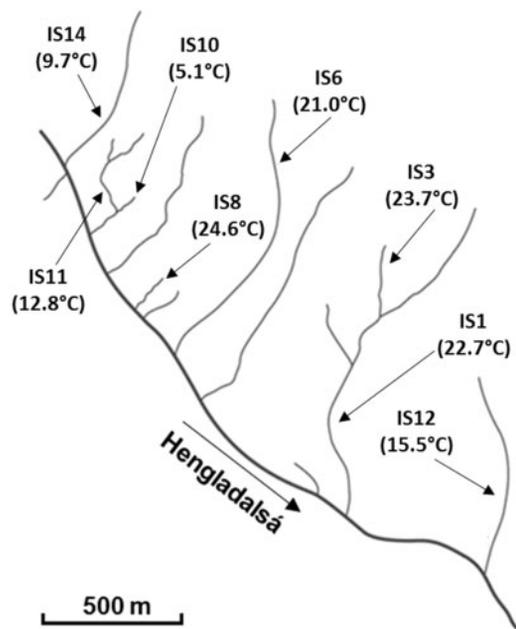
Figure 1. Map of the study site. Schematic of the Hengill geothermal streams, with labels indicating the eight streams used in this study and their associated mean temperatures in August 2008. Stream names are in keeping with the labelling system used in previous studies (e.g., O'Gorman et al. 2012).

species along a 15×0.1 mm transect of each slide, ensuring that a transect contained at least 300 individuals. Full details of stream benthos survey methods and results are reported by O'Gorman *et al.* (2012), including yield-effort curves which show that these sample numbers were sufficient to accurately describe the composition of both the invertebrate and diatom communities (Appendix C in O'Gorman et al. 2012).

Study species

Three prominent primary consumers from the Hengill system, each with a different functional feeding mode, were chosen for dietary analyses. The snail *Radix balthica* Linnaeus, 1758, is the dominant scraping grazer in the Hengill system (O'Gorman et al. 2012). The blackfly larva *Simulium aureum* Fries, 1824, may traditionally be thought of as a strict filter feeder, but has congeners that are able to collect small algal particles from the biofilm, *i.e.* collector gatherers (Burton 1973; Walsh 1985; Alder and McCreadie 1997), and this behaviour has been regularly observed in the Hengill system (personal observation). The midgefly larva *Eukiefferiella minor* Edwards, 1929, is thought to be a largely generalist collector gatherer (Henriques-Oliveira et al. 2003), as for most chironomids during some part of their larval lifespan (Berg 1995). These invertebrate consumer species are likely to play important ecological roles in both the bottom-up regulation of secondary consumers and the top-down control of epilithic algal assemblages in freshwater stream systems (Ledger et al. 2006; Gudmundsdóttir et al. 2011; Sturt et al. 2011; O'Gorman et al. 2012).

Gut content analyses

Dietary selectivity for epilithic diatom species at different temperatures was investigated using gut content analyses from all three invertebrate consumers. Diatoms were chosen for these assays as previous research from the system suggests that $> 90\%$ of invertebrate diets are composed of diatoms and fine particulate organic matter, with virtually no allochthonous inputs and minimal

predatory behavior among invertebrates (O'Gorman et al. 2017). Gut content analyses were carried out on individuals representing an even spread across the body size distributions present in the samples. Invertebrates were acid-digested for 18 h in 1.5 mL of 62% nitric acid (HNO_3) at $65°C$, in order to remove all organic matter except for silicate diatom frustules in the guts. Step-wise dilutions with distilled water were then carried out to achieve a minimum pH of 4.5 prior to slide mounting. One milliliter sub-samples of the resulting suspensions of diatom frustules were pipetted onto glass coverslips and allowed to dry overnight. Once dry, cover slips were fixed to glass slides by adding a drop of naphrax (Brunel Microscopes Ltd., Chippenham, UK) and heating to $60°C$ on a hotplate, before allowing the naphrax to dry for slide analysis.

Diatoms were identified using the species definitions of Krammer and Lange-Bertalot (1986–1991), in the same manner as the quantification of epilithic algal assemblages (O'Gorman et al. 2012; Adams et al. 2013). The relative abundance of individual diatom species in each gut was determined by recording the species identity of the first 100 diatom individuals encountered in a continuous, non-overlapping 100 µm-wide transect following a fixed route across the slide. Transects were continued until 100 individuals were encountered or the entire slide had been examined. To ensure that no additional diatom species were missed by only examining the first 100 individuals, the entirety of each slide was checked for novel species. This procedure never yielded extra species not present in the initial transect, suggesting that identifying the first 100 diatom individuals was enough to accurately characterize the species present on each slide.

The number of invertebrates per stream required to accurately quantify the diet was determined using yield-effort curves. The cumulative number of diatom species identified was used as an indicator of diet characterisation, and plotted against the number of invertebrate gut content slides examined. For each stream, cumulative diatom species count data were used to plot asymptotic curves ("*SSasymp*" function in the "*stats*" package of R 3.4.0; R Core Team 2017) of the form:

$$y = A + (R_0 - A)e^{-e^{\ln(c)x}}, \qquad (1)$$

where A is the horizontal asymptote, R_0 is the response when $x = 0$, and c is the rate constant. Curves were fitted for 1,000 randomizations of the sample order, and the median parameters of the 1,000 curves were used to calculate an overall yield-effort curve for each consumer species in each stream (Figure 2). The horizontal asymptote of these overall curves was taken to represent a theoretical maximum for the number of diatom species making up the diet of consumers in that stream. The difference between the theoretical and observed number of diatom species in the diet for a given stream never exceeded 3.7 for *E. minor*, 0.4 for *R. balthica*, and 2.3 for *S. aureum* (Figure 2). It was therefore assumed that the accuracy of diet characterization was adequate for this study.

Quantifying selectivity strategy

The level of generality or speciality of invertebrate feeding on diatom species was first assessed using diversity metrics of the dietary composition. Species richness, Pielou's evenness, and Shannon diversity metrics were calculated for the diatom communities present in each consumer's gut contents. A lower richness, evenness, or diversity of diatom species in the guts would indicate a more specialized feeding strategy.

To account for variation in diatom communities in each stream, the Chesson Selectivity Index (CSI; Chesson 1983) was used to
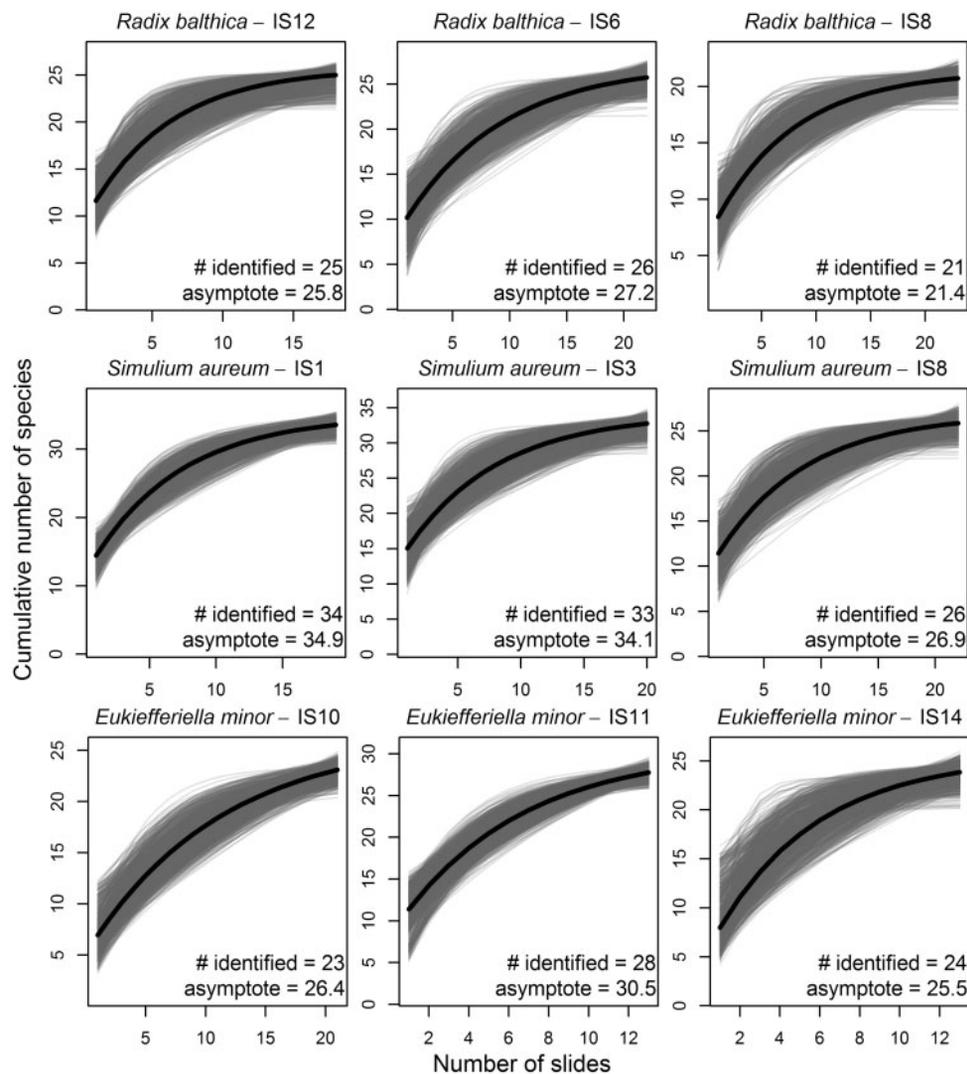
Figure 2. Yield-effort curves for invertebrate gut contents in each stream. Gray lines represent asymptotic curves fitted to 1,000 sample order randomizations of the cumulative species count; black lines represent the overall curve based on median parameters of the 1,000 randomized curves. Asymptote values for the overall curves were taken as theoretical maxima for the number of diatoms in each consumer's diet, and are given alongside the actual number of diatoms identified in each case.

compare the proportional representation of each diatom species in the gut contents with its proportional representation in the stream benthos. The CSI was calculated as follows:

$$CSI = \frac{g_i/b_i}{\sum_{j=1}^{n} g_j/b_j}, i = 1, \ldots, n, \qquad (2)$$

where n is the total number of diatom species in the gut contents, and g and b are the proportional representation of diatom species i or j in the gut contents and stream benthos, respectively. The CSI value for a given diatom species i reflects its presence in the gut contents relative to the stream benthos, divided by the sum of the equivalent calculation for all diatom species in the gut. This is therefore a proportional indicator of the level of selectivity for each species in the diet, with 0 indicating complete absence from the diet and 1 indicating exclusive feeding on that species. The distribution of CSI values for each resource species in a single consumer's gut was taken as a proxy for its overall selectivity strategy, with the median value for each individual consumer indicating its level of generality or speciality. A higher median CSI value would indicate a more specialist feeding strategy, with consumers feeding heavily on a few species, rather than feeding weakly on many species.

Quantifying preference for diatom taxa

Diatom species composition was different for each stream (O'Gorman et al. 2012; Adams et al. 2013), making it difficult to objectively assess preference for individual species. As such, diatom species were classified into three distinct ecological guilds (low profile, high profile, and motile) based on morphology and accessibility to consumers, following previous work by Fore and Grafe (2002), Passy (2007), and Rimet and Bouchez (2012). Diatom classifications are broadly similar in all three approaches, but this study most closely resembled Passy (2007) as it resulted in an even spread of the diatom species in this dataset across the three guilds (e.g., there are only two species from the Hengill streams that would fit in the additional planktonic guild of Rimet and Bouchez 2012). All guild designations were made on a species-by-species basis using trait information sourced from the "Diatoms of the United States" online guide (https://westerndiatoms.colorado.edu).
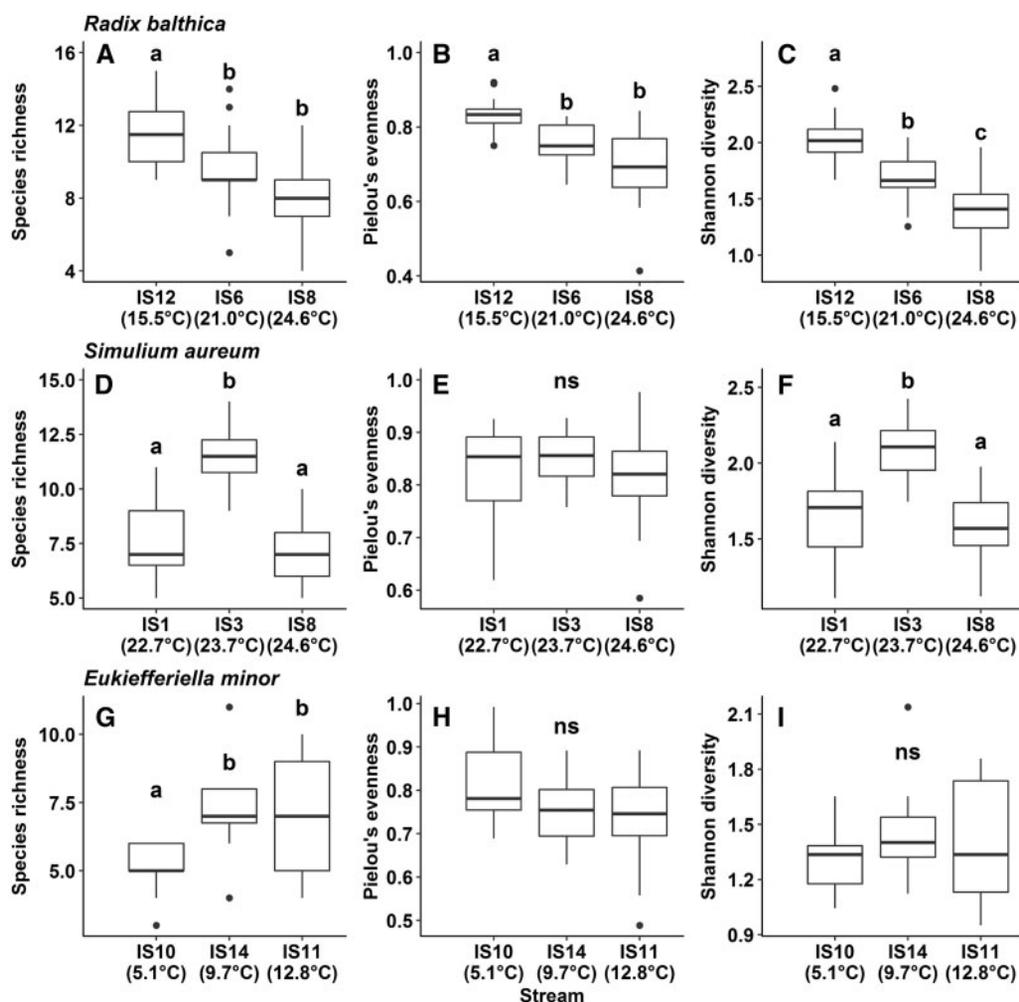
Figure 3. Diversity of diatom species in the guts of invertebrate consumers. Box plots display species richness, Pielou's evenness, and Shannon diversity of diatom species in the guts of (A–C) *Radix balthica*, (D–F) *Simulium aureum*, and (G–I) *Eukiefferiella minor* in different streams. Boxes represent the median ± interquartile range; whiskers represent the 5–95% range; single points represent outliers. Bars not sharing a common letter (a, b, or c) were significantly different from each other (Tukey test: $P < 0.05$), while "ns" indicates no significant difference between streams.

Low profile diatoms comprise slow-moving or non-motile species that attach directly and closely to the substrate without forming branches or colonies. This guild is characterized by a short stature, potentially making them difficult for grazing or filter-feeding consumers to acquire, and includes diatoms from the genera *Achnanthes* Bory de Saint-Vincent, 1822, *Amphora* Ehrenberg ex Kützing, 1844, *Aulacoseira* Thwaites, 1848, *Cocconeis* Ehrenberg, 1837, *Cyclotella* (Kützing) Brébbisson, 1838, *Hannaea* Patrick, 1961, *Karayevia* Round et Bukhtiyarova ex Round, 1998, *Meridion* Agardh, 1824, and *Planothidium* Round et Bukhtiyarova, 1996. High profile diatoms comprise species that attach to the substrate and either have stalks or form long, branching colonies extending beyond the boundary layer. This guild is characterized by a tall stature, potentially making them more accessible to grazing consumers, and includes diatoms from the genera *Cymbella* Agardh, 1830, *Diatoma* Bory de Saint Vincent, 1824, *Encyonema* Kützing, 1849, *Eunotia* Ehrenberg, 1837, *Fragilaria* Lynbye, 1819, *Gomphonema* Ehrenberg, 1832, *Melosira* Agardh, 1824, *Rhoicosphenia* Grunow, 1860, *Staurosirella* Williams et Round, 1987, and *Ulnaria* (Kützing) Compére, 2001. Motile diatoms comprise comparatively fast-moving species with well-developed raphe structures. This guild is characterised by its movements over surfaces, potentially making it

more accessible to less motile, filter-feeding consumers, and includes diatoms from the genera *Caloneis* Cleve, 1894, *Cavinula* Mann et Stickle ex Round *et al*, 1990, *Diploneis* (Ehrenberg) Cleve, 1894, *Eolimna* Lange-Bertalot et Schiller, 1997, *Epithemia* Kützing, 1844, *Frustulia* Rabenhorst, 1853, *Mayamaea* Lange-Bertalot, 1997, *Navicula* Bory de Saint Vincent, 1822, *Nitzschia* Hassall, 1845, *Pinnularia* Ehrenberg, 1843, *Placoneis* Mereschkowsky, 1903, *Rhopalodia* Müller, 1895, and *Surirella* Turpin, 1828.

The proportional representation of each diatom guild in the gut contents of invertebrate consumers was calculated and used in place of species identity in Equation 2 to estimate CSI at the guild-level. All diatom guilds were present in the guts of all consumer species in all of the streams, facilitating a less biased comparison of preference for the various guilds across the stream temperature gradient.

Statistical analysis

All statistical analysis and figure plotting was carried out in R 3.4.0 (R Core Team 2017). Response variables included the species richness, Pielou's evenness, and Shannon diversity of diatom species in the guts, the median CSI value for diatom species, and the CSI for low profile, high profile, and motile diatom guilds. All response

Table 1. Statistical outputs from ANOVA and Tukey's HSD tests comparing the gut content diversity metrics presented in Figure 3, the Chesson Selectivity Index (CSI) values presented in Figure 4, and the preference for different diatom guilds presented in Figure 5 for the three study organisms (*R. balthica*, *S. aureum*, and *E. minor*) across the various study streams

Metric	Figure	*Radix balthica*		*Simulium aureum*		*Eukiefferiella minor*	
		ANOVA	Tukey's HSD	ANOVA	Tukey's HSD	ANOVA	Tukey's HSD
Species richness	3	$F_{2,41} = 5.58$ $P = 0.006$	IS6–IS12 $P = 0.050$ IS8–IS12 $P = 0.004$ IS8–IS6 $P = 0.685$	$F_{2,58} = 10.70$ $P < 0.001$	IS3–IS1 $P < 0.001$ IS8–IS1 $P = 0.997$ IS8–IS3 $P < 0.001$	$F_{2,41} = 10.54$ $P < 0.001$	IS11–IS10 $P = 0.002$ IS14–IS10 $P < 0.001$ IS14–IS11 $P = 0.960$
Pielou's evenness	3	$F_{2,41} = 21.11$ $P = 0.006$	IS6–IS12 $P = 0.001$ IS8–IS12 $P < 0.001$ IS8–IS6 $P = 0.018$	$F_{2,58} = 1.99$ $P = 0.148$	NA	$F_{2,41} = 3.23$ $P = 0.062$	NA
Shannon diversity	3	$F_{2,67} = 46.15$ $P < 0.001$	IS6–IS12 $P < 0.001$ IS8–IS12 $P < 0.001$ IS8–IS6 $P < 0.001$	$F_{2,58} = 31.77$ $P < 0.001$	IS3–IS1 $P < 0.001$ IS8–IS1 $P = 0.628$ IS8–IS3 $P < 0.001$	$F_{2,41} = 1.59$ $P = 0.216$	NA
Median CSI value	4	$F_{2,67} = 10.89$ $P < 0.001$	IS6–IS12 $P = 0.001$ IS8–IS12 $P < 0.001$ IS8–IS6 $P = 0.781$	$F_{2,58} = 0.33$ $P = 0.724$	NA	$F_{2,41} = 1.64$ $P = 0.206$	NA
CSI: High profile	5	$F_{2,67} = 19.11$ $P < 0.001$	IS6–IS12 $P = 0.702$ IS8–IS12 $P < 0.001$ IS8–IS6 $P < 0.001$	$F_{2,58} = 99.48$ $P < 0.001$	IS3–IS1 $P < 0.001$ IS8–IS1 $P < 0.001$ IS8–IS3 $P < 0.001$	$F_{2,41} = 0.52$ $P = 0.596$	NA
CSI: Low profile	5	$F_{2,67} = 14.68$ $P < 0.001$	IS6–IS12 $P = 0.943$ IS8–IS12 $P < 0.001$ IS8–IS6 $P < 0.001$	$F_{2,58} = 33.43$ $P < 0.001$	IS3–IS1 $P < 0.001$ IS8–IS1 $P = 0.004$ IS8–IS3 $P = 0.823$	$F_{2,41} = 0.96$ $P = 0.393$	NA
CSI: Motile	5	$F_{2,67} = 2.50$ $P = 0.090$	NA	$F_{2,58} = 8.56$ $P < 0.001$	IS3–IS1 $P = 0.068$ IS8–IS1 $P < 0.001$ IS8–IS3 $P < 0.001$	$F_{2,41} = 1.54$ $P = 0.226$	NA

variables were analysed separately using one-way Analysis of Variance (ANOVA; "*aov*" function in the "*stats*" package; R Core Team 2017). In each case, stream identity was treated as a categorical explanatory variable with three levels and a separate analysis was performed for each consumer species. Tukey's HSD post-hoc test was used to assess which streams were significantly different from each other ("*TukeyHSD*" function in the "*stats*" package; R Core Team 2017). Assumptions of normality and heteroscedasticity were confirmed using visual analyses of residual plots and the Fisher–Pearson standardised third moment coefficient, with no transformation of the data required. Differences in each of the response variables across streams and consumer species were visualised with boxplots. To help inform the species-level investigation of CSI values, a probability density function was fitted to the distribution of CSI values for each diatom species in a single consumer gut. To help inform the guild-level investigation of CSI values, the relative abundance of diatom guilds in the stream benthos and in the gut contents were plotted alongside the CSI values for each diatom guild.

Results

Selectivity strategy

The three invertebrate consumers exhibited different changes in selectivity strategy for diatom species along the stream temperature gradient (Figure 3). There was a significant reduction in the species richness, Pielou's evenness, and Shannon diversity of diatom species in the diet of *R. balthica* in the warmer streams (Figure 3A–C; Table 1). In contrast, there was a significant increase in the species richness and Shannon diversity of diatom species in the diet of *S. aureum* in the intermediate-temperature stream (i.e., IS3), although there was no significant difference in Pielou's evenness (Figure 3D–F; Table 1). There was a significant increase in the species richness

of *E. minor* in the warmer streams, but no significant differences in Pielou's evenness or Shannon diversity (Figure 3G–I; Table 1).

Distributions of CSI values were generally skewed towards lower values for all three invertebrate consumers, suggesting they fed quite generally on all diatom species (Figure 4). There was a significant increase in the median CSI value for *R. balthica* in the warmer streams (Figure 4D; Table 1). There was no significant change in the median CSI value of either *S. aureum* or *E. minor* across the stream temperature gradient (Figure 4H and L, Table 1).

Preference for diatom taxa

Radix balthica had a significantly stronger preference for high profile diatoms and a significantly weaker preference for low profile diatoms in the warmest stream, with no significant change in preference for motile diatoms (Figure 5A–C; Table 1). *Simulium aureum* had a significantly weaker preference for high profile diatoms as stream temperature increased and a significantly stronger preference for both low profile diatoms and motile diatoms in the warmest stream (Figure 5D–F; Table 1). *Eukiefferiella minor* exhibited no change in preference for high profile diatoms, low profile diatoms, or motile diatoms (Figure 5G–I; Table 1).

Comparison of the relative abundances of diatom guilds in the stream benthos and gut contents revealed further insights into the feeding behavior of the invertebrate consumers (Figure 6). For *R. balthica*, the weaker preference for low profile diatoms in the warmest stream (Figure 6G) was unrelated to their environmental availability, with a similar relative abundance of low profile diatoms in all streams (Figure 6A). Instead, *R. balthica* appeared to increase its preference for high profile diatoms in the warmest stream (Figure 6G), perhaps due to their ubiquity in that stream (Figure 6A). In contrast, the decreasing preference for high profile diatoms with increasing stream temperature in *S. aureum* (Figure 6H) occurred despite a large increase in their availability in
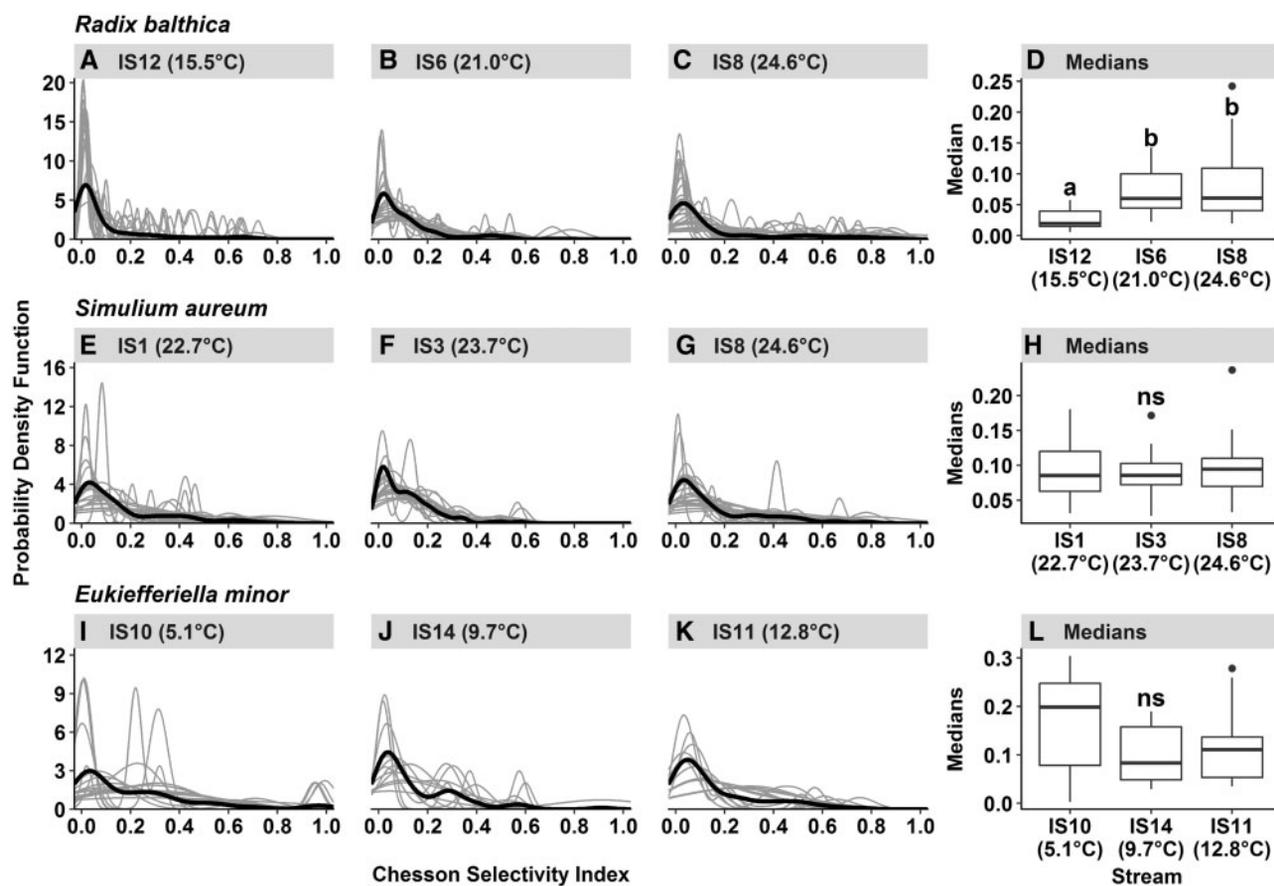
Figure 4. Feeding selectivity of invertebrate consumers for diatom species. Chesson Selectivity Index (CSI) metrics are shown for (A–D) *Radix balthica*, (E–H) *Simulium aureum*, and (I–L) *Eukiefferiella minor*. The first three columns display CSI distributions for consumers in different streams; gray lines represent probability density functions for each individual consumer's diet, black lines represent a probability density function of all individuals' diets combined. The last column displays boxplots of the median CSI value for each consumer in each stream; boxes represent the median ± interquartile range; whiskers represent the 5–95% range; single points represent outliers. Bars not sharing a common letter (a, b, or c) were significantly different from each other (Tukey test: $P < 0.05$), while "ns" indicates no significant difference between streams.

the stream benthos (Figure 6B), with the opposite trend occurring for motile diatoms. The composition of diatom guilds in the guts of *E. minor* (Figure 6F) mirrored the availability of resources in the stream benthos (Figure 6C) and thus the lack of any effects on feeding selectivity (Figure 6I).

Discussion

This study compared the relative abundance of diatom species in the guts of invertebrate consumers with their relative abundance in the benthos of geothermally heated streams to investigate feeding selectivity at different temperatures in a natural setting. Multiple aspects of feeding selectivity were considered, with results suggesting that different invertebrate species exhibit contrasting changes to their feeding selectivity in different thermal regimes. The use of the Hengill geothermal system facilitated ecological validity in natural conditions, but these results would now benefit from additional experiments and research on other naturally heated systems to achieve increased control, replication, and geographic coverage.

The scraping grazer *R. balthica* fed more selectively in warmer streams, as shown by a decline in gut content diversity (Figure 3A–C) and an increase in the median value of its CSI distribution (Figure 4D). This suggests a shift towards a more specialist diet at warmer temperatures, in agreement with the first hypothesis.

Similar effects have been shown for brown trout in the same study system, who select for more energetically valuable prey at higher temperatures (O'Gorman *et al.* 2016) and in latitudinal shifts in the dominance of omnivorous and herbivorous fish due to the higher nutrient quality of plant material in warmer waters (Behrens and Lafferty 2007). Specifically, *R. balthica* exhibited a greater preference for high profile over low profile diatoms in the warmest stream studied here (Figure 5A–B), supporting the second hypothesis. These patterns occurred despite a similar proportional representation of its most selectively consumed resource in each stream, suggesting that the snails actively switched their feeding to the more prevalent high profile diatom guild (Figure 6A). Benthic diatoms can exhibit both species-specific depth zonation (Cantonati et al. 2009) and form dense assemblages of varying degrees of heterospecificity in response to environmental parameters such as salinity and nutrient availability (Snoeijs and Murasi 2004; Häusler et al. 2014). Similarly, the warmest stream here was dominated by dense patches of high profile diatoms and so it may have been energetically more favorable for *R. balthica* to feed on those, rather than seeking out its preferred low profile resource. Indeed, previous laboratory studies have shown that *R. balthica* feeds unselectively on whatever resources are widely available to it (Brendelberger 1997).

Simulium aureum showed relatively little change in overall feeding strategy in different streams (Figure 4E–H), despite indications
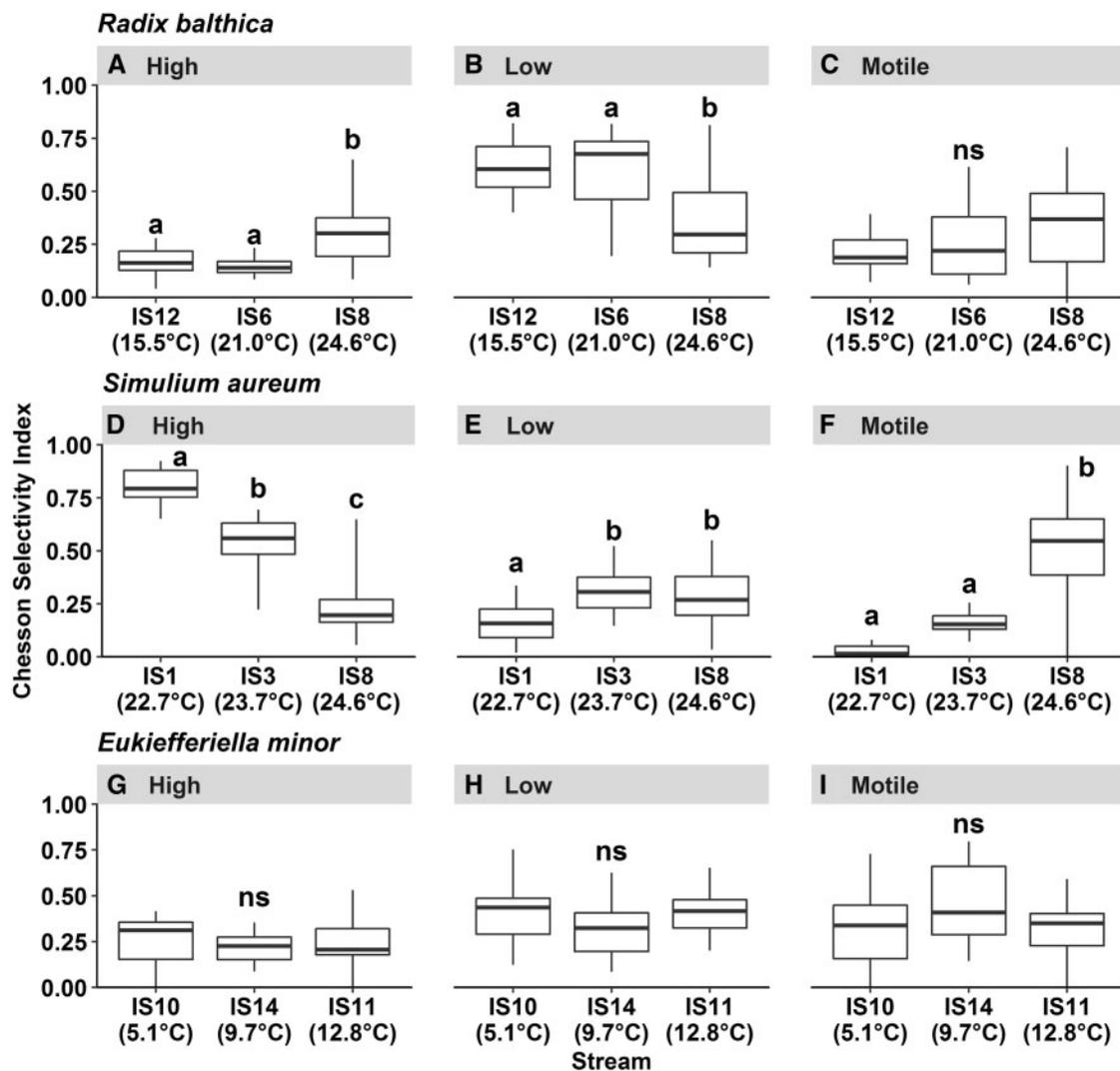
Figure 5. Preference of invertebrate consumers for diatom guilds. Box plots display Chesson Selectivity Index (CSI) values of (A–C) *Radix balthica*, (D–F) *Simulium aureum*, and (G–I) *Eukiefferiella minor* for high profile, low profile, and motile diatoms in different streams. Boxes represent the median ± interquartile range; whiskers represent the 5–95% range; single points represent outliers. Bars not sharing a common letter (a, b, or c) were significantly different from each other (Tukey test: $P < 0.05$), while "ns" indicates no significant difference between streams.

of elevated diversity of diatom species in the diet in the intermediate-temperature stream (Figure 3D–F). This is in contrast to the first hypothesis, indicating that *S. aureum* is quite a generalist feeder in all the studied streams. Analyses of diatom guilds, however, revealed a shift in preference from high profile to motile diatoms in the warmer stream (Figure 5E–H), offering support for the second hypothesis. The lack of agreement between the environmental composition, gut contents, and CSI values for *S. aureum* (Figure 6) seems to suggest active selection by the consumer, in contrast with previous studies indicating that gut contents of blackfly larvae typically reflect the composition of their environment (Wotton 1977; Wallace and Merrit 1980; Thompson 1987). The mechanism underpinning this contradictory finding, however, may lie in the feeding mode employed by the blackfly larvae. The switch from feeding on sessile high profile to motile diatoms suggests a shift from active collector gathering to filter feeding behavior. Indeed, previous studies suggest that other *Simulium* species have the capability to feed by both collector gathering and filter feeding (Burton 1973; Walsh 1985; Alder and McCreadie 1997). The latter may be a

more energetically efficient feeding strategy in warmer environments because it is a more passive mode of capturing prey, thus expending less energy through movement and contributing to Simuliidae having one of the highest growth conversion efficiencies among freshwater invertebrates (Cummins and Klug 1979).

There was little evidence for altered feeding strategy in the larvae of the collector gatherer *E. minor* in the studied streams, in contrast to the first hypothesis. The increased species richness of diatoms in the guts (Figure 3G) suggests that *E. minor* may be feeding on a broader selection of diatom species in the warmer streams, but there were no concurrent changes in evenness or diversity (Figure 3H–I), and the distribution of CSI values suggested a highly generalist diet (Figure 4I–L). Indeed, many other chironomid larvae are shown to exhibit generalist feeding behaviour (Berg 1995; Henriques-Oliveira et al. 2003; Butakka et al. 2016). There was also no evidence to suggest that *E. minor* changed its preference for any of the diatom guilds (Figure 5G–I), in contrast to the second hypothesis. Further, the relative abundance of diatom guilds in the environment closely mirrored the relative abundance in the gut contents, suggesting that
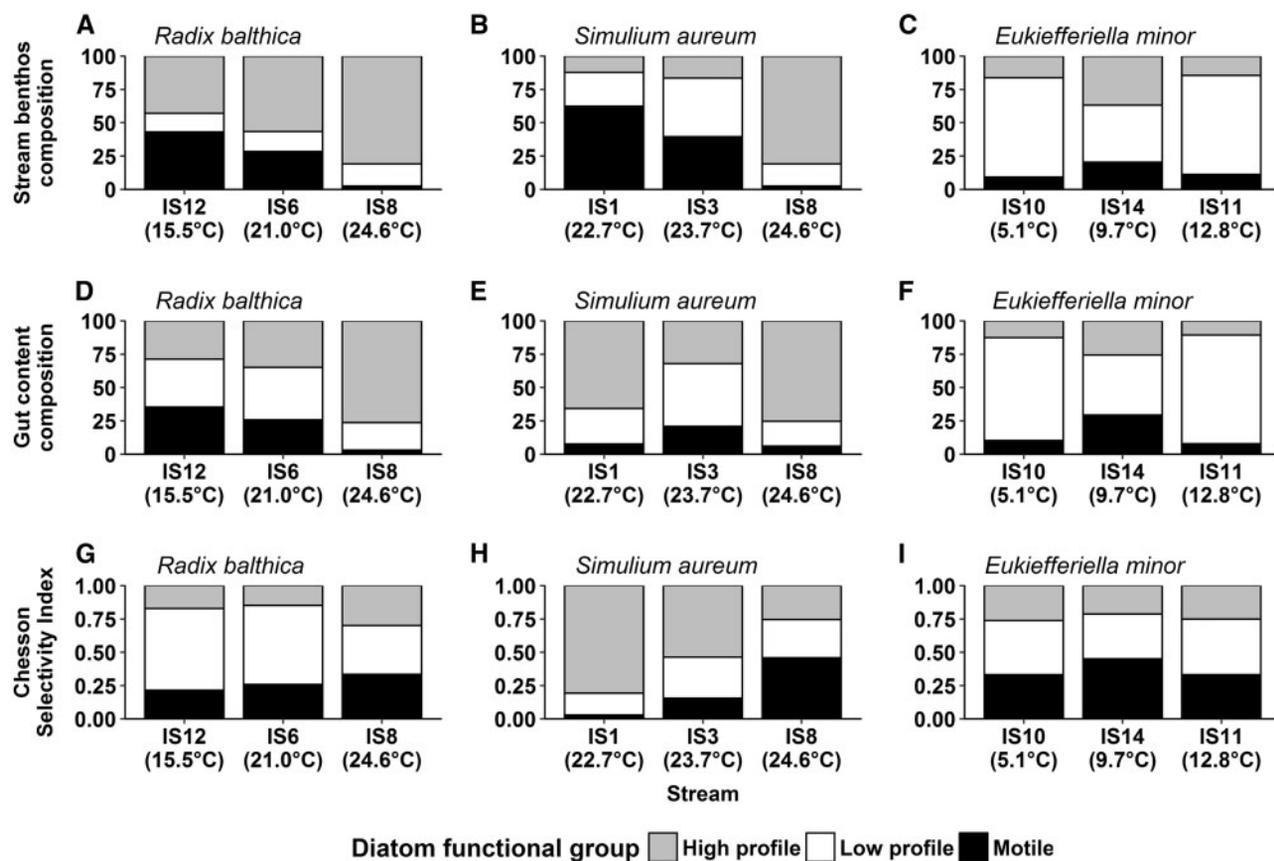
Figure 6. Key drivers of feeding preferences for different diatom guilds. Stacked barplots display relative abundances of diatom guilds (A–C) in the environment and (D–F) in the guts of invertebrate consumers. Chesson Selectivity Index values in (G–I) are the median values shown in Figure 5.

this species exhibits very little selectivity in its diet (Figure 6). Given the ability of E. minor to survive in a much wider temperature range than that covered by this study (Hannesdóttir et al. 2012), it is possible that its feeding strategy is altered at higher or lower temperatures than in the streams examined here. Alternatively, E. minor might be altering its feeding strategy by mechanisms other than selection for different diatom species or guilds. Variables such as foraging intensity, size-selection, ingestion rate, and egestion rate are known to vary with temperature in other invertebrate consumers (Hylleberg 1975; Kingsley-Smith et al. 2003; Yee and Murray 2004), and are likely to play an important role in this stream system as well. For example, R. balthica has been shown to have higher overall grazing rates in warmer streams at Hengill (O'Gorman et al. 2012). It is important to note, however, that the number of diatom species identified in the diet of E. minor was below the asymptote of the yield-effort curve for each stream. Thus, interpretation of the dietary analyses for E. minor should be treated with caution due to slight under-sampling.

Feeding efficiency can be increased by either targeting resources that require less effort to assimilate, or by targeting resources of higher nutritional value. Both of these options are possible explanations for the differences in feeding selectivity observed in R. balthica and S. aureum here. The observed shifts in the diatom guilds that were targeted may reflect a switch in preference for diatoms that were easier to acquire at higher temperatures (i.e., high profile diatoms as more prominent and easily grazed material for R. balthica than low profile diatoms; filter feeding as a less energetically

expensive feeding mechanism for S. aureum than collector gathering). However, diatoms are also known to have considerable interspecific variation in their cellular concentrations of carbon, nitrogen, and other nutrients (Moal et al. 1987; Menden-Deuer and Lessard 2000), and epithemoids such as Rhopalodia gibba (Ehrenberg) Müller, 1895, are known to fix atmospheric nitrogen via cyanobacterial endosymbionts (Prechtl et al. 2004). Further, both the ratios of cellular nutrients within individual diatom species and the rates of nitrogen fixation by R. gibba are known to change with temperature (Montagnes and Franklin 2001; Marcarelli and Wurtsbaugh 2006). It may be that the observed changes in feeding selectivity are due to consumers varying their preferences for individual species based on changing nutritional values of different diatom species with temperature. Further, it is important to note that these two potential mechanisms are not mutually exclusive, and may be working in combination or as a trade-off.

We also cannot definitively say whether a more selective diet is due to direct effects of temperature on the target organism or indirect effects via the predators, competitors, and resources that it interacts with. There is increasing top-down control by the brown trout, Salmo trutta Linnaeus, 1758, on each of the three invertebrates studied here as stream temperature increases (O'Gorman et al. 2012, 2016). Thus, changes in the feeding behavior of invertebrates may be an indirect consequence of altered habitat use as a predator avoidance mechanism (Werner and Peacor 2003). Similarly, resource production has been shown to increase with stream temperature in the Hengill system (O'Gorman et al. 2012). This raises the possibility that the standing

stock of certain diatoms may be low, but rapid replenishment after consumption may make them more readily available to invertebrates. Such uncertainties are part of a necessary trade-off in studies that utilize natural gradients, which forsake the control of laboratory experiments for the realism of natural ecosystems. A tightly controlled laboratory experiment could exclude all predators and competitors of the target organism and standardize the biofilm available for consumption to give greater mechanistic insight, however, the conditions would be so unrealistic as to cast doubt on the relevance of the findings for the real world. In contrast, the changes in feeding behavior observed in the current study will not just be a consequence of the autecological response of the target organism, but also the synecological response of the entire community of which it is a part. This complexity is an inherent part of the ecological changes we will see as a result of planetary warming in the coming decades.

In conclusion, this study demonstrates that invertebrate consumers can alter their feeding selectivity in streams of different temperature, in species-specific ways. Developing a more specialist feeding strategy by targeting the most ubiquitous resource items and altering feeding mode to preferentially consume more optimal resources are both potential mechanisms for the changes observed here. Environmental warming exerts selection pressures on organisms, including the need to increase feeding efficiency to mitigate the disproportionate increase in metabolic demand relative to ingestion rate (Rall et al. 2010). The changes in feeding selectivity observed along the stream temperature gradient here suggest that species may express different behavioural adaptations to meet the higher energetic demands of a warmer environment. The subsequent impacts on the abundance and composition of the diatom community could lead to altered nutrient cycling (e.g., through changes in nitrogen fixation) and thus cascading effects throughout the food web (Furey et al. 2012, 2014). Caution should be taken before applying the results presented here to other systems, as the lack of experimental control or spatial replication precludes mechanistic insights or general conclusions. Further consideration of individual-based changes in feeding strategy and their effects on community dynamics are thus essential to increase our understanding of how future environmental warming will alter freshwater ecosystems.

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