

1 Running Head: Seasonality in diet variation

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3 **Temporal shifts in intraspecific and interspecific diet variation:**
4 **effects of predator body size and identity across seasons in a stream community**

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Abstract

Intraspecific variation is increasingly recognized as an important factor in ecological interactions, sometimes exceeding the role of interspecific variation. Few studies, however, have examined how intra- versus interspecific variation affect trophic interactions over time within a seasonally dynamic food web. We collected stomach contents from 2028 reticulate sculpin (*Cottus perplexus*), 479 cutthroat trout (*Oncorhynchus clarkii clarkii*), and 107 Pacific giant salamanders (*Dicamptodon tenebrosus*) in western Oregon streams and compared diets among predator species and size classes over three seasons. Predator body size and species identity both showed strong effects on dietary niche breadth, proportional prey composition, and prey size, with seasonal variation in the relative magnitudes of intraspecific and interspecific diet variation. Size-associated diet variation was high in summer and fall but was heavily outweighed by species-associated diet variation in spring. This pattern was driven primarily by a 50-fold increase in the consumption of terrestrial thrips (Order: Thysanoptera) by cutthroat trout in spring compared to summer and fall. Mean dietary niche breadth generally increased with body size and was roughly half as wide in sculpin as in trout and was intermediate in salamanders. Predator-specific responses to the seasonality of terrestrial prey availability were associated with interspecific differences in foraging mode (e.g., benthic vs drift-feeding) and contributed to temporal variation in the roles of predator size and identity in trophic niche differentiation. Our results thereby demonstrate that intraspecific and interspecific diet variation can exhibit strong seasonality in stream predators, emphasizing the dynamic nature of food webs and the need to incorporate sampling over relevant temporal scales in efforts to understand species interactions.

Key words: temporal diet variation, intraspecific, predator-prey interactions, food webs, terrestrial subsidies, body size, streams

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Introduction

48 Understanding the relative importance of interspecific versus intraspecific niche variation
49 has long been recognized as being key to understanding the structure and dynamics of
50 communities (May and MacArthur 1972, Shoener 1974, Wiens 1977, Lichstein et al. 2007,
51 Violle et al. 2012, Hart et al. 2016). Nevertheless, ecologists have largely focused the study of
52 interacting populations at the species level, often ignoring the role of variation within species
53 (Abrams and Ginzburg 2000, Bolnick et al. 2011, Novak et al. 2016). Individuals within species
54 often differ from one another in many ecologically meaningful ways, including prey preferences
55 (Estes et al. 2003), microhabitat use (Schlosser 1987), vulnerability to predation (Kusano 1981),
56 and competitive ability (Svanback and Bolnick 2007). For instance, phenotypic changes that
57 occur throughout ontogeny (e.g., body size, physiology, behavior) often alter the types and
58 strengths of interactions in which individuals participate (Polis 1984, Bolnick et al. 2003,
59 Bolnick et al. 2011). Because recent empirical studies have demonstrated that intraspecific
60 variation can influence community and ecosystem processes as much as or even more than
61 interspecific variation (Des Roches et al. 2018), a renewed emphasis is being placed on
62 understanding the mechanisms that drive variation within and among species.

63 A focal point for research on intraspecific variation has been its influence on species
64 coexistence (Lichstein et al. 2007, Miller and Rudolf 2011, Nakazawa 2015, Bassar et al. 2017).
65 According to the competitive exclusion principle, species cannot stably coexist if they occupy
66 the same ecological niche (Gause 1934, Hutchinson 1957), with only the differential use of
67 resources permitting the coexistence of ecologically similar species (Chesson 2000). Such niche
68 differentiation can be achieved through three basic means: specialization on a distinct set of
69 resources (MacArthur and Levins 1967, Chesson 2000), differential utilization of resources in

70 space (May and Hassell 1981), and differential utilization of resources in time (Armstrong and
71 McGehee 1980, Chesson 1985). Several recent studies have demonstrated the importance of
72 intraspecific variation for community dynamics and the maintenance of species coexistence
73 (Hughes et al. 2008, Clark et al. 2010, Jung et al. 2010, Messier et al. 2010, Bolnick et al. 2011,
74 Pruitt and Ferrari 2011, Violle et al. 2012), yet consensus on the underlying mechanisms and
75 their effects remains elusive. While some theory suggests that intraspecific variation should
76 promote coexistence (Clark et al. 2003, Hubbell 2005, Fridley et al. 2007, Lichstein et al. 2007),
77 other theory suggests that, if anything, individual variation is more likely to prevent species
78 coexistence (Taper and Case 1985, Crutsinger et al. 2008, Hart et al. 2016). Understanding the
79 context for these effects and their underlying mechanisms will benefit from studies that quantify
80 interspecific and intraspecific variation concurrently over space and time in natural communities.

81 While intraspecific variation is increasingly being quantified with respect to resource use
82 in particular (Araújo et al. 2007, Semmens et al 2009, Coblenz et al. 2017), few studies have
83 considered how the relative magnitudes of intraspecific versus interspecific diet variation may
84 change over time. This is important because failure to consider time scales may bias inferences
85 of the strength and consistency of diet variation within and among species, especially in
86 temporally variable environments (Tinker et al. 2012, Novak and Tinker 2015). For instance, in
87 aquatic communities, which often exhibit considerable within-species variation in body size,
88 interactions between predator and prey can vary greatly over time (Closs and Lake 1994, Dodds
89 et al. 2013, Peralta-Maraver et al. 2017, Heng et al. 2018). This temporal variation in trophic
90 interactions can have strong effects on community dynamics, especially in freshwater streams
91 that have recurrent seasonal changes in community structure, hydrological discharge, primary
92 production, nutrient dynamics, and riparian influences (Closs and Lake 1994, Chaplin et al.

93 1997, Nakano et al. 1999b, Baxter et al. 2005, Power et al. 2008, Li et al. 2016). Because
94 individuals that differ in species identity and body size typically interact differently with their
95 environment, the relative magnitudes of intra- versus interspecific diet variation in stream food
96 webs may be highly variable over time.

97 In the present study, we assessed seasonal variation in the interspecific (i.e., taxonomic
98 identity) and intraspecific (i.e., body size) feeding interactions of a stream community. We
99 focused on three generalist predators that co-occur in forested streams throughout western
100 Oregon: reticulate sculpin (*Cottus perplexus*), coastal cutthroat trout (*Oncorhynchus clarkii*
101 *clarkii*), and Pacific giant salamanders (*Dicamptodon tenebrosus*). We found substantial seasonal
102 variation in the magnitudes of intraspecific and interspecific diet variation among these three
103 focal predators. This resulted primarily due to species-specific responses to seasonal changes in
104 the prey community. Our study thereby demonstrates the importance of considering both forms
105 of variation across time when seeking to understand how trophic interactions influence
106 community dynamics.

107 **Methods**

108 *Study System* – We examined the stomach contents of reticulate sculpin, cutthroat trout,
109 and Pacific giant salamanders at nine sites in Soap, Oak, and Berry Creeks located within
110 Oregon State University’s McDonald-Dunn Research Forest northwest of Corvallis, Oregon
111 (44.638 N, 123.292 W). Reticulate sculpin are small benthic fishes that prey primarily on benthic
112 macroinvertebrates (Bond 1963, Petrosky and Waters 1975, Wydoski and Whitney 1979, Scott
113 and Crossman 1998, Preston et al. 2017). As aquatic larvae, Pacific giant salamanders are also
114 benthic stream predators that consume a range of prey, including benthic invertebrates, terrestrial
115 arthropods, and other stream-dwelling vertebrates (Kelsey 1995, Cudmore and Bury 2014). In

116 contrast to sculpin and salamanders, trout are active swimmers that feed at both the water surface
117 and the benthos on a relatively even mixture of terrestrial and aquatic prey (Chapman and Bjornn
118 1969, Jenkins et al. 1970, Elliot 1973, Ware 1973). Our study streams were small (~1 to 3 m in
119 width) and flowed through mixed deciduous-coniferous forests into higher order tributaries of
120 the Willamette River. These streams support a diverse community of aquatic macroinvertebrates
121 (>325 species) (Anderson and Hansen 1987).

122 *Data Collection* - To collect stomach contents, we conducted electro-fishing surveys in
123 summer (June and July 2015), fall (September 2015), and spring (April 2016). We conducted
124 surveys during the day (0900 – 1700) at three reaches within each stream. Each reach measured
125 ~45 m in length and contained a combination of pool and riffle habitats. To capture predators, a
126 crew of four researchers conducted a single pass of electro-fishing using a backpack
127 electroshocker (Smith-Root LR20B), a block net (1.0 x 1.0 m) and two dip nets (0.30 x 0.25 m).
128 Captured predator individuals were anesthetized, measured for total length, lavaged nonlethally
129 to collect stomach contents using a 60-cc syringe with a blunt 18-gauge needle, and released
130 back into the stream following a recovery period in aerated stream water. Large trout and
131 salamanders were lavaged using a small straw (2.5 mm in diameter) attached to a 500-mL bottle
132 of stream water. We did not lavage individuals smaller than ~25 mm. Stomach contents were
133 preserved in 70% ethanol and later identified in the laboratory using a dissecting microscope (8X
134 to 35X magnification) to the lowest possible taxonomic level (mostly family) according to
135 Merritt et al. (2008). Total lengths of whole, intact prey items were measured to the nearest 0.5
136 mm. Additional details about study sites and data collection may be obtained in Preston et al.
137 (2018a) and Preston et al. (2018b).

138 *Data Analyses* – The overall goals of our analyses were to describe and quantify how
139 diets differed by species, predator size, and season. We were especially interested in whether the
140 relative effects of species and size were consistent over time, or whether they varied seasonally.
141 To examine diet variation by predator size, we subdivided each predator species into size classes
142 based on the distribution of total lengths observed when the individuals of all seasons were
143 combined. Sculpin and trout were subdivided into small, medium, and large size-classes using
144 the 25th and 75th percentile of their distributions to ensure similar numbers of individuals in
145 each size class. Due to a relatively low sample size of salamanders, we used the 50th percentile
146 to divide salamanders into two size-classes: small and large.

147 Among species, size-classes, and seasons, we compared the proportional diet
148 composition by prey counts of seven primary groups: Diptera larvae (true flies), Ephemeroptera
149 larvae (mayflies), Trichoptera larvae (caddisflies), aquatic snails (*Juga sp.*), emergent adult
150 insects (i.e., aquatic insects that have emerged from the stream), terrestrial prey (i.e., organisms
151 with no aquatic life stage), and “other”. The “other” category represented <5% of total prey
152 items. We calculated proportional diet composition in each season by dividing the total number
153 of a given prey group found in the stomach contents of a given species (or size class) by the total
154 number of prey items found in the stomach contents of that species (or size class). Permutational
155 multivariate analysis of variance (PERMANOVA) was performed to assess the statistical
156 strength of differences in individual-level dietary composition due to predator species, body size,
157 and season using the ‘*adonis*’ function in the ‘*vegan*’ R-package (Oksanen 2015). Prey counts
158 were fourth-root transformed prior to PERMANOVA to decrease the effects of extremely large
159 counts of diet items.

160 We quantified dietary niche breadth at both the species and size-class levels using
161 Levins' standardized measure (Levins 1968, Hurlbert 1978),

$$162 \quad B_i = \frac{\left[\left(\frac{1}{\sum_{i=1}^n p_{ij}^2} \right) - 1 \right]}{(n-1)},$$

163 where p_{ij} is the proportion of prey type i in the stomachs of predator group j and n is the total
164 number of prey items consumed by predator group j . Standardized niche breadth values range
165 from 0 (highly specialized) to 1 (highly generalized). Prey items were not grouped into
166 categories for these niche breadth calculations. Instead, we used the lowest possible taxonomic
167 level of prey identification (as suggested by Greene and Jaksic 1983) and treated different prey
168 life stages (i.e., larval, pupal, adult) as distinct prey types. Niche breadth means and standard
169 errors were estimated by non-parametric bootstrapping (1000 draws of 20 prey items) to account
170 for differences in sample sizes among seasons and predator groups. To evaluate diet breadth in
171 the context of prey size, we performed quantile regression analyses (using the 90th and 10th
172 quantiles) on the total lengths of predator individuals and their diet items using the '*quantreg*'
173 package in R (Koenker 2015).

174 To classify feeding relationships by predator group, we applied a hierarchical cluster
175 analysis on dietary compositions using prey-type proportions and generated dendrograms
176 depicting dietary dissimilarity among size-classes of each predator species within each season.
177 Cluster analyses were performed using the unweighted pair-group method (UPGMA) with
178 Euclidean distance to describe the dissimilarity in dietary composition (Ward 1963, Krebs 1989,
179 Amundsen et al. 2003). To supplement the cluster analyses, we calculated dietary overlap among
180 species and size classes within each season using Schoener's index of percent overlap (Schoener
181 1970),

182
$$100(1 - \frac{1}{2} \sum_i |p_{xi} - p_{yi}|),$$

183 where p_{xi} and p_{yi} represent the proportion of prey type i in the stomachs of predator species (or
184 size classes) x and y , respectively. Percent overlap ranges from 0% (no overlap) to 100%
185 (complete overlap). Schoener's index is considered to be an adequate measure of dietary overlap
186 in the absence of prey availability data (Hurlbert 1978, Wallace 1981).

187 **Results**

188 We collected stomach contents from a total of 2028 sculpin, 479 trout, and 107
189 salamanders and found 22,798 identifiable prey items belonging to 104 prey types (entailing taxa
190 and life stages within them). Predator body sizes ranged from 27 to 242 mm in total length, with
191 salamanders and trout reaching considerably larger sizes than sculpin (Fig. 1). Diptera larvae and
192 Ephemeroptera larvae were the primary prey groups found in stomach contents, constituting
193 36.9% and 36.4% of all food items across all predators, respectively (Fig. 2). Cannibalism was
194 observed in 14 sculpin (13 singletons, 1 doubleton) and 2 trout (both singletons), and predation
195 on sculpin was observed in 2 salamanders (both singletons). We could not find identifiable prey
196 in 115 sculpin (5.67%), 19 trout (3.97%), and 13 salamanders (12.1%) (see Table S1 for numbers
197 of stomachs sampled and percent empty by size class and season).

198 In general, sculpin and salamander diets were comprised primarily of benthic aquatic
199 invertebrates, whereas trout diets were comprised of a more even mixture of terrestrial, aquatic,
200 and semi-aquatic prey. Trout diets, which contained the highest overall proportions of adult
201 aquatic insects (9.4%) and terrestrial prey (19.8%), also exhibited the greatest seasonal variation,
202 including a shift in proportional consumption of terrestrial thrips (Order: Thysanoptera) from less
203 than 1% in summer and fall to 49.8% in spring. Proportions of Diptera larvae and Ephemeroptera
204 larvae found in trout stomachs were also highly variable across seasons; trout diets contained

205 relatively high and even proportions of Diptera and Ephemeroptera in summer (~35% and ~33%,
206 respectively), high proportions of Diptera (~52%) and low proportions of Ephemeroptera (12%)
207 in fall, and low proportions of both in spring (~9% and ~15%) (Fig. 2). Sculpin and salamander
208 diets exhibited relatively minimal seasonal variation in proportional diet compositions compare
209 to trout (Tables S2-S4).

210 Dietary niche breadth varied seasonally within species but was highest (most generalized)
211 in trout, lowest (most specialized) in sculpin, and consistently higher in the larger size-classes
212 within each species (Fig. 3). Mean dietary niche breadth was roughly half as high in sculpin ($\overline{B_i}$
213 = 0.041; 95% CI = 0.023 to 0.059) as in trout ($\overline{B_i}$ = 0.078; 95% CI = 0.043 to 0.113) over all
214 seasons combined, with salamanders exhibiting intermediate values ($\overline{B_i}$ = 0.062; 95% CI =
215 0.033 to 0.091). Sculpin dietary niche breadth was lowest in summer ($\overline{B_i}$ = 0.034; 95% CI =
216 0.019 to 0.049) and highest in spring ($\overline{B_i}$ = 0.043; 95% CI = 0.028 to 0.058). Salamander dietary
217 niche breadth was also lowest in summer ($\overline{B_i}$ = 0.044; 95% CI = 0.029 to 0.059) but was highest
218 in fall ($\overline{B_i}$ = 0.063; 95% CI = 0.036 to 0.090). Trout dietary niche breadth was lowest in fall ($\overline{B_i}$
219 = 0.049; 95% CI = 0.023 to 0.075) and highest in spring ($\overline{B_i}$ = 0.086; 95% CI = 0.049 to 0.123).

220 Predators of differing body size and of differing identity both differed in the mean size
221 and composition of prey they consumed (Figs 3-4; Tables S2-S4). Mean prey length (\overline{TL}) was
222 much larger in salamanders (\overline{TL} = 7.6 mm, σ = 6.7) compared to sculpin (\overline{TL} = 2.8 mm, σ = 2.7)
223 and trout (\overline{TL} = 2.5 mm, σ = 2.7) and generally increased with increasing predator body size (Fig.
224 4). For sculpin and trout, Diptera larvae were generally found in higher proportions in the diets
225 of smaller size classes, whereas the proportions of Ephemeroptera larvae were higher in larger
226 size classes. Based on proportional diet composition, large sculpin consumed 19.1% (averaged
227 difference across seasons) fewer Diptera larvae and 19.5% more Ephemeroptera larvae than

228 small sculpin. Similarly, large trout consumed 27.4% fewer Diptera larvae and 11.3% more
229 Ephemeroptera larvae than small trout. Larger trout also consumed higher proportions of adult
230 aquatic insects and terrestrial prey than smaller trout. Small salamander diets contained higher
231 proportions of Ephemeroptera larvae but larger salamanders generally consumed more prey that
232 were not Ephemeroptera or Diptera (e.g., snails, crayfish, annelids, other rare prey).
233 PERMANOVA analysis confirmed the statistical strength of these dietary differences among
234 predator species (pseudo-F = 37.95, $p < 0.001$), body sizes (pseudo-F = 58.23, $p < 0.001$), and
235 season (pseudo-F = 73.57, $p < 0.001$; Table 1).

236 The hierarchical clustering of size classes by diet dissimilarity varied across seasons (Fig.
237 5). Diet dissimilarity among size classes was lowest in summer (Fig. 5A), intermediate in fall
238 (Fig. 5B), and highest in spring (Fig. 5C). In summer and fall, the diets of heterospecific size-
239 classes were often more similar than the diets of conspecific size-classes. Only in spring were
240 size classes clustered according to predator species, with sculpin and salamander diets being
241 highly dissimilar to trout diets, a result that was driven primarily by a large increase in terrestrial
242 thrips found in trout stomachs. Calculations of percent overlap were consistent with results of the
243 cluster analyses (Table S3). Dietary overlap generally decreased with increased differences in
244 body size within and between species, and trout size-classes showed the lowest dietary overlap
245 with sculpin and salamander size-classes in spring.

246 Discussion

247 The relative magnitudes of intra- and interspecific diet variation are recognized as being
248 important to shaping community dynamics, yet few studies have evaluated the degree to which
249 these two types of variation are static or dynamic in time. In the present study, we compared
250 intraspecific and interspecific variation in feeding interactions within a stream community over

251 three seasons. Our primary finding is that size-associated diet variation had a strong influence on
252 feeding relationships in summer and fall but was heavily outweighed by species-associated diet
253 variation in spring. This pattern emerged largely due to predator-specific responses to seasonal
254 changes in prey availability. Our study therefore demonstrates that the relative roles of
255 intraspecific and interspecific variation can be temporally dynamic, thereby emphasizing the
256 importance of considering them at relevant temporal scales, beyond just ‘snapshots’ in time.

257 Seasonal changes in prey composition and availability contributed to the temporal
258 variation in intra- and interspecific diet variation. Trout diets were comprised of a mixture of
259 terrestrial and aquatic prey but were highly variable across seasons, with spring diets containing
260 high proportions of terrestrial prey. In contrast, sculpin and salamander diets were comprised
261 primarily of benthic aquatic prey and showed relatively low seasonal variation. While seasonal
262 inputs of terrestrial invertebrates can have strong effects on trophic interactions in streams
263 (Nakano et al. 1999b, Nakano and Murakami 2001, Kawaguchi et al. 2003, Baxter et al. 2005),
264 their relative effects can differ strongly across predator-prey interactions. For instance, seasonal
265 diet shifts are ubiquitous among freshwater salmonids but are not widely observed in sculpin or
266 salamanders (Wilhelm et al. 1999, Li et al. 2016, Cochran-Biederman and Vondracek 2017).
267 Preston et al. (2018a) also suggest that prey-specific sculpin feeding rates are relatively
268 consistent across space and time in our study streams, especially compared to the more variable
269 trout diets observed in the present study.

270 Differences in dietary niche breadth and in responses to changing prey availability among
271 our focal predators likely stem from differences in foraging strategies. Sculpin and salamanders
272 are bottom-dwellers that employ ambush predation to feed primarily on benthic
273 macroinvertebrates (Bond 1963, Daniels and Moyle 1978, Kratz and Vinyard 1981, Wells 2007,

274 Cudmore and Bury 2014). In contrast, trout are active swimmers that exhibit a wider diet breadth
275 because they feed on both aquatic and terrestrial prey in the benthos and throughout the water
276 column (Chapman and Bjornn 1969, Jenkins et al. 1970, Elliot 1973). Trout diets are therefore
277 expected to exhibit greater responses to the changes in availability of terrestrial prey, that are
278 inherent to streams, than are the diets of sculpin and salamanders. Because of the high seasonal
279 variation in availability of terrestrial prey compared to the relative consistency of the benthic
280 prey community in our study streams (Preston et al. 2018a), trout diets showed much greater
281 seasonal variation compared to sculpin and salamander diets. These results are consistent with
282 prior experimental work. By manipulating inputs of terrestrial invertebrates into streams, Gillette
283 (2012) demonstrated that stream predators can indeed exhibit species-specific responses to
284 changes in the availability of terrestrial prey based on differences in diet breadth and foraging
285 behavior. Species-specific responses are also observed in riparian consumers when aquatic
286 derived subsidies are manipulated (Paetzold et al. 2006, Marczak and Richardson 2007). Taken
287 together, these results emphasize how the interplay of predator characteristics (e.g., diet breadth
288 and foraging behavior) and prey characteristics (e.g., seasonal changes in availability) can
289 interact to drive temporal shifts in interspecific diet variation.

290 The high seasonal diet variation of trout was driven largely by consumption of western
291 flower thrips (Thysanoptera: Thripidae), which comprised nearly half of all prey consumed by
292 trout in the spring but comprised less than 1.0% in summer and fall. Thrips were not a major diet
293 item in sculpin or salamanders in any season. Thrips, which are considered widespread
294 agricultural pests (Teulon et al. 1993), hatch from eggs in plant tissues and later drop to the
295 ground before metamorphosing into adults (Sanderson 1990). The timing of the thrip lifecycle is
296 temperature dependent, with the larval stage lasting just five to 20 days. Thus, larval thrips

297 apparently dropped from overhanging canopy into our study streams prior to or during the spring
298 surveys and were subsequently consumed at disproportionately high rates by trout compared to
299 the consumption rates by sculpin and salamanders. Previous evidence of thrip consumption by
300 stream predators is scarce but has been documented in brook trout (Williams 1981) and
301 sticklebacks (Hynes 1950). However, similar temporally-pulsed inputs of terrestrial arthropods
302 are well documented in forested streams and are known to contribute a large portion of available
303 prey for streams predators (Wipfli 1997, Kawaguchi and Nakano 2001, Romero et al. 2005,
304 Chan et al. 2007). Consumption of cross-ecosystem subsidies by top predators such as trout can
305 reshape the structure and energetic dynamics of stream food webs (Perkins et al. 2018). Our
306 results exemplify how specific community members (i.e., thrips and cutthroat trout in our study)
307 can disproportionally contribute to cross-ecosystem fluxes of nutrients and matter from land to
308 water (Polis et al. 2004).

309 Predator-prey body sizes had a strong influence on feeding relationships, especially in
310 summer and fall. For instance, salamanders, which exhibited some of the largest body sizes
311 among our focal predators, fed on substantially larger prey, including prey taxa that were rare in
312 sculpin and trout diets (e.g., crayfish, caterpillars, snails). Despite aquatic snails (*Juga* sp.) being
313 the most abundant benthic macroinvertebrates by biomass in our study streams (Preston et al.
314 2018b, Hawkins and Furnish 1987), sculpin feeding rates on snails were among the lowest for all
315 observed prey, likely reflecting their low digestibility (Preston et al. 2018b) and morphological
316 constraints of predators (e.g., gape width and size of digestive tract). Additionally, cannibalism
317 and intraguild predation among our focal predators (i.e., sculpin eating sculpin, trout eating trout,
318 salamanders eating sculpin) was more common in larger individuals. The influence of body size
319 on feeding interactions is not surprising given that body size is widely recognized as a key trait

320 dictating an organism's trophic ecology and interactions with its environment (Werner and
321 Gilliam 1984, Woodward et al. 2005, Woodward and Warren 2005, Petchey et al. 2008, Rudolf
322 et al. 2014). For example, Woodward and Hildrew (2002) demonstrated that feeding
323 relationships within a guild of stream predators were driven primarily by body-size constraints
324 that led to less diverse diets in smaller predators by restricting consumption to a limited subset of
325 the prey-size spectrum. Consistent with this result, we found that both dietary niche breadth and
326 prey size generally increased with predator body size, and dietary overlap was generally higher
327 between groups of similar body size. In several cases, dietary overlap was higher between
328 heterospecifics of similar body size than between conspecifics of dissimilar body size (see Table
329 S5). In summer and fall, for example, higher dietary overlap was observed between small trout
330 and small sculpin than between small sculpin and large sculpin. In spring, however, dietary
331 overlap between small sculpin and small trout was less than half the overlap between small and
332 large sculpin, which again reflects the influence of terrestrial prey availability on feeding
333 relationships in our study.

334 Temporal variability in the magnitudes of intra- versus interspecific variation may play
335 an important role in the coexistence of our focal predators by limiting similarity in resource use
336 over time. According to classic niche theory, increased dissimilarity in resource use should lead
337 to decreased competition (MacArthur and Levins 1967, File et al. 2012). Thus, seasonal shifts in
338 intra- and interspecific diet variation, such as those caused by changes in prey availability,
339 should theoretically coincide with changes in the strength of competition (Zaret and Rand 1971,
340 Chase and Leibold 2003, Correa and Winemiller 2014, Neves et al. 2018). For instance, Zaret
341 and Rand (1971) suggest that increased interspecific competition during the dry season when
342 food resources in tropical streams are low provides a good explanation for seasonal diet shifts in

343 characin fishes. This flexibility of resource partitioning has been suggested as a key mechanism
344 for coexistence of stream predators (Nakano et al. 1999a, Dineen et al. 2007). Assuming classic
345 niche theory holds true, if interspecific diet variation is lower (i.e., higher species-level overlap
346 in diet) at times of the year when terrestrial prey inputs are scarce, then intraspecific diet
347 variation may provide a seasonally important mechanism to promote species coexistence by
348 reducing species-level resource overlap among our focal predators. However, because (1) we did
349 not estimate feeding rates nor quantify the limiting availability of prey, (2) species overlapping
350 in resources do not necessarily compete (Menge 1979), (3) competition may occur along
351 multiple niche dimensions beyond diet (Pianka 1975), and (4) patterns of niche overlap may
352 reflect “ghosts of competition past” (Connell 1980), we are here unable to infer the strength of
353 competition in our system. Our results nevertheless provide strong evidence that the relative
354 magnitudes of intra- and interspecific diet variation can change over time, and hence competition
355 is likely to exhibit temporal variation as well. Our study therefore suggests that temporal scales
356 are an important consideration in efforts to understand coexistence.

357 Given that seasonality in environmental factors and the strength of predator-prey
358 interactions is widespread across various ecosystems and taxa (Ostfeld and Keesing 2000,
359 Thompson et al. 2012, Humphries et al. 2017, Calizza et al. 2018), temporal variation in the
360 relative magnitudes of intraspecific and interspecific diet variation is likely to be inherent to most
361 food webs. The seasonal influx of a single prey type, terrestrial thrips, into our study streams was
362 enough to substantially increase interspecific diet variation in spring. Examples of temporal
363 pulses in the availability of even a single prey type are widespread and occur across various time
364 scales (Yang et al. 2010): diurnal pulses of marine copepods consumed by pelagic fishes (Godin
365 1981), annual pulses of anadromous fish carcasses providing food for minks (Ben-David 1997),

366 and multiannual fluctuations in abundances of rodents consumed by owls (Korpimäki 1992).
367 Diet studies conducted on time scales that are poorly matched to the relevant intrinsic and
368 extrinsic drivers, such as seasonal variation in prey communities, may not capture the full picture
369 of how temporally dynamic trophic interactions can be in nature. In the present study, our
370 estimates of diet variation are averaged over multiple weeks and compared across seasons,
371 whereas higher (or lower) diet variation may be revealed on much different time scales (e.g.,
372 diurnal, annual, decadal). We recommend that future studies of trophic interactions should
373 consider temporal changes in prey populations and incorporate time scales that are relevant to the
374 life histories of the interacting species.

375

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675

Figure Captions

676 **Figure 1.** Frequency histograms of total lengths for sculpin (A-C), trout (D-F), and salamanders
677 (G-I) in summer, fall, and spring. Dashed vertical red lines depict the division of size classes
678 (25th and 75th percentile of cumulative size distribution for sculpin and trout; 50th percentile for
679 salamanders).

680 **Figure 2.** Proportional composition (based on counts) of primary prey groups in diets of sculpin
681 (CP), trout (OC), and salamanders (DT) in summer (A), fall (B), and spring (C). Adult stages of
682 aquatic insects are grouped separately from terrestrial organisms that undergo no aquatic life
683 stages. The “other” category is comprised of aquatic and semi-aquatic prey that individually
684 amounted to less than 5% of predator diets.

685 **Figure 3.** Mean dietary niche breadth (Levins’ standardized measure) by size class for sculpin
686 (CP), trout (OC), and salamanders (DT) in summer (A), fall (B), and spring (C). Lower niche
687 breadth values indicate more specialized (less diverse) diets. Error bars represent 95%
688 confidence intervals around the mean.

689 **Figure 4.** Regression plots depicting the 10th and 90th quantiles for the relationships between
690 total lengths of sculpin (A-C), trout (D-F), and salamanders (G-I) and whole, intact food items in
691 their stomach contents in summer, fall, and spring.

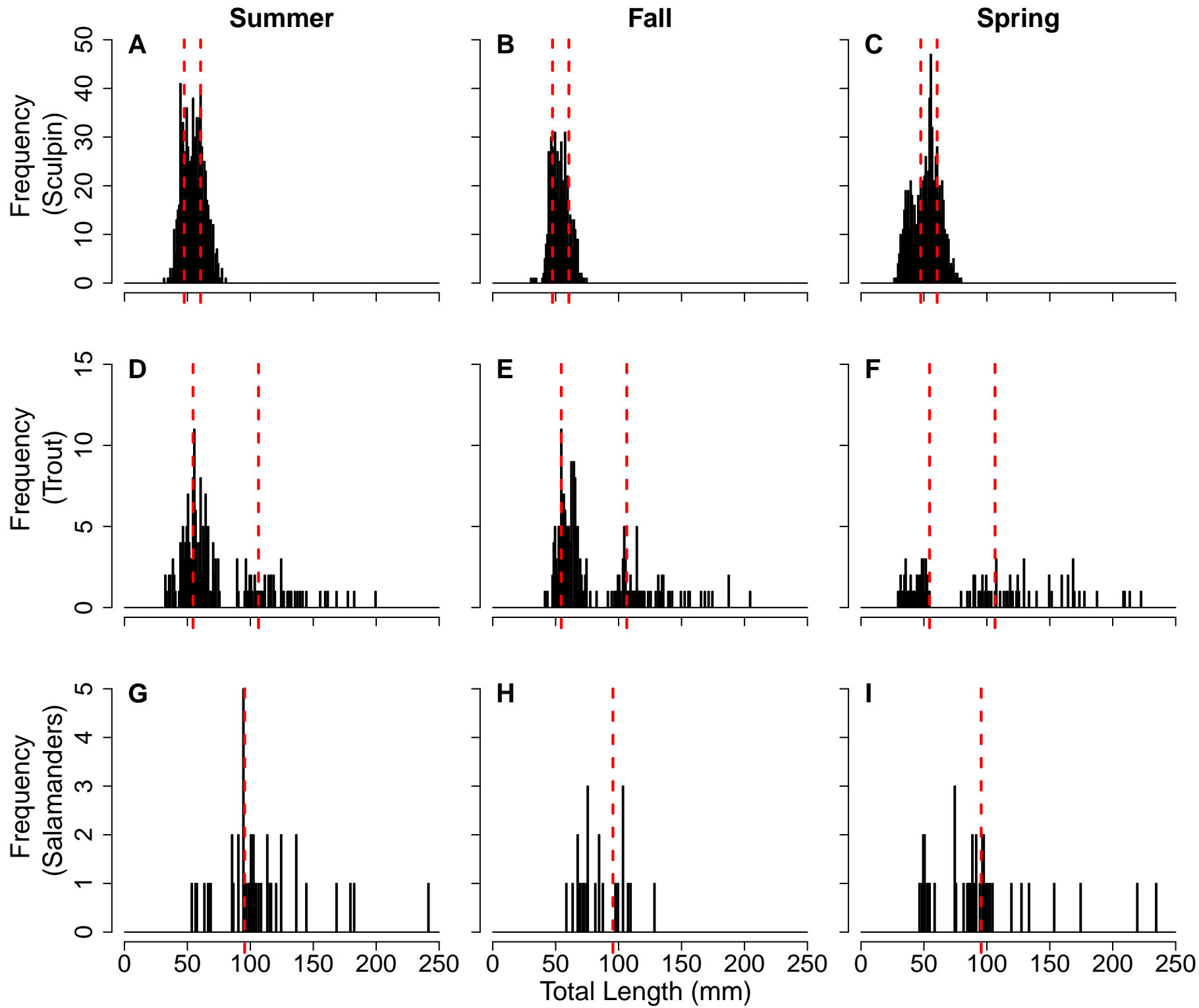
692 **Figure 5.** Dendrograms generated from hierarchical cluster analyses of proportional diet
693 composition in size classes of sculpin (CP), trout (OC), and salamanders (DT) in summer (A),
694 fall (B), and spring (C). Shorter branches represent greater similarity in dietary composition
695 between the connected groups.

696 **Table 1.** Permutational multivariate analysis of variance (PERMANOVA) of dietary
697 composition with stomachs as sites and predator size, season, and species as fixed factors.

Factor	df	SS	MS	psuedo-F	P-value
Predator size (TL)	1	15.23	15.225	58.233	<0.001 ^a
Season	2	38.47	19.234	73.566	<0.001 ^a
Species	2	19.84	9.9206	37.945	<0.001 ^a
Residuals	2461	643.43	0.2614	-	-
Total	2466	716.96	-	-	-

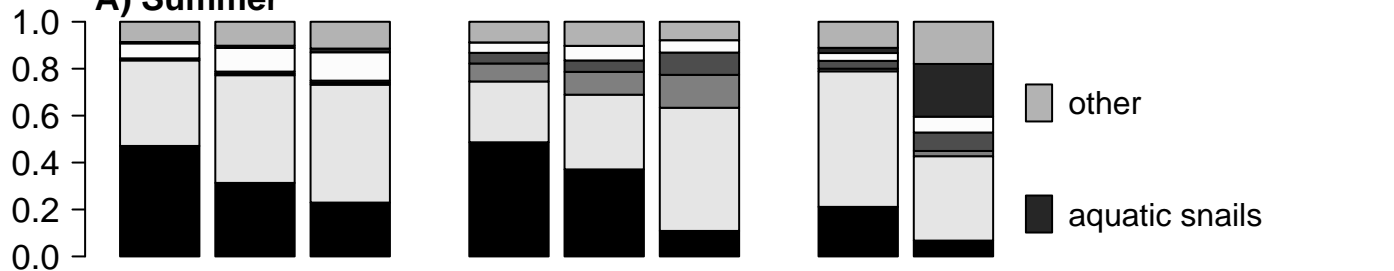
^a Indicates significant results

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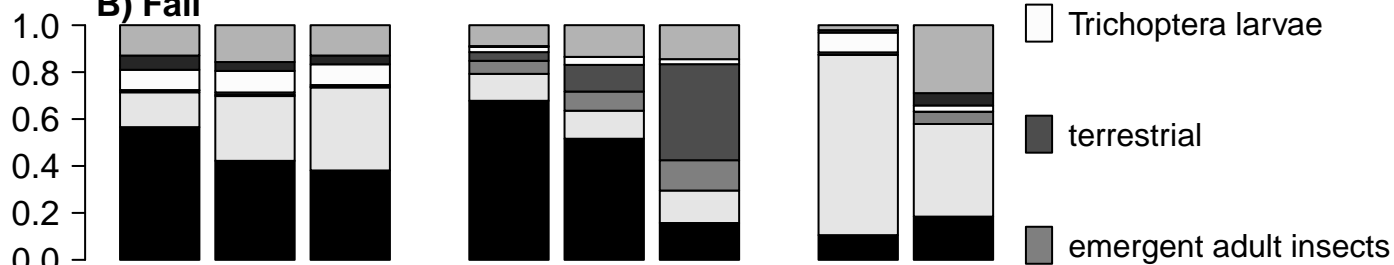


Proportional diet composition (counts)

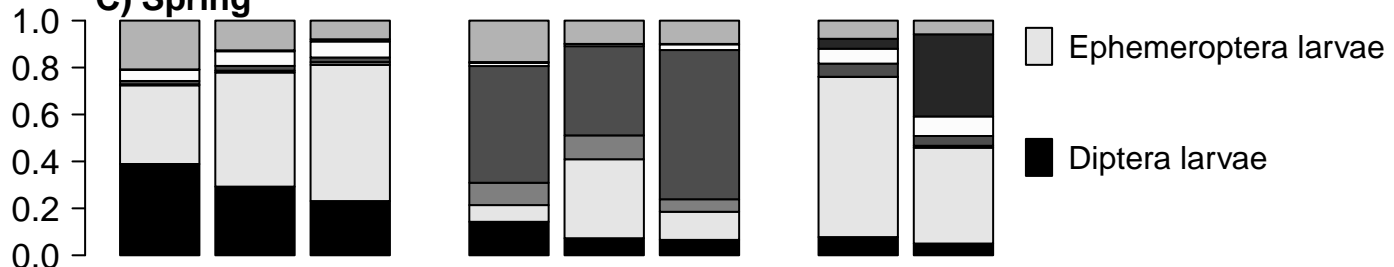
A) Summer

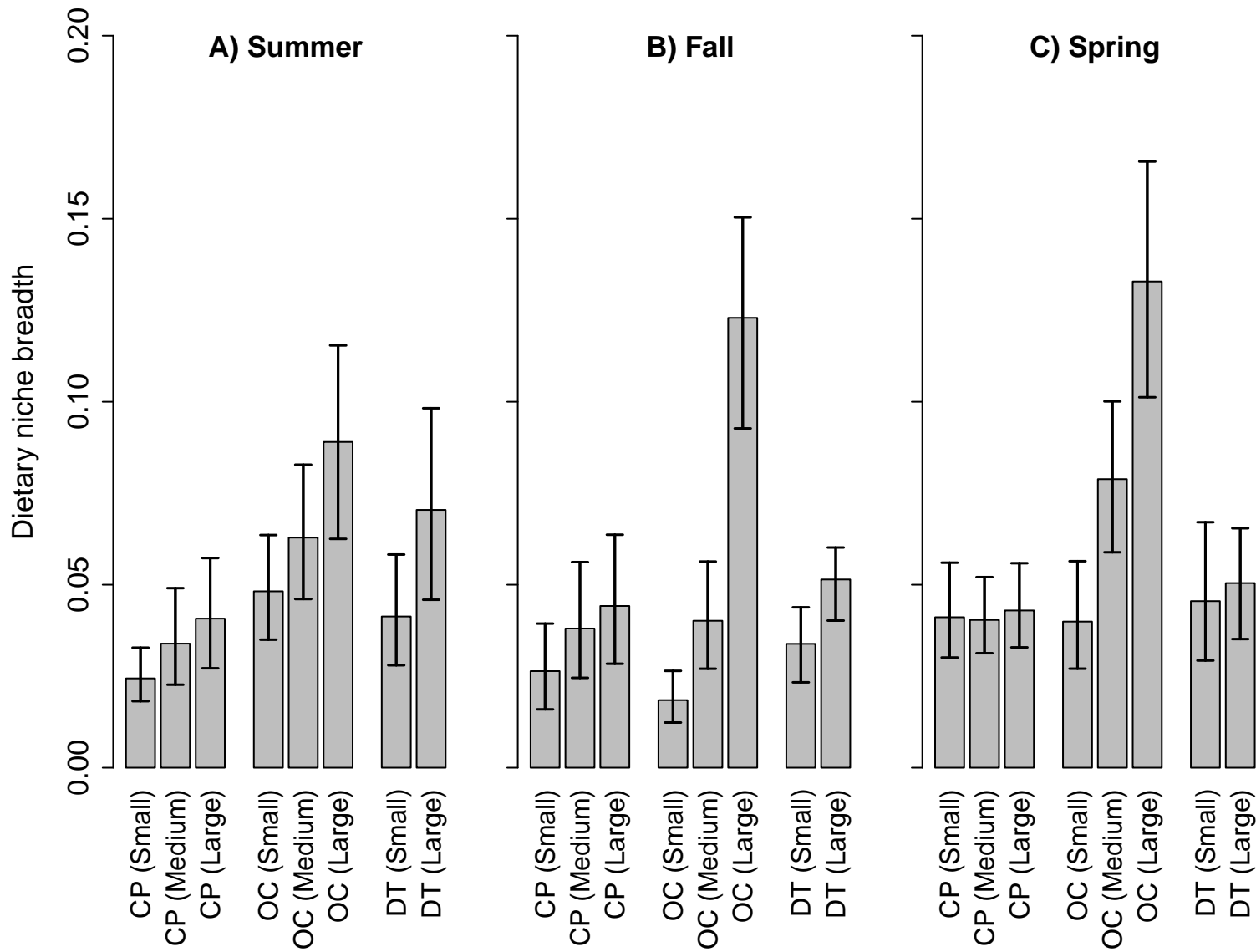


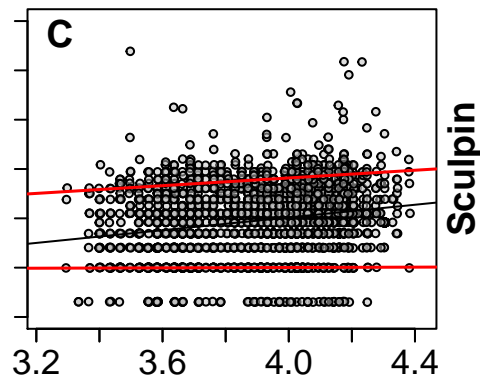
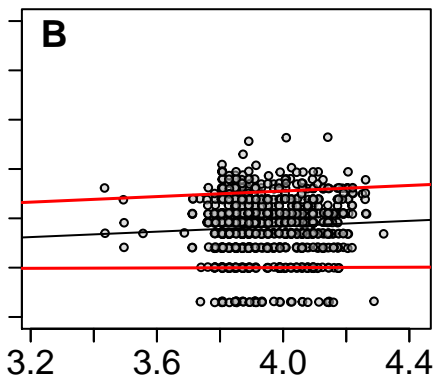
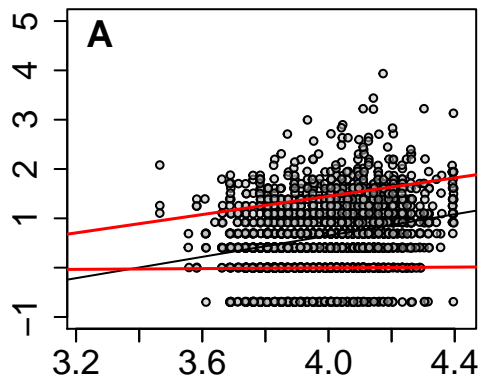
B) Fall



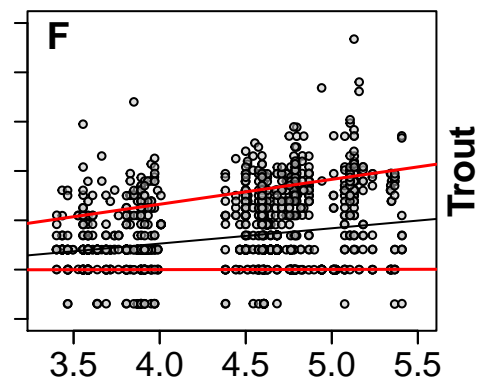
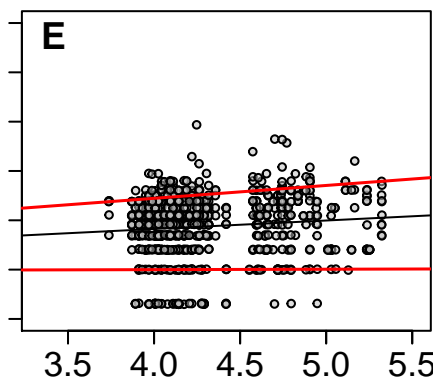
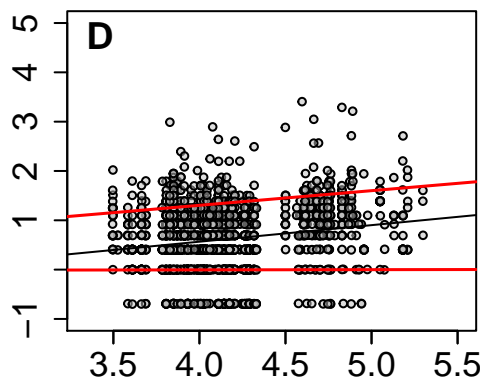
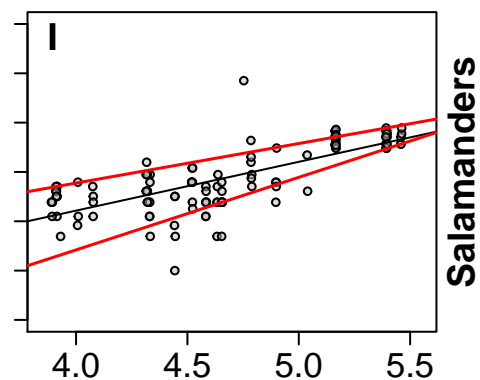
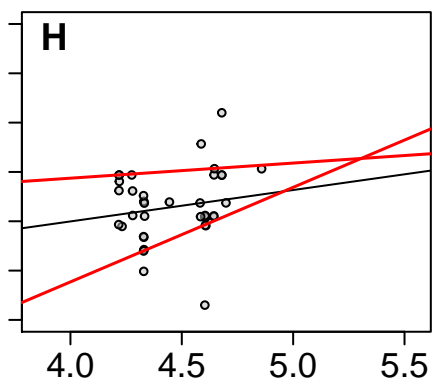
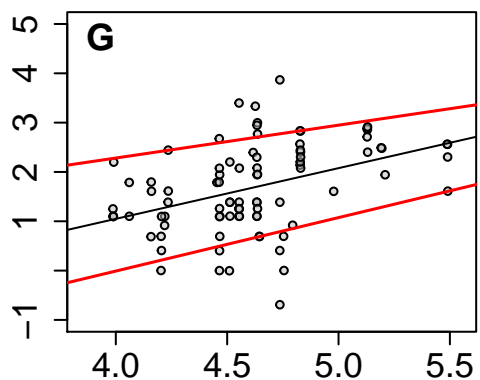
C) Spring





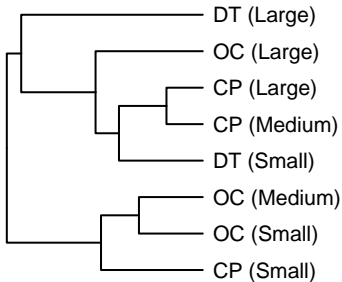
Summer**Fall****Spring****Sculpin**

Log Prey Total Length (mm)

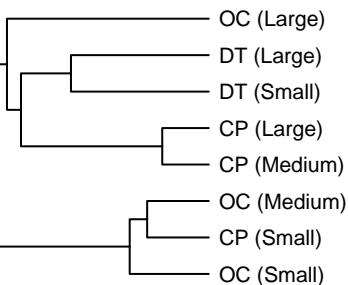
**Trout****Salamanders**

Log Predator Total Length (mm)

A) Summer



B) Fall



C) Spring

