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**Importance of non-native isopods and other terrestrial prey resources to steelhead/rainbow trout *Oncorhynchus mykiss* in coastal streams in Big Sur, California.**

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Running title: Non-native terrestrial isopods in *O. mykiss* diets in Big Sur, California.

**Abstract**

Terrestrial invertebrates provide important prey subsidies to many stream fishes. Non-native invertebrates are widespread in many ecosystems, yet they have received little attention in studies of subsidies to stream food webs. We sampled coastal basins in Big Sur, California, to determine the importance of non-native isopods and other terrestrial invertebrates in the summer diet of steelhead/rainbow trout (*Oncorhynchus mykiss*) and to estimate the density of isopods along streambanks. Terrestrial invertebrates contributed more than 40% of the

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29 energetic value of *O. mykiss* stomach contents at most sites and up to 75% at some locations.  
30 Non-native isopods *Armadillidium vulgare* or *Porcellio scaber* occurred at all sites, reaching  
31 mean densities of up to 13 individuals/m<sup>2</sup> on streambanks, and accounted for up to 20% of the  
32 energy in the diet. The proportion of non-native isopods in the diet was positively correlated  
33 with their density at a site, and the frequency and energetic value of terrestrial invertebrates  
34 and non-native isopods in *O. mykiss* diets increased with fish size. In terms of the broader diet,  
35 the energetic value and taxonomic composition of stomach contents varied among sites but  
36 there was no major geographic pattern or trend to the variation and overall *O. mykiss* diets  
37 were generally similar across the region. Our results highlight that non-native terrestrial  
38 invertebrates may provide a considerable but overlooked subsidy to stream fishes.

39  
40 Keywords: Diet, non-native species, riparian, salmonid, stream, subsidies.

## 41 **1 | INTRODUCTION**

42 Terrestrial invertebrates provide important prey subsidies to many stream fishes, and a large  
43 number of studies have examined various aspects of their occurrence and ecological effects  
44 (reviewed in Baxter et al., 2005; Paetzold et al. 2007; Richardson et al., 2010; Wipfli & Baxter,  
45 2010). In forested basins in particular, terrestrial invertebrates often compose the majority of  
46 the biomass or energy in the diets of stream salmonids in certain seasons, typically summer and  
47 fall (Bridcut, 2000; Romero et al., 2005; Utz & Hartman, 2007; Rundio & Lindley, 2008; Li et al.,  
48 2016), and provide more than half of the annual energy budget in some cases (Nakano &  
49 Murakami, 2001; Sweka & Hartman, 2008; Sato et al.; 2011). Subsidies of terrestrial  
50 invertebrates have been shown to affect the growth, local abundance, and movement of  
51 stream salmonids (Kawaguchi et al., 2003; Baxter et al., 2007; Erős et al., 2012; Atlas et al.,  
52 2013) and alter trophic interactions and reciprocal prey fluxes in adjacent stream and riparian  
53 food webs (Nakano et al., 1999; Baxter et al., 2004; Sato et al., 2012).

54 Non-native invertebrates are widespread in many ecosystems and can have strong  
55 ecological effects (e.g., Niemelä & Mattson, 1996; Holway et al., 2002; Bohlen et al., 2004; Kenis  
56 et al., 2009; Jackson et al. 2017), yet they have received almost no attention in studies of  
57 terrestrial prey subsidies to streams. Roon et al. (2018) documented that non-native green

58 alder sawflies (*Monsoma pulveratum*) reduced riparian foliage and both increased the biomass  
59 and altered the taxonomic composition of terrestrial prey inputs to streams in Alaska during  
60 summer months. Despite these effects, however, sawflies did not alter the biomass of native  
61 invertebrates on foliage or in terrestrial infauna to streams. Further, sawflies did not alter the  
62 biomass of native invertebrates in the diets of juvenile coho salmon (*Oncorhynchus kisutch*) and  
63 themselves constituted only a minor portion of the diet (11% by biomass) even in the month  
64 when they were most abundant and dominated terrestrial subsidies (Roon et al., 2018).

65 In contrast to the minor importance of invasive sawflies to the diet of juvenile coho  
66 salmon in Alaska streams (Roon et al., 2018), we previously found that non-native terrestrial  
67 isopods are a major component of the diet of *Oncorhynchus mykiss* (steelhead/rainbow trout)  
68 in a small basin on the central coast of California (Rundio & Lindley, 2008). Non-native  
69 European isopods, particularly *Armadillidium vulgare* and *Porcellio scaber*, have become  
70 established globally in temperate regions. They can reach densities of hundreds to thousands of  
71 individuals/m<sup>2</sup> (Miller & Cameron, 1987; Frouz et al., 2004) and dominate the arthropod  
72 assemblages in some riparian areas (Holway, 1998; Ellis et al., 2001; Catron et al., 2003).  
73 Despite their abundance and potential influence on litter decomposition and nutrient dynamics  
74 (Hassall et al., 1987; Zimmer et al., 2002; Frouz et al., 2008; Špaldeňová & Frouz, 2014), little is  
75 known about their effects in invaded ecosystems. In California, non-native isopods were first  
76 reported in the San Francisco Bay area in the early 1900s and apparently became established in  
77 the region within several decades (Paris, 1963). In our prior study of seasonal patterns of prey  
78 resources and *O. mykiss* diet, we found that non-native isopods provided 30–40% of the total  
79 biomass and 20–30% of the energy consumed by *O. mykiss* over a 15-month period in two  
80 study reaches in Big Creek, a small basin in the relatively undeveloped Big Sur coast more than  
81 100 km south of San Francisco Bay (Rundio & Lindley, 2008).

82 Our primary objectives in this study were to assess the importance of non-native  
83 isopods and other terrestrial prey to *O. mykiss* and estimate the riparian density of non-native  
84 isopods in basins across the entire Big Sur coast, and to evaluate whether diet or isopod density  
85 were related to geographic or landscape variables within the region. In addition, because there  
86 are few diet data for coastal *O. mykiss* populations in south-central California where they are

87 listed as threatened under the U.S. Endangered Species Act, our secondary objective was to  
88 evaluate basic aspects of energy content and composition of the diet. This included differences  
89 related to fish size, which is often a large source of diet variation in stream salmonids and in  
90 particular may influence the use of terrestrial prey (Dineen et al. 2007; Gustafsson et al. 2010;  
91 Syrjänen et al., 2011) including non-native isopods (Rundio & Lindley, 2019). Finally, although  
92 landscape conditions across the Big Sur coast are relatively similar in terms of major features  
93 such as landform, forest type, low level of development, and climate, the region is large (> 100  
94 km from north to south) and there is some local variation in geology and other environmental  
95 conditions (Rundio 2009), so we also sought to determine whether there were large-scale  
96 geographic patterns or trends in diet or riparian isopod abundance. Specifically, we sampled *O.*  
97 *mykiss* diets and riparian isopods in 11 basins on the Big Sur coast (including Big Creek) during  
98 summer to evaluate (1) variation in the energetic value, taxonomic composition, and  
99 proportions of terrestrial prey and non-native isopods in the diet among sites and with respect  
100 to fish size; (2) the occurrence and density of non-native isopods on streambanks and  
101 correlations with occurrence in the diet; and (3) relationships between diet and isopod density  
102 and geographic/landscape variables. Ultimately, our study was meant to provide an example to  
103 highlight the potential but overlooked importance of subsidies of non-native terrestrial  
104 invertebrates to stream fishes that may occur in many systems.

105

## 106 **2 | METHODS**

### 107 **2.1 | Study area**

108 The Big Sur coast in central California consists of relatively small basins that drain the Santa  
109 Lucia Mountains (Figure 1). Stream channels generally have high gradients and are confined in  
110 steep hillsides. The primary channel types are step-pool and cascade, although plane-bed and  
111 pool-riffle channels (Montgomery & Buffington, 1997) occur at lower elevations in some basins.  
112 The region has a Mediterranean-type climate with moderate temperatures (monthly means  
113 between 10–16 C), dry but foggy summers, and precipitation coming as rainfall from winter  
114 storms. Stream flows generally are stable from late spring through fall and increase during  
115 winter with high flow events during storms. Riparian forests are dominated by coast redwood

116 (*Sequoia sempervirens*), white alder (*Alnus rhombifolia*), and bigleaf maple (*Acer*  
117 *macrophyllum*). Limited farming, livestock grazing, logging, and mining occurred in many of the  
118 basins in the previous century. Present land use is relatively low and most of the region is in  
119 national forest with isolated homes, roads and recreation trails. There are no urban areas in the  
120 region, although services are concentrated in the unincorporated community of Big Sur (Figure  
121 1).

122 We sampled *O. mykiss* diets and riparian isopods in 11 basins on the Big Sur coast  
123 (Figure 1, Table 1). Basins were selected to span the range of *O. mykiss* and coast redwood-  
124 dominated riparian forests within this region, within constraints of limited access to non-public  
125 property. Sites were selected non-randomly, dictated by land ownership and physical access in  
126 often steep stream canyons; however, sites were well distributed across the region (Figure 1)  
127 and represented a range of geographic/landscape variables such as drainage area, elevation,  
128 and gradient (Table S1), so this did not appear to bias the study. Single sites were sampled in 10  
129 of the basins, and three sites were sampled in Big Creek where we have conducted intensive  
130 studies on *O. mykiss* and the stream food web (Rundio & Lindley, 2008, 2012, 2019; Rundio et  
131 al., 2012). At each site, we selected a 100-m reach that was representative of habitat conditions  
132 of the surrounding area. Latitude (UTM northing), drainage area (km<sup>2</sup>), elevation (m), and  
133 gradient (m/km) of each site were obtained from GIS. All sites were located in areas with intact  
134 riparian forest where canopy closure over the stream was > 75%. All sites were below barriers  
135 where *O. mykiss* populations were composed of both anadromous and non-anadromous (i.e.,  
136 resident) life-history forms. Coastrange sculpin (*Cottus aleuticus*) was the only other fish species  
137 present at some sites.

138

## 139 **2.2 | Field sampling**

140 All field sampling was conducted during early summer from June 22–30, 2006. Terrestrial  
141 invertebrate subsidies in this region are highest from early summer through fall, and surface  
142 activity by nonnative isopods, and their abundance in the diet, is highest in spring through early  
143 summer before declining as the dry season progresses (Rundio & Lindley 2008, 2019). Diet  
144 samples were collected from 25 fish per site. We captured fish during daytime (0830–1630

145 hours) using a backpack electrofisher (Smith-Root, Inc.; Model 12-B) and collected all size  
146 classes  $\geq 60$  mm fork length (FL, the minimum size for taking diet samples using our equipment)  
147 in approximate proportion to their abundance. Fish were lightly anesthetized with CO<sub>2</sub> (from  
148 sodium bicarbonate), measured (FL, nearest mm), and weighed (nearest 0.1 g). We collected  
149 stomach contents by gently flushing stomachs with stream water using a wash bottle fitted  
150 with a narrow straw (Meeham & Miller, 1978; Twomey & Giller, 1990). Stomach contents were  
151 then rinsed on a 225- $\mu$ m sieve and preserved with 80% ethanol. All fish were allowed to  
152 recover and then released. Capture and sampling methods were authorized and approved by  
153 National Marine Fisheries Service Scientific Research Permit 1044 under Section 10(a)(1)(A) of  
154 the U.S. Endangered Species Act and the University of California Santa Cruz Institutional Animal  
155 Care and Use Committee.

156 At each site, we also quantitatively sampled the stream banks for terrestrial isopods at  
157 five locations. The starting location was randomly selected within the first (downstream) 20 m  
158 of the reach, and the remaining four locations were spaced sequentially every 20 m upstream.  
159 At each location, both left and right banks were searched using a 0.10 m<sup>2</sup> quadrat, with the  
160 quadrat placed 0, 0.5, or 1.0 m away from the stream edge determined by a random draw, for a  
161 total of 10 quadrats per site. We searched the ground surface and under rocks, leaves, and  
162 other cover, and collected and preserved all isopods in 80% ethanol. We choose this approach  
163 for estimating the abundance of isopods because our previous study in Big Creek indicated that  
164 isopods were greatly underrepresented in floating pan traps, which typically are used to sample  
165 terrestrial invertebrate subsidies to streams, relative to their occurrence in the diet (Rundio &  
166 Lindley, 2008).

167

### 168 **2.3 | Sample processing**

169 Invertebrates from the diet samples were identified, counted, and measured to the nearest mm  
170 in body length. All aquatic insects were identified at least to family, and most to genus or  
171 species, and non-insects and most terrestrial invertebrates were identified to order, suborder  
172 (some Diptera), or family. Isopods in both the diet and riparian samples were identified to  
173 species in order to distinguish native and non-native taxa. Only recently ingested prey were

174 counted and measured to reduce bias associated with differences in digestion rates among taxa  
175 (Elliot, 1972; Hyslop, 1980); in particular, we did not want to overestimate the importance of  
176 terrestrial isopods due to their heavily sclerotized bodies that likely had slower digestion rates  
177 than other prey taxa. Analyzed prey specimens included undigested prey, partially digested  
178 prey as long as there was a significant amount of soft tissue left inside the integument, and  
179 fragmented specimens as long as there was a consistent, identifiable part that could be  
180 enumerated and the length estimated from more intact specimens of the same taxa in the  
181 sample (e.g., thorax for many of the insects); prey digested beyond this point were excluded.  
182 We estimated invertebrate prey mass (mg dry mass) from taxon-specific length-mass  
183 regressions in the literature (Rogers et al., 1977; Gowing & Recher, 1984; Sample et al., 1993;  
184 Benke et al., 1999; Sabo et al., 2002). We then estimated energy content (Joules) for all prey  
185 items by multiplying dry mass by taxon-specific energy densities (calories/mg) from Cummins  
186 and Wuycheck (1971) and converting to Joules.

187

## 188 **2.4 | Statistical analyses**

189 We used a variety of analyses to examine how the proportion of terrestrial prey and non-native  
190 isopods in the diet, the taxonomic composition of the diet, and the energetic value of stomach  
191 contents varied among sites and with fish size, and to evaluate relationships between  
192 geographic/landscape variables and diet and isopod density. These included both univariate  
193 (for energetic values and proportions) and multivariate (for taxonomic composition based on all  
194 prey taxa) methods. Although the underlying goals of the analyses were to detect relatively  
195 simple differences or patterns, in several cases aspects of the data (e.g., heterogeneity among  
196 sites, or proportions with many zero or one values) did not meet assumptions of simple linear  
197 methods (e.g., ANOVA or ANCOVA) and required the use of more complicated statistical  
198 approaches to properly account for the structure of the data and produce unbiased results.

199

200

### 201 **2.4.1 | Proportion of terrestrial prey and non-native isopods in the diet**

202 To evaluate the importance of terrestrial prey and non-native isopods to *O. mykiss*, we assessed  
203 what proportion of the diet they constituted at each site and whether the proportion varied  
204 with fish size. Because the proportions among individual fish contained many values of zero or  
205 one, we used Bayesian zero-one inflated beta regression models to account for the data  
206 structure and avoid biased results. We estimated the proportion of terrestrial prey and non-  
207 native isopods (separately) out of the total energetic value of the stomach contents of  
208 individual fish as a function of site and fork length by fitting Bayesian zero-one inflated beta  
209 regression models in the R package *zoib* (Liu & Kong, 2019). The *zoib* package estimates  
210 parameters by Markov Chain Monte Carlo (MCMC) sampling by implementing MCMC methods  
211 from the program *JAGS* (Plummer, 2017) via the R package *rjags* (Plummer, 2019). Models were  
212 of the general form

$$y \sim x_1 | x_2 | x_3 | x_4$$

213  
214 where  $x_1$  are the fixed-effect factors (i.e., site and FL) in the link function of the mean of the  
215 beta distribution,  $x_2$  are the factors in the link function of the precision parameter of the beta  
216 distribution,  $x_3$  are the factors in the link function of  $\Pr(y = 0)$ , and  $x_4$  are the factors in the link  
217 function of  $\Pr(y = 1)$  (Liu & Kong, 2019). Models were fit using diffuse normal priors and logit  
218 link function, and posterior samples drawn from two MCMC chains with 6,000 iterations per  
219 chain, burn-in of 1,000 iterations, and thinning interval of five. Proportions of terrestrial prey  
220 were both zero- and one-inflated so included terms for both  $x_3$  and  $x_4$  in models, while  
221 proportions of non-native isopods were zero-inflated only so did not include terms for  $x_4$ . To  
222 determine whether site and fork length were significant predictors, we compared models with  
223 one or both variables and a null model with neither using the deviance information criterion  
224 (DIC) to identify the top model. Then the posterior predictive values from the top model were  
225 used to estimate the median proportion (and 95% credible interval) of terrestrial prey or non-  
226 native isopods at each site.

227

#### 228 **2.4.2 | Taxonomic composition of the diet**

229 We summarized the frequency and relative abundance (percentage of energy content) of prey  
230 taxa across all samples, as well as by site and by four *O. mykiss* size classes (60–89, 90–119,



231 120–149, and  $\geq 150$  mm FL), to identify important prey types. To test for differences in  
232 taxonomic composition of the diet among sites and with respect to fish size, we ran non-  
233 parametric, permutational multivariate analysis of variance (PERMANOVA) using the  
234 PERMANOVA+ for PRIMER software package (Anderson et al., 2008). Stomach contents (Joules)  
235 of individual fish were standardized to relative abundances of 84 prey taxa (Table S2), where  
236 taxa were aggregated to family or order to avoid parent-offspring taxa pairs (e.g., Baetidae and  
237 *Baetis*) due to variable condition of prey items (Cuffney et al., 2007). Bray-Curtis similarity was  
238 calculated between all pairs of samples (i.e., individual fish) on untransformed relative  
239 abundance data, and PERMANOVA (using type I sums of squares and 9,999 permutations under  
240 a reduced model) was run on the resulting similarity matrix with site and FL as factors. We used  
241 the estimated components of variation (square root-transformed to put them in the original  
242 units of Bray-Curtis similarity) to assess the amount of variation in diet composition related to  
243 each factor (Anderson et al., 2008).

244 Next, we used similarity percentages (SIMPER) and non-metric multidimensional scaling  
245 (NMDS) in PRIMER version 7 (Clarke & Gorley, 2015) to interpret and visualize the differences in  
246 diet composition indicated by PERMANOVA. SIMPER calculates the contributions of individual  
247 taxa to the average Bray-Curtis dissimilarity between groups. We used one-way SIMPER  
248 analyses to identify taxa driving differences in diet between sites and with fork length, grouping  
249 fish into four size classes (60–89, 90–119, 120–149, and  $\geq 150$  mm FL). We then used NMDS and  
250 bar plots to display patterns in diet composition among sites and size classes. Because diet  
251 variation among fish was high, to summarize general patterns we averaged the individual diet  
252 data (the relative prey abundances [Joules] per fish) by site or size class. To ordinate sites based  
253 on rank similarity in diet composition, we calculated Bray-Curtis similarity on these averaged  
254 values, and ran two-dimensional NMDS using default settings (25 random restarts, minimum  
255 stress = 0.01, Kruskal fit scheme = 1, convergence on the global minimum verified from multiple  
256 restarts that produced the lowest stress solution).

257

258 **2.4.3 | Energetic value of aquatic, terrestrial, and all prey**

259 To determine whether energetic value in the diet varied among sites or with respect to fish size,  
260 we fit generalized least squares (GLS) models to stomach contents (Joules) of aquatic,  
261 terrestrial, and all prey in the diets of individual fish with site and fork length as explanatory  
262 variables. Stomach contents (Joules) were  $\log_e$ -transformed for normality and fork lengths were  
263 centered, and models were fitted using the *nlme* package (Pinheiro et al., 2018) in R version  
264 3.5.3 (R Core Team, 2019). Examination of residuals from simple linear models indicated  
265 heterogeneity in variances, so we used the *varComb* function to allow variances to differ both  
266 among sites and with respect to fork length (increasing with FL for aquatic prey and decreasing  
267 with FL for terrestrial and all prey).

268  
269 **2.4.4 | Geographic/landscape associations with diet and isopod density**

270 We assessed whether the occurrence of non-native isopods in the diet was related to their  
271 riparian density and whether variation in isopod density and *O. mykiss* diet were related to  
272 geographic/landscape variables as follows. We used Spearman rank correlation tests in the  
273 base *stats* package in R to evaluate whether the frequency or proportion of non-native isopods  
274 in the diet was correlated with riparian density of isopods at a site. Frequency was based on the  
275 number of fish at a site that contained isopods in the stomach contents, and the proportion of  
276 isopods out of the total energetic value (Joules) in the stomach contents was based on the  
277 median predicted value for each site from the zero-one inflated beta regression model with  
278 most support (lowest DIC). We also used Spearman correlation tests to determine whether  
279 various diet metrics and riparian density of non-native isopods were related to four  
280 geographic/landscape variables obtained from GIS (latitude, drainage area, elevation, and  
281 channel gradient; Table S1). We considered six diet metrics: median energetic value (Joules) of  
282 aquatic, terrestrial, and all prey for each site predicted from the generalized least squares  
283 models; the frequency and proportion of non-native isopods (as described above); and the  
284 proportion of all terrestrial prey items out of the energetic value of the stomach contents  
285 (median predicted value for each site from the zero-one inflated beta regression model). As this  
286 resulted in 28 pairwise tests between environmental variables and the diet metrics or riparian

287 isopod density, statistical significance was assessed after Bonferroni correction for multiple  
288 comparisons.

289 Finally, we used the BIOENV method within the BEST routine in PRIMER to determine  
290 whether the pattern of similarity in taxonomic structure of *O. mykiss* diets among sites was  
291 correlated with the pattern of similarity in the four geographic/landscape variables among sites.  
292 BIOENV evaluates all combinations of the habitat variables to identify the set that produces a  
293 similarity matrix with the highest rank correlation ( $\rho_s$ ) with the diet-structure similarity matrix,  
294 and uses a permutation and randomization test to determine whether this correlation is  
295 statistically significant. For this test, the diet matrix was based on Bray-Curtis similarity of the  
296 relative abundances of the 84 prey taxa groups averaged for each site (i.e., based on site means  
297 rather than individual fish). The geographic variables were log-transformed as necessary to  
298 improve spread and normalized prior to analysis, and BIOENV was run with 999 permutations.

299

### 300 **3 | RESULTS**

301 We analyzed diets of 325 *O. mykiss* from the 13 sites. The majority (80%) of fish were between  
302 80–160 mm FL (Figure S1). The diet samples contained 11,888 identifiable prey items from 84  
303 taxa groups (Table S2). The most frequent taxonomic orders in the stomach contents were  
304 aquatic Diptera (90%), Ephemeroptera (87%), and Trichoptera (76%), and terrestrial Diptera  
305 (56%), Coleoptera (47%), Hymenoptera (46%), and Homoptera (46%). In particular, diets were  
306 dominated by the aquatic families Baetidae (82% frequency), Chironomidae (68%), and  
307 Simuliidae (60%). In terms of energy, the most important taxonomic orders were aquatic  
308 Ephemeroptera (16%), Trichoptera (15%), and Diptera (13%), followed by terrestrial Coleoptera  
309 (13%), Hymenoptera (11%), and Isopoda (8%).

310 Non-native terrestrial isopods occurred in *O. mykiss* diets at all 13 sampling sites and in  
311 riparian samples at eight sites (Table 1). Two species of non-native isopods were found:  
312 *Armadillidium vulgare* was the most common and abundant, occurring at all sites except  
313 Garrapata Creek and representing all but one specimen in the riparian samples, while *Porcellio*  
314 *scaber* was less abundant and occurred at eight sites in six basins (Table 1). In addition, one  
315 species of native terrestrial isopod, *Ligidium gracile*, was found in low numbers in the diets in

316 five basins (Big, Partington, Mill, Limekiln, and Salmon). Mean riparian densities of non-native  
317 isopods were up to 13 individuals/m<sup>2</sup> (Table 1). There were moderate correlations between  
318 riparian isopod density and geographic/landscape variables suggesting that density decreased  
319 with latitude and increased with elevation, however these trends were not statistically  
320 significant (Table S3 and Figure S2).

321 The proportion of non-native isopods out of the total energetic value of the stomach  
322 contents of individual fish differed among sites and with respect to fork length, as the zero-one  
323 inflated beta regression model that included both of these terms received the most support  
324 from the data by 21 DIC (Table S4). Among sites, the median proportion of isopods in the diet  
325 ranged from less than 1% to over 20% (Figure 2a). Consumption of isopods increased with fish  
326 size: 10% of fish 60–89 mm FL had consumed isopods compared to nearly 40% of fish > 150 mm  
327 (Figure 3a), and the energetic value similarly increased from 2% to 14% of the diet across size  
328 classes (Figure 4). The median proportion of non-native isopods (Joules) in the diet was  
329 positively correlated with riparian density at a site (Spearman rank correlation,  $r_s = 0.62$ ,  $p =$   
330  $0.02$ ; Figure S3) but the frequency of occurrence in the diet was not ( $r_s = 0.32$ ,  $p = 0.29$ ).

331 In terms of broader spatial patterns in diet, all measures of the taxonomic composition  
332 and energetic value of *O. mykiss* stomach contents varied significantly among sites (proportion  
333 of terrestrial prey, Table S4; taxonomic composition, Table S5; mean energetic value, Table S6)  
334 but there were no major geographic patterns or trends to the variation. Spearman correlations  
335 between diet metrics and geographic/landscape variables were not statistically significant and  
336 were generally weak, although there were a few moderate correlations suggesting that  
337 energetic value of all prey decreased with drainage area and that frequency and proportion of  
338 non-native isopods increased with channel gradient (Table S3 and Figure S2). With regard to  
339 mean energetic value, stomach contents were relatively similar across most sites, and  
340 differences were driven by one or two sites with high or low values (Figure 5). Specifically, the  
341 energetic value of aquatic prey was much higher at Partington Creek (site code P, Figure 5a)  
342 than other sites due to higher than average consumption of many aquatic taxa by all fish at the  
343 site (i.e., not driven just by a few fish eating a few specific taxa). In contrast, fish in the South  
344 Fork Little Sur River and Salmon Creek had consumed little terrestrial prey compared to fish at

345 other sites (Figure 5b). Terrestrial prey accounted for about 25% of the total energy content in  
346 the diet at these two sites, whereas they represented 40–50% at six sites and 60–75% at five  
347 sites (Figure 2b). In total, however, the mean energetic value of all prey in the stomach  
348 contents was more similar among sites and showed less variation than when viewed separately  
349 by source (Figure 5c).

350 Taxonomic composition of *O. mykiss* diets varied significantly among sites  
351 (PERMANOVA,  $F_{12,311} = 5.82$ ,  $p < 0.0001$ ; Table S5), and this was driven primarily by differences  
352 in the relative abundances (based on energetic value) of 12 aquatic and terrestrial prey taxa  
353 (Table 2). These included both taxa that were frequent and common across nearly all sites, such  
354 as aquatic Baetidae, Chironomidae, Simuliidae, and terrestrial Coleoptera, as well as rarer taxa  
355 such as Diplopoda that were highly important at just a few sites (Table 2). Variation in the  
356 relative abundance of non-native terrestrial isopods *A. vulgare* also contributed to the  
357 differences in diet composition among sites (Table 2). Despite these differences among sites,  
358 there was no apparent geographic pattern (e.g., north–south trend or clustering of groups of  
359 sites) to the variation in diet composition (Figures 6 and S4) and no significant correlation  
360 between geographic/landscape variables and taxonomic composition of the diet (BIOENV,  $\rho_s =$   
361  $0.30$ ,  $p = 0.09$  for the top selected model that included latitude and gradient). Furthermore, the  
362 largest component of variation in the PERMANOVA model was the residual, indicating that  
363 variation between individual fish was a much larger source of variation than among sites (Table  
364 S5).

365 The energetic value of *O. mykiss* stomach contents increased significantly with FL for  
366 both aquatic (GLS,  $F_{1,311} = 4.534$ ,  $p = 0.034$ ) and terrestrial prey ( $F_{1,311} = 74.756$ ,  $p < 0.001$ )  
367 (Table S6). However, consumption of terrestrial prey increased much more than consumption  
368 of aquatic prey, and this drove the main change in diet composition with fish size, which was  
369 increasing relative abundance of terrestrial prey (Figure 4). The frequency of terrestrial prey in  
370 the diet was high across all size classes (72–100%, Figure 3b) but the energetic value increased  
371 dramatically from 30% in fish 60–89 mm FL to 75% in fish > 150 mm (Figure 4). With respect to  
372 the taxa contributing to the differences in diet composition among size classes, the relative  
373 abundance (based on energy) of aquatic Ephemeroptera and Diptera (particularly Baetidae and

374 Simuliidae, respectively) declined with fish size while terrestrial Isopoda (particularly *A.*  
375 *vulgare*), Coleoptera, and Hymenoptera increased (Table 3, Figure 4).

376

#### 377 **4 | DISCUSSION**

378 Terrestrial invertebrates, including non-native isopods, were a major source of energy in the  
379 summer diet of *O. mykiss* in our study streams along the Big Sur coast, accounting for more  
380 than 40% of the energetic value of the stomach contents for the average-sized fish at most  
381 sites. Non-native isopods were present throughout the region and, along with terrestrial  
382 invertebrates in general, increased in importance as prey with increasing fish size. Although the  
383 energetic content and taxonomic composition of *O. mykiss* diets varied among sites, there was  
384 no clear spatial pattern or trend to the variation and overall diets were generally similar across  
385 sites. The importance of terrestrial prey resources, including isopods, to *O. mykiss* populations  
386 across the Big Sur coast broadens our previous findings from a single basin (Rundio & Lindley,  
387 2008, 2019) and highlights that non-native terrestrial invertebrates can be an important prey  
388 subsidy to salmonids in some systems.

389 Non-native isopods were present in *O. mykiss* diets at all sites, even where they were  
390 not found in riparian samples, although their occurrence in the diet and riparian density varied  
391 considerably among sites. Isopods occurred in 20–40% of fish sampled at the majority of sites  
392 but accounted for >10% of the mean energetic value of the stomach contents at only four sites.  
393 The energetic value of non-native isopods in the diet at sites was positively correlated with  
394 riparian density of isopods, which reached up to 13 individuals/m<sup>2</sup>. These densities were lower  
395 than densities of non-native isopods in other studies, where isopod densities in upland habitats  
396 reached hundreds to thousands per meter in the surface and upper soil layer during peak  
397 abundance and activity period in spring (California: Paris & Pitelka, 1962; Paris, 1963; Florida:  
398 Frouz et al., 2004; Texas: Miller & Cameron, 1987). Comparable quadrat-based estimates are  
399 not available for riparian areas, although non-native isopods dominated arthropod samples  
400 from pitfall traps and numbered in up to tens per trap in New Mexico (Ellis et al., 2001; Catron  
401 et al., 2003) and an inland basin in northern California (Holway, 1998). However, similar to  
402 other studies, peak abundance and surface activity of isopods in Big Sur appears to be in spring

403 (March–May) based on our diet samples and observations in Big Creek (Rundio & Lindley,  
404 2019). Consequently, the diet and density data presented here based on sampling in late June  
405 probably underestimate the abundance of isopods compared to the annual maximum.  
406 Additionally, our estimates of riparian density are somewhat limited by the relatively small area  
407 we sampled (1.0 m<sup>2</sup> total per site) considering the highly patchy distribution and abundance of  
408 isopods.

409 Terrestrial isopods have been reported in the diets of stream salmonids in several  
410 previous studies in the United States, but coarse or ambiguous identifications make it unclear  
411 whether they were non-native. Surber (1933) reported that “terrestrial sowbugs (Oniscidae)”  
412 occurred in the diets of five percent of introduced rainbow trout sampled in a Virginia stream,  
413 and Lord (1933) found that “terrestrial sowbugs” were three percent of the annual diet (and up  
414 to 10–14% in some winter months) of brook trout (*Salvelinus fontinalis*) in a Vermont stream.  
415 While most species of abundant terrestrial isopods in North America are non-native, there are a  
416 number of native isopods, including in the eastern United States (Jass & Klausmeier, 2000,  
417 2001), making the origin of the sowbugs in these studies uncertain. Embury and Gordon (1924)  
418 cited a study finding “terrestrial sow bugs (Porcello)” were about one percent of the diet of  
419 brook trout in a Wisconsin stream; if these were in fact Porcellionidae then they were non-  
420 native, as the three species from this family that have been reported in Wisconsin (*Porcellio*  
421 *scaber*, *P. spinicornis*, and *Porcellionides pruinosus*) are introduced (Jass & Klausmeier, 1996,  
422 2001). Although the taxonomic details of these old studies are uncertain, they suggest that non-  
423 native terrestrial isopods might occur in salmonid diets in many regions in addition to our study  
424 area in California and, in cases such as Lord (1933), may be a considerable subsidy in some  
425 seasons, similar to our results. Overall, this suggests that non-native isopods may contribute a  
426 larger subsidy to stream fishes than previously recognized.

427 While isopods were the only non-native taxa that were abundant in *O. mykiss* diets in  
428 our study, several other non-native invertebrates occurred in low numbers. A total of 13  
429 European honeybees (Hymenoptera, Apidae) were present in the diet samples from eight sites,  
430 and a European earwig (Dermaptera: Forficulidae) occurred at one site. There were a total of 15  
431 oligochaetes in the diet samples from five sites, and they were presumed to be primarily native

432 aquatic worms during the original processing and identification of samples but were not  
433 identified to family. However, a subsequent examination of a small number of specimens from  
434 diet and benthic samples from the study streams revealed that several oligochaete families  
435 were present: native aquatic Enchytraeidae and Naididae as well as non-native Lumbricidae  
436 including genera from both aquatic and riparian habitats. Therefore, it is likely that some of the  
437 oligochaetes in the diet samples from the present study were non-native Lumbricidae but it is  
438 unclear if they were terrestrial. Similarly, there may have been other non-native taxa among  
439 the terrestrial invertebrate orders present in the diet samples that we did not detect due to the  
440 resolution of our identifications. Nevertheless, if additional non-native terrestrial invertebrates  
441 occurred, they were too rare to represent an important summer prey resource.

442 While non-native fish (Baxter et al., 2004; Benjamin et al., 2013; Jackson et al., 2016)  
443 and aquatic invertebrates (Gergs et al., 2014) have been shown to have strong effects on  
444 community structure and flows of energy and material between stream and riparian food webs,  
445 the prevalence and importance of non-native invertebrate prey subsidies to streams has not  
446 been well studied. Roon et al. (2018) found that invasive green alder sawflies were only a minor  
447 prey item for juvenile coho salmon in Alaska and did not affect the biomass of native terrestrial  
448 invertebrates as in fall or prey, although they speculated that these results might change as the  
449 recent sawfly invasion progresses. Introduced earthworms (Oligochaeta, Lumbricidae) are  
450 widespread in North America (Bohlen et al., 2004) and appear to be important prey to stream  
451 predators in some cases. Kerby and Kats (1998) reported that terrestrial earthworms (*Eisenia*  
452 *rosea*, since revised to *Aporrectodea rosea*) became common in a southern California stream  
453 following a wildfire and landslides and also became abundant in the diets of adult California  
454 newts (*Taricha torosa*), which reduced cannibalism on larvae; *A. rosea* is a non-native lumbricid,  
455 although this aspect was not mentioned. Similarly, White and Harvey (2007) documented that  
456 oligochaetes dominated the biomass of resident *O. mykiss* diets during periods of high stream  
457 flow and turbidity in two streams in northern California, and bioenergetics models suggested  
458 that these episodic feeding events were critical for meeting energy demand during winter. The  
459 oligochaetes were not identified at the time but were assumed to be terrestrial based on their  
460 apparent increase in availability during high flows (B. Harvey, pers. comm.). In a later analysis of



461 eleven archived diet samples from the same streams, all oligochaetes appeared to be non-  
462 native Lumbricidae, and of the specimens in best condition (i.e., least digested) most were  
463 tentatively identified as *Eiseniella tetraedra* (B. Harvey and S. Fend, pers. comm.), which is  
464 common in gravel-bedded streams in the western U.S. (S. Fend, pers. comm.) but also occurs in  
465 riparian habitats (Wood & James, 1993; Costello et al., 2011). Therefore, it is uncertain whether  
466 the oligochaetes in the trout diets originated from aquatic versus terrestrial habitats, although  
467 input of riparian oligochaetes during winter storms and high flows would be consistent with the  
468 mechanism reported by Kerby and Kats (1998). Together, the results of these studies and ours,  
469 along with the widespread distribution and often high abundance of introduced invertebrates  
470 (Niemelä & Mattson, 1996; Bohlen et al., 2004; Kenis et al., 2009; Jackson et al. 2017), suggest  
471 that subsidies of non-native terrestrial prey to stream food webs may be more common than  
472 has been appreciated.

473 The energetic importance of terrestrial invertebrates to *O. mykiss* in Big Sur streams  
474 during summer is consistent with previous studies of subsidies to stream salmonids (Baxter et  
475 al., 2005; Paetzold et al. 2007; Richardson et al., 2010; Wipfli & Baxter, 2010). Terrestrial  
476 invertebrates provided 40% or more of the energetic value of the stomach contents at all but  
477 two sites and up to 75% at almost a quarter of sites, similar to values in other forested systems.  
478 The importance of terrestrial prey also increased with fish size, in line with previous studies  
479 (Hunt, 1975; Bisson, 1978; Dineen et al. 2007; Gustafsson et al. 2010; Syrjänen et al., 2011;  
480 Rundio & Lindley, 2019). Terrestrial invertebrates were 75% of the energy in the diet for *O.*  
481 *mykiss* larger than 150 mm FL, but were a substantial proportion (>30%) even for the smallest  
482 size class examined (60–89 mm). *O. mykiss* populations in these basins are partially migratory  
483 and anadromous individuals appear to outmigrate as smolts generally at 150–180 mm in spring  
484 whereas fish > 150 mm in late spring and summer appear to be primarily non-anadromous  
485 individuals (Rundio et al., 2012; Pearse et al., 2019). Therefore, terrestrial invertebrate  
486 subsidies may be especially important to juvenile anadromous fish as they approach the size  
487 threshold for smolting and to mature non-anadromous (resident) fish.

488 Although *O. mykiss* diets varied among streams in Big Sur both in terms of energy  
489 content and taxonomic composition, diets were generally similar across sites and there was no

490 geographic pattern or trend to the variation. The most frequent and numerous prey items  
491 across all sites were aquatic insects (Baetidae, Chironomidae, and Simuliidae), whereas  
492 energetic contribution was more evenly balanced among a number of aquatic (Ephemeroptera,  
493 Trichoptera, and Diptera) and terrestrial (Coleoptera, Hymenoptera, and Isopoda) taxonomic  
494 orders. The lack of geographic pattern or trend likely reflects the relatively similar  
495 environmental conditions along the Big Sur coast with regard to major large-scale features such  
496 as landform, forest type, low level of development, and climate. However, moderate (but  
497 statistically non-significant) correlations between several diet metrics and  
498 geographic/landscape variables (e.g., energy content of all prey in the stomach contents and  
499 drainage area, and frequency and proportion of isopods and channel gradient) suggest that  
500 there may be some finer scale diet–environment relationships within the region that were  
501 beyond the scope of our study. For instance, in previous studies in many of these same streams,  
502 we found that the abundance and taxonomic richness of benthic macroinvertebrates was lower  
503 in sites with travertine (calcium carbonate) deposition than in sites without (Rundio & Lindley,  
504 2008; Rundio, 2009), but there was no indication of differences in diet between sites with  
505 travertine (Partington, Devils, Limekiln, and Mill creeks) and those without (we did not conduct  
506 formal tests for differences due to small and unbalanced number of sites with and without  
507 travertine). Our ability to detect differences may have been limited by the high variability in  
508 diet among individual fish, by our samples being limited to a single date per site, and by our  
509 sample comprising all size and age classes, whereas differences corresponding to benthic  
510 invertebrates are most likely to occur among smaller size classes that feed predominantly on  
511 aquatic prey. Nevertheless, our results indicate that *O. mykiss* diets were similar across the  
512 range of conditions in these redwood-forested coastal basins in this region during the summer  
513 we sampled.

514 In conclusion, terrestrial invertebrates, including non-native isopods, provided an  
515 important energy subsidy to *O. mykiss* during summer in streams along the Big Sur coast. Non-  
516 native isopods, which have been introduced around the world, occurred in the diet at all sites  
517 and were abundant on streambanks in most sites. Although isopods were a substantial source  
518 of energy in the diet, their overall effects on *O. mykiss* and stream and riparian food webs is

519 unclear. Terrestrial isopods have lower energy density (Cummins & Wuycheck, 1971) and %C  
520 and %N (Tibbets & Molles, 2005) than most other invertebrates, so they may provide less  
521 nutritional value than alternative prey. However, they are most abundant in late winter and  
522 spring when abundances of other aquatic and terrestrial prey are low (Rundio & Lindley, 2008),  
523 which may make them seasonally important for feeding and growth of anadromous *O. mykiss*  
524 just prior to their smolt outmigration. For ecosystem effects, their abundance (Holway, 1998;  
525 Ellis et al., 2001; Catron et al., 2003) and capacity to consume large quantities of litter (Hassall  
526 et al., 1987; Zimmer et al., 2002; Frouz et al., 2008; Špaldeňová & Frouz, 2014) suggest that  
527 non-native isopods may influence invertebrate assemblages, decomposition rates, and organic  
528 matter cycling in riparian zones. Non-native earthworms have been shown to increase the flux  
529 of nitrogen from riparian soils to streams (Costello & Lamberti, 2008), so riparian isopods may  
530 potentially have effects that extend to other aspects of stream nutrient dynamics and food  
531 webs in addition to being prey for fish. The prevalence and abundance of non-native  
532 invertebrates suggests that they often may have important effects in linked stream and riparian  
533 food webs that are likely to become more common under continued global change (Larsen et  
534 al. 2016). As our results about the contribution of terrestrial isopods to the diet of threatened  
535 *O. mykiss* in Big Sur highlight, subsidies to stream predators are among the interactions  
536 involving non-native invertebrates that warrant further study.

537

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550

#### 551 **DATA AVAILABILITY STATEMENT**

552 The data that support the findings of this study are available from the corresponding author  
553 upon request.

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894 **Table 1.** Summary of riparian density of non-native terrestrial isopods and relative  
 895 frequency in *O. mykiss* diets at 13 sites in Big Sur, California. Sites are listed from north to  
 896 south, and code refers to site abbreviations in Figure 1. Isopod density is mean (SE).  
 897 Presence of non-native isopod species *Armadillidium vulgare* and *Porcellio scaber* at a site  
 898 is indicated with an “x”.  
 899

Site	Code	Basin	Non-native isopods			
			Riparian density (no./m <sup>2</sup> )	Frequency in trout diet	<i>A.</i> <i>vulgare</i>	<i>P.</i> <i>scaber</i>
San Jose Creek	SJC	San Jose	0	0.12	x	x
Garrapata Creek	GC	Garrapata	0	0.12		x
Rocky Creek	RC	Rocky	0	0.20	x	x
South Fork Little Sur River	SFLS	Little Sur	4.0 (3.1)	0.04	x	
Partington Creek	P	Partington	0	0.28	x	x
Mainstem Big Creek	MBC	Big	1.0 (1.0)	0.40	x	x
Big Creek	BC	Big	6.0 (3.1)	0.40	x	x
Devils Creek	DC	Big	2.0 (2.0)	0.28	x	x
Limekiln Creek	LC	Limekiln	0	0.12	x	
Mill Creek	MC	Mill	6.0 (4.0)	0.36	x	
Prewitt Creek	PC	Prewitt	1.0 (1.0)	0.12	x	x
Upper Willow Creek	UWC	Willow	5.0 (2.7)	0.12	x	
Salmon Creek	SC	Salmon	13.0 (5.6)	0.20	x	

900

901 **Table 2.** Mean relative abundance (percent of Joules) of prey taxa that contributed to > 5% of the Bray-Curtis dissimilarity in *O.*  
 902 *mykiss* diet composition between any two sites based on SIMPER analysis. Site codes are defined in Table 1.  
 903

Taxon	Site												
	SJC	GC	RC	SFLS	P	MBC	BC	DC	LC	MC	PC	UWC	SC
<i>Aquatic</i>													
Baetidae	1.31	5.70	2.99	50.21	4.16	14.99	6.48	14.64	8.41	2.20	4.73	7.84	21.17
Blephariceridae	0	0	0.96	1.57	0.83	1.91	3.09	8.69	3.99	5.33	0	3.65	0.27
Chironomidae	5.71	2.91	1.4	0.69	1.68	1.72	1.11	0.63	0.37	1.17	6.07	5.11	0.14
Glossosomatidae	1.40	0	1.04	0.03	1.86	4.54	5.22	0.24	7.38	18.31	1.08	1.21	0
Hydropsychidae	0	0.77	8.05	3.76	11.53	1.28	4.72	3.51	14.57	7.32	2.34	1.08	4.80
Simuliidae	1.85	2.33	0.44	8.03	0.03	10.94	1.53	11.13	1.66	0.05	2.38	7.77	9.24
<i>Terrestrial</i>													
Armadillidiidae	1.52	0	4.33	0	7.16	13.36	9.94	4.84	1.71	24.37	2.02	5.05	6.75
Coleoptera	22.21	24.90	15.46	8.24	6.31	5.29	7.51	5.74	25.87	8.74	18.15	15.10	4.54
Diplopoda <sup>†</sup>	0	20.29	16.47	0	1.84	0.04	0	1.59	0	0	2.48	0	0
Hemiptera	2.58	0.66	1.31	0.92	1.84	4.57	6.51	2.29	1.92	1.3	0.81	9.33	0.03
Hymenoptera <sup>‡</sup>	5.53	4.16	3.91	0	12.41	5.93	7.75	2.94	8.13	1.18	32.59	9.31	5.11

Lepidoptera	19.28	8.42	6.81	0.02	3.58	0.27	0.09	0	0	0	1.88	4.06	0.64
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904 † Excluding Xystodesmidae which was identified and analyzed as a family.

905 ‡ Excluding Apidae and Formicidae, which were identified and analyzed as families.

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906 **Table 3.** Mean relative abundance (percent of Joules) of prey taxa that contributed to > 5%  
 907 of the Bray-Curtis dissimilarity in *O. mykiss* diet composition between any two size classes  
 908 based on SIMPER analysis.

Taxon	Size class (FL, mm)			
	60-89	90-119	120-149	≥ 150
<i>Aquatic</i>				
Baetidae	31.62	14.11	7.51	2.85
Hydropsychidae	3.05	5.25	7.47	1.03
Simuliidae	11.77	6.21	2.79	0.64
<i>Terrestrial</i>				
Armadillidiidae	0	2.28	8.38	12.81
Coleoptera	7.89	7.92	14.4	21.67
Hymenoptera <sup>†</sup>	2.33	7.84	7.81	9.13

910 <sup>†</sup> Excluding Apidae and Formicidae, which were identified and analyzed as families.

911 **FIGURE LEGENDS**

912

913 **Figure 1.** Locations of the 13 study sites in Big Sur, California. Site codes correspond to  
 914 Table 1, where full location names are given. The community of Big Sur and California State  
 915 Route 1 are shown for reference.

916

917 **Figure 2.** Proportion (median and 95% credible interval) of (a) non-native terrestrial  
 918 isopods and (b) all terrestrial prey out of the energetic value (Joules) in stomach contents  
 919 of *O. mykiss* from 13 sites in Big Sur, California. Estimates are medians of posterior  
 920 predictive values from zero-one inflated beta regression models for the mean-sized fish  
 921 (127 mm FL). Sites are ordered from north to south and site codes are defined in Table 1.  
 922 Note that y-axis scale differs between panels.

923

924 **Figure 3.** Relative frequency (percentage) of individual *O. mykiss* diets containing (a) non-  
925 native isopods and (b) all terrestrial prey by size class (mm FL).

926

927 **Figure 4.** Relative abundances (percentage) by energy content (Joules) of the main prey  
928 orders in diets of different size classes (mm FL) of *O. mykiss*. Values are relative  
929 abundances from individual fish averaged across all sites.

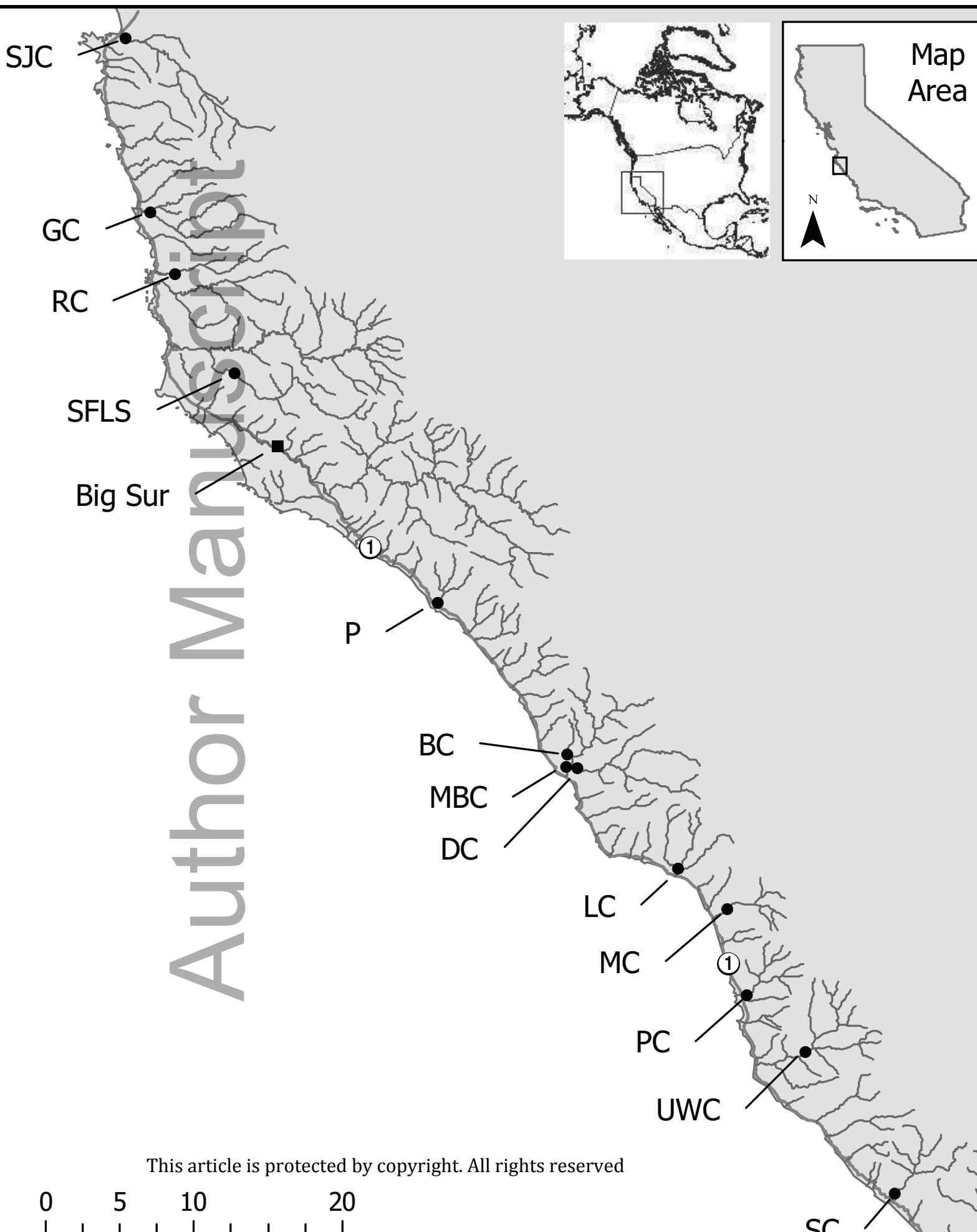
930

931 **Figure 5.** Energetic value (Joules, median and 95% confidence interval) of *O. mykiss*  
932 stomach contents of (a) aquatic, (b) terrestrial, and (c) all prey from 13 sites in Big Sur,  
933 California. Estimates are predicted values from generalized least squares (GLS) models for  
934 the mean-sized fish (127 mm FL) back-transformed to the original scale. Sites are ordered  
935 from north to south and site codes are defined in Table 1. Note that y-axis scale differs  
936 among panels.

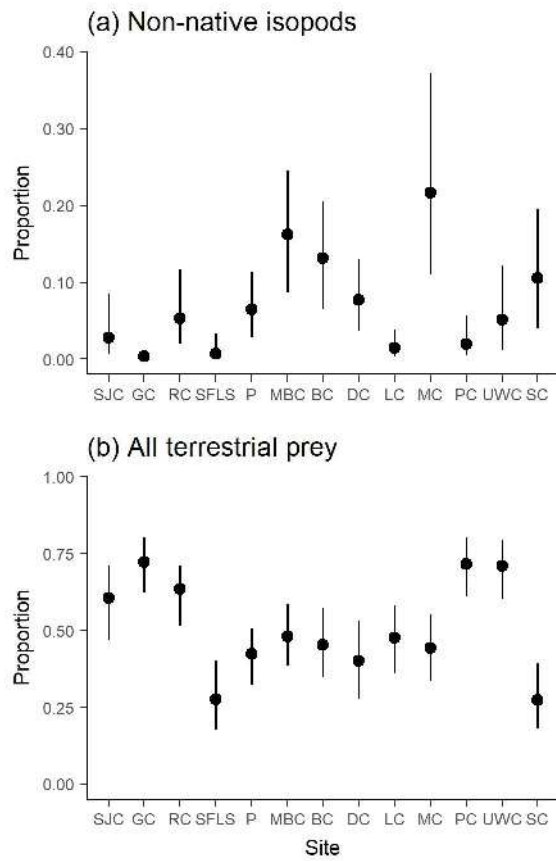
937

938 **Figure 6.** Nonmetric multidimensional scaling (NMDS) ordination of study sites in Big Sur  
939 based on Bray-Curtis similarity of average *O. mykiss* diet composition (relative energetic  
940 abundance of 84 prey taxa). Symbols for sites are shaded by latitude from north (dark) to  
941 south (lighter)

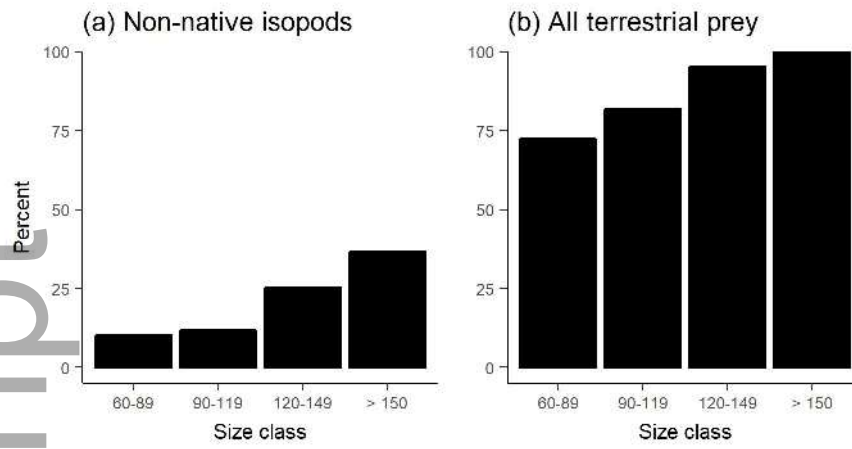
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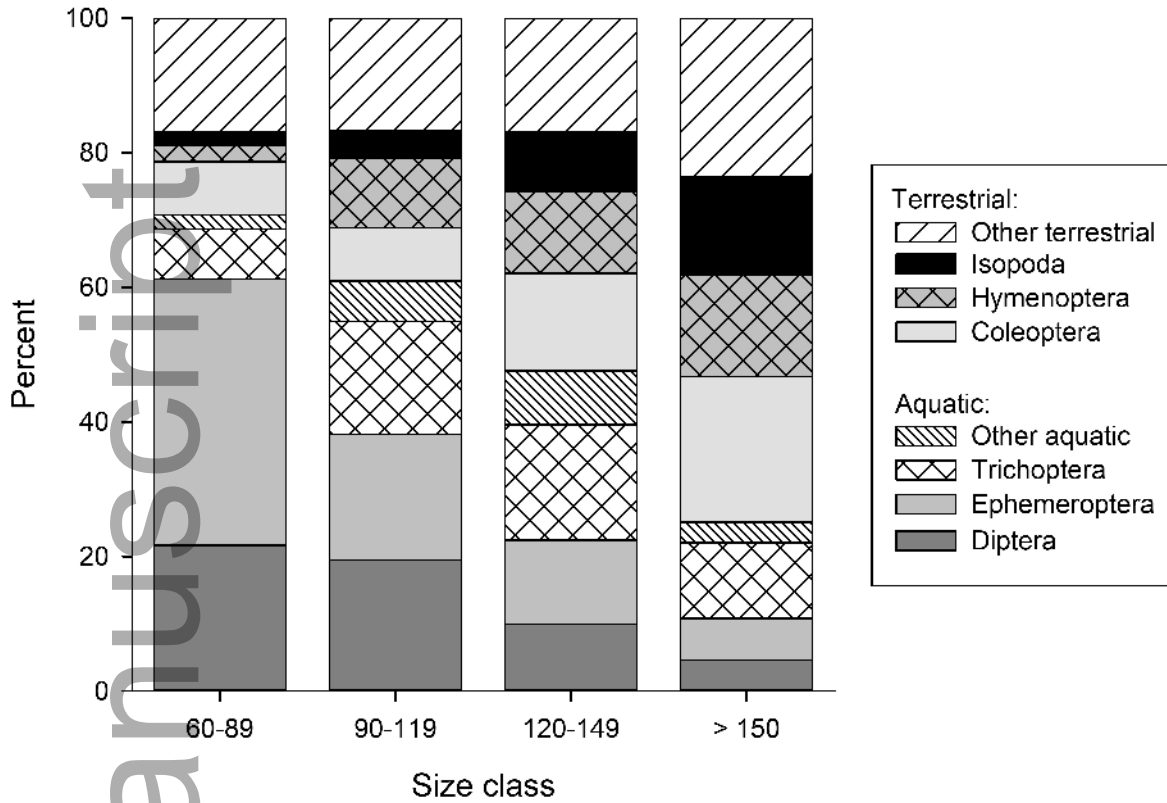


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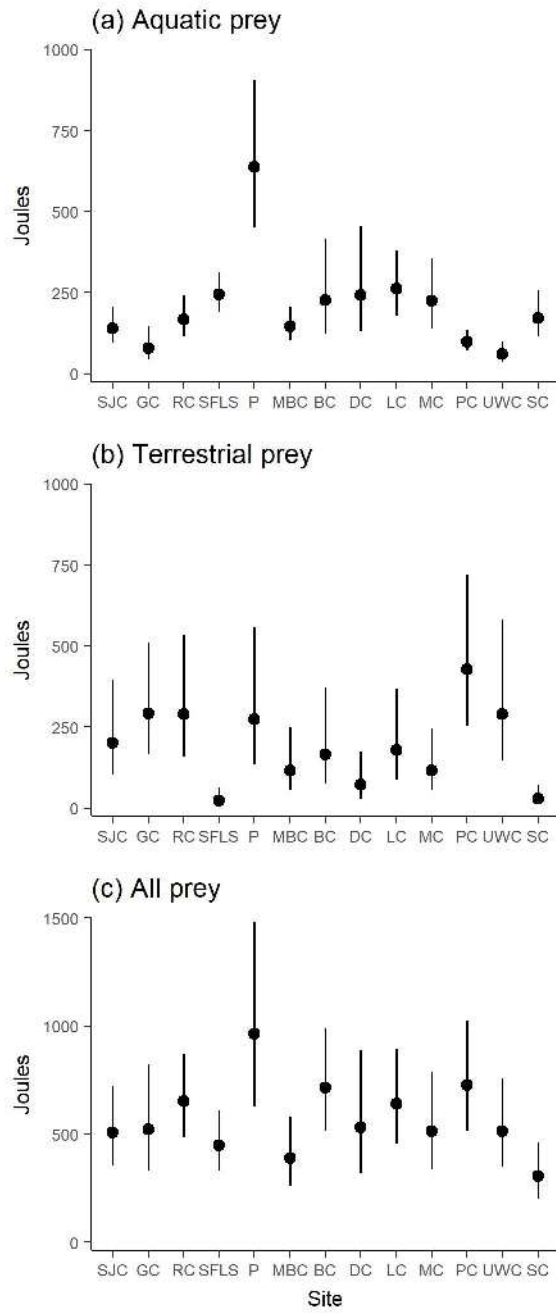


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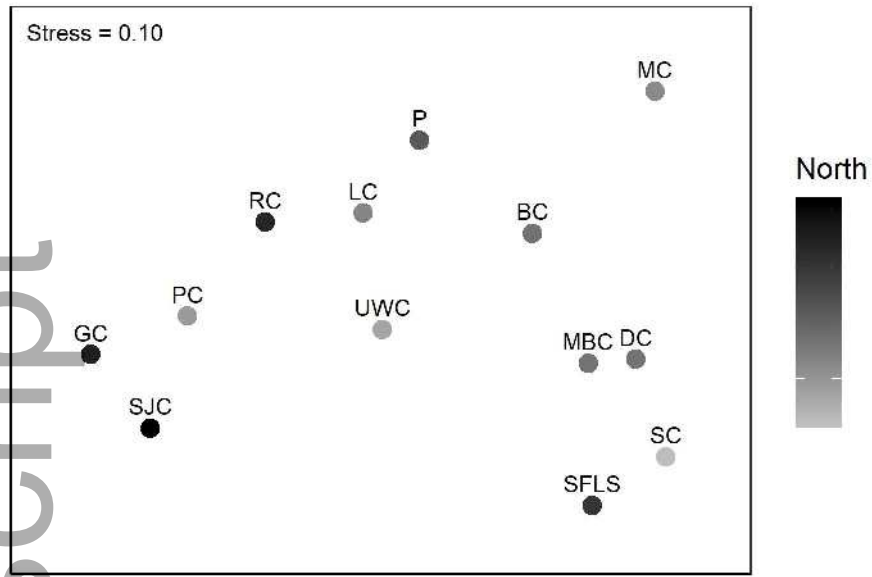




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