

EXPORT OF INVERTEBRATE DRIFT FROM FISHLESS HEADWATER STREAMS

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A Thesis Presented to

The Faculty of Humboldt State University

In Partial Fulfillment of the Requirements for the Degree

Master of Science in Natural Resources: Fisheries

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December 2018

ABSTRACT

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An understanding of ecological linkages between headwater systems and downstream habitats is needed to enhance management practices for aquatic conservation. I quantified and described the export of invertebrate drift from fishless headwater streams to assess its potential importance to downstream populations of Coastal Cutthroat Trout (*Oncorhynchus clarki clarki*) in the lower Klamath River in northern California. From June 2015 through April 2016, I sampled invertebrate drift in six fishless headwaters in the sub-basins of Tectah, Ah Pah, and Tarup creeks. Concurrently, I collected invertebrate drift and trout diet samples from adjoining fish-bearing streams. Drift export rates were lowest in October and greatest in April, and ranged from 98 - 1331 mg dry mass stream⁻¹ d⁻¹. Invertebrate taxa of aquatic origin dominated drift biomass in fishless streams on all four sampling occasions; the proportion of terrestrially-derived biomass was highest in October. Estimates of daily drift flux in fish-bearing streams exceeded the delivery of drift mass from fishless streams throughout the year. Trout diet samples demonstrated tremendous variability in invertebrate biomass among individuals within seasons. However, average biomass per diet sample differed strongly among sampling occasions, and was greatest in April. Terrestrial taxa dominated

the biomass of trout diets in June and October. Both drift and diet samples were taxonomically rich, but exhibited little similarity to each other. I estimated drift exports from fishless headwaters could support a maximum of 37 g dry mass stream⁻¹ year⁻¹ of trout, theoretically accounting for one-tenth to one-quarter of the annual production of over-yearling trout in the study streams.

ACKNOWLEDGEMENTS

This research was supported with funding and technical assistance from Green Diamond Resources Company. I especially thank Matt House, Pat Righter, and Chuck Holt. Additional financial support was generously provided by Dr. Richard Ridenhour (Fisheries Founding Faculty Scholarship), Dr. Terry Roelofs (Danielle Plum Zumbrun Memorial Scholarship), the Marin Rod & Gun Club, and Granite Bay Flycasters.

Many thanks to my adviser, Dr. Peggy Wilzbach, whose availability and guidance were invaluable throughout this endeavor. I thank my committee, Dr. Darren Ward and Dr. Bret Harvey, for their humor, thoughtful advice, and remarkable attention to this project. Thank you to Anthony Desch for supplying me with field and lab equipment, and fabricating new equipment when the need arose. I thank Thomas Starkey-Owens for his expertise and assistance in the laboratory. Thanks to Leslie Farrar for administrative support, and especially all the chocolate. I thank David Roon for sharing his enthusiasm and knowledge of stream ecology. Thanks to my comrades in the Fisheries Cooperative and those in the Fish Ecology lab. Lastly, I thank my partner Laura Lalemand for her infinite and unending love and support throughout this experience.

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INTRODUCTION

Low-order, headwater streams often have insufficient water volume or passage barriers that prevent year-round residence by salmonid fishes. While fishless headwater streams do not provide fish habitat, they may serve as an important source of energy subsidies, transporting invertebrates and organic detritus from forested upland habitats to downstream waters occupied by fish. A central theme in the study of food web dynamics is the exchange of such subsidies across habitat boundaries (Polis et al. 1997). For example, in stream ecosystems, small headwaters interact strongly with surrounding terrestrial habitats, receiving terrestrial inputs such as sediments, nutrients, detritus, invertebrates, and woody debris (Gomi et al 2002). The fluvial transport of these resources to downstream habitats makes them available to downstream food webs.

Drift is the process by which aquatic organisms are transported downstream in current, and is an important mechanism for delivering prey resources to fish (Waters 1968). Drifting invertebrates are a key food source for stream-dwelling salmonids, and fishless headwater streams are thought to be an important donor of this subsidy to downstream fish-bearing habitats (Wipfli et al. 2007, Richardson and Danehy 2007).

Prey subsidies from fishless headwaters can be substantial. For example, Wipfli and Gregovich (2002) estimated headwater streams in southeastern Alaska exported 0.44 grams dry mass m^{-2} stream area $year^{-1}$, and concluded that every kilometer of salmonid-bearing stream could receive enough energy from headwater streams in the form of exported prey and detritus to support 100-2000 young of the year salmonids. Considering

that the majority of the total length of a river network is made up of low-order, headwater streams (Wipfli et al. 2007), and the substantial prey biomass these streams export, these habitats may be of vital importance to salmonid production.

Export of invertebrate prey from fishless headwaters has been quantified in relatively few systems. In those systems for which estimates exist, the extent to which invertebrate prey subsidies from fishless headwaters are actually used by fish and how they contribute to biological production relative to other sources has not been established. While researchers have demonstrated that headwater drift subsidies can make significant contributions to the availability of downstream prey, the circumstances under which such prey is actually consumed and assimilated needs further investigation.

The goals of this study were to characterize invertebrate drift from fishless headwater streams draining timberlands in the lower Klamath River, describe prey consumption by Coastal Cutthroat Trout (*Oncorhynchus clarki clarki*) residing in recipient streams, and to evaluate the implications for trout production. My primary objectives were to describe the magnitude, taxonomic composition, and seasonal variation in the export of invertebrate drift from fishless headwater streams. This exploratory and descriptive research is intended to serve as a baseline for evaluating the effects of past and future management activities on stream food webs in the region.

MATERIALS AND METHODS

Study Location

I selected six fishless headwater streams and adjoining fish-bearing mainstem reaches in three sub-basins of the lower Klamath River watershed in coastal northern California: one site in Ah Pah creek, three sites in East Fork Tectah creek, one site in West Fork Tectah creek, and one site in Tarup creek (Figure 1). These headwaters were classified as Class II (fishless) streams according to the California Forest Practice Rules (California Department of Forestry and Fire Protection 2013) based on previous fish surveys by Green Diamond Resource Company. However, field reconnaissance in May and June 2015 revealed small numbers (< 5 individuals per stream) of trout fry occupying confluence pools in the lowest portions of four headwaters. Therefore, I visually assessed each site to ensure trout fry were not present in the vicinity of invertebrate sampling.

The study streams were located in 30- to 60-year-old timber stands managed for coast redwood (*Sequoia sempervirens*) and Douglas-fir (*Pseudotsuga menziesii*) production. Red alder (*Alnus rubra*), tanoak (*Notholithocarpus densiflorus*), coast redwood (*Sequoia sempervirens*), western hemlock (*Tsuga heterophylla*), and Douglas-fir (*Pseudotsuga menziesii*) dominated the riparian canopy. Also present in smaller numbers were bigleaf maple (*Acer macrophyllum*), willow (*Salix spp.*), cascara buckthorn (*Rhamnus purshiana*), California bay laurel (*Umbellularia californica*), vine maple (*Acer circinatum*), Pacific madrone (*Arbutus menziesii*), and giant chinquapin (*Chrysolepus*

chrysophylla). Catchment area (mean 0.59 kilometers²) and mean bankfull width (mean 2.4 meters) of the selected fishless headwaters were similar among sites (Table 1).

Sample sites were in non-anadromous portions of each sub-basin; only resident individuals of Coastal Cutthroat Trout (*Oncorhynchus clarki clarki*) occurred in each of the mainstem study reaches. Other aquatic vertebrates encountered within the study reaches included Coastal giant salamanders (*Dicamptodon tenebrosus*), California red-legged frog (*Rana draytonii*), and coastal tailed frog (*Ascaphus truei*).

Regional climate is described as marine-west-coast, with precipitation falling almost entirely as rain, the majority of which occurs between November and March. Total rainfall averages 205 cm per year. Average air temperatures range from 16-20° Celsius in the summer, and 4-10° Celsius in the winter. Bedrock of the Klamath River is of the Franciscan complex (California Division of Mines and Geology 1964), and soils are of the Hugo-Josephine association (United States Soil Conservation Service 1967).

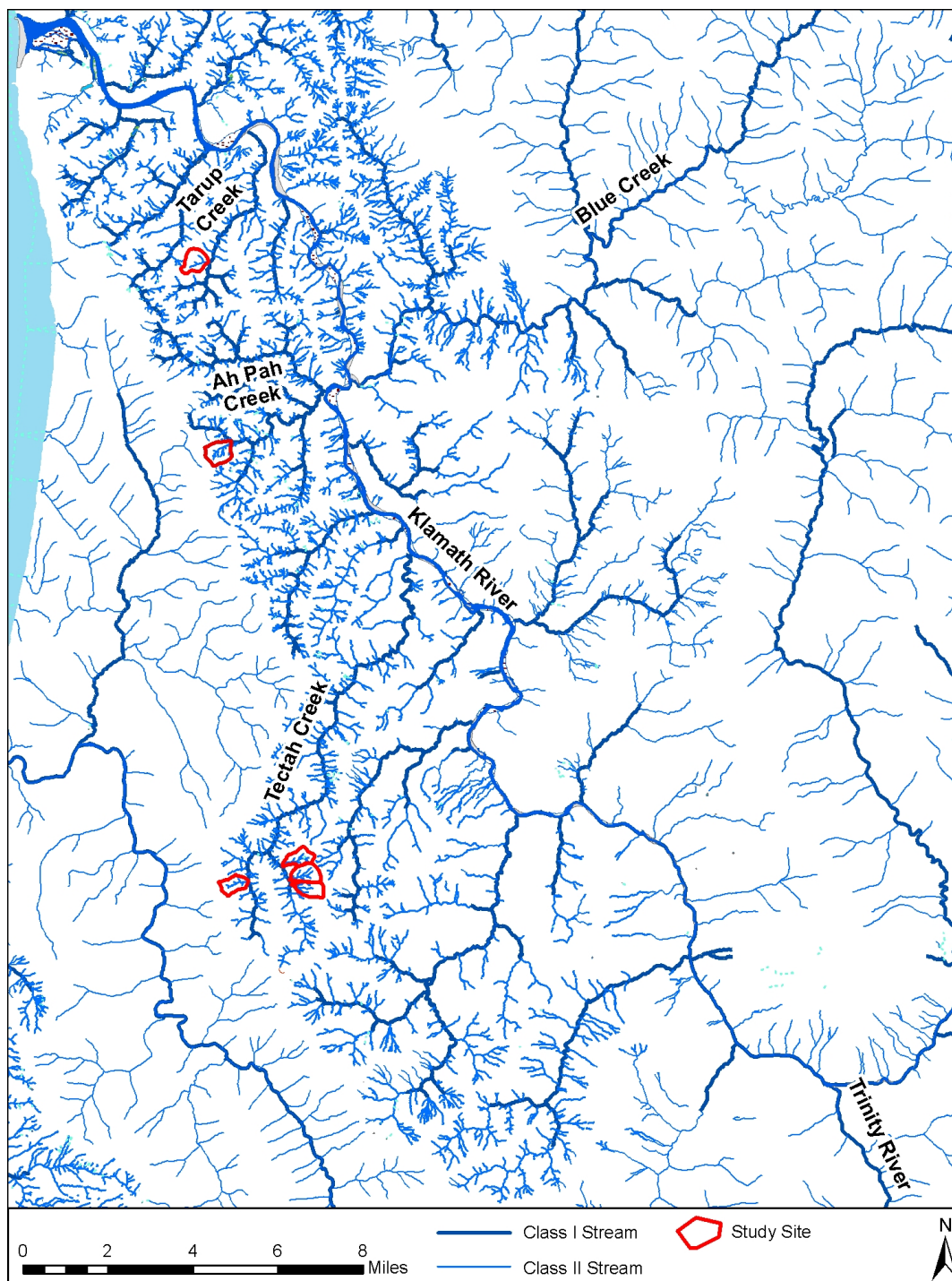


Figure 1. Study sites within the lower Klamath River basin of coastal northern California (Source: Green Diamond Resources Company).

Site Characteristics

In July 2015, I collected environmental and site characteristic data at each of the six fishless stream sites (Table 1) to ascertain site similarity and evaluate potential relationships with export of invertebrate drift. Data were collected from reaches originating at the confluence with fish-bearing streams, upstream for a distance of at least 200 meters (300 m in WF3). I identified and enumerated living stems of riparian trees ≥ 5 cm diameter at breast height within 5 meters of either bank, and measured channel width, gradient, and overstory density at transects located perpendicular to stream flow every 10 m within each reach.

Table 1. Geographic coordinates, catchment area, stream width and gradient, and overstory density and riparian conifer coverage of 200 – 300 m reaches in fishless streams originating at the confluence with fish-bearing streams.

Site ID	Geographic coordinates (UTM)	Catchment area (km ²)	Mean bankfull width (m)	Mean channel gradient (%)	Mean overstory density (%)	Riparian conifer (%)
Ah Pah 2	0417811, 4583998	0.71	3.0	19	98.2	36
EF Tectah 1	0419766, 4567881	0.51	2.7	22	99.7	30
EF Tectah 2	0420005, 4567372	0.64	2.3	12	99.3	45
EF Tectah 3	0420069, 4567204	0.52	2.2	23	92.9	48
Tarup 1	0416950, 4590805	0.63	2.0	15	99.4	29
WF Tectah 3	0418467, 4567346	0.51	2.1	11	99.3	62

Invertebrate Sampling

I sampled drifting invertebrates with 250- μm -mesh nets on four occasions (June 2015, October 2015, February 2016, and April 2016) at each of the six study sites. Two nets were deployed simultaneously per sampling occasion in each fishless stream; one near the confluence and one approximately 100 m upstream. Additionally, a single drift net was deployed in the fish-bearing receiving stream, just upstream of the confluence with the fishless headwater stream. Drift sampling occurred over 24-hour sampling periods. Standard-sized drift nets (45.7 cm x 30.5 cm) were used when surface flow allowed. However, during periods of reduced surface flow, when standard drift nets could not be effectively employed, smaller custom-made cylindrical drift nets (radius 11 cm) were used. Drift nets were placed at riffle tails, and secured with rebar, so that the bottom of each net opening was 2 cm above the stream bed and the top was above the surface of the water. This placement ensured the capture of invertebrates both within the water column and at the water surface. Mean current velocity (m s^{-1}) was measured in the vicinity of drift sampling using a Marsh McBirney Flo-Mate. I averaged a minimum of 10 flow measurements in the stream channel, excluding shallow margins, as well as in the opening of the drift net. Wetted width was measured perpendicular to flow, and depth measurements taken at 15-20 cm intervals. Discharge passing through the sampling net (cross-sectional area of the submerged portion of the net opening multiplied by mean current velocity entering the center of the net), and total streamflow (cross-sectional area of the stream multiplied by mean current velocity of the stream) were measured at the

beginning and end of each 24-h sampling period. Beginning and ending values were averaged and used to estimate drift concentration (biomass of invertebrates m^{-3} estimated from a 24-h sample) and drift export (biomass of invertebrates $\text{stream}^{-1} \text{day}^{-1}$, estimated as the product of drift concentration and daily streamflow).

All invertebrate samples (fishless drift: $n = 35$, fish-bearing drift: $n = 24$) were washed into a 250- μm sieve, transferred to Whirl-Paks®, and preserved in the field using 90% ethanol.

Drought conditions in 2015 resulted in dewatering of some fishless headwaters in summer and fall (Figure 2). According to the United States Drought Monitor, near-record and record low flows in USGS monitored coastal streams of California's Humboldt and Mendocino counties in the month of June warranted a change in drought status from severe to extreme (National Drought Mitigation Center, U.S. Department of Agriculture, and National Oceanic and Atmospheric Association). While drift sampling in fish-bearing mainstem streams was not affected, my ability to collect invertebrate drift samples from fishless headwaters in June and October was limited (Table 2). As a result, I obtained information about drift from fishless headwaters in October from only three of the 12 tributary sampling sites.

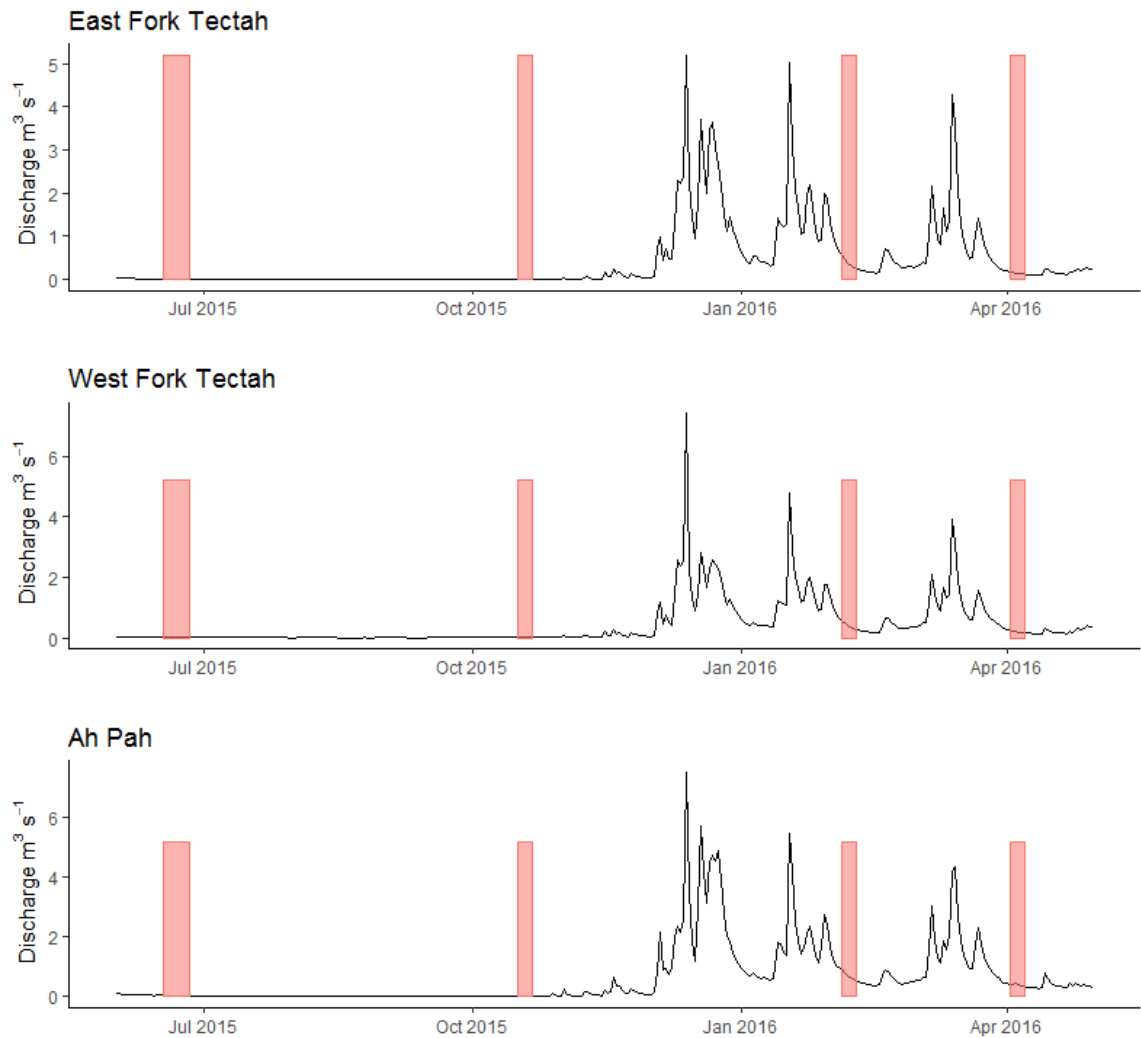


Figure 2. Hydrograph data from Green Diamond Resource Company gauging stations for the mainstems of East Fork Tectah, West Fork Tectah, and Ah Pah creeks for the period of this study (June 1, 2015 – April 30, 2016). Surface flows were very low during June and October sampling efforts, and peaked following winter and spring rain events. Bars represent the timing of drift and fish sampling efforts.

Table 2. Number of drift samples obtained from each site during four seasonal sampling efforts. Zeros indicate when a lack of streamflow prevented drift sampling. When only one sample was collected in a fishless headwater, that sample was collected at a downstream location near its confluence with the mainstem.

	June	October	February	April	<i>Total</i>
Ah Pah 2					
<i>fishless</i>	2	2	2	2	8
<i>mainstem</i>	1	1	1	1	4
EF Tectah 1					
<i>fishless</i>	1	0	2	2	5
<i>mainstem</i>	1	1	1	1	4
EF Tectah 2					
<i>fishless</i>	2	0	2	2	6
<i>mainstem</i>	1	1	1	1	4
EF Tectah 3					
<i>fishless</i>	1	0	2	2	5
<i>mainstem</i>	1	1	1	1	4
WF Tectah 3					
<i>fishless</i>	2	1	2	2	7
<i>mainstem</i>	1	1	1	1	4
Tarup 1					
<i>fishless</i>	1	0	2	1	4
<i>mainstem</i>	1	1	1	1	4

Capture, Diet Sampling, and Tagging

All fish capture and handling was conducted using methods approved by the Humboldt State University Institutional Animal Care and Use Committee under protocol number 14/15.F.95-A.

Electrofishing

I collected yearling and older resident cutthroat trout ($n = 296$ individuals; 360 encounters; Table 3) from downstream fish-bearing reaches associated with invertebrate sampling sites with a battery powered, backpack electrofisher (Smith-Root Inc., Vancouver, Washington) using pulsed DC of 200 volts. Electrofishing took place in the

morning prior to invertebrate drift sampling during each sampling event. A thorough single pass was made in a downstream direction in 100-meter reaches originating at the confluence with fishless streams. Sampling was conducted slowly and deliberately to cover all available water. Higher flows in February and April necessitated the use of block nets placed at riffle crests to prevent trout from moving downstream and out of the sampling reach. Multi-pass electrofishing in the study systems indicates first-pass capture efficiency averages 75% (B.C. Harvey, personal communication), thus I estimated total trout biomass in the study reaches by dividing the biomass captured by 0.75. Trout larger than 65 millimeters fork length were retained with dip nets and transferred to buckets containing creek water for temporary holding prior to measurement and collection of diet samples.

Table 3. Number and size of trout collected from mainstem streams on four occasions. Trout were not collected from EF2 in February due to staffing constraints. Recaptured trout were collected on two or more occasions. Young-of-the-year (YOY) fish were not collected for processing, but counts were recorded in the field.

Sampling date	Sites sampled	N	Mean N reach ⁻¹	Length (mm)			Mass (g)			Recap.	YOY tally
				Mean	Min	Max	Mean	Min	Max		
June	6	113	18.8	117.2	84	199	18.81	5.8	75.1	NA	48
October	6	103	17.2	112.9	76	200	16.99	4.4	79.5	33	45
February	5	59	11.6	106.9	71	225	17.48	3.9	114.7	18	18
April	6	85	14.2	98.12	71	185	11.58	2.9	59.5	15	1

Processing and handling

Captured trout were anesthetized with buffered MS-222 (tricaine methanesulfonate) at a dosage of 100 ppm and measured (fork length, nearest millimeter). Stomach contents were collected by gastric lavage from a maximum of 20

trout per site, per sampling occasion (Meehan and Miller, 1978; Kamler and Pope, 2001). I performed lavage using a 3.8-L, hand-pumped garden sprayer fitted with a modified tip (2 x 80 mm) inserted through the fish's mouth and foregut into the stomach. A gentle, continuous spray of creek water and massaging of the belly were employed to empty the foregut and evacuate excess water. Green Diamond fisheries personnel inserted individually numbered Passive Integrated Transponder (PIT) tags (Biomark, Inc. Boise, ID) into each fish. PIT tags provided an identifying marker to develop growth records for individuals recaptured on subsequent occasions. Trout were weighed (wet mass, nearest 0.1 gram) following lavage so that stomach contents would not contribute to mass measurements, and after receiving a PIT tag to account for the mass of the tag during ensuing sampling events. Trout were transferred to buckets filled with creek water and/or net pens and allowed to fully recover. Upon recovery, we promptly returned trout to the reach from which they were collected.

Diet samples and fish measurements were collected at each of the six study sites on each of the four seasonal sampling occasions, with the exception of EF2 in February, when field support could not be procured.

Laboratory Procedures

I identified, enumerated, and measured (nearest mm) all macroinvertebrates from fishless headwater stream drift samples (n = 35) and fish diet samples (n = 350). Jon Lee Consulting subsampled and processed drift samples collected from fish-bearing streams (n = 24) following the California Stream Bioassessment Procedure (2003) protocol.

Invertebrates from all samples were measured from the tip of the head to the end of the abdomen, excluding projections and cerci. Maximum shell length was measured for Mollusca and carapace length was measured for Decapoda. In instances of damaged or fragmented individuals, only the number of heads was enumerated, and the length was estimated using measurements from intact individuals of similar head size. Biomass (dry mass mg) estimates were derived using taxon-specific length-mass regressions (McCauley 1984, Sample et al. 1993, Hodar 1996, Benke et al. 1999, Sabo et al. 2002, Baumgartner and Rothhaupt 2003, Takahara et al. 2008, Wardhaugh 2013, M. A. Wilzbach and K. W. Cummins, personal communication). I chose to identify specimens to family level because this is the finest level of taxonomic resolution for which length-mass relationships commonly exist.

Data Analysis

I performed all statistical analyses with R version 3.5.1 (R Core Team 2018) in RStudio version 1.1.456 (RStudio Team 2016).

Determining the implications of drift exports from fishless streams for downstream prey availability and trout production was the primary motivation of this study. Thus, my analysis focuses on invertebrate biomass rather than numerical data, as biomass has greater biological relevance for production.

Invertebrate drift

The magnitude of invertebrate drift was evaluated by drift concentration (dry mass of invertebrates per m³ of water filtered), and drift flux (drift concentration

multiplied by estimated daily streamflow) for fishless headwaters and fish-bearing mainstem streams. I compared drift magnitude among fishless headwater streams, among sampling occasions, and among fishless headwaters and fish-bearing streams. I used linear regression to assess relationships between drift concentration and streamflow, streamflow and the percentage of terrestrially-derived drift, and drift export from fishless streams and riparian canopy composition (percentage coniferous).

Drift composition was evaluated gravimetrically and numerically by origin (aquatic or terrestrial) and by taxon at the Order and Family levels (for insects). Comparisons were made among fishless headwaters and sampling occasions, and between fishless headwaters and fish-bearing streams. Additionally, I examined the similarities in taxonomic composition among samples collected in fishless headwaters at upstream locations with their counterparts collected downstream, near the confluence with a fish-bearing stream. I hypothesized that the upstream faunal assemblages would be similar in composition to those found downstream.

Trout diet

I compared the invertebrate mass of trout diet samples from different sampling occasions to assess seasonal feeding patterns. Diet samples were log-transformed to normalize variance and were compared using ANOVA with Tukey HSD pair-wise comparison tests ($P < 0.05$).

I assessed diet composition in a similar fashion to drift composition, using mass and abundance to determine proportions by origin and by taxon.

Drift / Diet similarity

Comparisons of taxonomic composition of tributary drift exports and fish diet samples were made using the Bray-Curtis dissimilarity index (Bray and Curtis 1957):

$$D = \frac{\sum |a_s - a_d|}{\sum a_s + \sum a_d}$$

where a_s is the proportion of a particular taxon found in the stomach contents of trout, and a_d is the proportion of that taxon found in drift samples collected from fishless headwaters. To express the measures as a similarity, the complement of the dissimilarity was used ($1.0 - D$). The measures were thus scored from 0 (samples completely disjoint) to 1 (samples identical).

Additionally, I assessed similarities between drift and diet samples qualitatively by plotting the proportions of the most dominant taxa of each sample type against one another. This assessment was made between drift from fishless headwaters and diet samples, drift from mainstem streams and diet samples, and drift from both fishless headwaters and mainstem streams.

Contribution of drift export to trout production

To assess how drift export from fishless headwaters may contribute to local trout production, I averaged estimates of daily export and multiplied by 365 to obtain an estimate of average annual export. I multiplied the estimate of average annual export by a food conversion efficiency for stream trout from the literature (Waters 1988) to determine the maximal contribution of export to annual trout production. To assess the proportion of

local trout production potentially supported by drift export, I first estimated annual production of over-yearling trout encountered in 100 m survey reaches using a literature value for annual production to mean annual biomass for resident stream-dwelling Coastal Cutthroat Trout (Lowry 1966). Then, I estimated the proportion of annual production of over-yearling trout as the maximal contribution to production made by export, divided by the estimate of annual production.

To provide context for the proportion of trout production attributable to drift export, I determined the number of fishless tributaries feeding West Fork Tectah, and attributed 100 m (the length of my study reaches) to each. Those numbers were summed and divided by the total length of fish-bearing habitat in West Fork Tectah. I then multiplied the resulting proportion of stream length and the estimated proportion of annual production of trout for the study reaches to obtain an estimate of the proportion of production on the stream scale.

RESULTS

Drift from Fishless Headwaters

Drift magnitude

Drift magnitude was highly variable among fishless streams during a given sampling occasion, and differed greatly from season to season. Drift concentration (excluding dry streams) was highest in October and lowest in February, ranging from 0.17 – 2.15 mg dry mass per cubic meter water sampled over the course of the year (Figure 3).

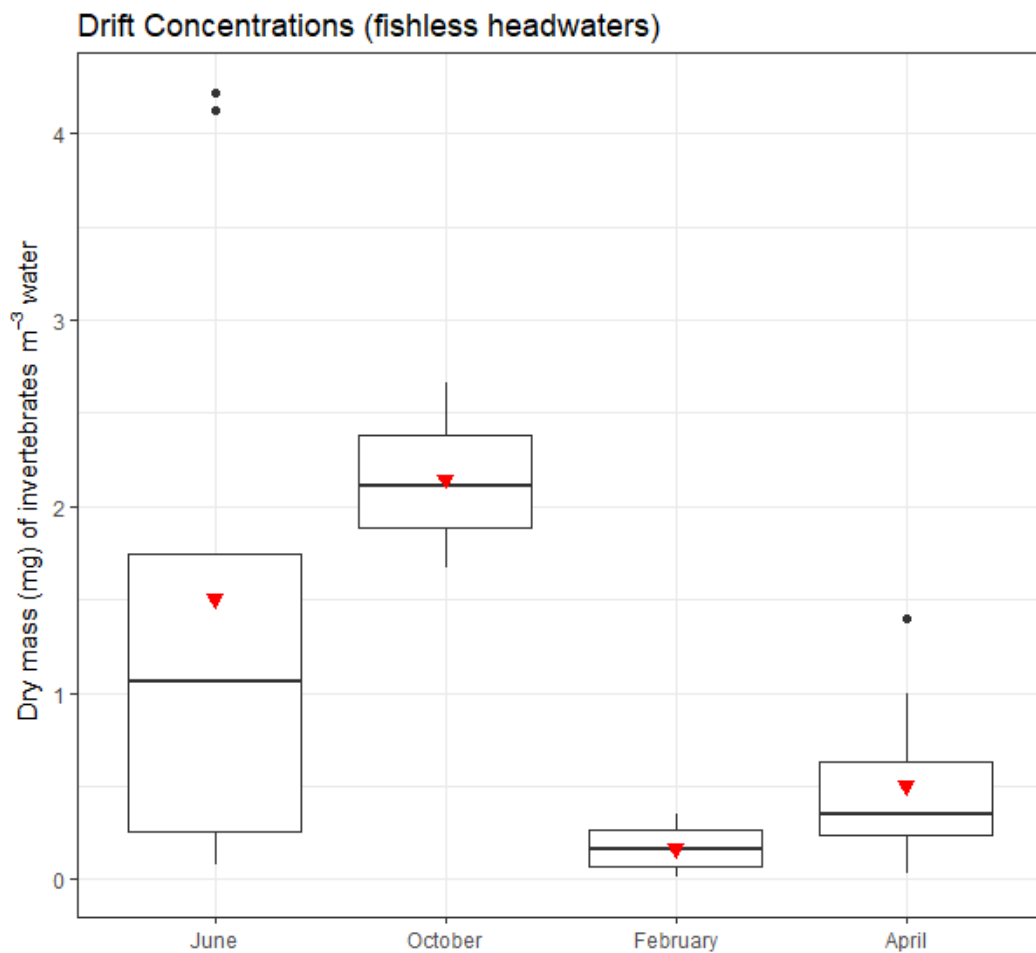


Figure 3. Box plots of seasonal drift concentration in fishless headwaters in the lower Klamath River, California during 2015-2016. Triangles indicate mean drift concentration values. Total n = 35 samples.

Drift concentrations differed between upstream and downstream sampling locations for number of individuals m^{-3} water ($t = 2.89$, d.f. = 5, $p = 0.02$) but not by mass ($t = 1.07$, d.f. = 5, $p = 0.17$). In general, downstream locations exhibited higher drift concentrations than upstream locations during this study (Figure 4). Acknowledging this difference in magnitude and proximity to fish-bearing streams, I used drift concentrations measured at downstream sampling locations only when estimating values of drift export.

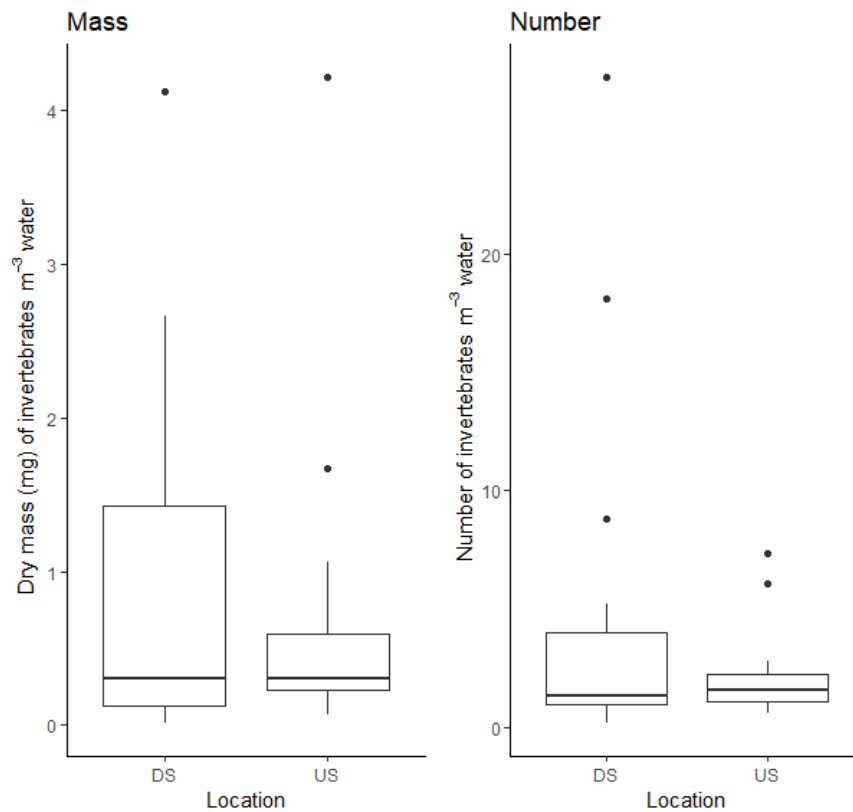


Figure 4. Comparison of annual drift concentrations at upstream (US) and downstream (DS) locations for six fishless headwater streams of the lower Klamath River. Drift concentrations were summed over 4 seasonal sampling events for each site during 2015-2016. A paired t-test revealed drift concentrations by number to be significantly greater at downstream sampling locations.

Daily export from fishless headwaters to fish-bearing streams was estimated to range from 98 – 1331 mg dry mass per stream per day (Figure 5). With the exception of site AP2, the greatest amount of drift export from fishless streams generally corresponded with measurements of peak discharge during this study.

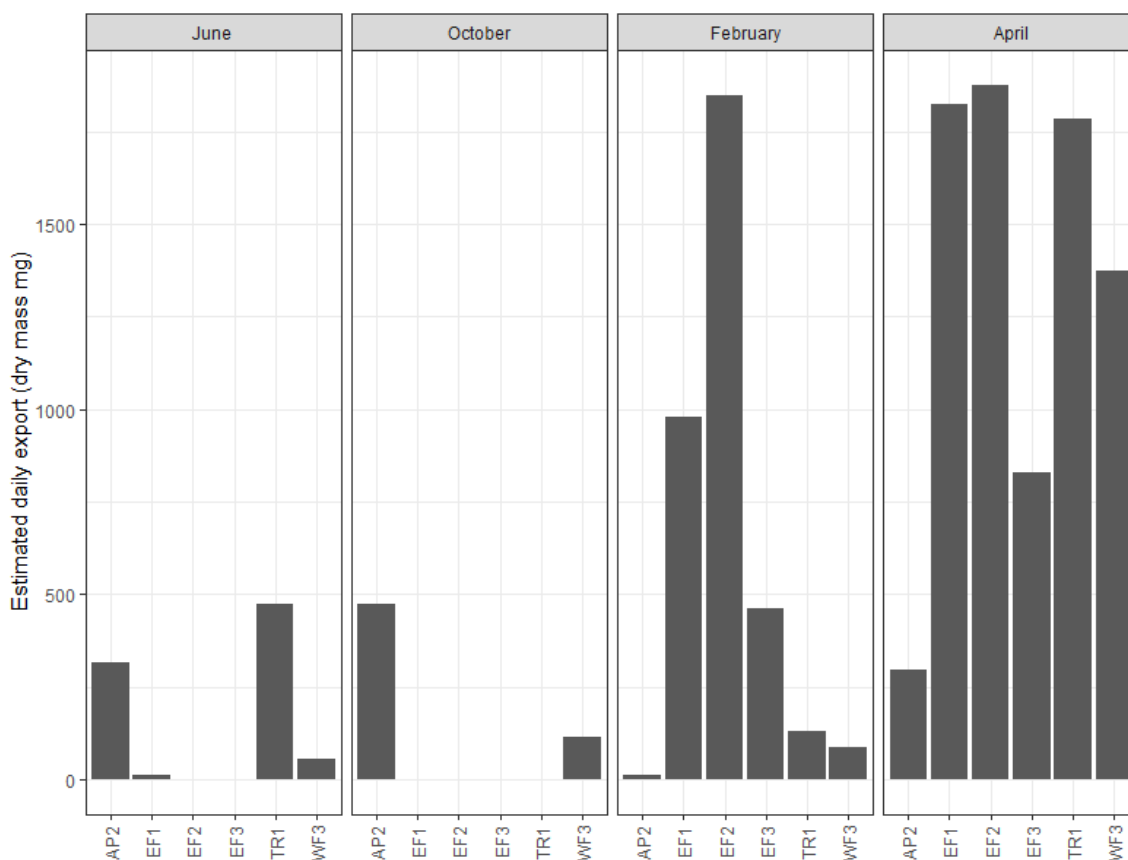


Figure 5. Seasonal comparison of estimated daily exports of invertebrate drift from six fishless headwater catchments in the lower Klamath River during 2015-2016. Estimates for each season are the product of drift concentration and channel discharge. AP2 is in Ah Pah creek; EF1, EF2, and EF3 are in East Fork Tectah creek; TR1 is in Tarup creek; WF3 is in West Fork Tectah creek.

Discernable patterns in the relationship between discharge and drift concentration were not observed, though the highest drift concentrations occurred during periods of very low flow (Figure 6). Nor was a relationship observed between discharge and percentage of drift biomass comprising invertebrate taxa of terrestrial fauna (Figure 7). A relationship between the amount of invertebrate export and percentage of coniferous riparian trees was not apparent (Figure 8).

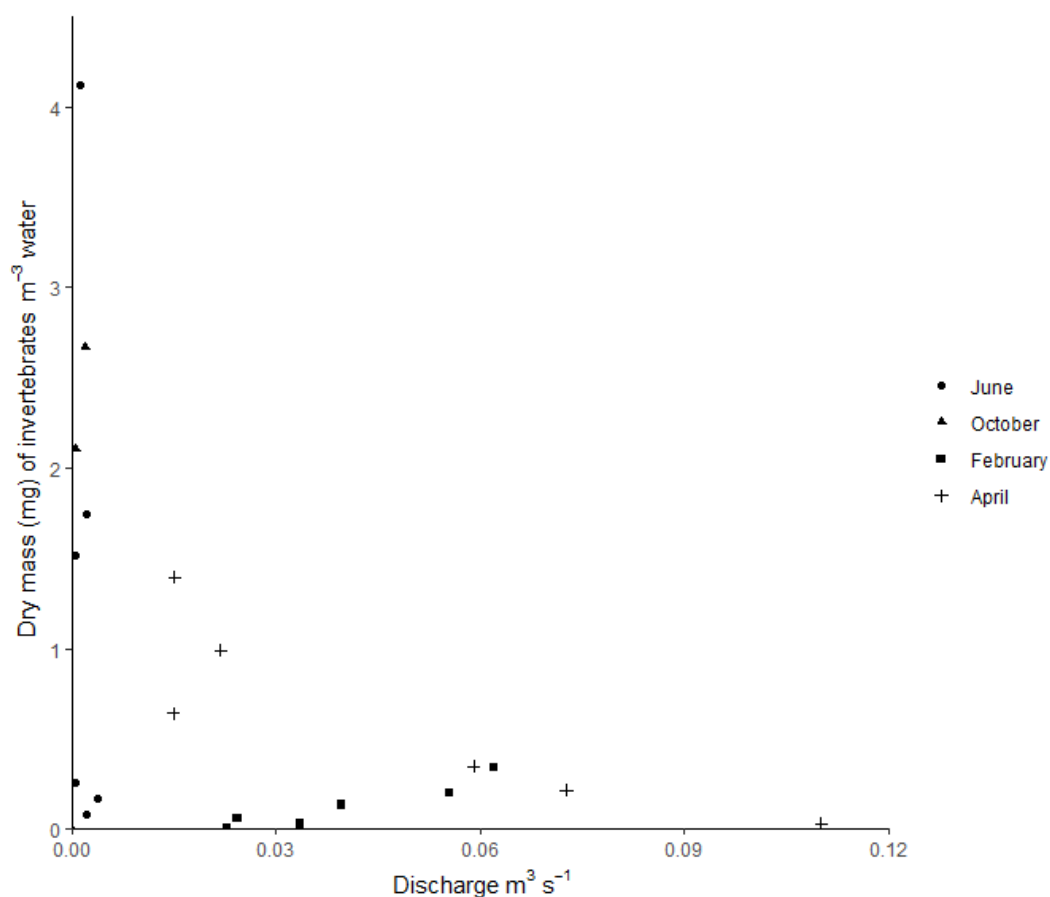


Figure 6. Stream discharge measurements and drift concentrations of samples collected at downstream locations in six fishless headwater streams of the lower Klamath River Basin in northern California during 2015-2016.

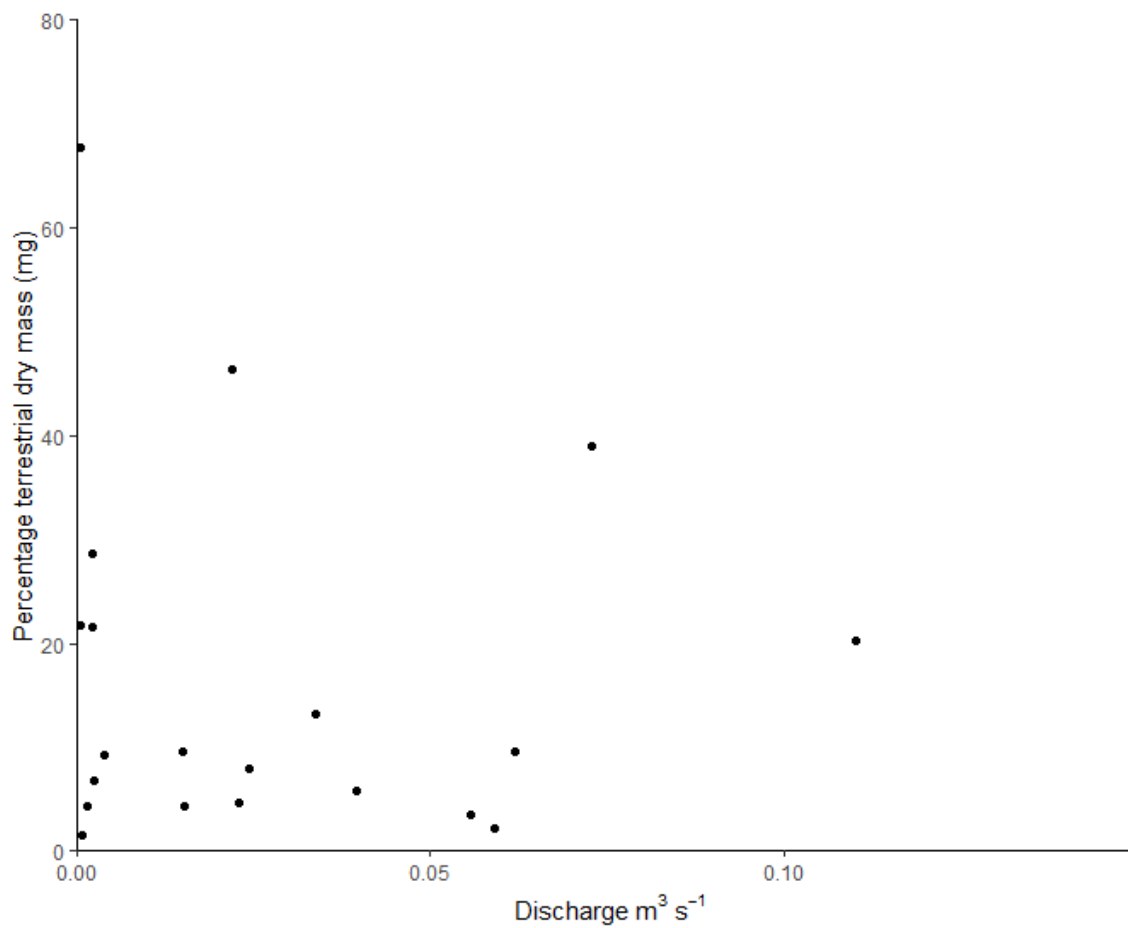


Figure 7. Stream discharge measurements and percentage of drift concentration biomass composed of taxa of terrestrial origin in six fishless headwater streams in the lower Klamath River Basin in northern California during 2015 – 2016.

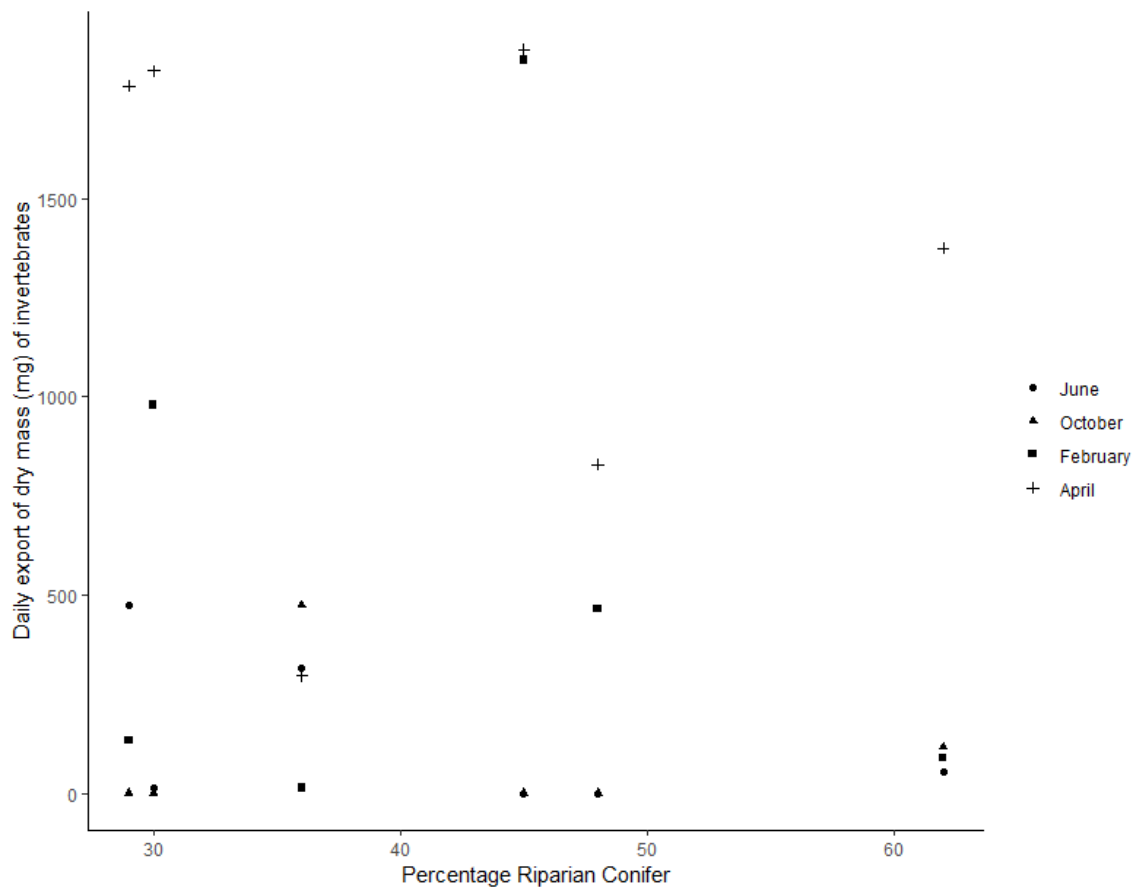


Figure 8. Seasonal estimates of daily invertebrate exports and the percentage of riparian conifers from six fishless headwater catchments in the lower Klamath River Basin in northern California during 2015-2016.

Drift composition

Drift samples from fishless headwater streams contained invertebrates of aquatic, semi-aquatic, and terrestrial origin. The drift exhibited high taxonomic diversity, with all of the major aquatic insect orders represented. Baetidae, Rhyacophilidae, Oligochaeta, Heptageniidae, and Acari composed the greatest biomass, representing 12%, 8%, 7%,

7%, and 6% respectively. Acari, Collembola, Chironomidae, Baetidae, and Peltoperlidae were the most numerous taxa (23%, 20%, 10%, 7%, and 5% respectively). Dominant drift taxa varied seasonally (Appendix B). The taxonomic composition of the drift varied widely between streams, and to a lesser extent between sampling locations (i.e. upstream vs. downstream within a fishless reach). Seasonal variation in taxonomic composition within a given stream was substantial in some instances, but in general was smallest in streams with year-round flow, and smallest between the February and April sampling occasions. Upstream and downstream sampling locations typically shared dominant taxa throughout the study. No single taxon achieved a majority of the drift, either gravimetrically or numerically, during any of the seasonal sampling occasions. The greatest dominance by mass occurred in June, with Rhyacophilidae composing 22% of the biomass collected. The greatest numerical dominance occurred in October, when Chironomidae composed 33% of the drift collected. Several taxa appeared in the drift during all sampling occasions (e.g. Baetidae, Heptageniidae, Chironomidae, Dixidae, Nemouridae, Peltoperlidae). Even in streams that were dry in October, numerous taxa that had been found in June were again found in the drift in both February and April.

Aquatic taxa were more numerous and accounted for a greater percentage of the total biomass of the drift than terrestrial taxa throughout this study, representing up to 59 – 77% of the total biomass and 44 – 78% of the total number of individuals collected per sampling event (Figure 9). The largest contribution by terrestrial invertebrates to the total drifting biomass occurred in October (32%). Insect taxa dominated the drift numerically in June, composing 85% of total numbers, and declined steadily on each subsequent

sampling event to 48% of the total abundance in April. In spite of this numerical decline, insect biomass dominated the drift across all four seasonal sampling events, ranging from 68 – 92% of the total biomass collected per sampling effort (Figure 10).

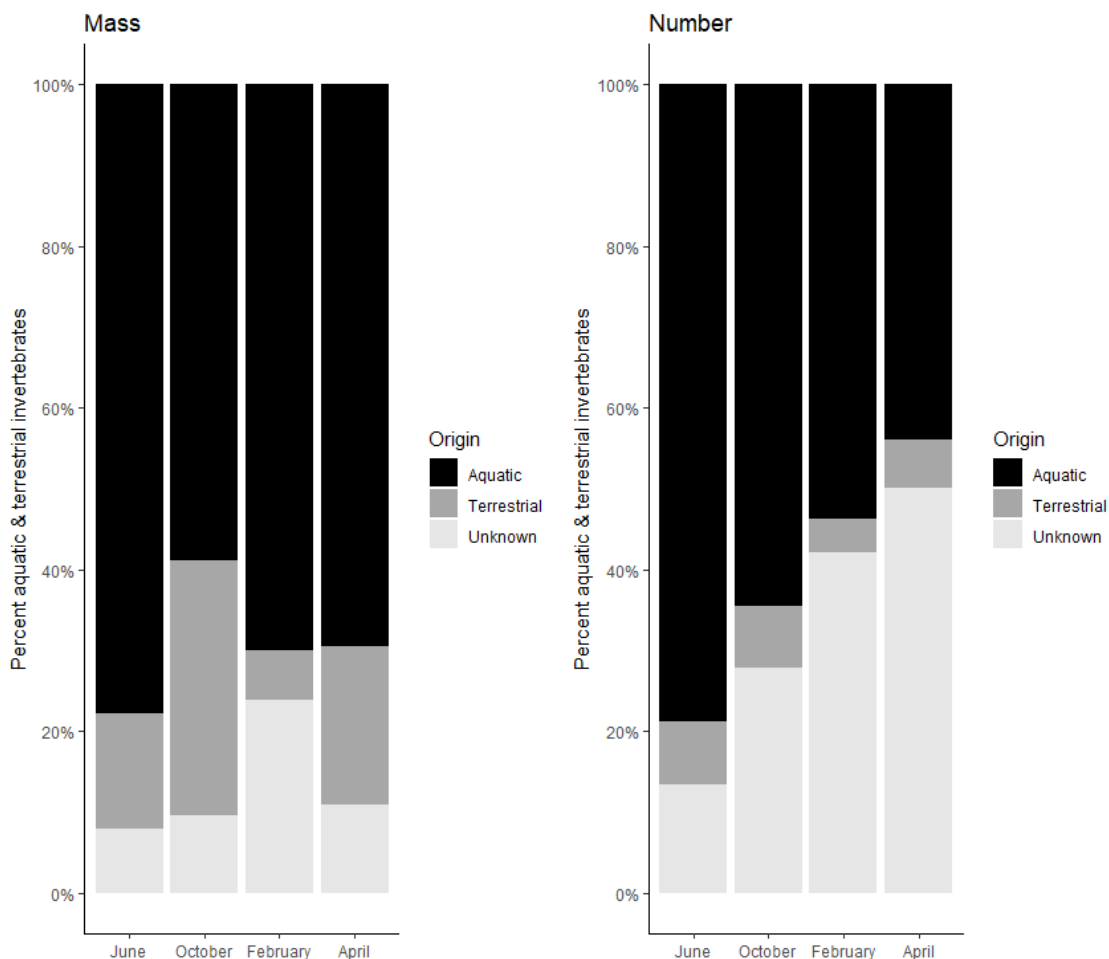


Figure 9. Percentages of aquatic and terrestrial invertebrates found in drift samples ($n = 35$) collected in six fishless headwater catchments in the lower Klamath River Basin in northern California during 2015-2016. Invertebrates of “unknown” origin included taxa for which origin could not be determined (Acari, Collembola, Nematoda, Oligochaeta, some Coleoptera and Diptera larvae, and Nematomorpha). Seasonal changes in the proportion of invertebrates of “unknown” origin were attributed almost entirely to changes in Acari and Collembola, except in February when Oligochaeta also contributed a substantial increase in biomass.

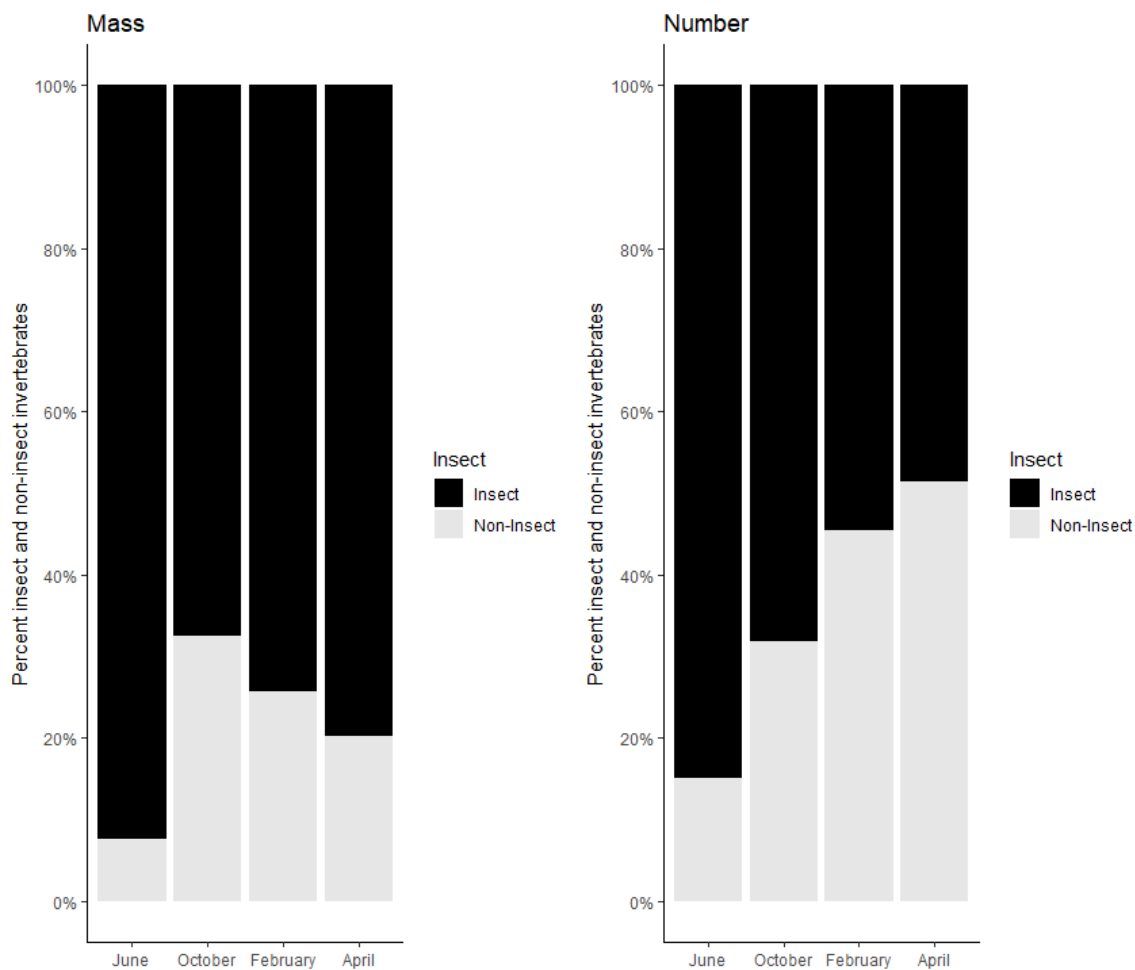


Figure 10. Percentages of insect and non-insect invertebrates found in drift samples ($n = 35$) collected in six fishless headwater catchments in the lower Klamath River Basin in northern California during 2015-2016.

Drift from Fish-Bearing Mainstem Streams

Drift magnitude

Drift concentrations in fish-bearing streams exhibited patterns of seasonal change similar to those observed in fishless headwaters, demonstrating a high degree of seasonality. The highest mean concentrations occurred in June and the lowest in February. Mean 24-h drift concentrations ranged from 0.04 – 1.44 mg dry mass per cubic meter water sampled over the course of the year. Numerically and gravimetrically, concentrations were lower than those observed in fishless streams (Figure 11).

Daily drift flux ranged seasonally from an estimated 202 – 5353 mg dry mass per stream per day. Greater mainstem discharge resulted in daily drift flux values for mainstem reaches that generally exceeded export from fishless headwaters (Figure 12), although in a few notable instances, estimates of invertebrate export from fishless headwaters exceeded estimates of mainstem flux (Figure 13).

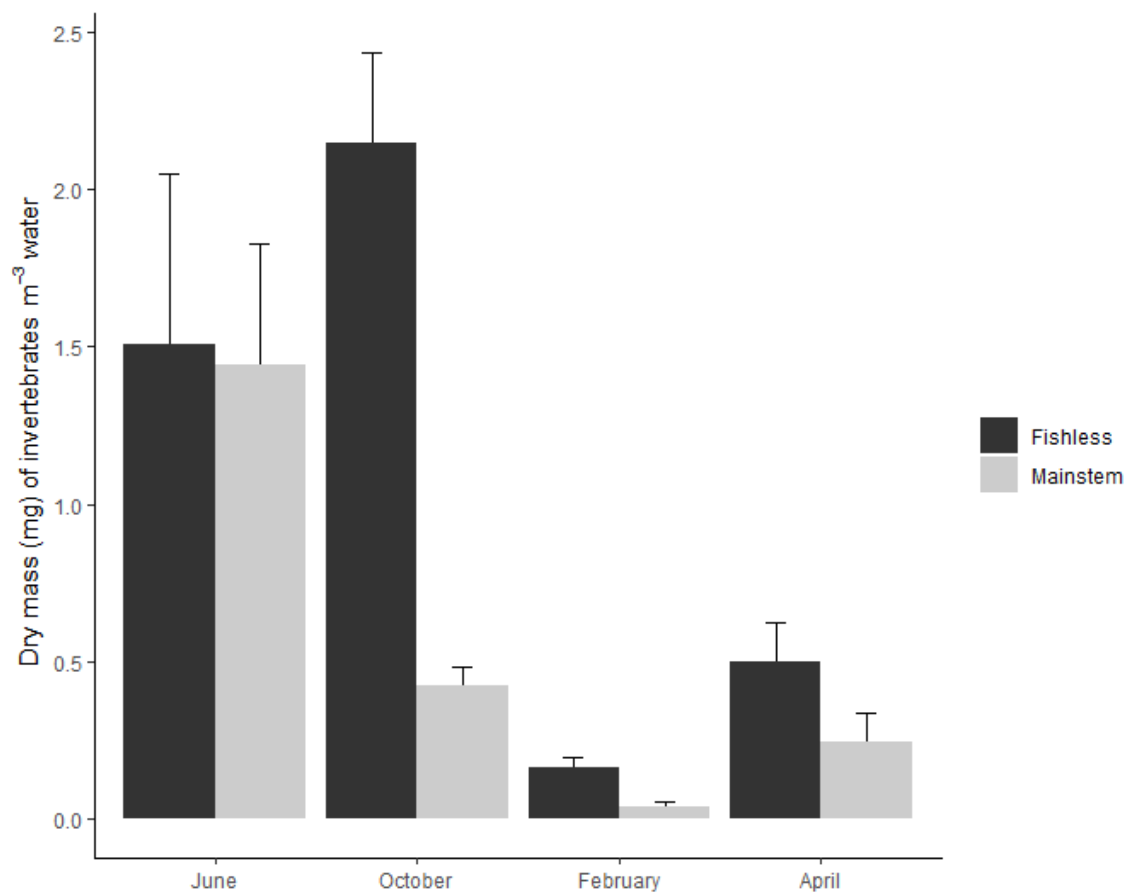


Figure 11. Mean 24-h drift concentrations from fishless headwaters (n = 35) and fish-bearing, mainstem streams (n = 24) in the lower Klamath River Basin during 2015-2016. Error bars represent 1-standard error of the mean.

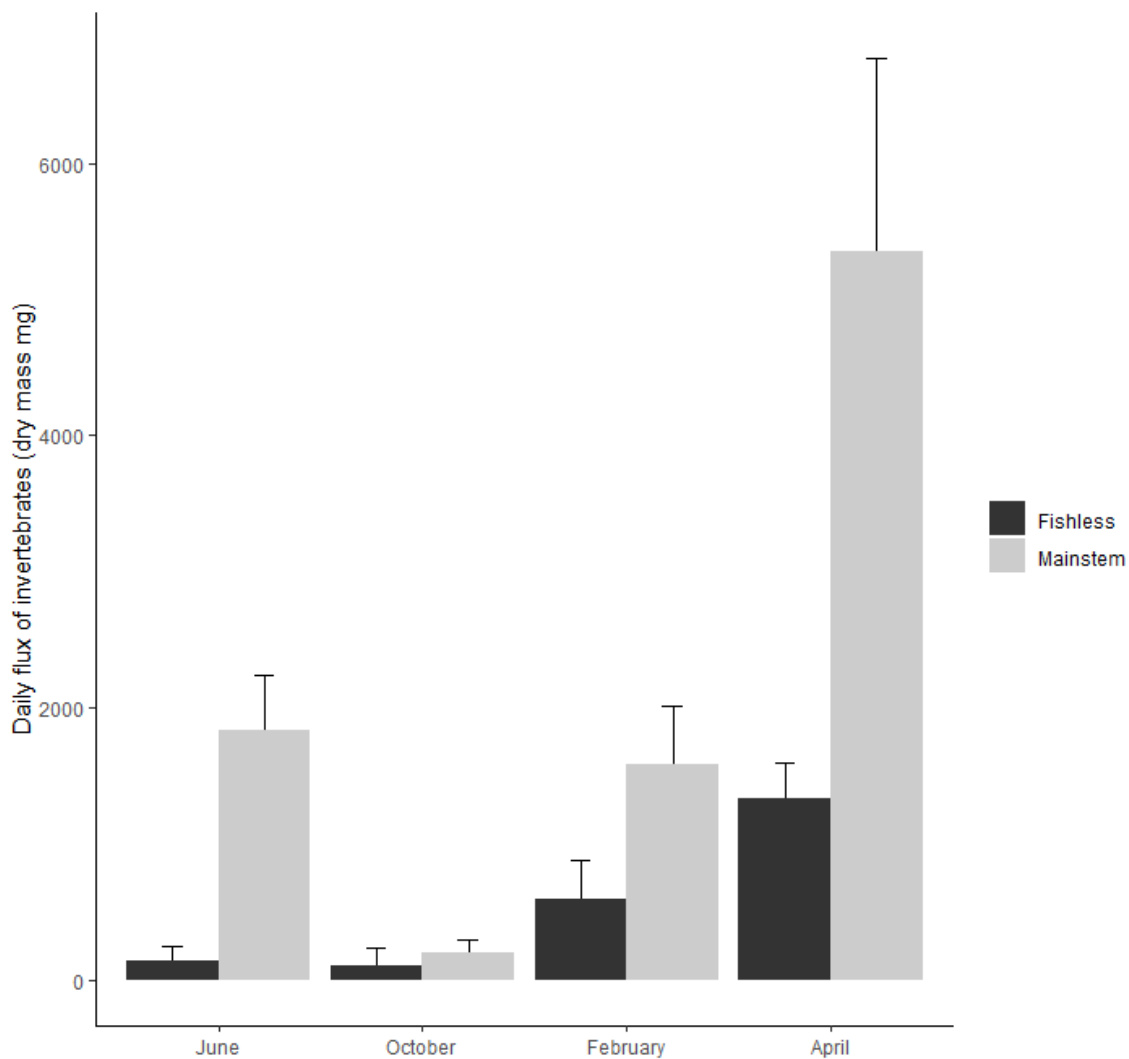


Figure 12. Seasonal estimates of mean daily export of invertebrate drift from fishless headwater streams and mean daily flux of invertebrate drift in adjacent fish-bearing, mainstem streams in the lower Klamath River Basin in northern California during 2015-2106. Error bars represent 1-standard error of the mean.

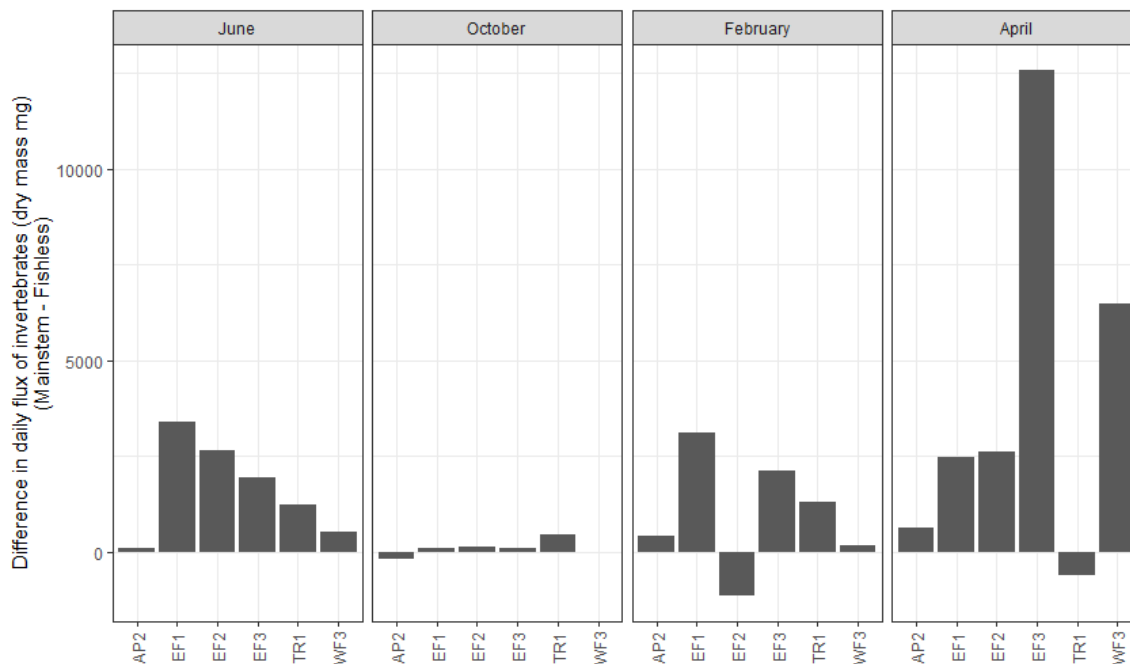


Figure 13. Differences in daily drift flux (mainstem fish-bearing streams minus fishless streams) at sites in six catchments in the lower Klamath River Basin, northern California during 2015-2016. AP2 is in Ah Pah creek; EF1, EF2, and EF3 are in East Fork Tectah creek; TR1 is in Tarup creek; WF3 is in West Fork Tectah creek.

Drift composition

The drift fauna of fish-bearing streams was similar to that observed in fishless headwaters. Notable differences in mainstem drift were the presence of dragonfly larvae, and a higher incidence of large predaceous stoneflies. Perlidae, Acari, Baetidae, Ameletidae, Chloroperlidae, and Chironomidae composed the greatest drifting biomass in mainstem streams (15%, 12%, 11%, 4%, 4%, and 4% respectively). The most numerous taxa were Chironomidae, Baetidae, Acari, Capniidae, Heptageniidae, and Sialidae (18%,

18%, 9%, 6%, 5%, and 4% respectively). As with drift from fishless headwaters, the dominant taxa observed in drift samples varied seasonally (Appendix B). Aquatic taxa composed 75 – 88% of the total biomass and 75 – 97% of the total abundance per sampling effort (Figure 14). While the origin of some taxonomic groups could not be determined for drift samples from fishless headwaters, mainstem samples were identified to a finer taxonomic resolution, and thus all invertebrate taxa (with the exception of Oligochaeta) were classified as either aquatic or terrestrial. In the case of Acari, the numerical percentage of aquatic representatives ranged from 38% in October to 76% in April. Collembola were entirely of terrestrial origin. Insect taxa accounted for 77 – 94% of the biomass and 77 – 97% of the number of invertebrates collected (Figure 15). The taxonomic composition of mainstem drift samples was more consistent among streams during a given sampling occasion than it was in fishless headwaters, and while seasonal variability existed, the most dominant taxa were fairly consistent across seasons, relative to fishless headwaters. The drift composition of fishless headwaters and mainstem reaches was not strongly correlated over the course of this study (Figure 16), and failed to demonstrate any strong seasonal similarities during the four sampling efforts.

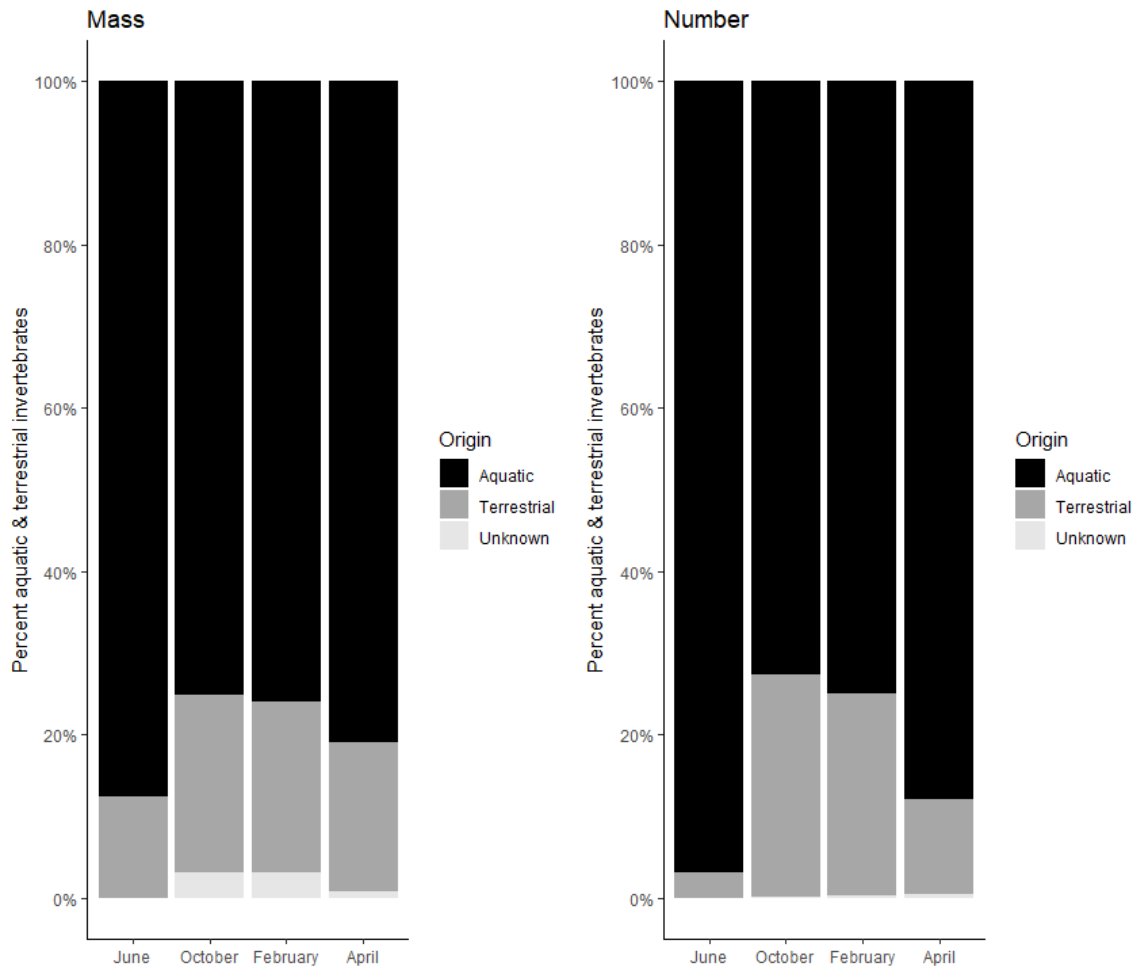


Figure 14. Estimated percentages of aquatic and terrestrial invertebrates found in drift samples ($n = 24$) from six fish-bearing, mainstem streams in the lower Klamath River Basin in northern California during 2015-2016. Mainstem drift samples were identified to a finer taxonomic resolution than samples from fishless headwaters, which allowed origin classifications to be assigned to a greater number of taxa. Here, invertebrates of “unknown” origin represented Oligochaeta only.

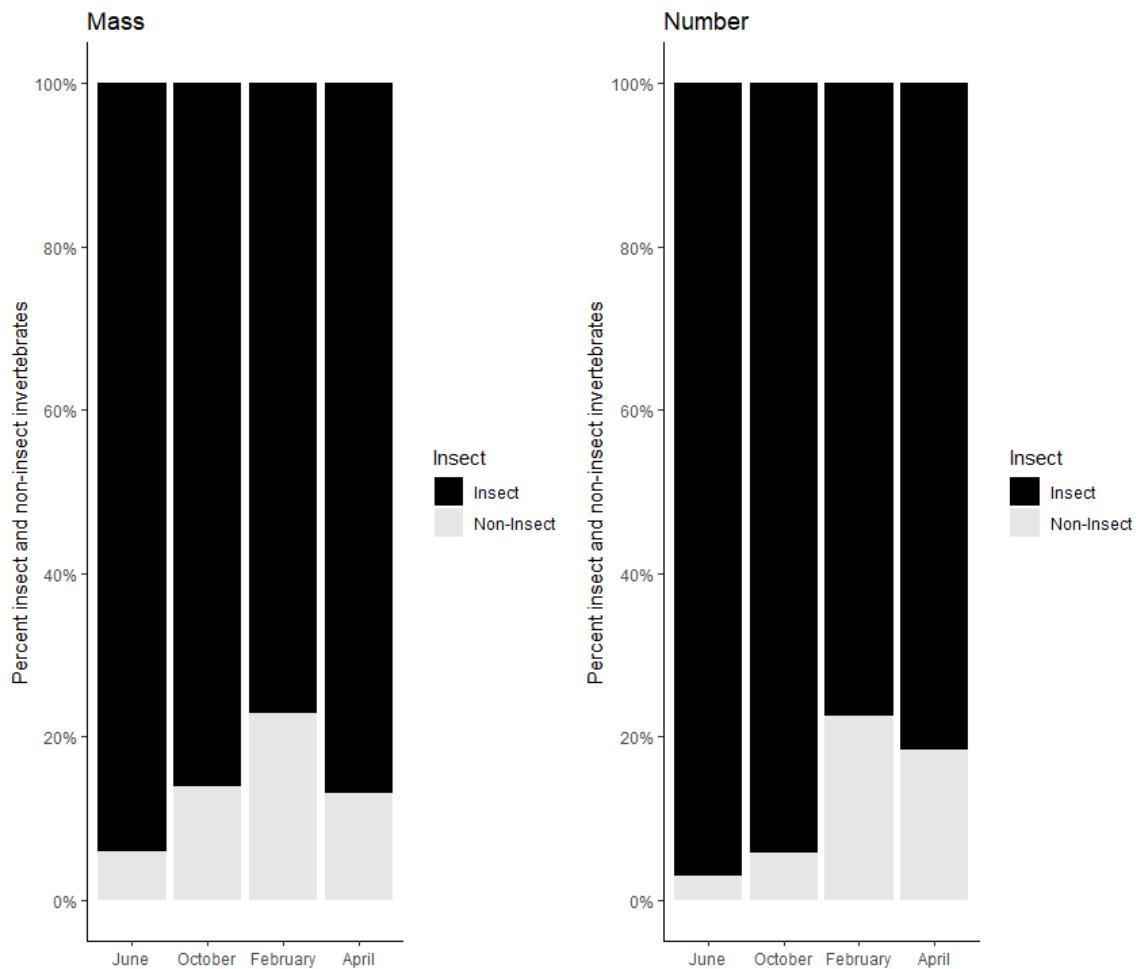


Figure 15. Estimated percentages of insect and non-insect invertebrates found in drift samples ($n = 24$) from six fish-bearing, mainstem streams in the lower Klamath River Basin in northern California during 2015-2016.

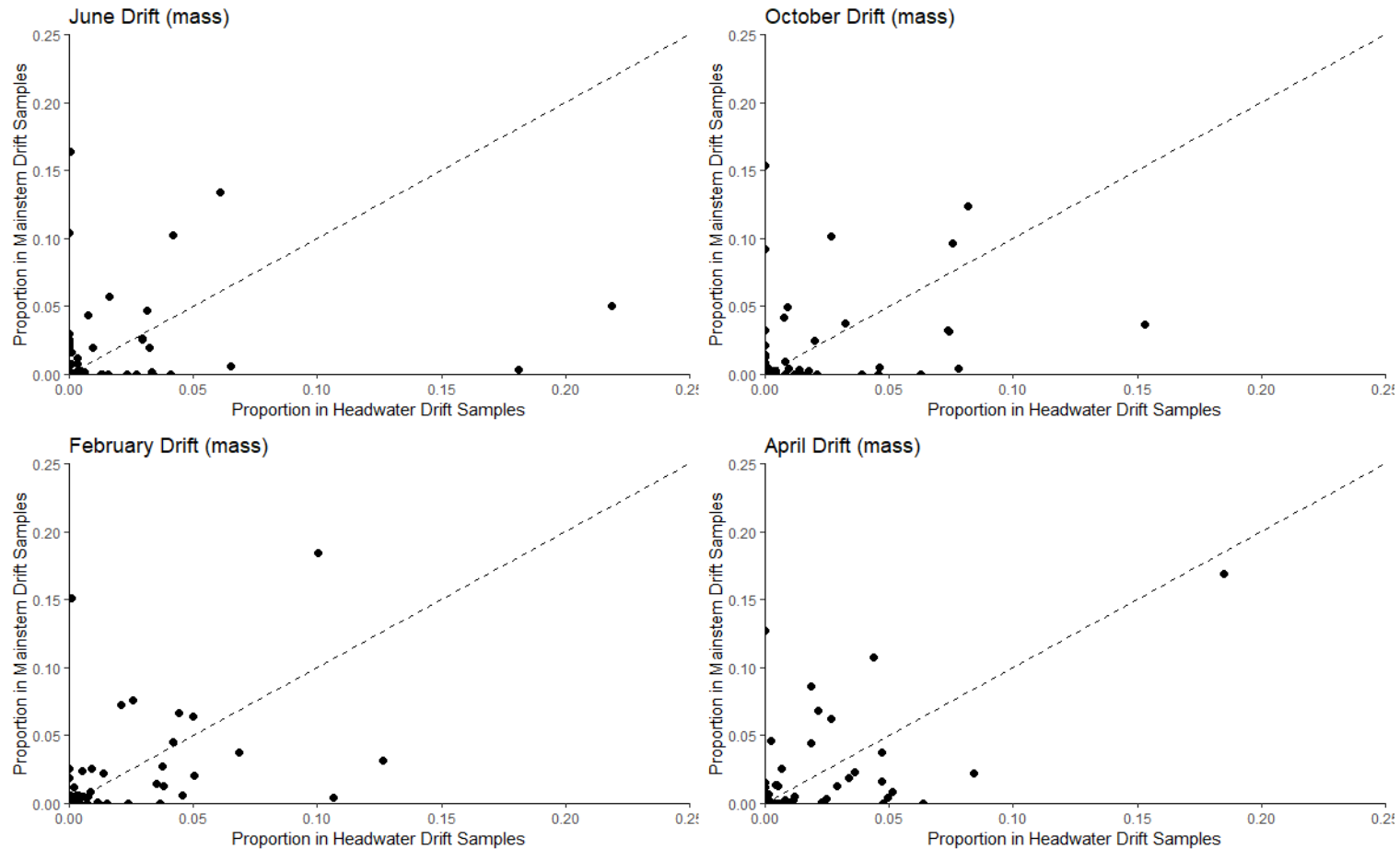


Figure 16. Relationship between proportion of invertebrate taxa dry mass in mainstem drift samples and proportion in fishless headwaters drift samples in the lower Klamath River Basin in northern California during 2015-2016. Dots represent individual taxa. June Spearman's $r_s = 0.11$, $p = 0.33$. October Spearman's $r_s = 0.005$, $p = 0.96$. February Spearman's $r_s = 0.49$, $p < 0.001$. April Spearman's $r_s = 0.35$, $p < 0.001$.

Diet Samples

Diet magnitude

Mean biomass per diet sample differed among sampling occasions (d.f. = 3, d.f. = 346, $F = 9.489$, $p < 0.001$), with the greatest biomass occurring in April (Figure 17). Rations demonstrated a propensity for high variability among individuals within a season. While mean rations ranged from 13 – 35 mg dry mass per trout per sampling effort, a number of extreme outlier rations obtained from certain individuals were observed in October. Extreme gravimetric outliers frequently contained Gastropods (slugs) and/or Diplopoda. The most extraordinary instances of numerical outliers occurred when a single trout consumed 814 Cecidomyiidae larvae, and another trout consumed 468 Mycetophilidae larvae, among other prey items.

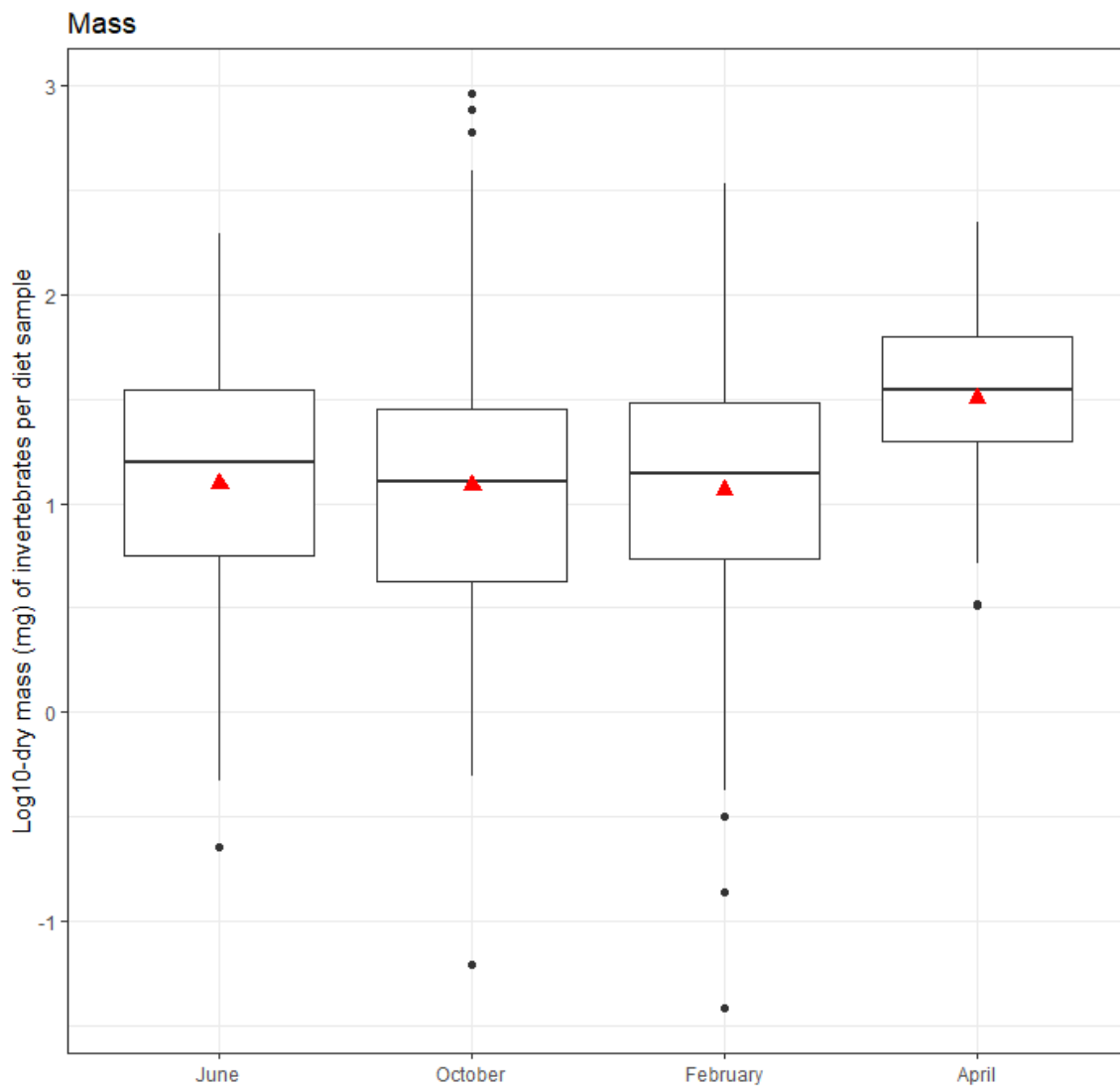


Figure 17. Log base 10-transformed dry mass (mg) per diet sample based on seasonal sampling of Coastal Cutthroat Trout. Triangles indicate mean values and dots represent outliers.

Diet composition

Diet samples contained both vertebrate and invertebrate prey. Nine vertebrates composed <0.1% of the total numbers of prey consumed, but 29% of the total diet sample biomass. Gastropoda (slugs), Oligochaeta, Diplopoda, adult terrestrial Coleoptera, and Hydropsychidae composed the greatest invertebrate biomass (12%, 9%, 7%, 5%, and 3% respectively). Turbellaria, Cecidomyiidae, Chironomidae, Mycetophilidae, and Leptophlebiidae were the most numerous invertebrate taxa (18%, 11%, 6%, 5%, and 4% respectively). Dominant taxa varied by sampling event (Appendix B).

Terrestrial invertebrate taxa were represented more frequently in the diet than in the drift, and were especially dominant in June and October. From a numerical standpoint, this trend was largely driven by two individual trout consuming extraordinary numbers of terrestrial Diptera larvae. A greater incidence of large terrestrial prey such as Gastropoda (slugs), Diplopoda, Lepidoptera, Hemiptera, and Coleoptera account for the dominance of terrestrial prey in the biomass of diet samples collected in June and October. Aquatic taxa represented from 13 – 44% of the total invertebrate biomass and 32 – 76% of the total numbers of invertebrates consumed per sampling event (Figure 18). Insect taxa represented from 35 – 72% of the total invertebrate biomass and 56 – 78% of the total numbers of invertebrates consumed per sampling event (Figure 19).

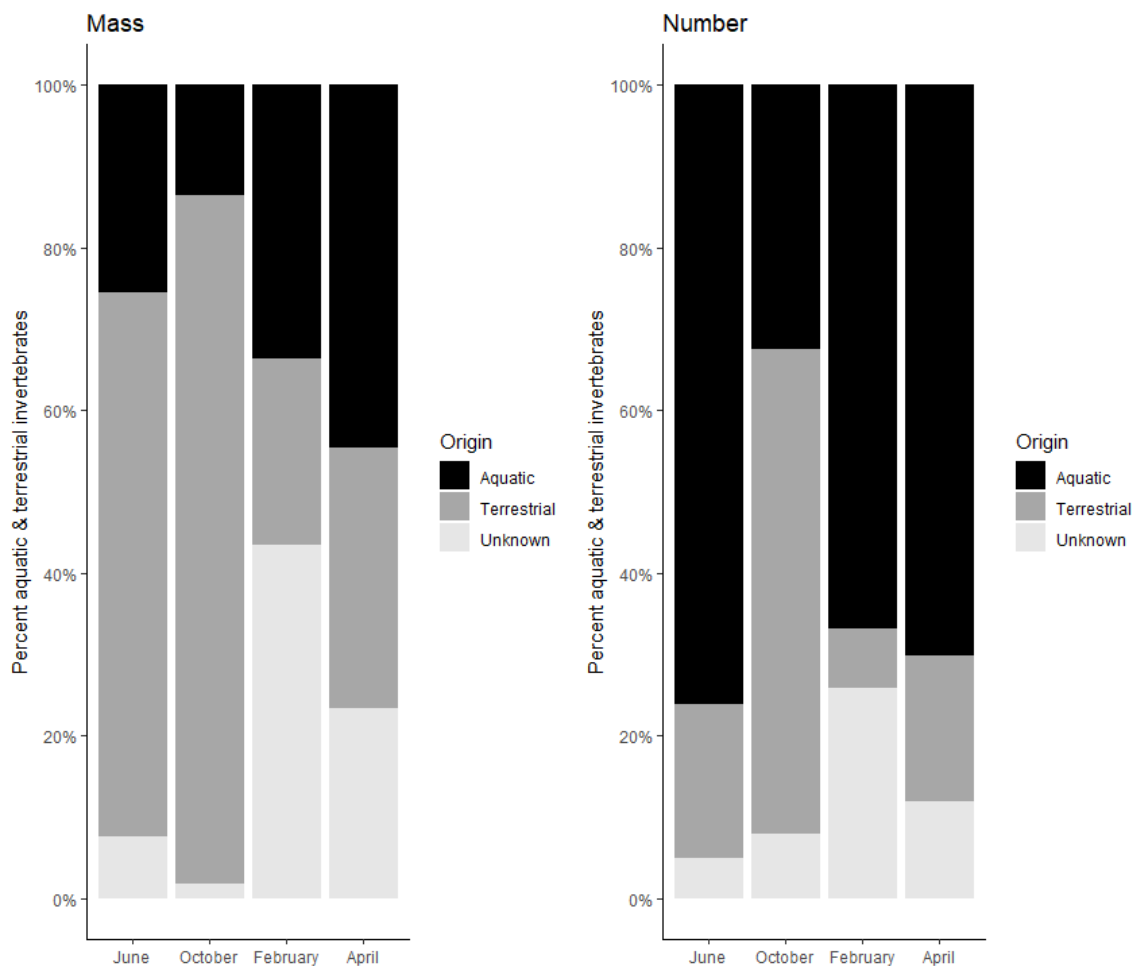


Figure 18. Percentages of aquatic and terrestrial invertebrates found in diet samples of Coastal Cutthroat Trout in six streams of the lower Klamath River Basin in northern California during 2015-2016. Invertebrates of “unknown” origin included the Acari, Collembola, Turbellaria, Nematoda, Oligochaeta, some Coleoptera and Diptera larvae, and Nematomorpha. Acari and Collembola made up a negligible proportion of fish diets during all sampling events. Invertebrates of unknown origin were primarily represented by Turbellaria, Nematoda, and Oligochaeta.

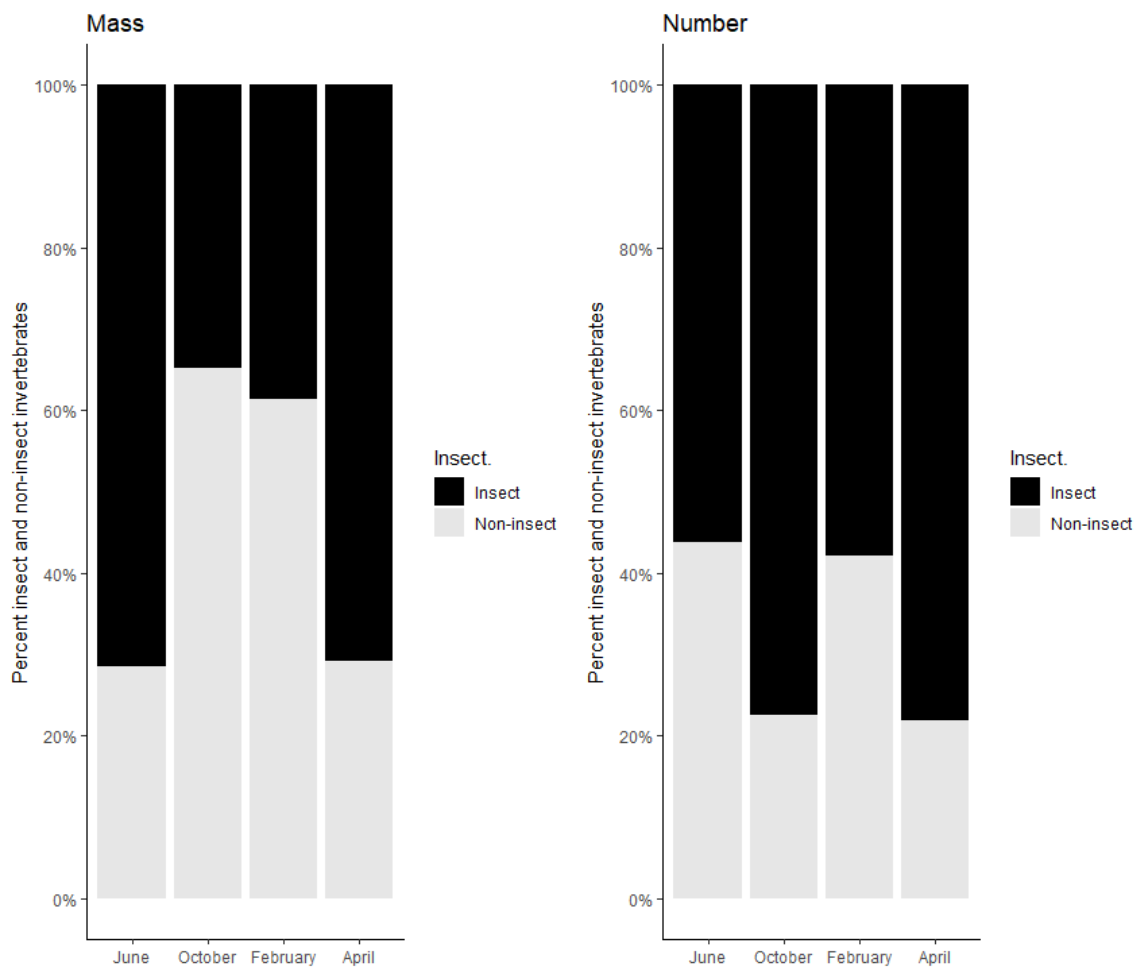


Figure 19. Percentages of insect and non-insect taxa found in diet samples of Coastal Cutthroat Trout in six streams of the lower Klamath River Basin in northern California during 2015-2016.

Drift and Diet Comparisons

Both drift and diet samples exhibited substantial taxonomic diversity, but little similarity to each other (Figure 20, Figure 21, and Table 4). In general, low similarity in dominant invertebrate taxa between drift from fishless headwaters and trout diet samples was observed in all four seasons. Similarity appeared weakest in October when terrestrial prey were most dominant in trout diets.

Table 4. Bray-Curtis similarity index (S) values between proportions of biomass of invertebrate taxa from drift samples collected in fishless headwaters and trout diet samples collected from adjoining streams in catchments of the lower Klamath River Basin in northern California during June 2015 – April 2016. Values range from 0 (samples completely disjoint) to 1 (samples identical).

Sampling occasion	S	
	Fishless	Mainstem
June	0.27	0.27
October	0.23	0.05
February	0.35	0.15
April	0.38	0.35
<i>All occasions combined</i>	0.35	0.21

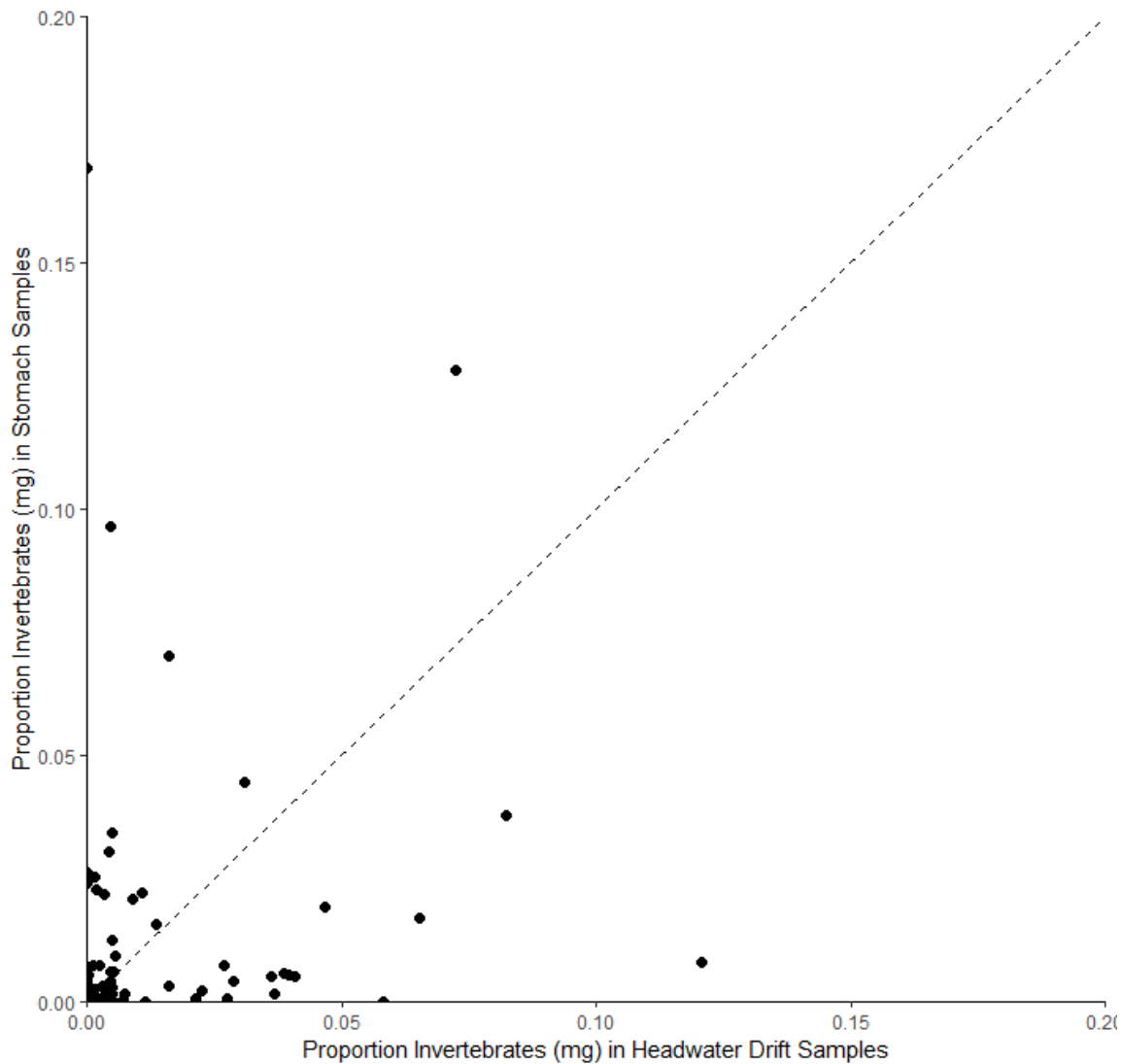


Figure 20. The proportion of all invertebrate taxa found in diet samples of Coastal Cutthroat Trout versus the proportion of all invertebrate taxa collected from adjoining fishless headwater streams in catchments of the lower Klamath River Basin in northern California during June 2015 – April 2016. The dashed line is a one-to-one line representing neutral electivity.

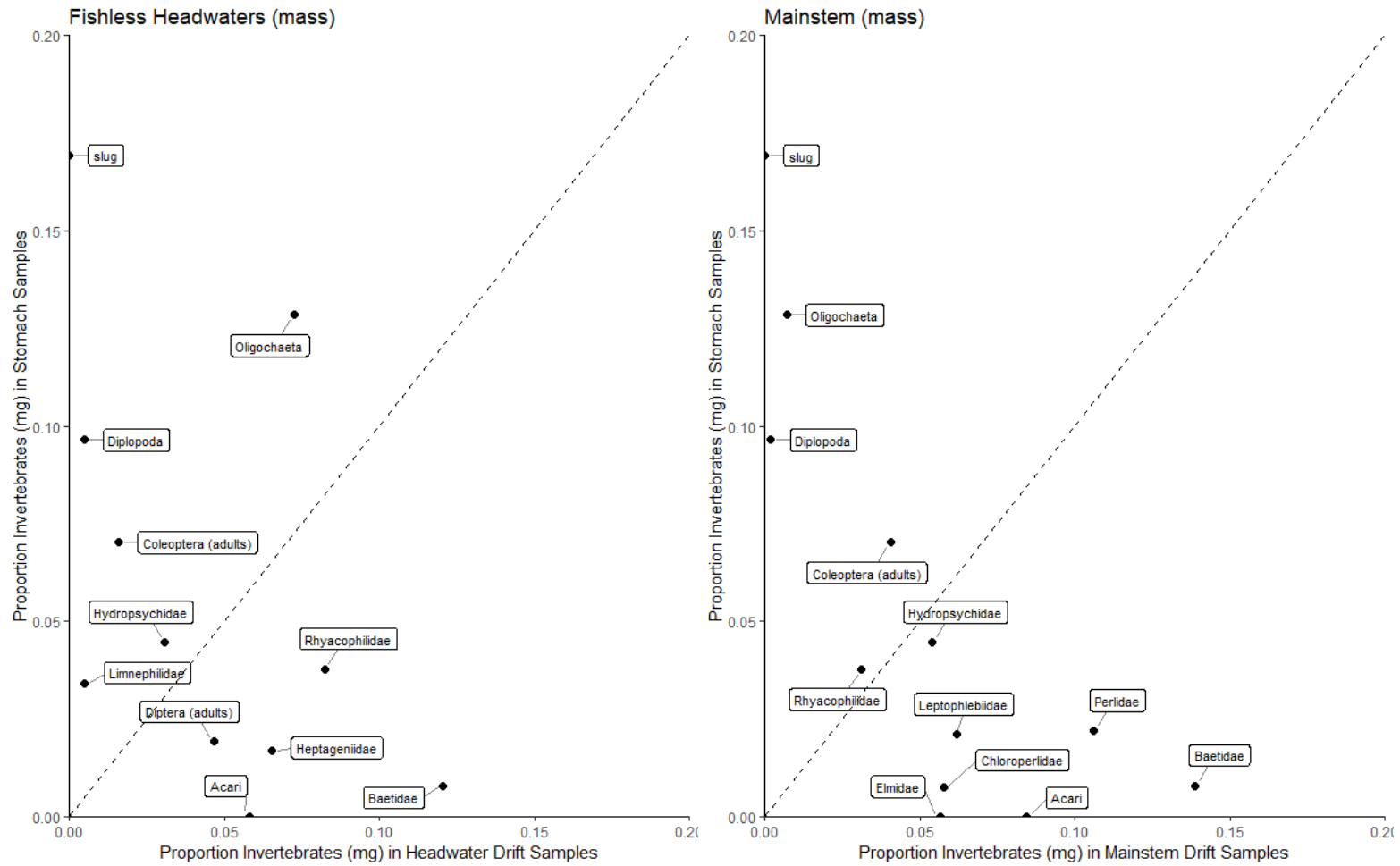


Figure 21. The proportion of dominant invertebrate taxa in trout diet samples versus the proportion of dominant invertebrate taxa dry mass in drift samples from fishless headwaters (left) and fish-bearing mainstem streams (right) of the lower Klamath River Basin in northern California during June 2015 – April 2016. Dashed lines represent neutral selectivity.

Contribution of Drift Export to Trout Production

To determine the maximal contribution export of invertebrate drift from fishless headwaters may make to annual trout production, I assumed drift exports were entirely consumed by trout. Average daily export from fishless streams was estimated at 540 mg dry mass stream⁻¹ day⁻¹. Thus, I estimated that a typical fishless headwater stream (0.5 – 0.75 km² catchment area) exports approximately 197.0 g dry mass stream⁻¹ year⁻¹. Using a food conversion efficiency of 0.20 (Waters 1988), annual drift export from a typical fishless headwater could support the production of approximately 39.4 g trout dry mass stream⁻¹ year⁻¹. I refined these estimates by including only the biomass of drifting taxa found in the diet of trout in the same season in which it was exported. This reduced estimated annual trout production to 37.0 g dry mass stream⁻¹ year⁻¹. Multiplying by a wet:dry mass ratio for juvenile salmonids of 4.5 (Darren Ward, unpublished data) resulted in an estimate of potential trout production of 167 g wet mass stream⁻¹ year⁻¹.

Literature values of the production to mean annual biomass ratio (P/\bar{B}) for Coastal Cutthroat Trout range from 0.87 - 1.04 (Lowry 1966). Mean annual biomass of Coastal Cutthroat Trout in the study reaches was an estimated 340 g per 100-meter-long reach (after accounting for capture efficiency). Assuming a P/\bar{B} ratio of 1 (Waters 1992), I estimated that export of invertebrate drift from fishless streams could theoretically account for nearly half of the annual production of over-yearling trout in the 100 m reaches I surveyed.

I related the estimate for the proportion of trout production derived for 100 m reaches to the scale of the total length of fish-bearing stream using West Fork Tectah as an example. I estimated the total length of fish-bearing habitat was 3930 m. Twenty fishless streams feed into West Fork Tectah over its length, thus 2000 m of the total length of West Fork Tectah comprises fish bearing reaches similar to those surveyed in this study (20 fishless streams * 100 m = 2000 m), or approximately half of its length. I multiplied my original estimate for the percentage of trout production by 0.5 to obtain one-quarter; therefore, I estimated drift export from fishless streams could theoretically account for one-quarter of the production of over-yearling trout in West Fork Tectah. If I included only fishless streams of a similar size or larger than those sampled in this study, the number of fishless streams delivering drift to West Fork Tectah is reduced to 10. In this case, I estimated that drift export from fishless streams could theoretically account for approximately one-tenth of the production of over-yearling trout in West Fork Tectah (10 fishless streams * 100 m = 1000 m, approximately 25% of the total length; $50\% * 0.25 = 12\%$).

DISCUSSION

Drift from Fishless Headwaters

The annual drift export values I observed in this study were within the range of values found in a similar study of 52 fishless headwaters in southeast Alaska, where mean annual drift transport ranged from 2 – 2460 mg stream⁻¹ day⁻¹ and averaged 163 mg stream⁻¹ day⁻¹ (Wipfli and Gregovich 2002). In that study and in the one presented here, the amount of export observed was highly variable among streams and sampling occasions, but California's strongly seasonal climate patterns appeared to have a stronger influence on the seasonal patterns I observed.

The finding in this study that the greatest export occurred during the highest discharge supports the well-established observation that increasing current velocity and discharge lead to increased drift flux (e.g., Ciborowski et al. 1987; Bond and Downes 2003; Gibbons et al. 2007). However, some notable exceptions occurred. For example, export at site AP2 was greatest in October when discharge measurements were lowest, and least in February despite a 10-fold increase in daily discharge. Severe drought conditions (i.e. record low flow) in the summer and fall of 2015 may partially explain the exceptionally high drift concentrations and export observed at AP2 in October. Minshall and Winger (1968) observed unusually high drift in a small diversion stream with dwindling flow, and discovered an increase in drift following experimental reductions in discharge. Other studies have documented increases in drift following rapid experimental

flow reductions in larger, regulated rivers (Gore 1977; Poff and Ward 1991) and in small, forested streams (James et al. 2008), and have proposed that such a phenomenon is an active behavioral response to unfavorable environmental conditions. This suggests a sudden pulse in drift export may occur prior to a stream running dry, as drift concentrations rapidly increase and flow is still sufficient to deliver invertebrates downstream. It is not clear if this process commonly occurs in these watersheds, as field sampling was not explicitly timed to coincide with declining stream flow. Furthermore, while rapidly declining stream flows have been linked to increases in drift flux, gradual reductions over weeks (Harvey et al. 2006), and naturally progressing seasonal declines (Leeseberg and Keeley 2014) have also been associated with reductions in drift flux, either because drift concentrations remained constant or flow was insufficient.

As I was unable to sample during peak flows, the largest annual export events were likely to have been missed in this study. Numerous studies have shown an increase in drift during sudden floods (Brittain and Eikeland 1988 and references therein) such as those caused by heavy rains. I observed evidence of bed-mobilizing and bank-scouring flows in the fishless headwaters following winter storms. Flows of that magnitude likely exceeded the thresholds necessary for catastrophic drift, and hydrograph data implies such flows occurred more than once between October and April. Failure to quantify peak export events has important implications for determining the total amount of prey transported to downstream fish populations from fishless headwaters as estimates of mean annual drift export and potential fish production will consequently not account for missed maximum values.

Predictors of drift, such as current velocity or discharge, could not clearly explain differences in drift magnitude among fishless headwaters during any given sampling occasion. It is notable that only two of the six streams selected for this study maintained permanent flow, and that one of those (AP2) exhibited seasonal patterns in drift export magnitude that were distinct from the other streams. For example, in June of 2015, the fishless streams at EF1 and EF2 had very little above ground flow, and by October both were virtually dry. Consequently, these streams made almost no contribution to drift exports during those sampling periods. Yet in February and April, these same streams made the largest contributions to drift exports by biomass of any of the streams sampled. By contrast, export from the fishless stream at AP2 was relatively small during all sampling occasions, with a peak in export in October. This observation may warrant further examination of the differences in patterns of drift exports between temporary and permanent streams in the lower Klamath River basin. It is possible perennial streams may provide a steady supply of drift throughout the year, with a modest peak in export occurring during the driest part of the year when most other streams have run dry. Conversely, temporary streams could provide large winter and spring pulses of prey subsidies, and little else during the rest of the year. Such differences in the timing and magnitude of prey subsidies originating from fishless streams could have implications for evaluating the seasonal importance and spatial distribution of these systems to downstream fish production.

As with discharge, riparian canopy composition also did not explain differences in drift magnitude among headwater reaches. Previous research has shown that forested

streams with deciduous-dominated young-growth riparian habitat, similar to those in this study, have greater inputs of terrestrial invertebrates relative to conifer-dominated streams (Allan et al. 2003; Romero et al. 2005), and potentially a greater supply of prey for fish (Piccolo and Wipfli 2002). This study revealed no clear relationship between riparian canopy type and the percentage of the drift comprising terrestrially derived invertebrates, although the range of values in conifer dominance among these highly shaded reaches was not large. It is also possible that drift rates do not accurately reflect terrestrial invertebrate input rates in these small streams. Drifting biomass was dominated by aquatic invertebrates throughout this study, but notable increases in terrestrial biomass occurred in October (one, large Diplopoda and 51 adult Diptera) when total export from the study streams was minimal as most were dry. An increase in invertebrates of unknown origin in February, largely attributable to Acari and Oligochaeta, corresponded with large peaks in the annual hydrograph, a result of seasonal precipitation events. Ground saturation, coupled with heavy rain may explain the higher incidence of Acari and Oligochaeta in February.

Drift from Fishless Headwaters versus Fish-bearing Streams

Drift concentrations were often higher in fishless streams than those observed in their corresponding mainstem streams, due in part, perhaps, to the presence of drift-feeding trout in mainstem streams. Conversely, daily drift export from fishless headwaters was typically less than daily drift flux in mainstem streams, the result of

smaller discharge in fishless streams. However, in some instances, export exceeded daily drift flux; this is perhaps surprising given the positive relationship between discharge or stream velocity and drift density that has been reported in the literature (e.g., references reviewed in Brittain and Eikeland 1988). It is not clear if exports from fishless streams commonly exceed levels of drift flux in the streams into which they flow. This is an important point to contemplate when determining the influence small headwaters have on the food-webs and energy supply of downstream habitats, especially when one considers the vast number of these small headwaters on the landscape. Wipfli and Gregovich (2002) concluded that fishless streams contribute substantially to downstream aquatic habitats in southeast Alaska simply through their sheer numbers, even without knowledge of the magnitude of their subsidies relative to in-stream production.

The taxonomic composition and magnitude of drift in mainstem streams was fairly consistent among streams in a given season. The dominant taxa of a given stream displayed some variability, but in general, if a certain taxon had been present in substantial numbers during a previous sampling event, it could be expected to be found in substantial numbers again on a subsequent sampling event. This was not necessarily true of fishless headwaters, where often a taxon not found (or found in very low abundance) in June or October could occur in the drift in February and April in tremendous numbers. Qualitative analysis between fishless stream and fish-bearing stream drift samples revealed weak similarities in the overall abundance and biomass of dominant drifting taxa with a few exceptions, notably Baetidae and Heptageniidae. However, close examination

of the data at the site level indicated substantial overlap of the most abundant taxa in both the fishless headwaters and adjacent mainstem streams exists throughout the year.

Trout Diet versus Drift

Drift and diet similarities were weaker than expected, particularly among the most dominant taxa from each. These results are contrary Allan's (1981) findings that the abundance and biomass of prey in the diets of brook trout (*Salvelinus fontinalis*) were strongly correlated with the abundance and biomass of prey in the drift. I found that drift and diet were especially dissimilar in June and October, when drift rates were lowest. On these occasions, streamflows were exceptionally low, and terrestrial biomass dominated diet samples. This suggests that drift samples, from either fish-bearing streams or fishless headwaters, may not fully represent the amount of food available to trout in the streams in this study. Large size, vulnerability in or on the water, and/or ease of capture during low flow may account for the over-representation of terrestrial prey in trout diets during summer and fall. Romero et al. (2005) found that aquatic insects dominated the diets of Coastal Cutthroat Trout (*Oncorhynchus clarki clarki*) throughout the year, but noted that the proportion of terrestrial prey biomass in diets was greatest during the summer and fall.

Implications for Trout Production

For the purposes of this analysis, I chose to assume trout consume 100% of the drift exported from fishless streams to ascertain a theoretical maximum value of trout

production. The estimates of production derived in this study may serve as a useful starting point for contemplating the importance of headwater stream subsidies to trout in coastal streams of northern California. However, it is unlikely that my findings accurately predicted production because the methods used fail to realistically account for the capture and assimilation of drift subsidies by trout. Several important biological considerations must be given attention before assessing the usefulness of my production estimates.

This study demonstrated that fishless streams may at times export substantial quantities of drift, but assuming exports are fully consumed by trout is unrealistic for several reasons. For instance, the majority of export from the fishless headwaters in this study occurred during elevated flows. Peak flows, especially in steep, narrow channels, may force trout to seek refuge, reducing their feeding efficiency. While I did not observe a cessation in feeding during high base (non-storm) flows in winter and spring, it is nevertheless important to consider there may be several occasions throughout the year where flood events temporarily impede a trout's ability to feed efficiently on drift. Turbidity associated with high flow may further reduce the importance of drift subsidies to trout, as feeding performance is impaired (Harvey and White 2008, but see White and Harvey 2007).

Conversely, drift subsidies may also be of little importance at very low flows if trout are unwilling to feed due to high predation risk associated with decreasing water depth. Trout occupying shallow pools may refuse to feed, even when prey inputs are high (Harvey and White 2017). The study area supported several predator species, including

Belted Kingfishers (*Megaceryle alcyon*), Common Mergansers (*Mergus merganser*), American Dippers (*Cinclus mexicanus*), river otters (*Lontra canadensis*), etc. Predation risk may partly explain why trout in this study did not appear to preferentially occupy confluence areas with perennial headwaters in summer and fall, and were instead typically found in areas with abundant cover.

The distance travelled by drift has implications for its importance to local trout production. I was unable to determine how far drift exports travelled upon entering fish-bearing streams; estimates in the literature vary considerably (reviewed in Brittain and Eikeland 1988), but range from centimeters at low current velocities to several hundred meters during spates. This sets up the possibility that drift exports often have little impact on the consumption of prey by most trout. In summer and fall, drift distances could be so short that the majority of drift exports does not reach trout occupying downstream waters; presumably these invertebrates become available prey for trout foraging on the benthos in areas where drift exports are deposited.

Empirical estimates of the proportion of drift consumed by trout range widely, but do not suggest total depletion of the drift. Using a bioenergetics approach, Leung et al. (2009) estimated young-of-the-year and 1+ to 2+ cutthroat trout consumed between 36 – 71% of the total drift flux of small streams in British Columbia. In an experimental feeding study, Wilzbach et al. (1986) found that cutthroat trout captured up to 80% of the drifting prey when provided at low prey densities, but in forested pools, like the ones in this study, the percent of prey captured tended to be much lower (i.e. 20 – 50%), especially at higher prey densities.

Peak drift abundance for most behavioral drifting taxa occurs at night (Brittain and Eikeland 1988), while feeding activity by visual predators like salmonids may be lower at night (Allan 1981, Sagar and Glova 1988), which sets up the possibility of a mismatch in the timing of the delivery and consumption of prey. This study did not examine diel patterns in the timing of drift export and trout feeding, thus it is not clear whether such a mismatch occurs in these streams.

Some taxa were very abundant in drift but had a negligible presence in diet samples (e.g. Acari, Collembola), especially invertebrates less than 1 mm in length, which composed 44% of the numerical abundance of drift from fishless streams but only 4% of the total number of invertebrates in diet samples. Including such apparently unimportant prey items in my calculations are bound to lead to an overestimation of fish production.

Lastly, these estimates do not account for other consumers of invertebrate prey occupying these streams such as invertebrate predators and salamanders. To my knowledge, the extent to which such consumers compete with trout for prey in the study area is not known, but competition for food resources has been documented among similar assemblages (e.g. Sepulveda et al. 2012). One could reasonably assume that such competition reduces the potential contribution of drift exports to trout production. However, the presence of predatory invertebrates (e.g. Rhyacophilidae) and salamanders in the diets of trout in these streams indicate losses in trout production via competing predators may eventually contribute to trout production indirectly as these predators are fed upon by trout.

The estimates of potential trout production supported by drift exports provided here are admittedly crude. Steps could be taken to refine my approach for deriving production estimates. First, taxon specific assimilation efficiencies of invertebrate taxa could be incorporated to account for differences in prey quality and digestibility among invertebrates. Alternatively, the caloric content of individual taxa could be estimated and used to determine the energetic content of drift exports. Next, dissimilarities in the proportions of prey types in trout diets and drift could be examined closely to more appropriately apportion the contribution of certain invertebrate taxa to predictions of production. For example, Acari composed a significant proportion of the drift biomass, yet their presence in the diets was negligible. Scaling back the contribution of underutilized taxa should reduce overestimating production. Last, I was unable to derive direct estimates for the annual production of Coastal Cutthroat Trout in this study due to an insufficient accounting of YOY trout. I therefore employed an annual P/\bar{B} ratio obtained from the literature; the value used is within the range commonly found for populations of stream salmonids (Waters 1992). Accurate annual production estimates, specifically derived for the trout in this study, would lend more credibility to my estimates for the percentage of trout production that drift exports are theoretically capable of supporting.

Despite the limitations and caveats described above, my estimate that export of invertebrate drift from fishless streams could account for one-tenth to one-quarter of the annual production of over-yearling trout in these systems supports the findings of others

(Wipfli and Gregovich 2002) that fishless headwater streams may provide important energy subsidies to downstream ecosystems.

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APPENDIX A

Coastal Cutthroat Trout length and mass measurements were fit using an allometric growth curve with multiplicative error using nonlinear least squares (Figure 22). The allometric growth function takes the form:

$$W_i = \alpha L_i^\beta e^\epsilon$$

where W is the mass of individual i , α is a scaling constant, L is the length of individual i , β is the growth parameter, and ϵ is the multiplicative error.

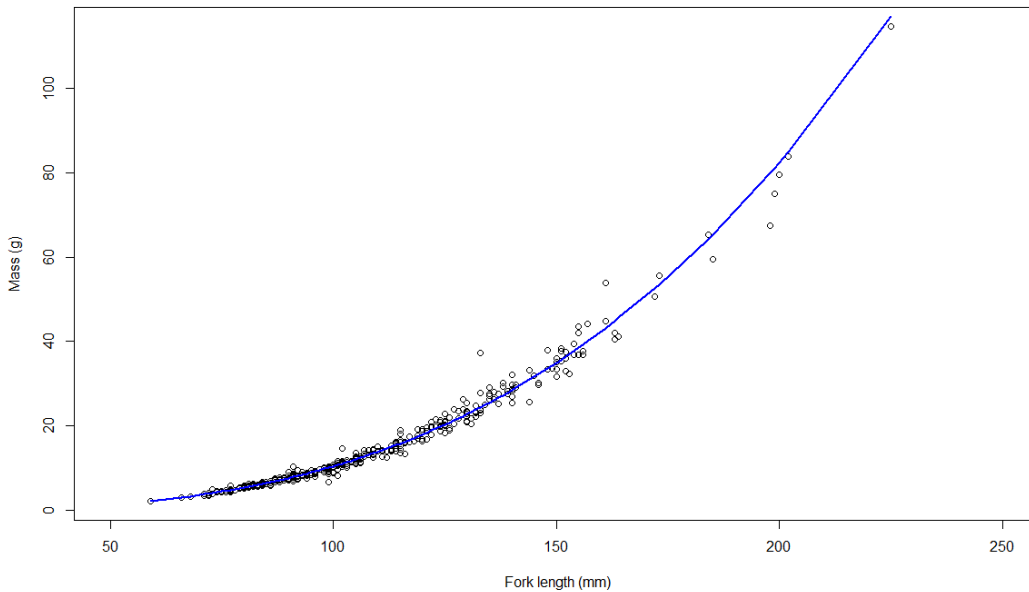


Figure 22. Length-to-mass relation ($n = 359$) for Coastal Cutthroat Trout collected June 2015 through April 2016 from the sub-basins of Ah Pah, Tarup, and Tectah creeks. The relationship between length and mass is described by the equation $W = -11.385 * L^{2.981}$.

For comparisons of fish condition between trout across different sites, the relative condition factor (Le Cren 1951) was calculated using the equation:

$$K_n = \frac{W}{W'}$$

where W is the weight of an individual, and W' is the predicted weight for the individual based on the population's mass-to-length equation. Condition factor varied slightly among streams and across seasons, but without apparent pattern (Figure 23).

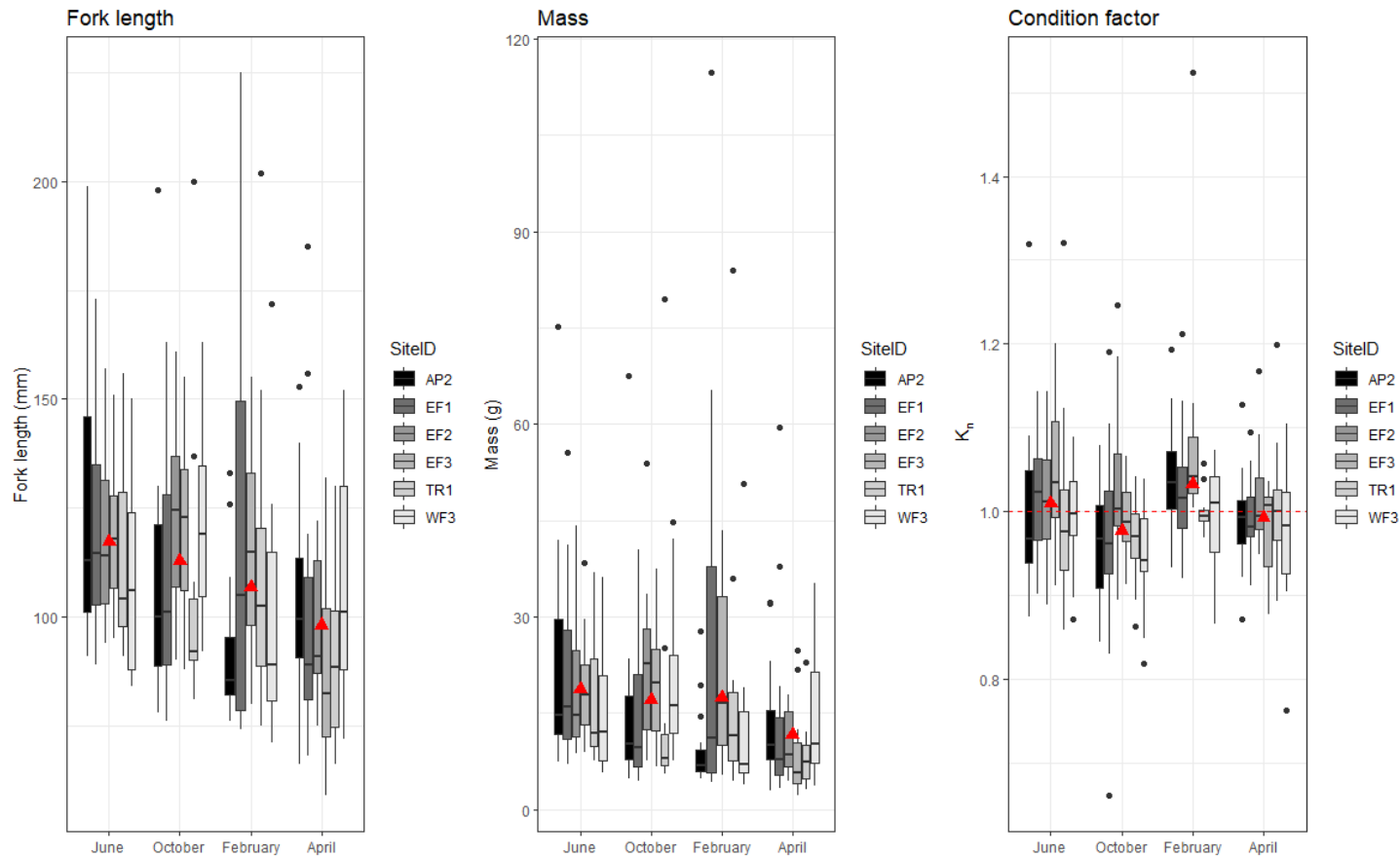


Figure 23. Fork length, mass, and relative condition factor (K_n) of Coastal Cutthroat Trout collected in seasonal sampling of mainstem streams in 100 m reaches originating at the confluence of fishless headwaters. Triangles represent mean values, and dots represent outliers.

Seasonal growth patterns for fish were estimated by calculating the specific growth rate (G) of recaptured fish using the equation:

$$G = 100 \left(\frac{\ln W_t - \ln W_0}{t} \right)$$

where W_t is the final mass, W_0 is the initial mass, and t is the number of days in the growth period. Seasonal growth patterns were evaluated by examining the differences in the relationship between specific growth rate and initial mass.

Seasonal size distributions of recaptured trout approximated the seasonal size distributions of all trout sampled (Figure 24). Thus, I assumed that specific growth rates of recaptured trout could be reasonably applied to trout not recaptured. Specific growth was lowest during the interval from June to October, with over half of recaptured trout exhibiting negative growth during that period (Figure 25). The highest specific growth rates were observed in recaptured trout from February to April, yet negative growth was observed in one individual during this interval.

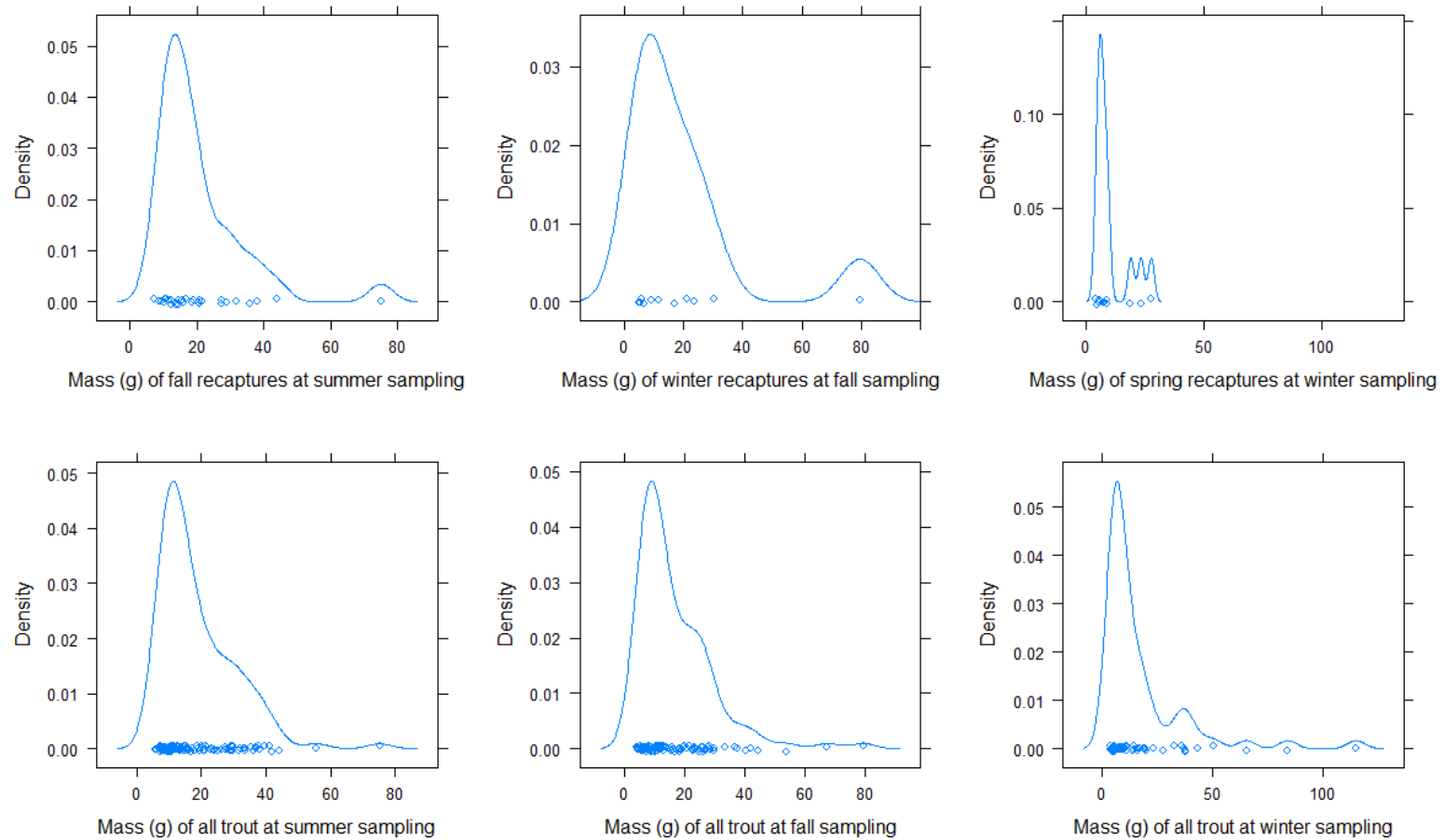


Figure 24. Comparisons of the mass distributions of recaptured trout to the mass distributions of all trout, as measured on prior sampling occasions. Trout were collected and recaptured from 100-meter reaches at six sites adjacent to fishless headwater streams located in the lower Klamath River basin. (Density refers to the distribution of the data).

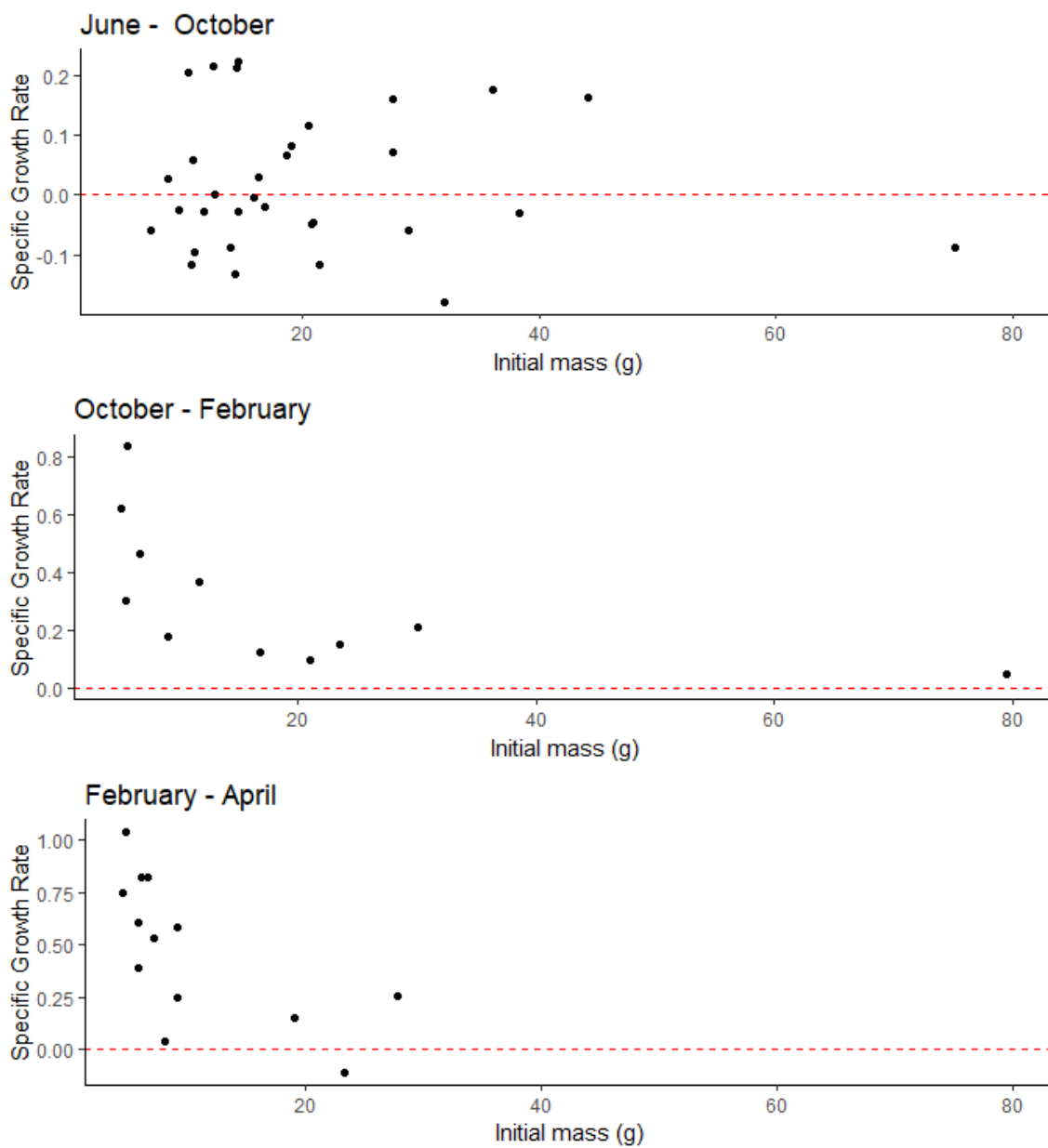


Figure 25. Specific growth rate (g d^{-1}) of recaptured Coastal Cutthroat Trout collected in mainstem stream reaches versus initial mass over three intervals: June – October ($n = 32$ trout), October – February ($n = 11$ trout), and February – April ($n = 13$ trout).

APPENDIX B

Ten most dominant invertebrate taxa (ranked by mass) found in 24-h drift samples from June 2015 (n = 9), October 2015 (n = 3), February 2016 (n = 12), and April 2016 (n = 11).

Taxon	Life stage	Mass (%)	Number (%)
<u>June</u>			
Rhyacophilidae	larvae	22	1
Hydropsychidae	larvae	18	<1
Diptera	adult	7	5
Baetidae	larvae	6	20
Leptophlebiidae	larvae	4	3
Philopotamidae	larvae	4	<1
Acanthosomatidae	adult	3	<1
Coleoptera	larvae	3	1
Dixidae	larvae	3	7
Chironomidae	larvae	3	22
<u>October</u>			
Diplopoda	-	15	<1
Dixidae	larvae	8	5
Diptera	adult	8	4
Rhyacophilidae	larvae	8	1
Baetidae	larvae	7	4
Oligochaeta	-	7	2
Hydrophilidae	larvae	6	<1
Calamoceratidae	larvae	5	<1
Hydropsychidae	larvae	5	<1
Cicadellidae	adult	4	<1
<u>February</u>			
Oligochaeta	-	13	1
Rhyacophilidae	larvae	11	<1
Acari	-	10	28
Simuliidae	larvae	7	6
Chloroperlidae	larvae	5	3
Chironomidae	larvae	5	5
Hydropsychidae	larvae	5	<1
Heptageniidae	larvae	4	4
Peltoperlidae	larvae	4	5
Diptera	adult	4	2
<u>April</u>			
Baetidae	larvae	18	8
Heptageniidae	larvae	8	3
Chilopoda	-	6	<1
Oligochaeta	-	5	1
Rhyacophilidae	larvae	5	<1

Taxon	Life stage	Mass (%)	Number (%)
Gerridae	-	5	<1
Ameletidae	larvae	5	2
Diptera	adult	5	4
Acari	-	4	21
Chironomidae	larvae	4	10

Ten most dominant invertebrate taxa (ranked by mass) estimated from 24-h drift samples collected from fish-bearing, mainstem streams upstream of the confluence with a fishless headwater.

Taxon	Life stage	Mass (%)	Number (%)
<u>June (mainstem)</u>			
Perlidae	larvae	42	3
Baetidae	larvae	10	38
Leptophlebiidae	larvae	6	6
Elmidae	adult	5	1
Ephemerellidae	larvae	5	1
Lepidoptera	larvae	4	<1
Acari	-	3	2
Chironomidae	larvae	3	13
Chloroperlidae	larvae	2	2
Coleoptera	adult	2	<1
<u>October (mainstem)</u>			
Rhyacophilidae	larvae	13	2
Dixidae	larvae	9	4
Capniidae	larvae	9	26
Chironomidae	larvae	9	32
Diplopoda	-	7	<1
Leptophlebiidae	larvae	7	2
Perlidae	larvae	6	1
Oligochaeta	-	5	<1
Ameletidae	larvae	4	3
Heptageniidae	larvae	3	4
<u>February (mainstem)</u>			
Acari	-	19	12
Limnephilidae	larvae	16	10
Ameletidae	larvae	10	8
Baetidae	larvae	8	10
Heptageniidae	larvae	6	12
Diptera	adult	5	7
Peltoperlidae	larvae	4	3
Simuliidae	larvae	4	2
Oligochaeta	-	3	<1
Perlidae	larvae	3	4
<u>April (mainstem)</u>			
Acari	-	18	21
Baetidae	larvae	16	15

Taxon	Life stage	Mass (%)	Number (%)
Perlidae	larvae	9	1
Chloroperlidae	larvae	7	2
Coleoptera	larvae	6	<1
Hydropsychidae	larvae	6	<1
Coleoptera	adult	5	1
Ameletidae	larvae	4	2
Hydrophilidae	larvae	4	1

Ten most dominant taxa (ranked by mass) found in diet samples (n = 109) collected from Coastal Cutthroat Trout in June 2015 from mainstem stream reaches adjacent to fishless headwaters.

Taxon	Life stage	Mass (%)	Number (%)	Trout (%)
<u>June (diet)</u>				
Dicamptodontidae	-	17	<1	1
Coleoptera	adult	9	2	33
Diplopoda	-	7	1	14
Hemiptera	-	6	1	14
Perlidae	larvae	5	<1	5
Vertebrate (unidentifiable)	-	5	<1	1
Oligochaeta	-	5	1	9
Diptera	adult	4	6	62
Araneae	-	4	1	28
Isopoda (terrestrial)	-	3	1	20
<u>October (diet)</u>				
Salamander (unidentifiable)	-	33	<1	1
Gastropoda (slug)	-	27	<1	3
Diplopoda	-	13	3	44
Limnephilidae	larvae	4	7	40
Mycetophilidae	larvae	4	16	2
Trichoptera	adult	3	1	8
Araneae	-	2	1	20
Hemiptera	-	1	1	19
Leptophlebiidae	larvae	1	3	40
Lepidoptera	larvae	1	<1	4
<u>February (diet)</u>				
Fish (unidentifiable)	-	50	<1	3
Oligochaeta	-	20	10	41
Gastropoda (slug)	-	5	<1	3
Hydropsychidae	larvae	5	<1	2
Rhyacophilidae	larvae	3	1	17
Isopoda (terrestrial)	-	2	1	19
Heptageniidae	larvae	1	6	53
Perlidae	larvae	1	1	7
Diplopoda	-	1	1	14
Coleoptera	larvae	1	1	12

Taxon	Life stage	Mass (%)	Number (%)	Trout (%)
<u>April (diet)</u>				
Oligochaeta	-	20	7	50
Coleoptera	adult	12	5	56
Hydropsychidae	larvae	10	1	18
Rhyacophilidae	larvae	8	1	29
Fish (unidentifiable)	-	6	<1	1
Heptageniidae	larvae	4	9	78
Hymenoptera	adult	3	<1	10
Araneae	-	3	2	39
Lepidoptera	larvae	2	<1	6
Limnephilidae	larvae	2	1	14