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DIVERSITY AND PHENOLOGY OF STONEFLIES (PLECOPTERA) FROM INTERMITTENT AND PERENNIAL STREAMS IN PINNACLES NATIONAL PARK, CALIFORNIA, U.S.A.

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ABSTRACT

Stoneflies are often associated with cool perennial streams, but some species can thrive in intermittent streams that cease flowing or dry completely during some parts of the year. The vast majority of stonefly records in California come from perennial streams, and few collection efforts have focused on intermittent streams. In this study, we surveyed 26 intermittent and perennial reaches of the Chalone Creek basin in Pinnacles National Park (California, USA) between 2014 and 2018. We quantified the flow regime at many of these reaches and compared stonefly assemblages with flow metrics. We found at least 14 species of stoneflies, including 8 species of Capniidae and 1 or 2 species each in four other families. Only *Malenka californica* (Claassen, 1923) was restricted to perennial reaches. All other species were primarily or exclusively found in intermittent reaches, even in reaches with flow permanence values as low as 13%. On average, we found more species in intermittent reaches than perennial reaches, with stonefly species richness peaking at about 60% flow permanence. Many species appeared to have rapid development times (2-3 months) to complete their larval life stage and emerge during brief winter flow periods (Dec-Mar). Given the relatively rich and unique stonefly assemblages we observed, intermittent streams in California deserve further research and conservation attention.

Keywords: Plecoptera, biodiversity, California, drying, drought, flow

INTRODUCTION

At least 186 species of stoneflies (Plecoptera) have been recorded from California, 39% of which are endemic to the state (Baumann & Kondratieff 2011). Most collecting of stoneflies in the state has been opportunistic; few streams have been surveyed across multiple seasons or across multiple locations within a basin. Further research attention is certainly warranted, as new stonefly species are still being described from California (e.g. Baumann & Nelson 2007, Lee & Baumann 2011, Verdone & Kondratieff 2018). The most detailed snapshots of local stonefly assemblages have occurred at Sagehen Creek (Nevada County), where 31 species were found (Sheldon & Jewett 1967), and Irish Gulch (Mendocino County), where 23 species were found (Bottorff & Bottorff 2007). Both of these sites are perennial headwater streams, with Sagehen Creek receiving its flow from snowmelt and groundwater and Irish Gulch supported by rainfall and groundwater. However, very few published stonefly biodiversity studies in California have focused specifically on intermittent streams, which comprise 66% of the total length of stream networks in the state (Levick et al. 2008).

Although stoneflies are often associated with cool perennial streams, a number of species are known to occur in intermittent streams (e.g. Baumann & Gaufin 1970, Jacobi & Cary 1996). In fact, at least two genera of stoneflies appear to be endemic to intermittent streams in California (*Calileuctra*: Shepard & Baumann 1995; *Cosumnoperla*: Bottorff 2007). Furthermore, several other genera have individual species which may be endemic to intermittent streams [e.g. *Isoperla adunca* Jewett, 1962: (Sandberg & Kondratieff 2013); *Mesocapnia arizonensis* (Baumann & Gaufin, 1969): (Bogan 2017); *Malenka diablo* Verdone & Kondratieff, 2018). Occasional collections from intermittent streams on the west slope of the Sierra Nevada have identified a group of eight stonefly species that occur in these streams but are rarely found in nearby perennial streams (Baumann & Kondratieff 2011).

Many parts of California are significantly drier than the west slope of the Sierra Nevada, and it is unknown what types of stoneflies may occur in the harsher intermittent streams of these regions. In this study, we surveyed for stonefly adults and larvae at intermittent and perennial reaches in the Chalone Creek basin, located in the Inner Coast Range of central California. We quantified flow regime at the majority of these reaches from 2014 to 2018, and we surveyed for stoneflies between one and five times a year at each reach. Our goals were to: (1) report on stonefly species richness within reaches and across the basin, (2) describe emergence periods of individual species, (3) compare assemblages in perennial vs intermittent reaches, and (4) explore the effects of drying and flow duration on stonefly assemblages.

MATERIAL AND METHODS

Study area

Chalone Creek drains approximately 100 km² of land within and adjacent to Pinnacles National Park in the Gabilan Range, one of the Inner Coast Ranges of central California (Fig. 1). The basin has a semi-arid Mediterranean climate, with an annual average precipitation of 420 mm, 75% of which falls between December and March. Accordingly, intermittent stream reaches often flow from December to April but generally are dry the rest of the year (Fig. 2). Due to its inland location, air temperatures vary greatly through the year, with highs that exceed 40°C in summer and lows below 0°C in winter. Upland vegetation is primarily live oak (*Quercus* spp.) and Gray Pine (*Pinus sabiniana* Douglas ex D. Don) woodland on mesic north-facing slopes and chaparral on drier south-facing slopes. When present, riparian vegetation consists of California Sycamore (*Plantanus racemose* Nutt.), willows (*Salix* spp.), Fremont Cottonwoods (*Populus fremontii* S. Watson), and seep-willow (*Baccharis salicifolia* (Ruiz & Pav.) Pers.). In highly intermittent reaches, there is no phreatophytic vegetation. Instead, upland shrubs such as buckwheat (*Eriogonum* spp.) and chamise (*Adenostoma fasciculatum* Hook. & Arn.) grow in and along stream channels. We surveyed a total of 25 reaches in the Chalone Creek basin (Fig. 1): 16 were primary study reaches with flow sensors installed (see below) and the remaining 9 reaches were surveyed for stonefly adults but benthic samples were not collected and the duration of dry periods were not quantified.

Survey methods

We surveyed for stonefly adults at each of the study reaches during 18 visits between 2014 and 2018, including three visits in 2014 (May, Jun, Dec), nine in 2015 (Jan, Feb, Mar, Apr, May, Jun, Jul, Nov, Dec), three in 2016 (Jan, Feb, May), two in 2017 (May, Jun), and one in 2018 (Jun). Adult stoneflies were sought by searching streamside rocks and leaf litter, and shaking streamside vegetation over a beating sheet, for at least 20 minutes per visit. All adults were preserved in 95% ethanol and identified using the keys in Jewett (1960), Baumann & Gaufin (1970), Nelson &

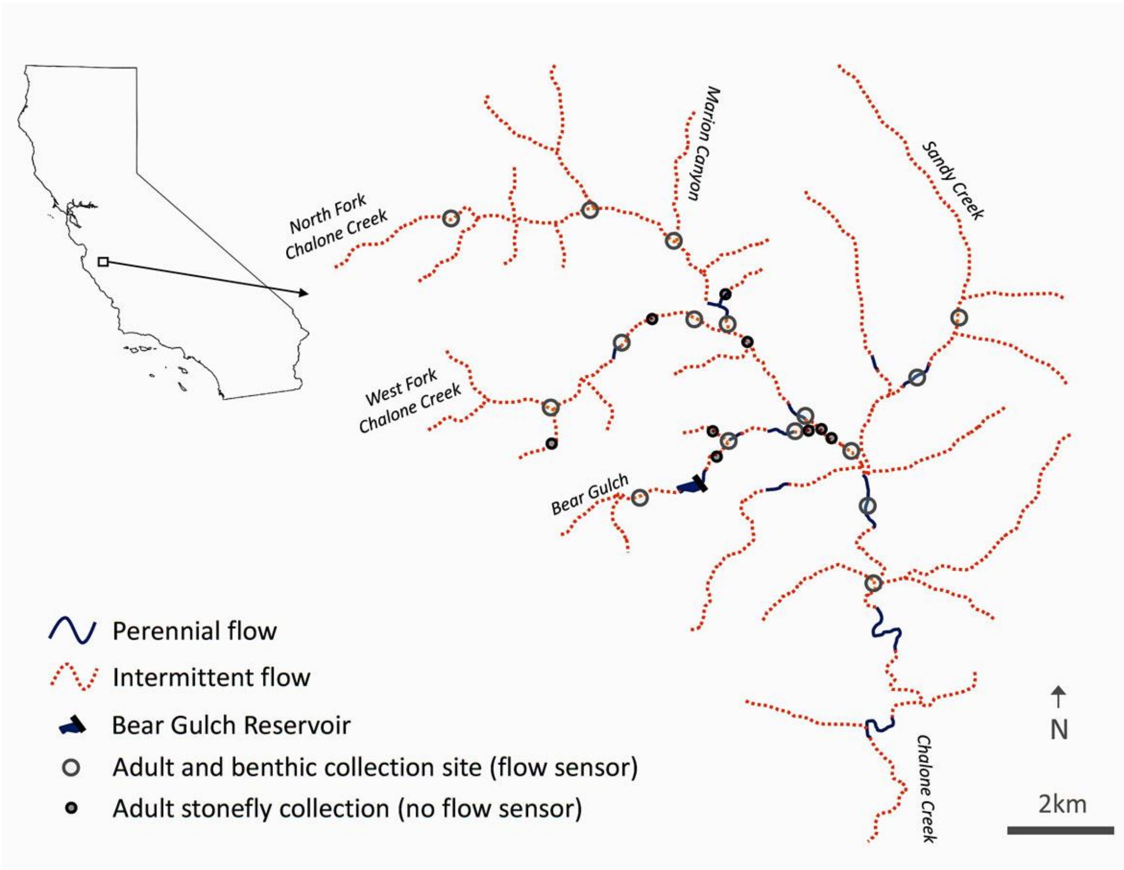

Fig. 1. Map of the Chalone Creek basin within and immediately adjacent to Pinnacles National Park, illustrating the dominance of intermittent flow regimes across the basin.

Baumann (1989, 1990), Stanger & Baumann (1993), and Zenger & Baumann (2004). Frequently, many of the reaches were dry during our visits, but when surface water was present we also surveyed for stonefly larvae. Benthic kick samples were collected using a D-frame net (500-micron mesh) when water was deeper than 10 cm (e.g. Fig. 2) and a 130 mm wide aquarium net (250-micron mesh) when only a trickle of flow was present. All stonefly specimens are currently in the personal collection of the first author (MTB) and representative specimens for each species and site will be deposited in the University of Arizona Insect Collection.

Flow sensors

At a subset of 16 stream reaches (Fig. 1), we deployed modified Onset HOBO Pendant waterproof temperature and light data loggers (Model UA-002-64, Onset Computer Corp, Bourne, MA, USA) to record flow condition (wet vs dry: Jaeger & Olden 2012). Data loggers were modified aftermarket using the approach of Chapin et al. (2014) to record electrical conductance instead of light intensity, thus providing a record of when streams had surface water (high conductivity) and when they were dry (no conductivity). With these loggers, we were able to quantify (1) how many days the reach had been flowing when stonefly adults were collected and (2) the overall flow permanence of any given reach (i.e. the percentage of days a given reach was wet between May 2014 and June 2018).

Data analysis

For each stonefly species, we calculated the

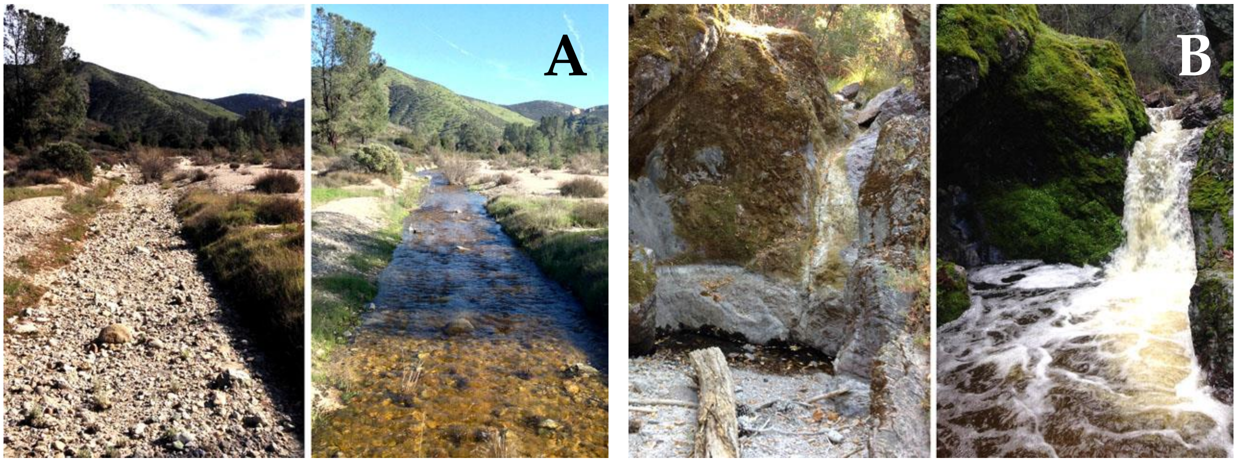

Fig. 2. Examples of dry and flowing phases at two of the twenty five study reaches at Pinnacles National Park: (A.) Chalone Creek below Highway 146 bridge and (B.) Bear Gulch at Green Gully.

percentage of all study reaches (n = 25) occupied at Pinnacles National Park. We also examined whether individual species were more likely to be found in perennial versus intermittent reaches. We then calculated the mean and standard deviation of the number of days reaches had been flowing when adults were collected. Perennial reaches were assigned a flow duration value of 365 days. To explore the phenology of each species, collection dates across all reaches and years (2014-2018) were used to determine activity periods for stonefly adults. Finally, we used least-squares regression to explore the relationship between stonefly species richness values and flow permanence values for each reach. The raw specimen data are available in a comma separated values file PinnaclesPlecoptera.csv.

RESULTS

We collected 710 adult stoneflies and thousands of larvae from Pinnacles National Park and identified at least 14 species (Table 1). The family Capniidae was represented by eight species, while Chloroperlidae, Nemouridae, Perlodidae, and Taeniopterygidae each were represented by one or two species. The two most commonly encountered species were *Bolshecapnia maculata* (Jewett, 1954) (76% of reaches) and *Taenionema californicum* (Needham & Claassen, 1925) (88% of reaches). The least common species were *Mesocapnia werneri* (Baumann & Gaufin, 1970) and *Sweltsa tamalpa* (Ricker, 1952), each found at only a single reach. Stonefly species richness per reach varied from one to nine. We found an average of 2.75 species at perennial reaches (n = 4) and 4.1 species at intermittent reaches (n = 21). *Malenka californica* (Claassen, 1923) was the only species that was mostly restricted to perennial reaches. Five larvae of *B. maculata*, one larva of *Isoperla adunca*, and 70 larvae of *T. californicum* also were collected from perennial reaches, but all other stonefly species were only found in intermittent reaches. We failed to find any stoneflies at just one intermittent reach, Sandy Creek above Pinnacles campground (36.504°N, 121.139°W). This reach was dry for nearly three years (from May 2014 until March 2017), and no stoneflies were found during subsequent visits when the reach had surface water.

In intermittent reaches, adult stoneflies were collected as early as six weeks after flow resumed, with *Mesocapnia arizonensis* and *M. projecta* (Frison, 1937) adults emerging on average 51 days after flow resumed (Table 1). Across all capniid species, adults were present on average after 77 days of flow. *Nemoura spiniloba* Jewett, 1954 and *T. californicum* also appeared to have rapid development times, with adults emerging about three months after flow resumed. Adults of two

Table 1. Stoneflies collected from streams in Pinnacles National Park between 2014 and 2018, including the percentage of collection reaches each taxon was found at, the mean number of days the stream had been flowing when adults were collected, and the standard deviation in the number of days flowing (if collected at multiple reaches or on multiple visits). Occasionally, only adult females were collected (*Mesocapnia* sp.) and could not be identified beyond genus.

Taxon	Occurrence (%)	Days flowing (mean)	SD (days)
Capniidae			
Bolshecapnia maculata (Jewett, 1954)	76	71	±21
Capnia saratoga Nelson & Baumann, 1987	4	74	±25
Capnia spinulosa Claassen, 1937	12	78	±32
Capnia ventura Nelson & Baumann, 1987	16	99	±7
Isocapnia abbreviata Frison, 1942	8	104	±6
Mesocapnia arizonensis (Baumann & Gaufin, 1969)	8	51	±22
Mesocapnia projecta (Frison, 1937)	8	51	±21
Mesocapnia werneri (Baumann & Gaufin, 1970)	4	90	n/a
Chloroperlidae			
Sweltsa tamalpa (Ricker, 1952)	4	159	±58
Nemouridae			
Malenka californica (Claassen, 1923)	24	365	±0
Nemoura spiniloba Jewett, 1954	28	95	±19
Perlodidae			
Baumannella alameda (Needham & Claassen, 1925)	24	130	±2
Isoperla adunca Jewett, 1962	44	133	±21
Taeniopterygidae			
Taenionema californicum (Needham & Claassen, 1925)	88	96	±4

perlodid species (*Baumannella alameda* (Needham & Claassen, 1925) and *I. adunca*) were collected after approximately 130 days of flow, suggesting a longer development time. *Sweltsa tamalpa* appeared to have the longest development time for species found in intermittent reaches, with adults emerging nearly five and a half months after flow resumed.

Malenka californica and *B. maculata* had extended emergence periods (Fig. 3), where adults were found across a timespan of five months (February-June and November-March, respectively). Two other species, *T. californicum* and *S. tamalpa*, had emergence periods stretching over three months. The remaining 10 species appeared to have more constrained emergence periods of one or two months (Fig. 3).

We did not sample each reach during the same months in each of the four study years, but we can make limited observations about interannual variation in the emergence patterns of common species. For example, the same winter stoneflies (*B. maculata*, *Capnia ventura* Nelson & Baumann, 1987, *I. abbreviata* Frison, 1942, *T. californicum*) were collected at Bear Gulch at Green Gully (36.483°N, 121.167°W) during 2014-2015 and 2015-2016.

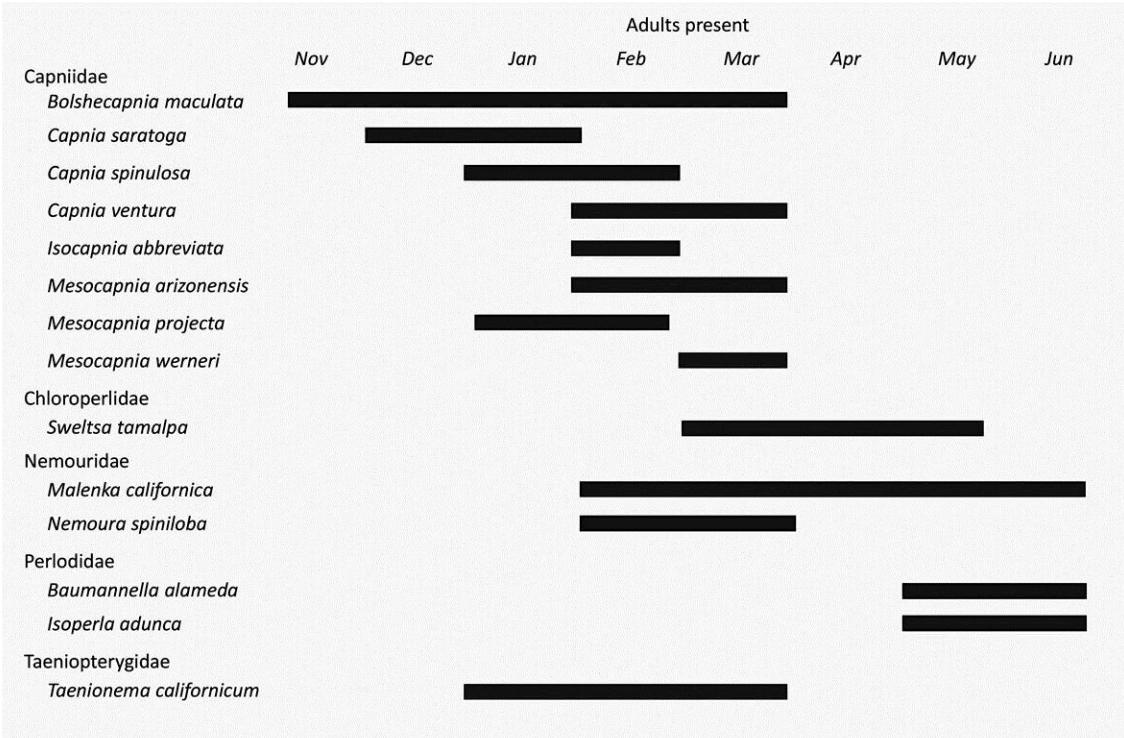

Fig. 3. Phenology of stoneflies in the Chalone Creek basin of Pinnacles National Park based on adult collection efforts between May 2014 and June 2018.

However, more intermittent reaches (e.g. the three reaches of North Fork Chalone Creek: Fig. 1) had flow during winter 2015-2016 but remained dry during all of the winter and summer of 2014-2015. At these reaches, no adult or larval stoneflies were present in winter 2014-2015, but both *B. maculata* and *T. californicum* were abundant in winter 2015-2016. The summer stoneflies *I. adunca* and *Baumannella alameda* emerged in May-June each year from Bear Gulch at Green Gully, but were only found at more intermittent reaches during wetter years. For example, at our downstream-most reach on Chalone Creek (36.455°N, 121.153°W), flow ceased by April in three years (2014, 2015, and 2018), likely preventing *I. adunca* and *B. alameda* from completing their life cycles. However, flow persisted into June of 2016 and 2017, allowing both species to successfully emerge into the adult stage. *Malenka californica*, which only was found in perennial reaches, emerged successfully in each year of our study.

Overall flow permanence values across the 16 study reaches with flow sensors ranged from 13% to 100% (as measured from May 2014 to June 2018). Three stonefly species were abundant at reaches with low flow permanence values (13-25%): *B. maculata*, *N. spiniloba*, and *T. californicum*. In contrast, *S. tamalpa* was only found at West Fork Chalone Creek below Balconies Cave (36.502°N, 121.200°W) where flow permanence was 50% and shallow groundwater was easily found by digging in the streambed during dry periods. Stonefly species richness tended to increase with flow permanence until about 60%, after which it declined (Fig. 4). At two of the perennial reaches, only a single stonefly species (*M. californica*) was collected. Regression analysis identified a polynomial curve as the best fit ($y = -0.0025x^2 + 0.2951x - 1.8919$) and flow permanence explained over 49% of the variation in stonefly species richness ($R^2 = 0.4926$).

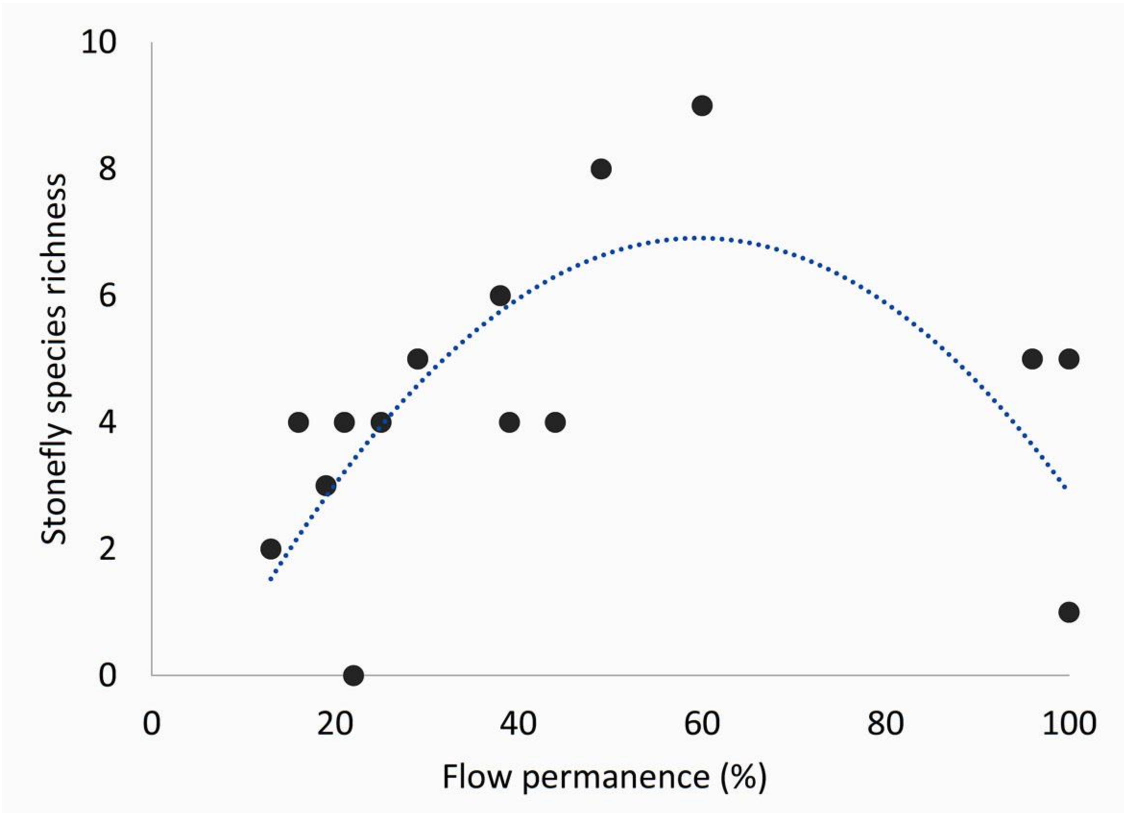

Fig. 4. Relationship between flow permanence (% of days with flow between May 2014 and June 2018) and stonefly species richness at 16 study reaches in the Chalone Creek basin of Pinnacles National Park.

DISCUSSION

Intermittent stream reaches at Pinnacles National Park support relatively diverse assemblages of stoneflies despite flow permanence values rarely exceeding 50%. In other arid regions of the southwest USA, stonefly richness in intermittent reaches rarely exceeds one or two species (Jacobi & Cary 1996, Bogan et al. 2013, Bogan 2017; Baumann et al. 2017), but as many as nine stonefly species co-occurred in intermittent reaches at Pinnacles. We found at least 14 species from a relatively small area (100 km^2), whereas only 13 species of stonefly are known from intermittent streams across an enormous region of Arizona, Nevada, and New Mexico (>500,000 km^2: Jacobi & Cary 1996, Cary & Jacobi 2008, Bogan 2017; Baumann et al. 2017). Furthermore, studies from intermittent streams in other parts of California have identified numerous additional species that we did not encounter at Pinnacles (e.g. Shepard & Baumann 1995, Bottorff 2007, Baumann & Kondratieff 2011), suggesting that stonefly diversity is quite high in California intermittent streams when compared to other parts of the western USA. Potential mechanisms that could explain this surprisingly high diversity such as more predictable flow regimes and higher groundwater levels during dry seasons deserve further study.

Although much additional work remains to understand how stonefly assemblages vary across intermittent streams within California, some initial comparisons can be made. For example, the presence of remnant pools during the dry season, and abiotic conditions in those pools, likely influence stonefly assemblages. In coastal intermittent streams, remnant pools persist through the dry season and coastal fog helps maintain cool water temperatures in those pools (~15-20°C: Hwan & Carlson 2016). Perhaps as a result of this relatively benign environment, stonefly assemblages in intermittent streams at Point Reyes National Seashore largely overlap with those of neighboring perennial streams, and include numerous genera absent from Pinnacles (e.g. *Calineuria*, *Despaxia*, *Yoraperla*, *Soyedina*, *Suwallia*, *Yoraperla*, and *Zapada*: Bogan et al. 2015; Bogan et al. 2017). Other regions of California have intermittent streams with intense drying regimes and summer temperatures similar to Pinnacles, and yet support distinct assemblages of stoneflies. For example, Baumann & Kondratieff (2011) identify eight species associated with intermittent streams in the western Sierra Nevada, only two of which (*I. adunca* and *N. spiniloba*) are also known from Pinnacles. Indeed, the genus *Cosumnoperla* is endemic to intermittent streams of the western Sierra Nevada (Bottorff 2007) and other stonefly species are only known from intermittent streams in southern California, e.g. *Taenionema jeanae* (Baumann & Nelson 2007). Systematic surveys across California are needed to fully describe biogeographic patterns in intermittent stream stonefly assemblages.

Surprisingly, stonefly species richness was lower in perennial reaches than moderately intermittent reaches at Pinnacles, with peak richness observed at ~60% flow permanence (Fig. 4). Additionally, all but one species of stonefly at Pinnacles appear capable of completing their larval stages in less than six months. In other parts of the Southwest, only *Mesocapnia arizonensis* is known to complete its life cycle in as little as three months (Bogan 2017), but at least eight species appear capable of doing the same at Pinnacles (Table 1). We suggest that the broad extent of intermittent reaches and the predictability of drying and rewetting cycles at Pinnacles drive life history adaptations for surviving drought. Over 90% of the stream network at Pinnacles dries for at least part of every year (Fig. 1), with some reaches being dry for over a year at a time. This drying intensity could promote the development of a "stonefly seed bank", with dormant egg or larval stages passing the dry season in the streambed (Snellen & Stewart 1979, Zwick 1996). And unlike more arid parts of the Southwest, at least some intermittent reaches at Pinnacles flow every year, meaning that drought-resistant eggs or larvae would not necessarily have to persist through multiple consecutive dry years (Jacobi and Cary 1996, Bogan et al. 2013, Bogan 2017).

At least some parts of the stream network at Pinnacles maintain high water table levels during the dry season, which may allow some species to remain active in hyporheic habitats after the surface dries. This may explain the presence of species such as *Isocapnia abbreviata* and *Sweltsa tamalpa*, which have been demonstrated to use perennial streams or those with well-developed hyporheic zones (Dieterich & Anderson 1995, Zenger & Baumann 2004). Detailed hydrological studies are needed to better understand the availability of hyporheic refuges across the intermittent stream reaches at Pinnacles.

The low diversity of stoneflies in perennial reaches at Pinnacles may be due to the small size and high isolation of these reaches. Many perennial reaches are less than 200 meters long, or are isolated from other perennial reaches by many kilometers of dry steam bed, or both (Fig. 1). The small sizes of perennial reaches may limit physical habitat diversity and niche availability for perennial-specialist stoneflies, and the high isolation of these habitats may decrease colonization potential and increase local extinction risk (MacArthur & Wilson 1967). Thus, while other perennial stream reaches in California may support dozens of stonefly species (Sheldon & Jewett 1967, Bottorff & Bottorff 2007), those of Pinnacles appear to support less than half a dozen.

Our findings at Pinnacles also prompt biogeographic and taxonomic questions with regard to the genus *Mesocapnia.* Some experts have suggested recently that the western *Mesocapnia* key (Baumann & Gaufin 1970) may not work well to distinguish species (J.B. Sandberg, pers. comm.), so we caution that our specific identifications in this genus remain provisional. We identified two ostensibly Southwestern species (*M. arizonensis* and *M. werneri*) at the northwestern edges of their known ranges (Baumann et al. 1977) and a typically Northwestern species close to the southern edge of its range (*M. projecta* (Frison, 1937): Jewett 1960). Additionally, the isolated populations of *M. arizonensis* we found at Pinnacles are nearly 500 kilometers away from the nearest known population in Mojave National Preserve (Bogan 2017), but only 100 kilometers away from populations of the morphologically similar *M. bulbosa* (Nelson & Baumann 1990). New morphological and genetic analyses of western *Mesocapnia* would aid in sorting out both taxonomic concerns and biogeographic history of intermittent stream stonefly assemblages in western North America.

In conclusion, intermittent streams historically have been considered to support less diverse invertebrate faunas, with few unique species (e.g. Datry et al. 2014). However, our findings here and the results of other recent studies (e.g. Bottorff 2007, Baumann & Kondratieff 2011) suggest that we have greatly underestimated the diversity and uniqueness of intermittent stream stonefly assemblages in California. In fact, just this year a new species of *Malenka* was described from intermittent streams in the Diablo Range just north of Pinnacles (Verdone & Kondratieff 2018). Further study of intermittent stream stonefly assemblages could help refine biomonitoring protocols for non-perennial streams (Mazor et al. 2014), solve outstanding biogeographic mysteries, and contribute to the long-term conservation of these undervalued ecosystems.

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