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Biodiversity value of remnant pools in an intermittent stream during the great California drought

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Abstract

1. In many intermittent streams, remnant pools persist after flow ceases and provide refuge for aquatic organisms able to tolerate stagnant water conditions. The conservation value of these pools may be greatly under-appreciated, especially in regions with a Mediterranean climate, where perennial streams have been substantially modified or disturbed by human activities.
2. Fish, amphibians, aquatic reptiles, and aquatic invertebrates were sampled from 15 remnant pools and three seeps at Coyote Creek, California, USA, in the late summer of 2014, during the height of the most intense drought that California has experienced in 500 years. Patterns of vertebrate and invertebrate species richness and community composition were compared with abiotic factors (e.g. water quality and habitat size).
3. Thirteen vertebrate species and 172 invertebrate taxa were identified from remnant pools and seeps. Overall vertebrate richness and composition were not correlated with abiotic factors, but fish species richness increased with remnant pool size and depth. Invertebrate taxon richness increased with pool size. Invertebrate community composition differed by habitat type (pool versus seep) and gradients in composition were correlated with several abiotic factors (e.g. pool size, substrate, and canopy cover).
4. Remnant pools at Coyote Creek supported a full assemblage of native fishes and numerous imperilled taxa, including California red-legged frogs and California floater mussels. Nearly all native fishes and imperilled taxa are absent from artificially perennial and urbanized reaches of Coyote Creek just a few kilometres downstream of the study area.
5. Remnant pools in intermittent streams should be a focus of conservation efforts in regions with a Mediterranean climate, especially during extreme droughts. Native fauna adapted to harsh intermittent flow regimes can thrive in these habitats, whereas non-native taxa may fare poorly. Furthermore, remnant pools supported by deep groundwater sources, such as those along geological faults, may provide both ecological refuge and evolutionary refugia for freshwater biota.

KEYWORDS
amphibians, aquatic invertebrates, drought, drying, fishes, refuge, refugia, reptiles

1 | INTRODUCTION

Stream drying is widely recognized as a significant factor shaping the ecology and biodiversity of lotic ecosystems (Boulton, 2003; Datry, Larned, & Tockner, 2014; Lake, 2011). Taxa living in intermittent streams, which cease flowing during part or much of the year, are confronted with contracting habitat area, potential stranding in drying reaches, and increasingly harsh abiotic conditions (e.g. higher temperatures or lower dissolved oxygen) in the remaining wetted habitats (Boulton, Rolls, Jaeger, & Datry, 2017; Gómez, Arce, Baldwin, & Dahm, 2017). Accordingly, aquatic biodiversity is often significantly lower in intermittent streams than in perennial streams (Tornes & Ruhi, 2013; Datry et al., 2014; Soria, Leigh, Datry, Bini, & Bonada, 2017). In many intermittent streams, however, remnant pools persist when flow ceases, providing refuge for aquatic organisms able to tolerate stagnant water conditions (Garcia-Roger et al., 2013; Stubbington et al., 2017). The conservation value of these remnant pools may be greatly under-appreciated (Hill & Milner, 2018), especially in regions where perennial streams have been substantially modified or disturbed by human activities.

In regions with a Mediterranean climate, intermittent streams often have high flow rates during the winter rainy season, but then surface flow ceases for several months during the long, dry summer and early autumn (Gasith & Resh, 1999). The magnitude of winter rain can vary dramatically from year to year, but at least some rain falls each year and promotes the persistence of remnant pools through the dry season (Bonada, Rieradevall, & Prat, 2007). In contrast, winter rains in more arid regions can fail almost wholly, leaving intermittent streams and remnant pools dry for multiple consecutive years (Bogan, Boersma, & Lytle, 2013). Many remnant pools in Mediterranean-climate streams are relatively stable and reliable, and have been shown to support numerous species of fish (Magalhães, Beja, Canas, & Collares-Pereira, 2002; Pires, Pires, Collares-Pereira, & Magalhães, 2010; Vardakas et al., 2017), herpetofauna (Sánchez-Montoya, Moleon, Sánchez-Zapata, & Escoriza, 2017), and aquatic invertebrates (Bogan, Hwan, & Carlson, 2015). The refuge from drying that these remnant pools provide is especially important, considering that Mediterranean-climate streams are ‘biodiversity hot spots’ facing threats from water abstraction, habitat alteration, climate change, and non-native species (Cid et al., 2017; Marr et al., 2010; Skoulikidis et al., 2017).

More than 66% of streams in Mediterranean-climate California, USA, cease to flow for part of each year (Levick et al., 2008), and remnant pools that persist through the dry season are found in many reaches (Bonada, Rieradevall, Prat, & Resh, 2006). Despite their numerical dominance, intermittent streams are the focus of far less ecological research and conservation than perennial streams (Acuña et al., 2014; Leigh et al., 2016). This lack of attention may undersell their biodiversity value in California, especially because intermittent streams are more likely to retain natural flow regimes than perennial streams, the majority of which are dammed (Mount, 1995). Natural flow regimes, including zero-flow periods with remnant pools, may facilitate the persistence of native species that would otherwise have been extirpated by the introduction of non-native species in modified reaches below dams (Kiernan, Moyle, & Crain, 2012; Moyle, 2013). Some intermittent streams in California are known to support diverse aquatic invertebrate communities (Bogan et al., 2015) and serve as critical spawning grounds for native fish (Boughton, Fish, Pope, & Holt, 2009; Hwan, Fernández-Chacón, Buoro, & Carlson, 2018); however, relatively little is known about their overall biodiversity value across taxonomic groups, especially during the dry season when only remnant pools remain.

In this study, the diversity and composition of aquatic invertebrate and vertebrate assemblages were documented in remnant pools of Coyote Creek, a third-order intermittent stream in northern California. Observations occurred during late summer 2014, coinciding with the peak of the most intense drought to strike the region in at least 500 years (Belmecheri, Babst, Wahl, Stahle, & Trouet, 2016; Griffin & Anchukaitis, 2014). The study goals were to describe the biodiversity found in remnant pools, to examine relationships between abiotic factors (e.g. pool size and water quality) and biotic community structure, and to contrast these findings with observations from tiny perennial seeps (with <1 m^2 of total wetted habitat) in the same reaches and from previously published surveys of artificially perennial reaches of Coyote Creek lower in the drainage.

2 | METHODS

2.1 | Study system

Coyote Creek is an 830-km^2 stream basin draining into the southern San Francisco Bay from its headwaters in the Diablo Range of northern California (Figure 1). The climate is typically Mediterranean, with warm, dry summers (from May to September) and cool, wet winters (from October to April); approximately 80% of the precipitation falls in winter (Leidy, Cervantes-Yoshida, & Carlson, 2011). The long-term average annual precipitation at Coyote Creek is 670 mm, but averaged only 450 mm in the 3 years that preceded the study period (2011–2013). Lower Coyote Creek is perennial because of releases of stored water from two impoundments (Coyote Dam and Anderson Dam) and overland run-off from urban sources. The stream channel in this lower portion is moderately to highly modified by urbanization (Leidy, 2007). Above the impoundments, however, the flow in upper Coyote Creek is naturally intermittent. Flow occurs during and after winter rains, and generally ceases by June or July each year, before

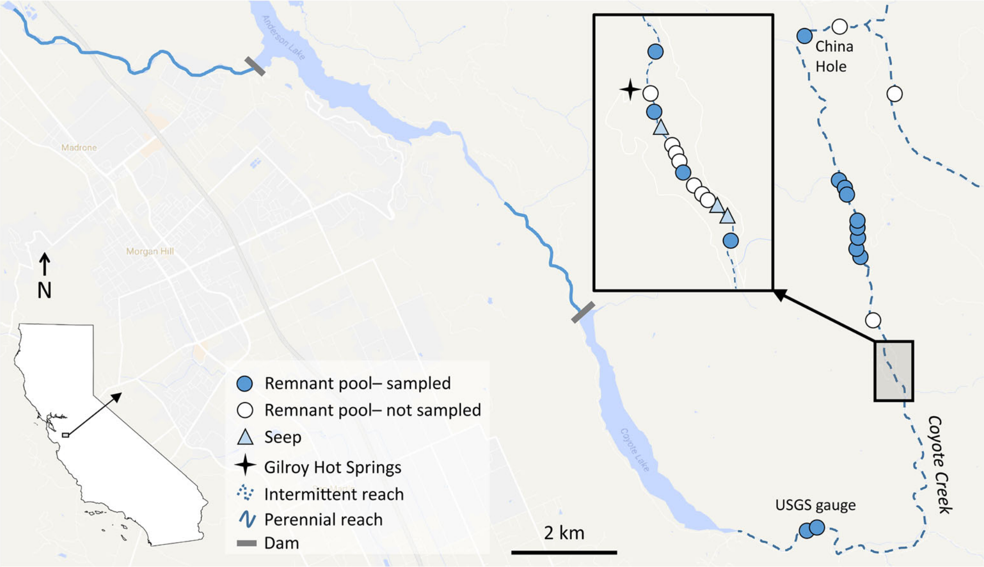

FIGURE 1 Map of the study area at Coyote Creek in Santa Clara County, California, USA. All sampling took place in the intermittent reaches above two reservoirs (Coyote Lake and Anderson Lake) in Henry Coe State Park. Downstream of the reservoirs, Coyote Creek is artificially perennial

resuming with the storms of the next winter, several months later (Figure 2). Surface water persists as a series of remnant pools during the summer dry season (Figure 3). The stream bed is composed primarily of gravel and cobble, with banks occasionally being bounded by boulders. Riparian vegetation in upper Coyote Creek is relatively sparse (Figure 3), with a scattered to moderately dense canopy of several willow (*Salix*) species, mulefat (*Baccharis salicifolia*), white alder (*Alnus rhombifolia*), and western sycamore (*Platanus racemosa*), and with a sparse-to-dense understory of torrent sedge (*Carex nudata*). In September and October 2014, during the height of the great California drought (2011–2016), surface water in 17 km of upper Coyote Creek (245–400 m a.s.l.) was restricted to approximately 25 remnant pools and three seeps (Figure 1). The seeps were small, narrow (<0.5 m width), and shallow (<0.05 m depth) habitats where groundwater surfaced and trickled over cobble or gravel substrate.

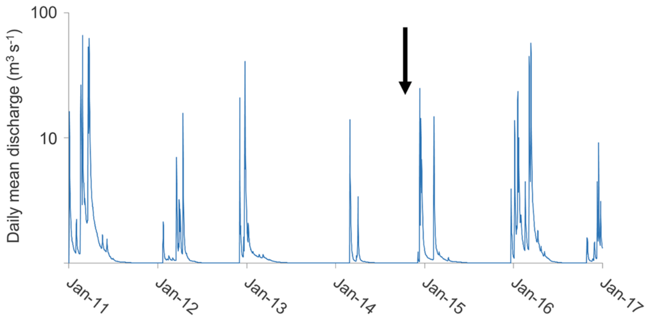

FIGURE 2 Daily average discharge (m^3 s^{-1}) at Coyote Creek from January 2011 to January 2017, demonstrating flow seasonality and the pronounced summer dry season. The driest years of the great California drought, which began in 2011 and ended in 2016, were 2013 and 2014. The black arrow signifies when the biological samples were collected in late September and October of 2014. Flow data are from USGS gauge #11169800

For this study, physical habitat variables were measured and biological communities were sampled in 15 randomly selected remnant pools and in all three seeps. All of the study sites were located in Henry Coe State Park and lands administered by the Santa Clara County Open Space Authority.

2.2 | Physical habitat measurements

Wetted surface area and maximum depth in remnant pools and all seeps were measured using metre tapes, metre sticks, and a Laser Technology TruPulse 200 digital rangefinder (Laser Technology, Inc., Centennial, CO). Visual estimates (%) were made for riparian canopy cover and benthic substrate cover (categories with particle diameters: silt, <0.25 mm; sand, 0.25–2 mm; gravel, >2–64 mm; cobble, >64–256 mm; and boulder/bedrock, >256 mm). The percentage of the benthic substrate that was covered by riparian leaf litter and aquatic vegetation was also visually estimated. Handheld meters were used to measure the water temperature, pH (Whatman pH Indicators; Whatman International, Maidstone, UK), and specific conductance (i.e. conductivity) (Milwaukee waterproof EC meter C65; Milwaukee Instruments, Rocky Mount, NC) in each pool.

2.3 | Biological sampling

Quantitative and qualitative collecting techniques were used to assess aquatic invertebrate, amphibian, reptile, and fish assemblages in 15 remnant pools and all remnant seeps. The goal was to document conditions at the height of the dry season in a very dry year. For aquatic invertebrates, pools were sampled with a D-net (0.5-mm mesh) using a timed-sweep method (Bogan & Lytle, 2007). Large pools (>15 m^2 surface area) were sampled by a combination of a timed sweep and

FIGURE 3 Variety of remnant pool sizes during the late summer dry season at Coyote Creek, California (September 2014)

searching of unique habitat features (e.g. submerged tree roots and vertical bedrock walls in pools) for target organisms (e.g. caddisflies and giant water bugs). Seeps were too shallow (>5 cm deep) to sample with a D-net or Surber sampler, so a 10-cm-wide aquarium net (0.25-mm mesh) was used instead. A 500-cm^2 area of seep substrate was disturbed, and dislodged invertebrates were swept by the current into the aquarium net placed downstream (Bogan et al., 2014). All invertebrates were preserved in 95% ethanol for transport and subsequent identification at the University of California, Berkeley. Most taxa were identified to genus or species, but a few challenging taxa were only identified to family or order (e.g. oligochaete worms).

Amphibians, reptiles, and fishes were sought using visual-encounter surveys along, in, and adjacent to remnant pools and seeps. Each survey lasted 20 min and was made during clear or partly cloudy warm daylight hours, at least 1 h after sunrise and before sunset. Air temperature at the time of the surveys exceeded 10°C. Surveys were conducted by first walking around and scanning the entire pool perimeter. For pools greater than 10 m^2, surveyors entered the pool and scanned the water column, substrate, and adjacent shoreline. In addition, larval amphibians (e.g. tadpoles) were sought during the timed-sweep sampling of pools for aquatic invertebrates. Surveyors scanned the shore to the bankfull elevation or within 3 m of the water's edge, whichever distance was smaller. Seine nets were used to capture fish for length measurements (see below) and to confirm the identity of small fishes seen during visual-encounter surveys.

The abundance of fish, amphibians, and reptiles was estimated for each pool using the following categories: 1, ≥1–10 individuals; 2, ≥10–100; 3, ≥100–1000; 4, ≥1000–5000; and 5, ≥5000. For accuracy, two observers first assigned fish, amphibians, and reptiles to an abundance category independently. If estimated abundances differed between the two observers, counts were reassessed until both observers agreed. Sculpin were difficult to sample visually, so a combination of dip netting (e.g. under banks and near root wads) and overturning cobbles was used to detect sculpin in interstitial spaces and to estimate their abundance. A subset of the total population of each species of fish in each pool was captured with seine nets to estimate distributions of size classes by species. In pools where fish were rare (<50 individuals), the length of each fish was measured. In pools where fish were abundant, the total lengths were measured for a random subset of 50 individuals for each species.

2.4 | Data analyses

After visual inspection of data plots, linear regression was used to quantify the relationship between each of two physical habitat factors (independent variables: remnant pool surface area and maximum depth) and each of three biological metrics (dependent variables: invertebrate taxon richness, vertebrate species richness, and fish species richness) across the 15 study pools. The log of remnant pool surface area was selected for analysis because surface areas varied across four orders of magnitude. Non-metric multidimensional scaling (NMS) ordination was used to visualize differences in community composition among remnant pools and seeps, with separate ordinations for the vertebrate and invertebrate taxa. Ordination analyses were conducted using 250 runs, random starting configurations, and Bray–Curtis distance as the measure of community dissimilarity. Prior to ordination, species abundances were square-root transformed to reduce the influence of dominant species (McCune & Grace, 2002). Measured abiotic factors were plotted as vectors on the ordination plot based on correlation coefficients between these factors and NMS axis values. Linear correlation values between species abundances and ordination axes were calculated to assess which species were most influential in the observed patterns.

Indicator species analysis (ISA; Dufrêne & Legendre, 1997) was used to identify species associated with remnant pool samples compared with seep samples. This analysis produces indicator value scores ranging from 0 (worst) to 100 (best) for each taxon, along with *P* values to assess the significance of each indicator value. Tests for significant compositional differences among habitat type (pools versus seeps) were made using the multi-response permutation procedure (MRPP; Mielke & Berry, 2001). All community analyses were performed using the program PC-ORD 5 (MJM Software, Gleneden Beach, OR).

3 | RESULTS

3.1 | Physical habitat

The surface area of remnant pools varied from 0.03 to 200 m^2 (58.9 ± 54.0 m^2, mean ± SD), with depths ranging from 0.03 to 1.9 m (0.7 ± 0.5 m) (also see Figure 3). The combined surface area of all 15 remnant pools surveyed was 884 m^2. Although there were no consistent longitudinal patterns in pool size, the pools furthest downstream, at the United States Geological Survey (USGS) flow gauge (Figure 1), were two of the largest pools. Riparian canopy cover was generally low across all the pools (34 ± 22%), and leaf litter covered only a small percentage of the benthic zone (6.6 ± 16%). Cobble and gravel were the most common benthic substrate classes (40 ± 17 and 32 ± 15%, respectively), with an average of less than 10% cover each for bedrock, sand, and fines. Surface flow was not recorded through remnant pools.

Small seeps were found in Coyote Creek below where input from Gilroy Hot Springs reaches the channel (Figure 1). The flow rate was meagre (~0.3 L s^{-1}), and the total wetted habitat area of the seeps was approximately 2 m^2. Seep habitats were very narrow (<0.2 m) and shallow (<0.02 m). In contrast to remnant pool habitat, seeps had dense riparian canopy cover (>95%).

FIGURE 4 Examples of the 184 aquatic taxa that inhabit remnant pools during the dry season at Coyote Creek, California: (a) California roach and floater mussel; (b) California red-legged frogs; (c) Diablo Range garter snake; (d) foothill yellow-legged frog; (e) Sierran tree frog; (f) California newts; (g) water scorpions (Nepidae); and (h) riffle sculpin (for scientific names, see Appendix 1 and Table 3)

Water temperature and conductivity values were relatively moderate across all pools and seeps within the sampling period, with temperatures ranging from 12°C to 22°C (18.1 ± 3.1°C) and with conductivity ranging from 462 to 1781 µS (803 ± 307). pH values were neutral and remarkably consistent across sampling locations (7.4 ± 0.3).

3.2 | Aquatic invertebrates

One-hundred and seventy-two aquatic invertebrate taxa were identified from the 15 pool and three seep samples collected in September and October 2014 (Appendix 1; Figure 4). Richness values for individual pools ranged from 21 to 77 taxa. The invertebrate fauna was dominated by insects such as true flies (Diptera, 49 taxa) and beetles (Coleoptera, 40 taxa), with smaller numbers of caddisfly (Trichoptera), true bug (Hemiptera), dragonfly (Odonata), stonefly (Plecoptera), and mayfly (Ephemeroptera) taxa. In addition, 35 taxa of non-insect invertebrates were collected, including freshwater sponges (Spongillidae) and the imperilled California floater mussel (*Anodonta californiensis*). On average, 49 ± 14 invertebrate taxa were found in each pool sample and 48 ± 10 taxa were found in each seep sample. Across the 15 pools, invertebrate taxonomic richness increased significantly with the log of pool surface area ($R^2 = 0.58$, $P < 0.01$) and with pool depth ($R^2 = 0.33$, $P = 0.03$). Fifteen taxa were unique to seep samples, including stoneflies (*Calineuria*, *Capnia*, *Malenka*, and *Pteronarcys*), a riffle beetle (*Zaitzevia*), mites (*Mesobates* and *Torrenticola*), a meniscus midge (*Meringodixa*), and several non-biting midges (*Parametriocnemus*, *Pentaneura*, *Rheocricotopus*, *Rheotanytarsus*, *Tanytarsus* (*Nimbocera*), *Thienemanniella*, and *Virgatanytarsus*).

Non-metric multidimensional scaling (NMS) ordination analysis of aquatic invertebrate community data resulted in a two-dimensional solution (stress = 0.10, final instability <0.0001, $P = 0.004$; Figure 5) that explained >86% of the variation in the original distance matrix. Flow rate, canopy cover, and percentage cobble were negatively correlated with axis 1 ($r = -0.85$, -0.64, and -0.51, respectively), whereas longitude was positively correlated with axis 1 ($r = 0.61$). Water depth and surface area were positively correlated with axis 2 ($r = 0.62$ and 0.59, respectively). Community composition was not correlated with water quality factors (all $r < 0.3$). The abundances of all the invertebrate taxa unique to seeps were negatively correlated with axis 1 ($r < -0.5$), whereas only abundances of the beetle *Peltodytes callosus* exhibited a strong positive correlation with axis 1 (Table 1). Abundances of eight true fly, amphipod, mite, caddisfly, and mayfly taxa were positively correlated with axis 2, whereas the abundances of three beetle taxa were negatively correlated with axis 2 (Table 1).

The invertebrate community composition differed significantly between pool and seep samples (MRPP, $A = 0.08$, $P < 0.001$). Nine invertebrate taxa were significant indicator taxa for pools, including five beetles, two mites, a damselfly, and an amphipod (Table 2). Eighteen stonefly, caddisfly, beetle, mite, and true fly taxa were significant indicators for seeps. Most of these taxa were exclusive or nearly exclusive to seep samples. Because seep samples were so distinct from pool samples, NMS analyses were also run with pool samples only, but the resulting ordination and abiotic correlation vectors were not significantly different from those of the full ordination.

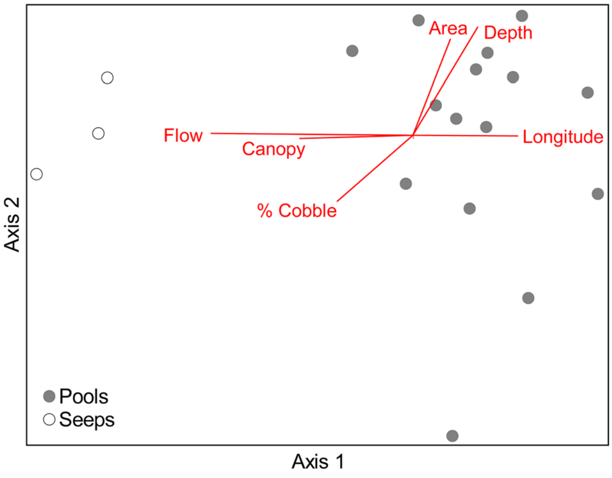

FIGURE 5 Non-metric multidimensional scaling ordination of aquatic invertebrate samples from pools and seeps at Coyote Creek in 2014. Vectors display which environmental variables were correlated with the ordination axes, and the length of each vector illustrates the strength of the correlation

TABLE 1 Aquatic invertebrate taxa with strong correlations ($|r| > 0.5$) with non-metric multidimensional scaling (NMS) ordination axis 1 or 2. For detailed taxonomic information regarding aquatic invertebrate genera and species, see Appendix 1

Taxon	Axis 1 *r*	Taxon	Axis 2 *r*
Peltodytes callosus	0.52	*Polypedilum*	0.57
Capnia	−0.61	*Hyalella*	0.54
Torrenticola	−0.62	*Enallagma/Coenagrion*	0.54
Rheocricotopus	−0.66	*Mystacides alafimbriata*	0.52
Lepidostoma	−0.68	*Callibaetis*	0.51
Helichus suturalis	−0.68	*Mideopsis*	0.51
Hydroptila	−0.69	*Dicrotendipes*	0.50
Tanytarus (*Nimbocera*)	−0.70	*Sigara mckinstryi*	0.50
Pentaneura	−0.70	*Gyraulus*	−0.44
Simulium	−0.74	*Neoclypeodytes leechi*	−0.72
Hydraena	−0.76	*Liodessus*	−0.72
Thienemanniella cf. *xena*	−0.76	*Enochrus pygmaeus*	−0.74
Calineuria	−0.78		
Eubrianax edwardsi	−0.78		
Tabanus	−0.80		
Parametriocnemus	−0.81		
Corynoneura	−0.85		
Micrasema	−0.90		
Zaitzevia parvula	−0.93		

TABLE 2 Indicator species analysis results for aquatic invertebrates collected from the two aquatic habitat types at Coyote Creek, pools and seeps

Habitat	Taxon	Indicator value	P
Pools	*Liodessus*	93	0.004
	Mideopsis	93	0.004
	Enallagma/Coenagrion	93	0.005
	Berosus	93	0.005
	Hyalella	87	0.016
	Hygrobates	87	0.012
	Peltodytes simplex	87	0.013
	Stictotarsus deceptus	80	0.032
	Peltodytes callosus	80	0.041
Seeps	*Calineuria*	100	0.001
	Parametriocnemus	100	0.001
	Pentaneura	100	0.001
	Rheocricotopus	100	0.001
	Tanytarsus (*Nimbocera*)	100	0.001
	Simulium	100	0.001
	Capnia	100	0.003
	Zaitzevia parvula	99	0.001
	Eubrianax edwardsi	98	0.001
	Tabanus	98	0.001
	Helicopsyche	80	0.021
	Helichus suturalis	67	0.019
	Hydropsyche	67	0.019
	Hydroptila	67	0.019
	Malenka	67	0.019
	Rheotanytarsus	67	0.019
	Lepidostoma	65	0.019
	Torrenticola	62	0.040

TABLE 3 Aquatic and semi-aquatic vertebrates detected at Coyote Creek in September–October 2014

Taxonomic group	Common name	Latin name
Fishes	California roach	*Lavinia symmetricus*
	Riffle sculpin	*Cottus gulosus*
	Brook lamprey[a]	*Lampetra* cf. *pacifica*
	Sacramento sucker	*Catostomus occidentalis*
	Sacramento pikeminnow	*Ptychocheilus grandis*
	Bluegill[b]	*Lepomis macrochirus*
Amphibians	California red-legged frog	*Rana draytonii*
	Foothill yellow-legged frog	*Rana boylii*
	Sierran tree frog	*Pseudacris sierrae*
	California newt	*Taricha torosa*
	California toad	*Anaxyrus boreas halophilus*
Reptiles	Western pond turtle	*Actinemys marmorata*
	Diablo Range garter snake	*Thamnophis atratus zaxanthus*

[a] Taxonomic status under revision.

[b] Non-native.

3.3 | Aquatic and semi-aquatic vertebrates

Thirteen species of aquatic and semi-aquatic vertebrates were identified from remnant pools (Figure 4; Table 3), including five native fishes and one non-native fish, five amphibians, and two reptiles. No vertebrates were documented from seep habitats. The overall vertebrate species richness per pool ranged from three to eight (mean = 4.6) and fish species richness ranged from two to five (mean = 3.0). There was no significant relationship between overall vertebrate species richness and the log surface area (R^2 = 0.01, P = 0.75) or maximum depth (R^2 = 0.21, P = 0.08) of remnant pools; however, when only fish were considered, species richness increased significantly with both the log surface area (R^2 = 0.32, P = 0.03) and maximum depth (R^2 = 0.28, P = 0.04) of remnant pools, similar to aquatic invertebrates. NMS analyses failed to produce a significant ordination of vertebrate community data, suggesting that there were no clear patterns of community composition across the 15 study pools. California roach (*Lavinia symmetricus*) was the most widespread and abundant species, occurring in all pools with abundances usually over 1000 individuals per pool (Figure 6). Sacramento sucker (*Catostomus occidentalis*) was abundant in many pools, and foothill yellow-legged frogs (*Rana boylii*) were widely distributed with lower abundances. Two species of conservation concern, the California red-legged frog (*Rana draytonii*) and the western pond turtle (*Actinemys marmorata*), were encountered in several pools. Non-native bluegill (*Lepomis macrochirus*) was only found at the USGS gauge pool (Figure 1), and all of the individuals were of the same large size class.

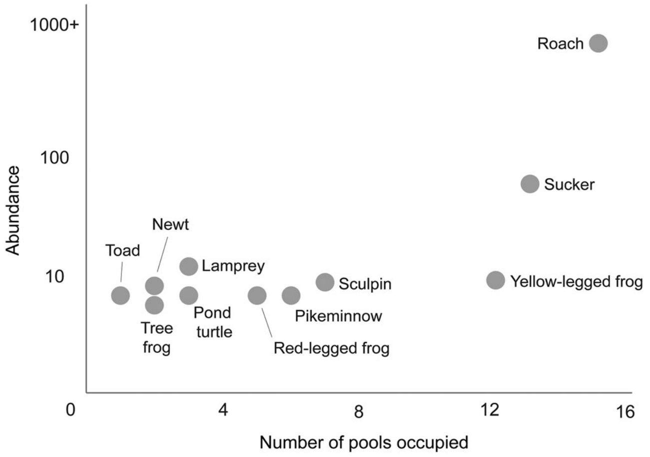

FIGURE 6 Relationship between the number of pools that each vertebrate species occupied at Coyote Creek and their average abundances in those pools on a log-scale. For the scientific names of these species, see Table 3

The presence of juvenile fishes in four of the most common native species (Figure 7) suggests evidence of successful reproduction during extreme drought conditions. The size distribution of California roach suggested abundant recruitment (young-of-year fish <40 mm total length, TL), with adults (>50 mm TL) also being common. For the Sacramento sucker, catches were dominated by young-of-year fish (<100 mm TL) and large adults (>350 mm TL), with few intermediate-

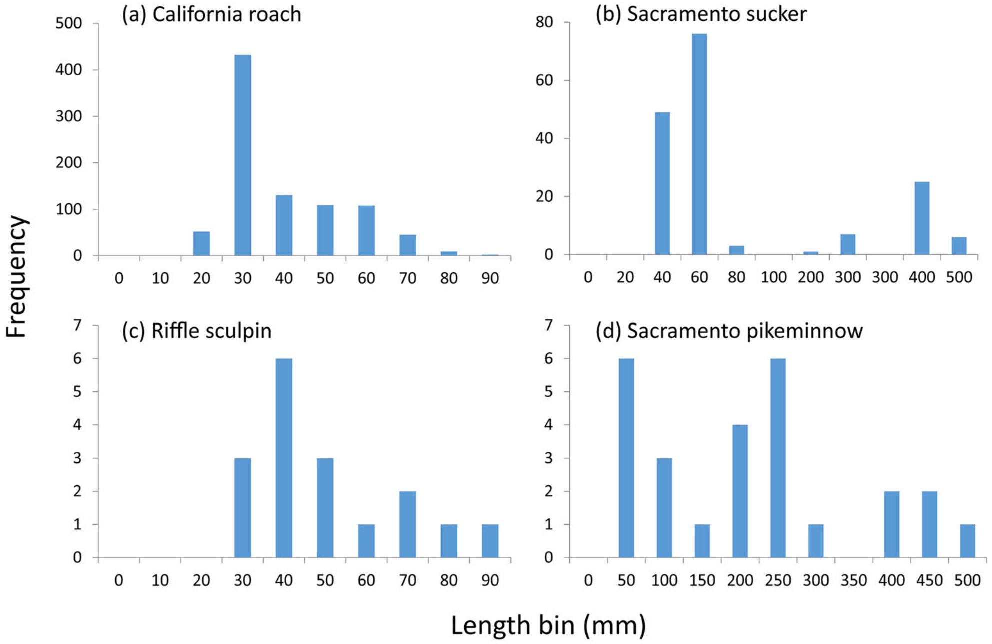

FIGURE 7 Length–frequency histogram for the four most common fishes found in remnant pools at Coyote Creek. The presence of juvenile fishes suggests evidence of successful reproduction in isolated pools during extreme drought conditions. The one exception is the Sacramento pikeminnow, which was rare overall, and for which all of the young-of-year fishes (<100 mm) were encountered in a single pool (China Hole). Note the differences in *x*- and *y*-axis values among species; bin sizes decrease for the Sacramento sucker for lengths of <100 mm to highlight the variation in the lengths of the young-of-year fishes

sized juveniles, suggesting reduced spawning success 2–3 years before sampling. For the Sacramento pikeminnow (*Ptychocheilus grandis*), three size classes were detected: young-of-year fish (<100 mm TL), juveniles, and adults (>350 mm TL). Pikeminnow were rare overall, however, and all nine individual young-of-year fish (<100 mm TL) were found in a single remnant pool. Too few individuals of brook lamprey (*Lampetra* cf. *pacifica*) were encountered to estimate their size class distributions.

4 | DISCUSSION

Remnant pools at Coyote Creek supported at least 172 invertebrate taxa and 13 vertebrate species through the most severe drought in more than 500 years. Although non-native fishes dominate many Californian streams (Moyle, 2013), including the artificially perennial lower reaches of Coyote Creek (Leidy, 2007), only a single non-native fish species was found in limited numbers in the intermittent upper reaches of Coyote Creek. Moreover, several imperilled species such as the California red-legged frog and the California floater mussel were common in remnant pools. These patterns suggest that intermittent streams with remnant pools may serve as valuable refuges for many native species adapted to highly variable flow regimes including shifts from lotic to lentic conditions; however, several invertebrate taxa were only encountered in tiny remnant seeps, demonstrating the limitations of remnant pool refuges for at least some rheophilic taxa.

4.1 | Aquatic vertebrates in remnant pools

Most fish species cannot breathe air or aestivate terrestrially, so remnant pools provide essential dry-season habitat for fish in intermittent streams (Kerezsy, Gido, Magalhaes, & Skelton, 2017). At Coyote Creek, five native fish species were found to use remnant pools. This is similar to values observed in other Mediterranean-climate systems (Magalhâes et al., 2002; Pires et al., 2010; Vardakas et al., 2017) and semiarid systems (Arthington, Balcombe, Wilson, Thoms, & Marshall, 2005; Beesley & Prince, 2010), but much lower than the fish species richness documented from intermittent streams in the wet–dry tropics (e.g. 20–30 species: Minshull, 2008; Pusey, Kennard, Douglas, & Allsop, 2018). The dominance of native fishes at Coyote Creek may be in large part the result of seasonal drying and habitat contraction to which non-native species are not adapted. Moyle (2013) hypothesized that the persistence of an endemic subspecies of California roach in Six Bit Gulch, California, results primarily from the drying regime of that stream and the harsh abiotic conditions in remnant pools. California roach was also the most abundant fish in Coyote Creek pools (Figure 6), but all native fishes showed clear evidence of successful reproduction in previous years (Figure 7). Recent studies from other intermittent streams have found that many native fish will disperse from remnant pools during intermittent flow events but frequently return to the same pools as flow ceases (Marshall et al., 2016). This site fidelity to reliable remnant pools may be lacking in non-native fishes, and probably facilitates the long-term persistence of native fishes in streams with highly variable flow regimes.

In addition to fishes, seven species of amphibians and reptiles were found in remnant pools at Coyote Creek. Many amphibians and aquatic reptiles have at least one life history stage that can survive in the terrestrial environment, making them especially well suited for life in intermittent streams, even where the flowing periods are as brief as 2 months per year (Sánchez-Montoya et al., 2017). For example, five of the seven species that were documented at Coyote Creek are capable of living or aestivating terrestrially for weeks to months each year (Stebbins, 2003). The decision to leave remnant pools for the terrestrial environment can come at a cost, however. For example, a high mortality of western pond turtles was documented at Coyote Creek during extreme drought conditions in the summer of 2014 (Leidy, Bogan, Neuhaus, Rosetti, & Carlson, 2016). Western pond turtles that depart from intermittent stream pools to aestivate terrestrially earlier in the dry season are also significantly smaller than those that remain in the stream longer (Bondi & Marks, 2013). Furthermore, some species, such as the ranid frogs encountered at Coyote Creek (*R. draytonii* and *R. boylii*), are entirely reliant on aquatic habitats for each life stage and cannot persist in intermittent streams that lack remnant pools (Hayes & Jennings, 1988).

Surprisingly, there was no significant relationship between vertebrate species richness and pool size or depth, and there were no discernible community composition patterns among the 15 study pools of varying sizes and physiochemical conditions. Remnant pool sizes varied across several orders of magnitude (0.03–200 m^2), but other abiotic factors exhibited narrow ranges. For example, although canopy cover was low in all pools, the water temperatures measured did not exceed 22°C. Amphibians and reptiles often tolerate wide temperature ranges (Stebbins, 2003) and many native fishes in Mediterranean-climate California can tolerate warmer temperatures (e.g. 25–30°C; Moyle, 2002). Thus, the abiotic gradients measured may not be strong enough to produce compositional differences in vertebrates among remnant pools; however, pool surface area and maximum depth explained the significant variation of fish species richness. Many previous studies from Mediterranean-climate and semiarid regions have found that fish species richness increases with increasing remnant pool size, perimeter, and depth (Arthington et al., 2005; Magalhâes et al., 2002; Pires et al., 2010). Habitat complexity, temperature variability with pool area and depth, and the exact locations of groundwater inputs were not quantified in this study, but it is possible that these or other factors might explain the positive effects of pool size and depth on fish species richness.

4.2 | Aquatic invertebrates in remnant pools and seeps

Remnant pools supported >170 taxa of aquatic invertebrates. Larger and deeper pools supported significantly more invertebrate taxa than smaller, shallower pools. Beetles, true bugs, and dragonflies and damselflies were the dominant taxonomic groups in all remnant pools, as has been observed in many other Mediterranean-climate and semiarid intermittent streams (Bonada et al., 2006; Stubbington et al., 2017). The seasonal colonization of remnant pools by nominally lentic invertebrate taxa (e.g. many beetles and water boatmen) has been observed in other systems (e.g. Bogan & Lytle, 2007; Bonada et al., 2007; Hill & Milner, 2018), and probably also explains some of the dominance of these taxa at Coyote Creek. Some taxa more often associated with flowing water habitat, however, such as mayflies and caddisflies, were also common in remnant pools. Hill and Milner (2018) noted similar overlap of lotic and lentic taxa in remnant pools of intermittent streams in the UK, with 38% of the rheophilic taxa present during flowing phases also occupying remnant pools during dry periods. It is important to note that remnant pools were sampled in only one dry season; longer-term extinction and colonization processes probably result in year-to-year changes in the composition of these communities (Cid et al., 2017; Gasith & Resh, 1999).

Although remnant pools provide refuge for some rheophilic invertebrate taxa in intermittent streams (Chester & Robson, 2011), observations from perennial seeps at Coyote Creek indicate the limited utility of these pools for other rheophilic taxa. Despite their tiny size (<2 m^2 total habitat area), perennial seeps supported 15 stonefly, caddisfly, and other rheophilic taxa that were never collected from remnant pools, leading to very distinct communities being found in seeps versus pools (Figure 5). Similar rheophilic stonefly and caddisfly taxa have been found in remnant pools in one other stream in the study region, but the canopy cover was much higher and the water temperatures remained cool (<15°C) all summer (Bogan, Hwan, Cervantes-Yoshida, Ponce, & Carlson, 2017). Such benign abiotic conditions are uncommon in intermittent stream pools (Gómez et al., 2017), suggesting that perennial seeps can play an essential role in augmenting local refuge capacity for more sensitive rheophilic taxa.

4.3 | Intermittent streams as refuges for imperilled species

Intermittent streams do not receive much conservation attention for their potential to support imperilled species. Instead, intermittent stream communities are frequently characterized as being composed of generalists or more tolerant species that form nested subsets of perennial stream communities (Datry, Larned, Fritz, et al., 2014). Several imperilled species or species of conservation concern were found in remnant pools at Coyote Creek, however. For example, it is uncommon to see a lowland stream in California with an intact native fish fauna, and many freshwater fishes in California are threatened with extinction (Moyle, 2002, 2013), but five native fish species were widespread in remnant pools at Coyote Creek, with only a single exotic species that was confined to one pool. These observations stand in sharp contrast to the artificially perennial lower reaches of Coyote Creek several kilometres downstream from the study sites and below two large water storage reservoirs. These lower perennial reaches typically support more than a dozen exotic fish species, several of which are characterized by widespread distributions and high population abundances (Leidy, 2007). A similar pattern of native fishes persisting in high abundances within the remnant pools of intermittent reaches has been documented in several other streams in the region (Leidy, 2007; Leidy et al., 2011). Similarly, three species of endangered cyprinid fishes are known to persist in intermittent rivers in Greece, and appear to seek deeper habitats at the onset of drought conditions (Vardakas et al., 2017).

Remnant pools at Coyote Creek supported robust populations of California red-legged frogs and foothill yellow-legged frogs, two threatened species that seldom overlap in distribution. Red-legged frogs prefer the lentic conditions of remnant pools but require year-round water for larval development, whereas yellow-legged frogs require flowing water to trigger reproduction (Hayes & Jennings, 1988). Coyote Creek, with its seasonally dynamic flow and persistent pools, appears to provide an ideal mix of lentic and lotic conditions, and lacks the non-native fish fauna and habitat alterations that threaten these ranids elsewhere in California.

Coyote Creek supports a robust population of California floaters, a large freshwater mussel that has been extirpated from nearly 70% of its historic localities (Howard, Furnish, Brim Box, & Jepsen, 2015). The primary factors cited in these extirpations are the construction of dams, which modify flow regimes and sediment dynamics, contaminants leading to poor water quality, and the loss of native fishes that serve as hosts for the larval stage of the California floater (Howard et al., 2015). The intact native fish fauna and natural flow regime of Coyote Creek, including the presence of remnant pools to serve as dry-season refuges, are probably why this freshwater mussel population persists while so many others have disappeared.

4.4 | Remnant pools as ecological refuges and evolutionary refugia

Remnant pools are ecological refuges, but can they also serve as 'evolutionary refugia' (Davis, Pavlova, Thompson, & Sunnucks, 2013) over longer timescales? Interannual variation in the level and timing of precipitation, antecedent flow conditions, geomorphology, and groundwater inputs all act to shape the distribution and persistence of remnant pools in intermittent streams (Arthington et al., 2005; Beesley & Prince, 2010; May & Lee, 2004). For species that can disperse easily and quickly when flow resumes (e.g. some fish; Marshall et al., 2016), the persistence of specific pools may not be that important to maintaining populations across longer timescales; however, taxa with poor dispersal abilities would rely upon the longer-term persistence of individual remnant pools. Groundwater inputs to pools can significantly enhance survival for many taxa (Beesley & Prince, 2010; Davis et al., 2013; Labbe & Fausch, 2000), helping to decouple short-term climate variability from pool habitat stability. Deep groundwater inputs are likely to have contributed to the stability of some aquatic habitat at Coyote Creek during the great California drought. One thermal spring (Gilroy Hot Springs) emerges along the Madrone Springs Fault and trickles into Coyote Creek (Figure 1), supporting three small seeps and several remnant pools in the stream channel. Isotopic analyses suggest that this deep spring may be integrating rainfall inputs over the last 80 000 years (Kharaka, Thordsen, Evans, & Kennedy, 1999), providing a small, but reliable, source of water even in the driest of years. Thus, surface water and shallow groundwater can create critical ecological refuges for many taxa, but deeper groundwater inputs may be essential in creating evolutionary refugia for more sensitive taxa (Davis et al., 2013). Conserving imperilled taxa in intermittent streams will require quantifying their dispersal abilities and understanding how well those abilities align with local habitat connectivity (during periods of flow) and the long-term persistence of remnant pools.

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APPENDIX A

AQUATIC INVERTEBRATE TAXA COLLECTED FROM REMNANT POOLS AND SEEPS AT COYOTE CREEK, CALIFORNIA, IN SEPTEMBER AND OCTOBER 2014

Type	Class/order	Family	Genus/species
Insect	Coleoptera	Dryopidae	*Helichus striatus*
			Helichus suturalis
			Postelichus
		Dytiscidae	*Agabus*
			Boreonectes striatellus
			Dytiscus marginicollis
			Hydroporus fortis
			Hygrotus intermedius
			Laccophilus maculosus
			Liodessus obscurellus
			Neoclypeodytes leechi
			Neoclypeodytes plicipennis
			Rhantus
			Sanfilippodytes
			Stictotarsus deceptus
			Stictotarsus eximius
			Stictotarsus griseostriatus
		Elmidae	*Dubiraphia giulianii*
			Optioservus
			Ordobrevia
			Zaitzevia parvula
		Gyrinidae	*Gyrinus plicifer*
		Haliplidae	*Haliplus* sp.
			Peltodytes callosus
			Peltodytes simplex
		Hydraenidae	*Hydraena*
			Octhebius holmbergi
		Hydrophilidae	*Anacaena limbata*
			Berosus punctatissimus
			Chaetarthria nigrella
			Cymbiodyta
			Enochrus pygmaeus pectoralis
			Enochrus sp.
			Helochares normatus
			Hydrochus
			Laccobius ellipticus
			Tropisternus californicus
			Tropisternus sp.
		Psephenidae	*Eubrianax edwardsi*
		Scirtidae	Scirtidae
	Diptera	Ceratopogonidae	*Atrichopogon*
			Bezzia/Palpomyia
			Ceratopogon
			Culicoides
			Forcipomyia
		Chaoboridae	*Chaoborus*
		Chironomidae	*Ablabesmyia*
			Apedilum
			Apsectrotanypus
			Brillia
			Chironomus
			Cladotanytarsus
			Corynoneura
			Cricotopus
			Dicrotendipes
			Heleniella
			Lauterborniella
			Nanocladius
			Nilotanypus
			Paracricotopus
			Paramerina
			Parametriocnemus
			Paratendipes
			Pentaneura
			Phaenopsectra
			Polypedilum
			Rheocricotopus
			Rheotanytarsus
			Stempellinella
			Tanytarsus s.str.
			Tanytarsus (*Nimbocera*)
			Thienemanniella cf. *fusca*
			Thienemanniella cf. *xena*
			Thienemannimyia group
			Virgatanytarsus
		Culicidae	*Anopheles*
			Culex
		Dixidae	*Dixella*
			Meringodixa
		Empididae	*Hemerodromia*
		Ephydridae	Ephydridae
		Psychodidae	*Maurina*
		Simuliidae	*Simulium* sp.
			Simulium piperi
		Stratiomyidae	*Caloparyphus/Euparyphus*
		Tabanidae	*Tabanus*
		Tipulidae	*Hexatoma*
			Limnophila
			Limonia
	Ephemeroptera	Baetidae	*Callibaetis*
			Centroptilum
		Caenidae	*Caenis*
		Heptageniidae	*Heptagenia*
		Leptohyphidae	*Tricorythodes*
		Leptophlebiidae	*Paraleptophlebia*
	Hempitera	Belostomatidae	*Abedus indentatus*
			Lethocerus americanus
		Corixidae	*Corisella decolor*
			Graptocorixa californica
			Hesperocorixa laevigata
			Sigara mckinstryi
			Trichocorixa calva
		Gelastocoridae	*Gelastocoris oculatus*

(Continued)

Type	Class/order	Family	Genus/species
		Gerridae	*Aquarius remigis*
		Naucoridae	*Ambrysus californicus*
			Ambrysus mormon mormon
		Nepidae	*Ranatra brevicollis*
		Notonectidae	*Notonecta kirbyi*
		Veliidae	*Microvelia*
	Megaloptera	Corydalidae	*Neohermes*
		Sialidae	*Sialis*
	Odonata	Aeshnidae	*Aeshna*
		Coenagrionidae	*Argia*
			Enallagma/Coenagrion
		Gomphidae	*Gomphus kurilis*
			Ophiogomphus
		Libellulidae	*Libellula*
			Paltothemis lineatipes
		Macromiidae	*Macromia magnifica*
	Plecoptera	Capniidae	*Capnia*
		Chloroperlidae	*Sweltsa*
		Nemouridae	*Malenka*
		Perlidae	*Calineuria californica*
		Pteronarcyidae	*Pteronarcys californica*
	Trichoptera	Brachycentridae	*Micrasema*
		Helicopsychidae	*Helicopsyche*
		Hydropsychidae	*Hydropsyche*
		Hydroptilidae	*Hydroptila*
			Neotrichia
			Oxyethira
		Lepidostomatidae	*Lepidostoma*
		Leptoceridae	*Mystacides alafimbriata*
			Oecetis
		Philopotamidae	*Wormaldia*
		Polycentropodidae	*Polycentropus*
		Psychomiidae	*Tinodes*
		Sericostomatidae	*Gumaga*

(Continued)

Type	Class/order	Family	Genus/species
Non-insect	Acari	Arrenuridae	*Arrenurus*
		Axonopsidae	*Ljania*
		Hydrozetidae	*Hydrozetes*
		Hygrobatidae	*Hygrobates*
			Mesobates
		Lebertiidae	*Lebertia*
		Mideopsidae	*Mideopsis*
			Nudomideopsis
		Protziidae	*Protzia*
		Sperchonidae	*Sperchon*
		Torrenticolidae	*Torrenticola*
		Unionicolidae	*Neumania*
			Unionicola
	Amphipoda	Gammaridae	*Hyalella*
	Bivalvia	Sphaeriidae	*Pisidium*
		Unionidae	*Anodonta californiensis*
	Branchiopoda	Cladocera	Cladocera
	Cnidaria	Hydridae	*Hydra*
	Copepoda	Copepoda	Copepoda
	Hirudinea	Hirudinea	Hirudinea
	Gastropoda	Ancylidae	*Ferrissia*
		Hydrobiidae	*Fluminicola*
		Lymnaeidae	*Radix*
		Physidae	Physidae
		Planorbidae	*Gyraulus*
		Planorbidae	*Helisoma*
		Planorbidae	*Planorbella*
		Planorbidae	*Vorticifex*
		Pomatiopsidae	*Pomatiopsis*
	Nematoda	Nematoda	Nematoda
	Oligochaeta	Oligochaeta	Oligochaeta (megadrile)
			Oligochaeta (microdrile)
	Ostracoda	Ostracoda	Ostracoda
	Platyhelminthes	Turbellaria	*Dugesia*
	Porifera	Spongillidae	Spongillidae