SEASONAL PROGRESSION OF AQUATIC ORGANISMS IN A TEMPORARY WETLAND IN NORTHERN CALIFORNIA

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ABSTRACT.—Seasonal wetlands are important habitats for biodiversity of both invertebrate and vertebrate fauna. Many aquatic species have life history traits adapted to colonizing and developing in temporary aquatic habitats, and these traits influence the annual succession of the macroinvertebrate community. The chronology of taxon appearance and the variation in relative abundances during the hydroperiod are important for understanding population dynamics, trophic interactions, and responses to drought. This study investigated the successional changes in macroinvertebrate abundances in a seasonal wetland in northern California. Water quality parameters were measured regularly, including dissolved oxygen, temperature, pH, surface area, and specific conductance during the wet season (January–July) in 2007–2009. Macroinvertebrates were collected with net sweeps (mesh > 500 µm), and the presence of life stages of amphibians were visually observed from March to June each year. As the hydroperiod progressed, wetland surface area decreased, while water temperature and specific conductance increased. Macroinvertebrate abundance increased with the progression of the hydroperiod, and the richness of macroinvertebrate predator taxa tripled from 2 families in March to 6 families in June. The earliest part of the hydroperiod in the wetland was dominated by *Cyzicus* clam shrimp and *Lindieriella occidentalis* fairy shrimp. *Limnephilus* caddisfly larvae were few in number but were found exclusively in the early season. Sequential changes of dominant invertebrate taxa and relative abundances of macroinvertebrates were evident, particularly among several macroinvertebrate predators. Among these predators, the early-season community was dominated by larval dytiscid beetles, while later-season communities demonstrated increased predator richness (e.g., *Notonecta* backswimmers) and were dominated by *Lestes* damselflies. Larvae of the vertebrate predator *Taricha torosa*, which may act as a top predator, were present during the later stages of the hydroperiod. The phenology of individual aquatic taxa and their specific life history strategies may impact the sensitivity of macroinvertebrate populations to increased annual variation in hydroperiod that may result from climate changes in this region.

RESUMEN.— Los humedales estacionales constituyen hábitats importantes para la biodiversidad de animales invertebrados y vertebrados. Varias especies acuáticas presentan características de sus historias de vida que les permiten colonizar y desarrollarse en ambientes acuáticos temporales y dichas características influyen la sucesión anual de la comunidad de macroinvertebrados. La cronología de la aparición de los diferentes taxones y la variación en las abundancias relativas durante el periodo húmedo son factores de importancia para poder entender la dinámica poblacional, interacciones tróficas y respuestas a la sequía. Este estudio aborda los cambios sucesionales en las abundancias de macroinvertebrados en un humedal estacional en el norte de California (EUA). Parámetros indicativos de la calidad del agua fueron registrados regularmente, incluyendo oxígeno disuelto, temperatura, pH, superficie cubierta y conductancia específica durante la temporada húmeda (Enero–Julio) entre 2007 y 2009. Los macroinvertebrados fueron recolectados usando barridos con una red (tramado > 500 µm) y se observó la presencia de distintos estados de vida de anfibios entre Marzo y Junio de cada año. A medida que el periodo húmedo continuaba, la superficie del humedal disminuyó, y en cambio tanto la temperatura como la conductancia incrementaron. La abundancia de macroinvertebrados aumentó a medida que transcurría el periodo húmedo y la riqueza de taxones de macroinvertebrados depredadores se triplicó de dos familias en Marzo a seis familias en Junio. Durante la primera parte del periodo húmedo, el humedal estuvo dominado por el branquiópodo *Cyzicus* y el anostráceo *Lindieriella occidentalis*. A pesar de encontrar un bajo número de larvas del tricáptero *Limnephilus*, estas fueron halladas exclusivamente al inicio de la temporada. Los cambios secuenciales en los taxones dominantes y abundancias relativas en la comunidad de invertebrados fueron evidentes, particularmente entre varios macroinvertebrados depredadores. Entre estos últimos, la comunidad al principio de la temporada estuvo dominada por larvas de escarabajos de la familia Dytiscidae, los que luego fueron desplazados para dar paso a una comunidad de depredadores más rica (e.g., *Notonecta* remeros), dominada por libélulas del género *Lestes*. Las larvas del vertebrado depredador *Taricha torosa*, el cual puede actuar como depredador tope, estuvieron presente durante los estados tardíos del periodo húmedo. La fenología de los taxones acuáticos individuales y estrategias específicas de historia de vida pueden impactar la sensibilidad de las poblaciones de macroinvertebrados frente a una variabilidad anual mayor durante el periodo húmedo, como resultado de cambios climáticos en esta región.

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Natural history studies contribute to our basic understanding of ecology by presenting patterns in nature in the context of biological and physical factors that may constrain or enhance species abundances (Resh and Rosenberg 2010). Studies that document the temporal co-occurrence of species in the same habitat (e.g., Poff and Matthews 1985, Berté and Pritchard 1986) or occurrences of species relative to seasonal abiotic fluctuations (Judson and Nelson 2010) can prompt hypotheses that address biotic interactions among species or document population effects of abiotic stressors. Syntheses of natural history information can inform ecological theory (McCreadie and Bedwell 2013) and are essential to mitigating impacts on threatened or endangered species. Moreover, discovery of the degree to which collective groups of species, such as guilds, have similar tolerances, traits, or habitat requirements allows for development of biological indices and other conceptual frameworks related to biological assessment (Karr 1991, Solimini et al. 2008, Lunde and Resh 2012a).

Seasonal wetlands provide aquatic habitat during certain times of year but are dry at other parts of the year. Although some organisms utilize microrefugia (Strachan et al. 2014), generally these wetlands do not support a diverse aquatic fauna when dry (Palik et al. 2001, Lunde and Resh 2012a). As water returns, macroinvertebrates access temporary wetlands via flight from nearby perennial habitat or through life history stages that survive in the sediment or nearby plants during the dry season (Batzer and Wissinger 1996, Williams 2006). During the wet season, physical and chemical factors in temporary aquatic environments, such as temperature and water chemistry, can constrain the occurrence and abundance of macroinvertebrate taxa (Williams 1996, Zamora-Muñoz and Svensson 1996). Though abiotic conditions may progress predictably across a season, high interannual variability in precipitation can lengthen or shorten the seasonal hydroperiod (Williams 1996, Boix et al. 2004, Biggs et al. 2005).

Aquatic insects have a diversity of life history strategies that enable them to utilize these temporary habitats (Williams 2006), and variability in hydroperiod length may be advantageous for some life history strategies over others (Williams 1983). For example, *Ironoquia* and *Limnephilus* caddisflies have rapid larval development, which results in

early-season adult emergence, far ahead of potential pond-drying events (Williams 1983). Libellulid dragonflies, on the other hand, have slower developmental rates, and their larvae are common in the late-season pond community (Williams 1983). In years where the hydroperiod is abbreviated, taxa that require late-season development time may risk severe larval mortality.

Temporary aquatic habitats are significant sources of biodiversity in the flora and fauna of many regions (Belk and Brtek 1995, Nicolet 2004, Moss et al. 2009). In northern California, seasonal wetlands are particularly important habitat for invertebrates, such as crustaceans (e.g., fairy shrimp, tadpole shrimp; Belk and Brtek 1995, King et al. 1996), and vertebrates, such as California tiger salamanders, California red-legged frogs (Alvarez et al. 2013), and migrating birds (Gilmer et al. 1982, Isola et al. 2000). Among freshwater ecosystems, less is known about the aquatic biology of many seasonal wetlands, such as ponds, than is known about streams and lakes (Boix et al. 2012, Pérez-Bilbao et al. 2015). Moreover, wetland habitats are often vulnerable to degradation as a result of human development, including in California, where 90% of original wetlands have been filled or altered (Dahl 1990). The impact of increased temperatures and precipitation variability on hydroperiods as a result of global climate change presents concerns for the conservation of biodiversity in seasonal aquatic habitats.

We investigated seasonal variation in the abiotic conditions and phenology of aquatic macroinvertebrates, California newts, and Pacific chorus frogs in a seasonal wetland in northern California over multiple years. The objectives of this study were to (1) examine the seasonal progression of abiotic conditions during the hydroperiod of a seasonal wetland over multiple years, (2) describe seasonal variability of taxonomic composition and taxon abundances in the macroinvertebrate community, and (3) assess the succession and co-occurrence of the common aquatic macroinvertebrate and vertebrate predators.

METHODS

Sampling Location

The focus of this study is a seasonal wetland known as Hog Lake (39.0316° N, 123.0789° W), located at the University of California Hopland

Fig. 1. The seasonal wetland Hog Lake at Hopland Research and Extension Center in northern California, USA, in May 2007.

Research and Extension Center in northern California (Mendocino County), USA. This type of small seasonal wetland (3200 m²; Fig. 1) is common in a Mediterranean-climate area that is characterized by hot, dry summers and mild, rainy winters. Approximately 75% of rainfall occurs during the wet months during late fall and winter (between November and February), and these storms provide the water to fill Hog Lake each year. The aquatic habitat generally remains until late June or July each summer. Although annual mean precipitation is approximately 100 cm (1952–2011), mean precipitation for the initial wet months of November and December (1952–2011) is 11.8 cm and 18.0 cm, respectively (Hopland Research and Extension Center weather records). In contrast, mean precipitation for summer and early fall (July–October) is only 6.8 cm (1952–2011, Hopland Research and Extension Center). For the specific years of the study, monthly rainfall showed high variability (Fig. 2). In addition, the lake was divided into 2 halves using a rubber barrier from December 2007 to August 2008 for a separate experiment.

Abiotic Measurements

Abiotic measurements were taken every 2–4 weeks from January to June in 2007,

2008, and 2009. Physical measurements of the length, width, and circumference of the wetland were measured on a subset of sampling days with a field tape measure and were used to calculate surface area. When possible, the most current images available in Google Earth Professional were also used to determine the size of the wetland. Temperature (°C) was measured using 2 approaches. To understand daily temperature fluctuations, a HOBO Pendant temperature logger (Onset, Bourne, MA) was placed at the bottom of Hog Lake from February through early July 2009. In addition, temperature, dissolved oxygen (mg · L⁻¹), specific conductance (μS · cm⁻¹), pH, and turbidity (NTU) were measured at 2 locations (east and west ends of the wetland) in Hog Lake as part of the general abiotic sampling design (2- to 4-week intervals). To measure dissolved oxygen, specific conductance, and temperature we used a Yellow Springs Instrument (YSI) MP 556. Turbidity was measured using a HACH 2100P turbidity meter, and pH was measured with an Oakton pHTstr 3 meter. For overall descriptions of the wetland, abiotic characteristics at the east and west sites were averaged to obtain a single value for each variable prior to analysis.

Fig. 2. Monthly precipitation (cm) at Hog Lake, Mendocino County, California, USA, during 2007, 2008, and 2009.

Biological Sampling

Aquatic macroinvertebrates were collected with a 500- μ m-mesh D-frame dipnet from the same 2 sites (east and west) where abiotic measurements were taken. The sampling interval was every 2–4 weeks during the months of March, April, May, and June 2007–2009. Five net sweeps each at the east and west areas of the wetland were collected in a way that included various depths and microhabitats in the limnetic zone, thereby capturing invertebrates in the benthos and water column.

All macroinvertebrates collected were stored in 70% ethyl alcohol in the field. In the laboratory, macroinvertebrates were sorted with a 25 $\times$ magnifying glass and identified to family. Some taxa were identified to genus, including *Limnephilus* (Trichoptera: Limnephilidae) caddisflies, *Lestes* (Odonata: Lestidae) damselflies, and *Notonecta* (Hemiptera: Notonectidae) backswimmers. Other taxa were identified to family, including dytiscid beetles and corixid water boatmen. All aquatic insects collected were identified, as well as the individuals of California fairy shrimp, *Linderiella occidentalis*, and the clam shrimp genus *Cyzicus*. Copepods were excluded because of their small sizes (they were inconsistently sampled in the <500- μ m-mesh D-frame net). For some samples, macroinvertebrates were subsampled and identified to family or genus by EcoAna-

lysts, Inc. For subsamples, total abundance estimates were calculated by converting from the percent subsampled.

In addition to aquatic invertebrates, Hog Lake provides habitat for frogs (Lunde and Resh 2012b), newts, and migrating birds. Visual observations of all vertebrates present in the wetland and surrounding vegetation, including amphibians, garter snakes, and birds, were recorded for each sampling date. Observations of the presence or absence of life history stages, including egg, larvae, and adult, were noted for the California newt, *Taricha torosa*, and the Pacific chorus frog, *Pseudacris regilla*, during each sampling trip.

Statistical Analyses

We used nonmetric multidimensional scaling (NMS; Kruskal 1964) to assess seasonal and site differences of square-root transformed macroinvertebrate abundances (counts) in the statistical program R, Version 3.2.1 (*vegan* package). Our NMS analysis (Kruskal 1964) used Sørensen (Bray–Curtis) distance to assess seasonal differences in both the abiotic factors and the aquatic invertebrate community in Hog Lake. Stress values <0.2 were considered significant. We used principle components analysis (PCA) to identify the abiotic factors that represented the majority of the seasonal variance and compared tested

TABLE 1. Abiotic factors, including water temperature, lake surface area, pH, turbidity, dissolved oxygen, calcium concentration, and specific conductance in Hog Lake samples from 2007, 2008, and 2009. Total abundance of macroinvertebrates collected at each date are also shown.

Day/month	Year	Water temp. (°C)	Surface area (m ²)	pH	Turbidity (NTU)	Dissolved oxygen (mg · L ⁻¹)	Calcium (mg · L ⁻¹)	Specific conductance	Total abundance
11 March	2007	16.8	3123	8.4	2.1	10.7	NA	70	NA
24 March	2007	20.4	2580	8.7	1.1	13.8	NA	109	NA
15 April	2007	14.6	2295	8.5	1.2	10.9	NA	123	NA
27 May	2007	24.0	1524	8.2	NA	6.1	NA	114	2323
8 June	2007	25.1	1160	8.2	2.5	8.1	1.8	126	3730
23 June	2007	22.6	500	8.4	2.5	9.0	1.5	136	66
2 March	2008	12.2	NA	8.9	4	8.4	NA	72	26
16 March	2008	9.4	NA	9.8	2.8	8.8	4	92	89
20 April	2008	12.8	1273	8.6	7.5	9.8	4	107	384
18 May	2008	27.1	900	8.3	12.9	6.8	5.1	144	233
2 June	2008	23.9	675	9.5	5.5	11.4	5.4	152	463
16 June	2008	28.2	NA	9.0	3.8	12.5	7.3	166	176
27 June	2008	26.1	NA	NA	8.6	6.8	NA	644	NA
15 March	2009	10.0	3200	8.2	4.5	7.7	NA	88	NA
11 April	2009	17.0	NA	7.0	NA	10.2	2	103	388
25 April	2009	13.7	NA	10.0	NA	9.9	NA	115	420
19 May	2009	27.9	1289	8.7	2.0	6.9	5.2	132	727

linear models with those factors. Finally, we used Akaike's information criterion (AIC) scores to determine the best model fit for abiotic factors with NMS axis 1. Furthermore, we used the analysis of similarity (ANOSIM) function in the *vegan* R package with relative abundances to examine the distinctness of invertebrate communities among months.

RESULTS

Abiotic Factors

The timing and magnitude of the winter precipitation that filled Hog Lake varied each year (Fig. 2), which affected the date of both wetland filling and wetland dry down. In November and December 2006, Hog Lake received 8.8 cm and 15.1 cm, respectively. In contrast, in 2007, Hog Lake received only 1.5 cm in November, but 15.5 cm in December. In 2008, Hog Lake received 9.9 cm and 8.2 cm in these months, respectively. In each case, precipitation filled the wetland to its peak by sampling dates in mid-January (2007 and 2008) or early February (2009). Total precipitation varied annually and was 58.9 cm for October 2006–September 2007, 68.4 cm for October 2007–September 2008, and 62.9 for October 2008–September 2009.

Precipitation in this area is limited from July through the end of October (Fig. 2), and Hog Lake did not fill until precipitation saturated

the area in late November or December. Physical measurements in 2007, 2008, and 2009 all demonstrated that Hog Lake began holding water sometime between November and January and was dry by mid-July. The largest surface area occurred each year in January or February and steadily decreased until drying out in late June or early July (Table 1). Full capacity of the wetland corresponded to a surface area of 3200 m², and mean surface areas for March and June were 2802 m² and 917.5 m², respectively.

Surface area was inversely related to water temperature each year (Table 1). Temperature ranged from 9.4 °C to >30 °C (Fig. 3), and median temperature was nearly twice as high in May and June than in March and April. Turbidity varied widely throughout the study, ranging from 1.0 to 12.8 NTU. Specific conductance and water calcium concentrations also increased throughout the hydroperiod and were correlated ($R > 0.8$; Table 1).

Dissolved oxygen and pH were highly variable in Hog Lake, demonstrating the influence of daily and seasonal cycles in primary productivity. Dissolved oxygen ranged widely from 6.1 to 13 mg · L⁻¹ and showed less directionality than temperature and specific conductance (Table 1). Dissolved oxygen in Hog Lake was relatively high (>10 mg · L⁻¹) on many sampling dates. The pH values were alkaline, ranging from 8 to 10.

Fig. 3. Temperature (upper panel), macroinvertebrate relative abundance, and vertebrate life-history-stage occurrences (lower panel) for Hog Lake, California. Temperature measurements are displayed from temperature loggers set for 15-min intervals and placed in the bottom of Hog Lake during the hydroperiod of 2009. Relative abundances of macroinvertebrates (middle panel) include samples from 2007 to 2009 and exclude baetid mayflies because of their extreme peak abundances (>1000 individuals) during late season.

TABLE 2. For each taxon, mean taxon abundances and life history strategies for surviving desiccation (Williams 2006) in samples collected by month from Hog Lake, Mendocino County, California, from the hydroperiods of 2007–2009.

Taxa	Life history traits	Mean abundance			
		March	April	May	June
Crustaceans					
<i>Linderiella occidentalis</i>	Resistant eggs	94.0	2.3	0.0	0.0
<i>Cyzicus</i>	Resistant eggs	139.0	208.3	100.3	107.3
Trichoptera	Semiresistant eggs				
Limnephilidae <i>Limnephilus</i>		3.5	0.0	0.0	0.0
Odonata					
Lestidae <i>Lestes</i>	Recolonizing adults	2.5	146.0	127.3	140.0
Libellulidae		0.0	63.0	73.0	69.0
Coenagrionidae		0.0	0.0	227.7	61.0
Coleoptera	Resistant eggs or recolonizing adults				
Dytiscidae		37.0	151.3	21.7	3.5
Belostomatidae		0.0	0.0	0.3	0.0
Naucoridae		0.0	0.0	3.0	0.0
Haliplidae		0.0	0.0	9.3	1.5
Hydrophilidae		3.5	22.3	6.3	5.8
Homoptera		0.0	0.0	5.0	0.0
Hemiptera	Recolonizing adults				
Notonectidae <i>Notonecta</i>		0.0	11.3	16.0	97.5
Corixidae		0.0	27.3	14.0	4.8
Diptera	Resistant larvae				
Dixidae		19.0	21.0	0.0	0.0
Chironomidae		0.5	26.3	68.7	1.3
Ephemeroptera					
Baetidae		0.0	0.0	524.0	793.0
TOTAL		316.5	679.0	1163.3	1284.5

Fauna and Dynamics

A total of 17 invertebrate families and 11,318 individuals were collected and counted over the 12 sampling events of this study. Total abundance and family richness of organisms increased from March to May or June each year (Table 1). Crustaceans were more than twice as abundant as aquatic insects in March, while the opposite was generally observed in May and June (Fig. 3). Two macroinvertebrate predator taxa were present in March, while 6 macroinvertebrate predator families were present in June (Fig. 3).

Certain taxa were exclusive to early or late months in the hydroperiod. *Limnephilus* caddisflies were only present in one month (March 2008). The fairy shrimp *Linderiella occidentalis* was only present during March and early April samples (Fig. 3). Dixid flies were also exclusive to March and April samples but were less abundant than *L. occidentalis* in March. Alternatively, baetid mayflies were exclusive to May and June samples, with high abundances in June (>3000 individuals) and making up the majority of the macroinvertebrate abundance at that time

(Table 1). In contrast, only *Cyzicus* clam shrimp were present in every sample, although *Lestes* damselflies occurred in all samples except the earliest March sample in 2008 (Table 2).

The dominant predator taxa varied during the wet season. In March, larval dytiscid beetles were the dominant predator in Hog Lake, representing >90% of the macroinvertebrate predators present. Although dytiscids were dominant in early April samples, representing >80% of the macroinvertebrate predators, *Lestes* damselflies were also observed but in lower numbers. By late April, the relative abundance of *Lestes* increased relative to that of earlier samples and *Lestes* damselflies became the dominant macroinvertebrate predator, followed in relative abundance by dytiscids, libellulid dragonflies, corixid water boatman, and *Notonecta* backswimmers, respectively.

Lestes damselflies continued to be the most abundant predator through the remainder of the hydroperiod. In May, *Notonecta* backswimmers and libellulids were less abundant than *Lestes* but more abundant than all other invertebrate predators. Relatively

Fig. 4. Nonmetric multidimensional scaling ordination (Stress = 0.051, $k = 2$) based on square-root-transformed macroinvertebrate abundances by sampling date and the directional influence of each taxon.

few dytiscids were found in late May. In June, *Lestres* remained the dominant predator, followed by *Notonecta*, libellulids, and dytiscids (Fig. 3).

Amphibians and reptiles were present in and around Hog Lake. Adult California newts, *Taricha torosa*, were observed frequently in December and January during the breeding season (Fig. 3). Eggs from the California newt were present from January through early April. Larvae were first observed in mid-April of each year, indicating emergence was occurring (Fig. 3). Newt larvae were then present at each sampling date until the wetland dried out. In addition, adult Pacific chorus frogs (*Pseudacris regilla*) were observed from January to May (Fig. 3). Eggs from Pacific chorus frogs were found from early to late April, larvae from late March through the end of the hydroperiod (early July), and metamorphs from mid-May through the end of the hydroperiod. Garter snakes (*Thamnophis* sp.) were observed on the shores of Hog Lake and numbers increased as the hydroperiod progressed in 2009. Garter snake observations ranged from 1 to 2 snakes per visit from January to early April 2009, but from 4 to 15 snakes per visit from early April to July 2009.

Community Analysis

Nonmetric multidimensional scaling of macroinvertebrate abundances indicated separation of samples by month in ordination space (Stress < 0.2; Fig. 4). Ordination distance was highly related to observed dissimilarity ($R^2 = 0.982$, linear fit; $R^2 = 0.995$, nonmetric fit). Moreover, samples were arranged in a progression from March to June, which is early to late spring (Fig. 4). In addition, comparisons of invertebrate communities among months using ANOSIM indicated distinct monthly communities ($R = 0.417$, $P = 0.018$).

The separation of March samples can be strongly attributed to the presence of *Limnephilus* caddisflies, *L. occidentalis* fairy shrimp, *Cyzicus* clam shrimp, and members of the fly family Dixidae. May and June samples were closer in space in some years than others, and separation between samples was associated with the abundances of many taxa, including the predators *Lestres*, *Notonecta*, libellulid dragonflies, and coenagrionid dragonflies, as well as baetid mayflies, which are collectors. Although abiotic factors varied by season (Table 1), the best regression model describing the relationship between abiotic factors and NMDS axis 1 included only temperature ($R^2 = 0.55$, $P = 0.006$).

DISCUSSION

Temporal variation in abiotic conditions typically occurs in perennial wetlands (Suren and Lambert 2010) and some lakes (Reid et al. 1995). Life cycles of aquatic organisms must match suitable seasonal conditions, such as temperature or food availability. Freshwater invertebrates in seasonal wetlands must be able to avoid or withstand the environmental conditions associated with the dry season and complete their aquatic life history stages, despite interannual variability in the length and timing of hydroperiods. For those species that avoid the dry season but utilize the wet season, further challenges include synchronizing colonization and emigration to the interannual variability in the hydroperiod length.

Aquatic invertebrates have a diversity of life history strategies that allow them to use temporary habitats, including rapid larval growth and ovarian diapause (Williams 1996, Bohonak and Jenkins 2003). Moreover, oviposition of desiccation-tolerant eggs in the terrestrial environment (Jannot et al. 2008) and desiccation-tolerant early-larval stages are life history characteristics also common in seasonal wetland fauna (Batzner and Wissinger 1996). In Hog Lake, for example, crustaceans are likely characterized by eggs that can tolerate dry habitats, whereas certain aquatic insects may emerge and relocate to nearby perennial habitats as the seasonal wetland dries (e.g., Hemipterans; Macan 1939).

Fairy shrimp and other crustaceans may become established earlier in the hydroperiod because they undergo their full life cycle in temporary aquatic habitat, including as desiccation-resistant eggs during the dry season (Gallagher 1996). Although Hog Lake exists in a Mediterranean climate, the early hydroperiod taxa and life history strategies show similarity to those observed in a pond in southern Ontario, Canada (Williams 1983). The occurrence of the fairy shrimp *L. occidentalis* was a good descriptor for the early-hydroperiod sampling dates in Hog Lake, which is consistent with rapid early-season growth rates and short life-cycle duration also observed in *Chirocephalopsis* fairy shrimp relative to other invertebrates from an intermittent pond in southern Ontario (Williams 1983).

In addition to the crustacean fairy shrimp, the presence of *Limnephilus* caddisflies early

in the successional state of Hog Lake (March 2008), when few other taxa were abundant, suggests that their larval growth occurs in the early months of the hydroperiod and that this taxon may be adapted to an early adult emergence. Occurrences of caddisfly species can vary along gradients of permanence in aquatic habitat (Wissinger et al. 2003, Wiggins 2004) and often have specific traits that reflect those habitats (Zamora-Muñoz and Svensson 1996, Wissinger et al. 1999). *Limnephilus* caddisflies were present early in the hydroperiod and had faster rates of development than many other aquatic insect taxa in temporary wetlands in southern Ontario (*Limnephilus indivisus*) and in the Rocky Mountains of Colorado (*Limnephilus coloradensis*, *Limnephilus picturatus*, and *Limnephilus externus*) (Williams 1983, Wissinger et al. 2003). In montane wetlands, *Limnephilus* caddisflies pupate in sediment (Wissinger et al. 2003), and *Limnephilus* in Hog Lake may employ a similar tactic. If so, that behavior would explain why we found relatively large larvae in March, but no specimens in later months. In addition, records from the Essig Museum of Entomology (University of California, Berkeley) indicate that *Limnephilus nogus* adults were caught in emergence traps at Hog Lake in early May, which suggests an emergence time earlier than the usual drying of the wetland in late June. Despite the fact that aquatic insects differ in evolutionary history compared with crustaceans (Will and Resh 2007) and therefore often demonstrate different life history traits that enable them to use temporary habitats, *Limnephilus* caddisflies, *Cyzicus* clam shrimp, and *L. occidentalis* fairy shrimp were characteristic of the early-season aquatic community.

The peak of larval dytiscid abundance also occurred early in the hydroperiod, in March and April, which suggests faster larval development than other aquatic insects or earlier establishment of dytiscid larvae in Hog Lake. Dytiscids are early colonizers of other seasonal wetlands (Williams 1983), which may be a result of drought- and cold-resistant eggs laid prior to wetland inundation (Nilsson and Söderström 1988), or colonization from perennial habitats (Nilsson and Svensson 1995, Schäfer et al. 2006). Additionally, high dytiscid abundances early in the hydroperiod, but not later, may suggest development and dispersal, or predation by other invertebrate (e.g., *Lestes*)

or vertebrate predators (e.g., newts) present later in the hydroperiod.

Increased abundances in libellulid dragonflies, *Notonecta* backswimmers, and *Lestes* damselflies as the hydroperiod progressed may suggest different abilities to colonize and become established at Hog Lake upon completion of filling, or different developmental or physiological adaptations for using temporary habitats. Previous studies with *Lestes* and *Notonecta* showed strong dispersal abilities and aerial colonization of both permanent and seasonal wetlands (McCauley 2006, 2008, Baines et al. 2015). Life history traits also suggest that both odonates and hemipterans likely rely on recolonization of temporary habitats as adults (Macan 1939, Hinton 1954), while *Limnephilus* caddisflies, fairy shrimp, and clam shrimp likely utilize dessication-resistant eggs and ovarian diapause in habitat close to the temporary wetland (Bishop 1967, Daborn 1971, Wiggins 1973, Williams 2006). Dytiscid beetles may use combinations of these strategies (Nilsson and Söderström 1988, Nilsson and Svensson 1995). In addition, in the intermittent pond in Ontario studied by Williams (1983), libellulid dragonflies and *Lestes* damselflies demonstrated longer aquatic life-cycle duration than *Limnephilus* caddisflies, *Chirocephalus* fairy shrimp, or dytiscid beetles, which would promote later-season habitat use.

Notonecta backswimmers and *Lestes* damselflies may co-occur late in the hydroperiod because they have different foraging behaviors and can therefore feed in different microhabitats. As predators, *Notonecta* and *Lestes* prey on many species of mosquitos (Blaustein et al. 1995) and microcrustacea (Havel et al. 1993), respectively. However, *Notonecta* has been observed to be more successful feeding in open water habitat (Blaustein et al. 1995), while *Lestes* was more successful in littoral habitat (Havel et al. 1993). Though we did not observe emergence events, increasing abundances of *Lestes* and *Notonecta* in May and June suggest later emergence relative to that of *Limnephilus* caddisflies and dytiscid beetles.

Increases in late-season predator abundance could be supported by increased prey density. For example, the surface area and estimated volume of Hog Lake decreased consistently from March to June. As habitat area decreases, organisms are concentrated, which

decreases the distances between predators and prey (Boix et al. 2004, 2012). High abundance of late-season baetid mayflies likely provides an important, high-density food source for the increasing abundances of predators. The narrow temporal window of baetid occurrences in Hog Lake was also similar to that reported by Williams (1983), where baetid mayflies underwent their entire larval stage in 2–3 weeks at the end of the hydroperiod.

Late-season conditions present tradeoffs for aquatic predators. For example, smaller wetland size increases prey density, which should benefit predators (Batzer and Wissinger 1996). In Hog Lake, June samples demonstrated the highest abundance of invertebrates and the smallest wetland surface area. Late in the hydroperiod, however, predator richness also increased, which may increase predation risks for invertebrate predators. In addition, as wetlands approach dryness, predators face an increased risk of not completing their life history, which can result in catastrophic mortality for both vertebrates and invertebrates alike (e.g., Jeffries 1994).

As habitat decreased in Hog Lake, temperature increased. These conditions caused increased metabolism in poikilothermic fauna, such as the macroinvertebrates and newts examined in this study. Temperature is important for seasonal regulation of certain aquatic insect species, including odonates (Corbet 1980). Previous studies indicate that *Lestes*, in particular, may be adapted for the late stages of the hydroperiod. For example, damselfly development can accelerate in response to shrinking habitat (Johansson et al. 2001). Specifically, a *Lestes* damselfly in North Carolina had progressively higher coefficients for growth rates in each successive instar (Lutz 1968, Corbet 2003), suggesting that as temperatures warm, *Lestes* damselflies may be able to increase growth rate and, therefore, develop more quickly when temporary habitats become small and warm.

The presence of amphibians as top predators in seasonal wetlands can influence the composition of the macroinvertebrate community (Wissinger et al. 1999). In Hog Lake, California newts are considered top predators in this study system. The presence of eggs before mid-April, but not after, combined with the presence of larvae in mid-April, but not before, indicates that emergence of newts

occurred in April in Hog Lake. This timing is advantageous for feeding on macroinvertebrates because both the total abundance of macroinvertebrates and the richness of macroinvertebrate families as potential prey had increased from March to April. Not only do newt larvae consume macroinvertebrates, but their chemical cues also affect macroinvertebrate behavior (Bucciarelli and Kats 2015).

The abundance of macroinvertebrates in our samples increased throughout May and June, suggesting that predation of macroinvertebrates by newts did not outpace macroinvertebrate production; however, individual taxa may have been impacted by the emergence of this predator. For example, dytiscid abundance in Hog Lake decreased concurrently with the emergence of newt larvae. Other amphibians, notably tiger salamanders in Arizona and Colorado, prey on limnephiliids and dytiscids as a minor proportion of their diet (Holomuzki and Collins 1987). Moreover, in montane wetlands, tiger salamanders preferentially prey on the most mobile or conspicuous caddisfly (Wissinger et al. 2003) and, therefore, the more mobile predators may be at heightened risk of predation. Finally, predator cues can promote aquatic insects, such as *Notonecta* backswimmers, to disperse at higher rates (McCauley and Rowe 2010), which could indirectly cause changes in the composition of macroinvertebrates in Hog Lake.

Variation in the annual hydroperiod of seasonal wetlands influences the macroinvertebrate community structure because aquatic organisms utilize diverse life history traits related to colonization, development, and reproduction (Jannot et al. 2008, Céréghino et al. 2012, Pérez-Bilbao et al. 2015). Certain life history strategies, such as long development time (e.g., certain trichopterans; Wiggins 1973) or low temperature needs (e.g., certain fairy shrimp) may be particularly vulnerable. Previous studies of Mediterranean-climate temporary wetlands with hydroperiods between 5 and 9 months indicate that hydroperiod length is positively related to invertebrate biodiversity (Waterkeyn et al. 2008). Hog Lake has an approximately 6-month-long hydroperiod, yet it is unknown which taxa would be vulnerable to shorter hydroperiods. Permanent wetlands can serve as source populations for some taxa to colonize seasonal wetlands and even small aquatic habitats can act as

dry-season refuges for other aquatic insect taxa (Strachan et al. 2014) or short-term refuges during intermittent early-season conditions (Strachan et al. 2016). Furthermore, some life history strategies, such as slower larval metabolism during dry seasons in leptocerid caddisflies (Wickson et al. 2012), may provide advantageous flexibility for interannual variability in environmental conditions. Therefore, threats to biodiversity may be specific to certain species and also to certain life history strategies of organisms inhabiting seasonal wetlands.

Increased occurrence of drought or of warmer air temperatures as a result of climate change may impact populations of aquatic insects in seasonal wetlands. While many macroinvertebrates develop more quickly under warmer temperatures, extremes in annual variability of hydroperiod, such as during droughts, may shorten hydroperiods to the exclusion of some taxa (Sim et al. 2013). In Hog Lake, decreased early-season precipitation could delay the initial establishment of aquatic habitat, or warmer air temperature may facilitate earlier drying. Both scenarios would contribute to shorter hydroperiods and longer dry periods, which could inhibit the occurrence or abundances of certain taxa and pose a long-term threat to regional biodiversity.

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