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Flow Management for Hydropower Extirpates Aquatic Insects, Undermining River Food Webs

THEODORE A. KENNEDY, JEFFREY D. MUEHLBAUER, CHARLES B. YACKULIC, DAVID A. LYTLE, SCOTT W. MILLER, KIMBERLY L. DIBBLE, ERIC W. KORTENHOEVEN, ANYA N. METCALFE, COLDEN V. BAXTER

Dams impound the majority of rivers and provide important societal benefits, especially daily water releases that enable on-peak hydroelectricity generation. Such "hydropeaking" is common worldwide, but its downstream impacts remain unclear. We evaluated the response of aquatic insects, a cornerstone of river food webs, to hydropeaking using a life history–hydrodynamic model. Our model predicts that aquatic-insect abundance will depend on a basic life-history trait—adult egg-laying behavior—such that open-water layers will be unaffected by hydropeaking, whereas ecologically important and widespread river-edge layers, such as mayflies, will be extirpated. These predictions are supported by a more-than-2500-sample, citizen-science data set of aquatic insects from the Colorado River in the Grand Canyon and by a survey of insect diversity and hydropeaking intensity across dammed rivers of the Western United States. Our study reveals a hydropeaking-related life history bottleneck that precludes viable populations of many aquatic insects from inhabiting regulated rivers.

Keywords: biodiversity, dams, biological traits, river ecology, citizen science

More than 800,000 dams exist worldwide (Richter and Thomas 2007), and the majority of Earth's rivers are dammed (Nilsson et al. 2005). Such flow management provides numerous societal benefits, including water storage, flood control, and hydropower production (World Commission on Dams 2000). The ecological upshot of all this damming is that rivers are some of the most extensively altered ecosystems on Earth (Carpenter et al. 2011), and flow regimes among large rivers are becoming homogenized as the timing and magnitude of impounded releases are engineered to meet societal needs (Poff et al. 2007). It is widely recognized that dams directly affect population viability for aquatic species by creating a barrier to movement and migration (Kareiva et al. 2000, Dugan et al. 2010). However, far less is known about the specific mechanisms underlying downstream ecological responses to hydrologic flow modification (Bunn and Arthington 2002, Poff and Zimmerman 2010).

Hydroelectricity production is a primary purpose of many dams, particularly the world's largest and most iconic, including the Three Gorges Dam on the Yangtze River in China, the Itaipu Dam on the Paraná River in Brazil and Paraguay, and the Hoover Dam on the Colorado River in the United States (World Commission on Dams 2000). Hydropower provides 19% of the world's electricity supply, far exceeding the generation of all other renewable sources combined (World Commission on Dams 2000, Zarfl et al. 2015). Governments around the world are also planning extensive new development of hydroelectricity potential in response to energy and climate crises (Kao et al. 2014, Zarfl et al. 2015), even though the damming of rivers has substantial environmental costs, including habitat loss, fishery collapse, and biological extinctions (Vörösmarty et al. 2010, Liermann et al. 2012). However, we contend that a key dimension of these environmental costs—and a mechanism underpinning many others—has been overlooked, contributing to an incomplete assessment of environmental trade-offs. As we demonstrate, this cost arises from a hitherto-unrecognized life-history bottleneck that flow management for hydropower production imposes on aquatic insects, ubiquitous organisms that play an essential role in food webs in and along the world's rivers.

Water releases from hydropower dams often vary at hourly timescales in a practice known as *load following* or *hydropeaking* (hereafter *hydropeaking*), whereby river flows are increased during the day when energy demand is high and decreased at night when demand is low (Førsund 2015). Hourly changes in discharge associated with hydropeaking can be substantial, with discharge varying by a factor of 10 or more within a day (Moog 1993, Topping et al. 2003).

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These large hourly changes in discharge produce kinematic waves that can propagate downstream for distances of more than 400 kilometers (km; Wiele and Smith 1996), creating an extensive intertidal zone along river shorelines that is absent from natural rivers and to which freshwater organisms are not adapted (Ward and Stanford 1979, Moog 1993). However, large dams impose multiple stressors on rivers, including altered flow, temperature, and sediment regimes (Poff et al. 2007, Schmidt and Wilcock 2008, Olden and Naiman 2010), and prior studies have struggled to disentangle the effects of hydropeaking from these other stressors (Arthington et al. 2006, Poff and Zimmerman 2010).

Hydropeaking and the artificial intertidal zone it creates have the potential to adversely affect numerous aquatic organisms, but strong deleterious impacts are particularly likely for organisms that rely on nearshore environments during one or more life stages. We selected aquatic insects for our investigation of hydropeaking impacts, because they are ubiquitous in freshwaters and represent the primary prey for myriad species of fish, birds, bats, and other wildlife living in and along rivers (Nakano and Murakami 2001, Baxter et al. 2005). These insect groups—especially mayflies, stoneflies, and caddisflies in the orders Ephemeroptera, Plecoptera, and Trichoptera (hereafter EPT)—are also widely used as bioindicators for rivers and are integral to freshwater regulatory policies in the United States, the European Union, and elsewhere (Fremling 1964, Lenat 1988, Carlisle et al. 2013).

Most aquatic insects have complex life cycles, with a winged adult life stage that is terrestrial whereas the egg, larval, and pupal stages are aquatic. Nonetheless, the vast majority of investigations into aquatic insects have focused on the larval life stages in isolation, whereas other life stages are traditionally ignored. However, this approach is currently undergoing a transformation, because the conditions necessary to support aquatic insects throughout their life cycles (egg, larva, pupa, and adult) are increasingly recognized as crucial to species persistence (Encalada and Peckarsky 2012, Muehlbauer et al. 2014).

The influence of *recruitment* (i.e., the number of eggs that develop into larvae) on population dynamics is poorly studied, particularly in the case of insects. Investigations into factors limiting the diversity or abundance of aquatic-insect assemblages have traditionally focused on studying larval life stages exclusively, because it was thought that the environmental conditions and biological interactions experienced by larvae (i.e., predation and competition) would invariably be the primary determinants of larval abundance. Aquatic insects spend a disproportionate amount of their lives in the larval stage, and adult females can lay hundreds to thousands of eggs, so it seemed unlikely that larval abundance would ever be limited by egg abundance or the environmental conditions experienced by nonlarval stages *per se*. However, several recent studies have called this assumption into question and demonstrate that the abundance of larvae can be strongly influenced by the quality and availability of egg-laying substrates at the start of the cohort (Encalada and Peckarsky 2012, Lancaster and Downes 2014, Macqueen and Downes 2015). In one compelling study, investigators experimentally varied the number of *Baetis* mayfly eggs present in stream reaches by simply manipulating the number of emergent rocks that were present in different pristine streams (Encalada and Peckarsky 2012). Adult *Baetis* females land on these rocks in fast water and then crawl under the rock to cement their eggs to the underside. Nearly a year after the emergent rocks were manipulated, the abundance of late-stage mayfly larvae had doubled in reaches where emergent rocks were added and declined by more than half in reaches where they had been eliminated. Therefore, recruitment dynamics—and the availability or quality of egg-laying substrates specifically—can be a primary determinant of aquatic-insect abundance in streams and rivers.

When viewed through this lens of egg laying and rearing, it becomes apparent that aquatic-insect populations below hydropeaking dams could be especially vulnerable to recruitment limitation. Over the course of a single day, these rivers are subject to large changes in river depth, which may dramatically affect the availability and quality of egg-laying substrates used by aquatic insects. For taxa such as *Baetis* that cement eggs to substrates, for example, a partially submerged rock that is wetted during high water at the time of egg laying could subsequently be exposed to air a few hours later during low water, potentially killing the eggs. Scaling up, acute egg mortality caused by hydropeaking could be capable of regulating aquatic-insect abundance throughout river segments via recruitment limitation and reducing biodiversity by extirpating aquatic insects with river-edge egg-laying behaviors, with attendant consequences for populations of insectivorous wildlife (Nakano and Murakami 2001, Baxter et al. 2005).

Encapsulating all of these insights, assumptions, and inferences, we propose the following novel hypothesis concerning the intersection of hydropeaking and aquatic-insect life history: Hydropeaking limits the recruitment of aquatic insects via acute egg mortality, constraining the abundance and diversity of aquatic-insect populations downstream of hydropeaking dams.

In the remainder of this article, we use multiple lines of evidence to test this novel hypothesis. We first formally test the two key assumptions implicit in this hypothesis: that most insects lay eggs in habitats vulnerable to drying by hydropeaking-induced water-level fluctuations and that drying reduces egg viability. Next, we develop a life history–hydrodynamic model that provides a predictive framework for exploring how different insect groups respond to hydropeaking, contingent on their specific egg-laying strategies. We then test predictions from this model using a large citizen-science data set of emergent insects collected throughout the 400-km-long Grand Canyon segment of the Colorado River. Finally, to investigate the consistency of hydropeaking effects on aquatic-insect assemblages, we compare insect diversity across 16 dammed rivers in the

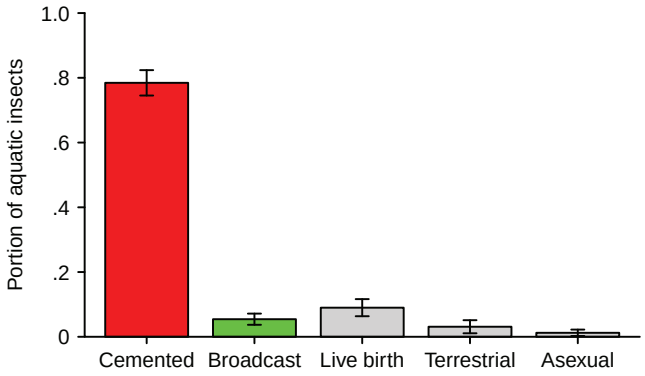

Figure 1. Aquatic insects often cement eggs to substrates along river margins. Represented here are the egg-laying strategies for the most common aquatic invertebrate genera in North America and Europe, representing 96 and 78 taxa, respectively. The error bars represent the standard error of the mean. Adapted with permission from Statzner and Beche 2010.

Western United States that span a range of hydropeaking intensity.

Where do aquatic insects lay their eggs?

One major assumption that is implicit in our recruitment-limitation hypothesis is that many aquatic insects lay eggs along river shorelines. We tested this assumption by drawing on a recent synthesis of biological trait databases (Statzner and Beche 2010). The use of biological traits as indicators has gained momentum as a powerful approach for disentangling the effects of multiple stressors in aquatic ecosystems (Poff et al. 2006), and the development of comprehensive databases of biological traits for aquatic invertebrates is making this approach feasible on a continental scale (e.g., Vieira et al. 2006). For the purposes of evaluating egg-laying traits of aquatic insects, Statzner and Beche (2010) included descriptions for invertebrate genera spanning 96 North American taxa and 78 European taxa.

These insect trait databases provide strong evidence that the majority of aquatic insects exhibit egg-laying behaviors that will be vulnerable to hydropeaking (figure 1). Specifically, more than three-quarters of aquatic insects exhibit the type of cementing behavior shown by females of *Baetis* that were studied in the Encalada and Peckarsky (2012) experiment described earlier. Significantly, this behavior generally requires the presence of substrates that are partially emerged out of the water surface on which females can alight before crawling under water or, alternatively, substrates that are in shallow water that females can swim to for the purposes of attaching their eggs. Both of these classes of substrates are vulnerable to hydropeaking-related flow variation, because partially submerged rocks and shallow habitats at high water can become fully exposed to air and dry out when the water is low. Although some taxa do exhibit egg-laying behaviors that will be unaffected by an artificial intertidal zone—such as species that give birth to live young (ovoviviparous) or broadcast eggs on the water surface—analysis of these traits databases indicates that such strategies are uncommon among aquatic insects (figure 1). Therefore, we conclude that this implicit assumption of our hypothesis is valid and well founded: The majority of insects lay eggs in habitats that are susceptible to drying via daily hydropeaking water-level fluctuations.

Does desiccation reduce egg viability?

In order for hydropeaking to limit aquatic-insect populations via acute egg mortality, desiccation on hydropeaking-relevant timescales must actually kill eggs. We directly tested this assumption by quantifying the viability of eggs that were exposed to brief periods of desiccation that are typical for hydropeaking rivers. Experiments were conducted using the eggs of a widespread genus of mayfly, *Baetis* (Baetidae), and two common, large river caddisfly genera, *Brachycentrus* (Brachycentridae) and *Hydropsyche* (Hydropsychidae). The experiments were conducted using insect eggs collected from the Green River downstream of the Flaming Gorge Dam, Utah, in June (caddisflies) and October (mayflies) of 2015. For caddisflies, egg masses attached to rocks were collected from nearshore habitats and assigned to one of four desiccation treatments: 0 (control), 4, 8, or 12 hours of streamside desiccation (n = 12–20, depending on the experiment and treatment level). Following the completion of each treatment, caddisfly egg masses were scraped from rocks, placed in individual vials, and stored in river water on ice. The treatments were initially conducted during both the day and the night, on the basis of the presumption that hotter air temperatures during the day would result in more rapid desiccation and egg mortality. However, both the day and night desiccation trials experienced extremely high mortality, and the ANOVA tests indicated that there was not a significant difference between day and night treatments (F-statistics = 0.001 and 0.042, and p-values = 0.978 and 0.837 for *Brachycentrus* and *Hydropsyche*, respectively). Therefore, the day and night treatments were combined for the remainder of the analysis, and the subsequent experiments on *Baetis* were conducted during the day only. The mayfly study also was conducted using eggs laid on slate tiles that had been placed throughout the stream rather than by scraping eggs off rocks, because low egg viability in the control groups for the caddisfly experiments indicated that scraping likely induced extraneous mortality. In addition, we added shorter duration treatments of one-half, 1, and 2 hours in the mayfly study to better identify critical desiccation exposure levels and conducted desiccation treatments in a laboratory setting instead of streamside. For both the caddisfly and mayfly experiments, the egg masses were reared at room temperature (23 degrees Celsius) on a 12-hour day–night light cycle for 5 weeks or until egg masses were no longer viable based on visual inspection. Egg viability was computed as the ratio of hatched eggs to the total number of eggs per egg mass.

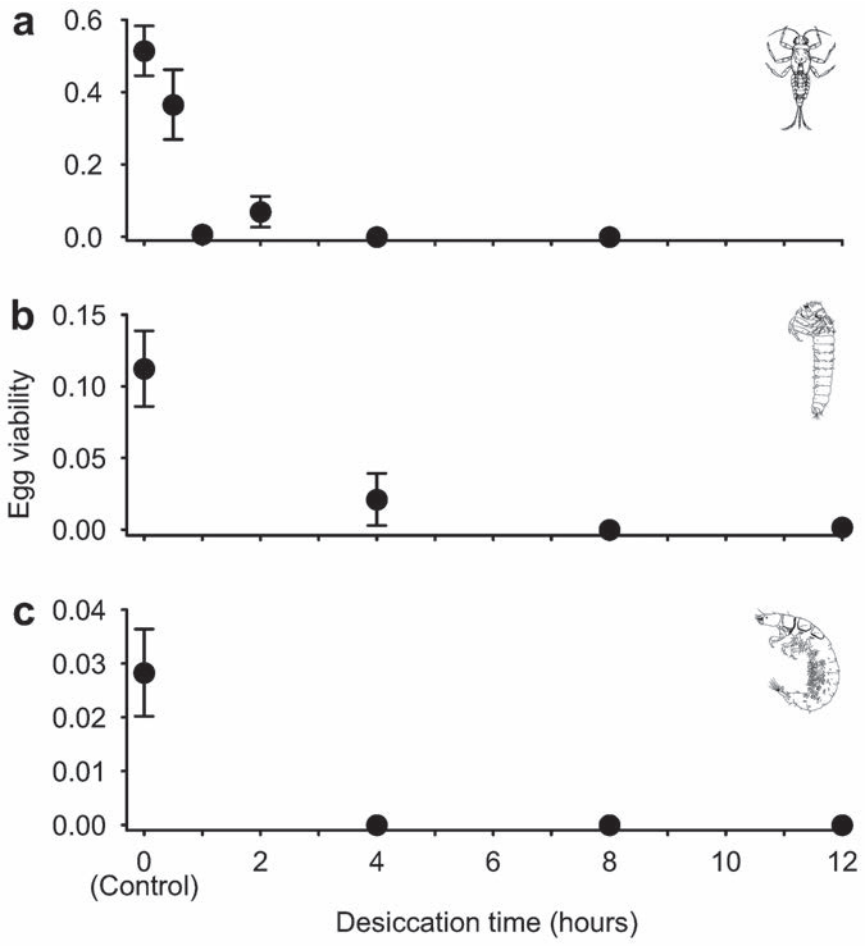

Figure 2. Desiccation causes high mortality of aquatic-insect eggs. Mean egg viability (number of hatched eggs/total eggs) after desiccation for (a) Baetis, (b) Brachycentrus, and (c) Hydropsyche egg masses. The points represent the mean viability of egg masses across 12–20 replicate experiments, depending on the treatment and taxon in question (see the main text for details). The error bars represent the standard error of the mean.

These experiments provide convincing evidence that this assumption is also valid and well founded: Even brief desiccation markedly reduced egg viability (figure 2, ANOVA F-statistics = 21.500, 10.332, and 13.403 for *Baetis*, *Brachycentrus*, and *Hydropsyche*, respectively, and p-statistics < 0.001 for all). We did find that a half-hour of desiccation did not significantly reduce the viability of mayfly egg masses relative to undesiccated, control egg masses (t-statistic = 1.326, p-statistic = 0.099). However, after 1 hour or longer of desiccation, egg viability was significantly reduced for all three taxa compared with the control treatments, based on *post hoc* Tukey's tests. In fact, egg viability in all of these desiccation treatments of 1 hour or longer did not differ significantly from 0 (i.e., total egg mortality), and no eggs hatched from 136 out of 164 (83%) of these treatments. It is worth noting that these treatments represent desiccation exposure for a single day along a hydropeaking river. Because many aquatic-insect eggs take days to weeks to hatch, they are in fact exposed to several cycles of inundation and drying prior to hatching. Therefore, our desiccation experiments should be viewed as conservative; field egg mortality after several such cycles is likely even higher than suggested by our laboratory rearing results. Conducting additional experiments on different aquatic-insect taxa (e.g., Plecoptera, stoneflies, or certain Diptera, true flies) would naturally be insightful and add nuance to the patterns we report here. However, our experiments included three globally common genera spanning two ecologically important aquatic-insect orders, and our results were unequivocal to the extent that they are likely to be broadly representative of other taxa. We therefore conclude that aquatic-insect eggs that are laid in the artificial intertidal zone created by daily hydropeaking will be subject to acute mortality later in the same day, when river stage is lower.

A life-history bottleneck arising from hydropeaking

Building on these egg-laying and desiccation results, we next developed a deterministic model to explore the interplay of hydropeaking waves with egg-laying strategies. Specifically, our model provides a predictive framework for understanding how these variables interact to affect aquatic-insect populations along a hydropeaking river continuum. Lateral (shoreline) inundation due to hydropeaking can be approximated as a sine wave with magnitude h at distance x downstream from a dam as follows:

$$h(x) = \frac{(h_{\max} + h_{\min\square})}{2} + \frac{(h_{\max} - h_{\min\square})}{2} * \cos(f * x) \quad (1)$$

where f determines the frequency of the wave, $h_{\max}$ is the maximum extent of lateral inundation, and $h_{\min}$ is the minimum extent of lateral inundation. As the sine wave propagates downstream, $h(x)$ describes the degree of hydropeaking inundation that occurs on a given river segment at dusk, when most insect taxa are assumed to be laying their eggs (Pinder 1995, Merritt et al. 2008). Therefore, $h(x)$ is an index of how severely hydropeaking affects recently deposited eggs at any location along the river. At locations with high values of h, eggs are laid when the river reach is at its daily high-flow peak, and deposited eggs will therefore be vulnerable to desiccation-induced mortality at low flow later that day and at the same time on each subsequent day.

In contrast, when $h(x) = 0$, the river is at low flow during the time of egg laying, so newly deposited eggs will never be subjected to any flows lower than those present during egg laying, and these eggs will never be subject to desiccation.

We assumed a trade-off between per-egg survival (s) and egg-laying location relative to the river edge ($0 \leq r \leq 1$), such that eggs cemented to substrates along river edges experience the highest relative survival in the absence of hydropeaking:

$$s(r) = e^{-r*c} \tag{2}$$

where c controls the steepness of the relationship. Such a trade-off occurs if shallow edge habitats provide more favorable rearing conditions for eggs (e.g., slower water that will allow river-edge specialists to cement eggs directly on suitable substrates) relative to midchannel habitats (e.g., only open-water generalists that dip eggs directly into the water are able to use these habitats for egg laying, and many of these eggs may settle on unsuitable substrates). Note that r is measured relative to the river edge (i.e., the river edge occurs at $r = 0$ and river center at $r = 1$), and this will change in response to hydropeaking. Therefore, exclusive of any hydropeaking effects, maximum total egg survival, w_{max}, in a river reach is given by the area under equation 2 bounded by the portion of the river cross-section used for egg laying (r_1 to r_2), which is a species-specific quantity:

$$w_{max} = \int_{r_1}^{r_2} e^{-r*c} dr_{max} \tag{3}$$

Although any egg-laying strategy is possible, we consider the case where each insect species uses a characteristic portion of the river with respect to the river's edge, and for simplicity, we treat the width of this proportion ($r_2 - r_1$) as constant. For example, river-edge specialists might lay eggs uniformly over the interval [0, 0.2] very near the shoreline, whereas open-water generalists might lay eggs uniformly in the thalweg [0.8, 1]. Under equation 3, the eggs of river-edge specialists will always have the highest potential survival (w_{max}) relative to other egg-laying strategies, but hydropeaking may strand some or all of the eggs deposited at a particular location such that the realized survival (w) is lower than w_{max}. The survival of eggs deposited within the zone affected by hydropeaking will be reduced by w_{hydro}, the portion of the egg-laying zone that is lost to desiccation:

$$w = w_{max} - w_{hydro} \tag{4}$$

$$\text{If } r_1 < h(k) < r_2,\ w_{hydro} = \int_{r_1}^{h(k)} e^{-rc} dr \tag{5}$$

$$\text{If } h(k) < r_1,\ w_{hydro} = \int_{r_1}^{r_1} e^{-rc} dr = 0 \tag{6}$$

$$\text{If } h(k) < r_2,\ w_{hydro} = \int_{r_1}^{r_2} e^{-rc} dr = w_{max} \tag{7}$$

In equation 5, only part of the egg-laying zone is lost because of hydropeaking, with concomitant effects for population level egg survival. In contrast, equations 6 and 7 describe scenarios in which none or all of the egg-laying zone, respectively, is lost.

Our life history–hydrodynamic model predicts that desiccation-induced egg mortality will extirpate river-edge egg layers from hydropeaking rivers (figure 3), particularly mayflies and other EPT taxa that cement eggs to substrates at the river margin or other zones subject to exposure under daily low hydropeaking flows (Statzner and Beche 2010, Encalada and Peckarsky 2012). In contrast, open-water egg layers, such as some blackfly species (e.g., *Simulium arcticum*; Adler et al. 2004), will be minimally affected by hydropeaking (figure 3). These divergent egg-laying strategies represent an example of a classic life-history trade-off that may even provide a basis for why EPT taxa are useful as bioindicators in the first place: Eggs laid by such river-edge specialists are likely to experience high survival when conditions remain ideal but are susceptible to complete mortality from environmental perturbations that cause conditions to suddenly change (e.g., shoreline desiccation). On the other end of the spectrum, eggs broadcast on the water surface by open-water generalists are likely to always experience relatively high mortality because many eggs will settle on unsuitable substrates; nonetheless, some eggs will just as invariably settle on ideal substrates. Finally, some taxa, such as midges (Chironomidae), exhibit an intermediate strategy. Taken as a group, midges lay their eggs generically along shorelines in a fashion that is neither strictly dependent on emergent rocks and vegetation nor broadcasting over open water (Pinder 1995). Specifically, most adult female midges tend to cement eggs to substrates, but some broadcast eggs freely (Williams 1982, Pinder 1995). Furthermore, when eggs are cemented, midge behavior differs from that of EPT taxa such as *Baetis* in that midges land at or on the water surface to release their eggs from their abdomen and do not actually crawl under water (Branch 1928, Pinder 1995). During this time between egg laying and cementing, many eggs are lost to open water; indeed, egg drift due to this behavior is substantial and has been estimated at 4000 eggs per hour per square meter through a river cross-section (Williams 1982). For intermediate strategists such as these midges, the model predicts a spatial periodicity in abundance that correlates with the timing of daily hydropeaking waves. Specifically, population abundance should be greatest in river reaches where the lowest daily flow occurs coincident with the peak timing of egg laying, because eggs laid in these locations will remain wetted and will never be subject to desiccation, but these insects should also be found at low abundance throughout the river.

Insect abundance and diversity along a hydropeaking river continuum

We parameterized our life history–hydrodynamic model for the specific conditions present along the Colorado River downstream from the Glen Canyon Dam in the Grand

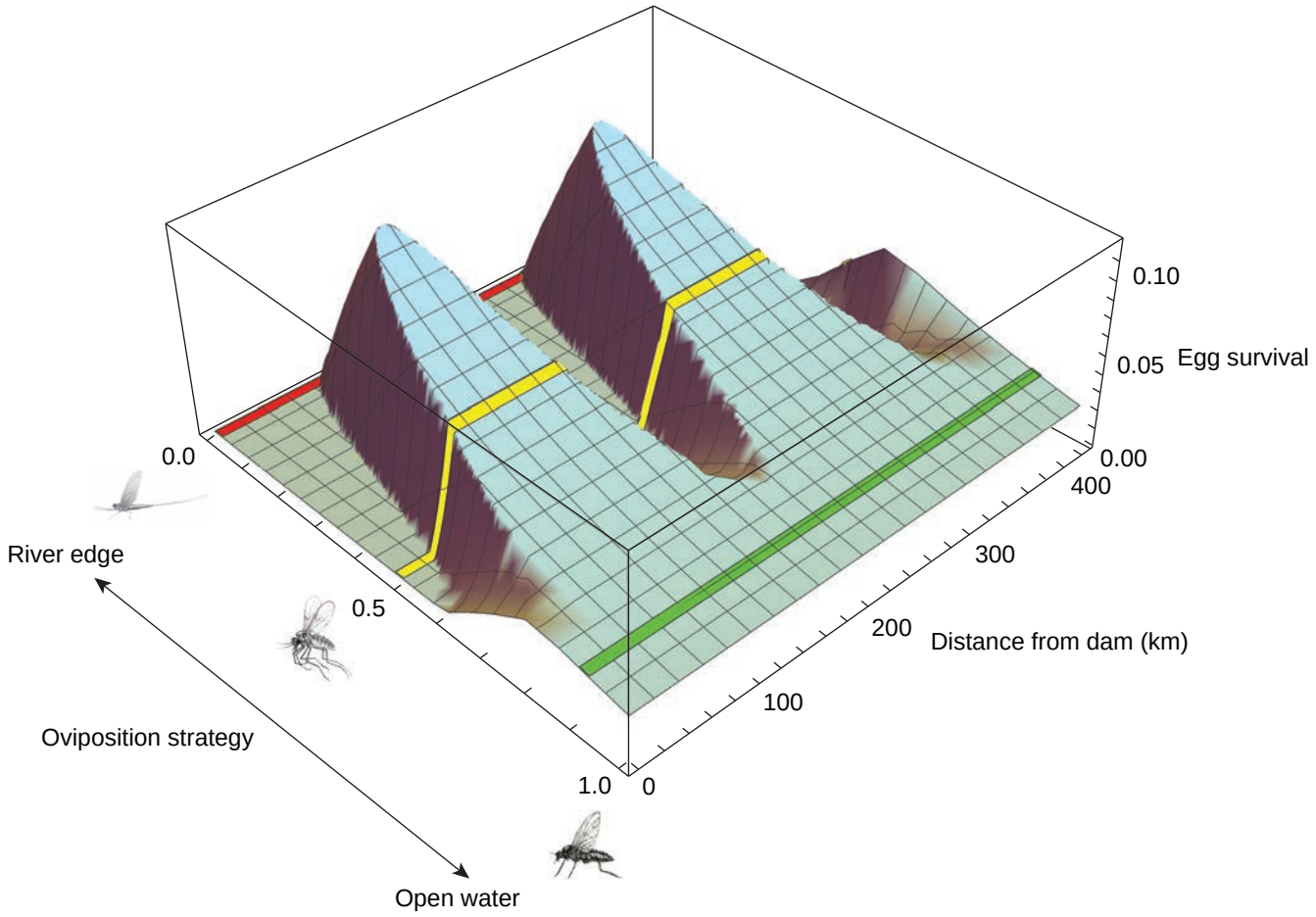

Figure 3. A life history–hydrodynamic model. Output from a life history–hydrodynamic model parameterized for the Colorado River in the Grand Canyon shows that as hydropeaking waves propagate downstream, the locations where daily flow minima occur at dusk are consistently located around river kilometer (km) 100 and 275. River-edge egg layers, such as mayflies (red line), are eliminated from hydropeaking rivers because of desiccation and the mortality of eggs. Open-water egg layers, such as* Simulium arcticum *(blackflies; green line) occur at all points along hydropeaking rivers. Intermediate strategists, such as midges (yellow line), exhibit spatial periodicity in abundance, with the highest abundance at locations where the timing of insect egg laying, generally at dusk, is in phase with daily flow minima. This figure illustrates equation 7, assuming $r_2 - r_1 = 0.2$, $c = 2$, *and* $f = 0.033$ *(see the main text for details).*

Canyon, United States. Because of its canyon-bound setting and the absence of large tributaries, the daily hydropeaking wave released from the Glen Canyon Dam propagates far downstream, with hourly changes of 1 meter in river stage still present more than 400 km downstream, where the Colorado River enters its next reservoir, Lake Mead (Wiele and Smith 1996). This makes the Colorado River in the Grand Canyon an ideal case study because there is a wide range of variation in the degree of synchrony between the timing of egg laying (i.e., dusk) and the timing of minimum flows. Sampling along this remote segment of the Colorado River nonetheless presents logistical challenges, because most reaches are only accessible by two-week-long rafting trips. Therefore, to quantify aquatic-insect abundance throughout the Grand Canyon, we collaborated with river rafters to sample the adult life stage of aquatic insects, the abundance of which is directly related to larval abundance (Statzner and Resh 1993). Each evening in camp, these citizen scientists deployed fluorescent light traps for 1 hour near the river's edge, ultimately collecting more than 2500 samples (see box 1, figure 4, and Acknowledgments).

We recruited citizen scientists to the project using an outreach video and through advertisement in Grand Canyon rafting publications (see box 1). Citizen-science light trapping occurred from April to October in 2012, 2013, and 2014. Each light trap consisted of a small plastic storage container and a fluorescent light that was placed along the short edge of the container (figure 4). Citizen scientists were provided with a table of sunset times to facilitate the consistent timing of trap deployment and were instructed to turn on light traps within 1 hour after nautical sunset. At the start of each deployment, citizen scientists poured the contents

Box 1. Little bugs, big data, and the Grand Canyon: The role of citizen science in Colorado River adaptive management.

The closure of the Glen Canyon Dam in 1963 fundamentally altered the physical template of the 400-kilometer-long segment of the Colorado River in the Glen, Marble, and Grand Canyons (Schmidt et al. 1998). For instance, water clarity is considerably higher because Lake Powell reservoir traps millions of tons of sediment and organic matter annually (Topping et al. 2000), hypolimnetic releases lead to relatively cold and constant water temperatures (Voichick and Wright 2007), and flow management dampens the annual low and high flow periods, whereas hydropeaking greatly increases hourly flow variation (Topping et al. 2003). These changes in the physical template, along with accidental and intentional introductions of organisms (Blinn and Cole 1991), have completely restructured aquatic food webs (Cross et al. 2013) and led to declines and local extirpations of native, endangered fish populations (Minckley 1991). Ongoing adaptive management of the Glen Canyon Dam releases seeks to rehabilitate the Grand Canyon ecosystem and benefit key resources, including native and desired nonnative fish populations (*www.gcdamp.gov*).

Science plays an essential role in the adaptive management of the Glen Canyon Dam, but it has proven challenging for professional scientists to collect the type of high-resolution data needed to inform the management of this highly altered and remote ecosystem. Specifically, most reaches of the Colorado River are only accessible by two-week-long river trips that travel the entire 400-kilometer-long segment, which greatly limits the spatial and temporal extent of sampling regimens. However, starting in the early 2000s, physical scientists began using automated sensors to continuously monitor suspended sediment concentration and, for the first time, demonstrated a clear link between hydropeaking operations, sediment transport, and the erosion of beaches in the Grand Canyon (Topping et al. 2004, Wright et al. 2008). More recently, the continuous measurement of ecosystem metabolism using dissolved oxygen monitors revealed that hydropeaking operations have a significant, albeit minor, effect on algae production in the Grand Canyon (Hall et al. 2015). Any similar solutions to the continuous monitoring of animal populations using sensors have proven elusive, however, so river trips staffed by professional scientists have remained the primary tool for investigations into animal population dynamics. However, testing predictions of our life history–hydrodynamic model using traditional benthic surveys of larval insects would have required dozens of such river trips through the Grand Canyon at a cost of millions of dollars.

The involvement of citizen scientists, whereby members of the public conducted standardized light trapping of adult aquatic insects, played a vital role in overcoming these logistical challenges (figure 4). Unlike many citizen-science projects, we elected to pay the participants on a per-sample basis to ensure high-quality data and continued involvement by professional river guides. Even with the $15-per-sample cost, this approach has proven to be extremely cost effective, which is an important consideration in the development of long-term monitoring programs. Somewhat unexpectedly, the broader impacts of this project have also been especially significant. For instance, our citizen-science monitoring project has proven to be a powerful tool for outreach and overall engagement with the public (*www.gcmrc.gov*). In addition, collaboration with Grand Canyon Youth (*www.gcyouth.org*) and other education groups has provided a unique opportunity to train the next generation of scientists about the scientific process and the important role that science plays in adaptive ecosystem management.

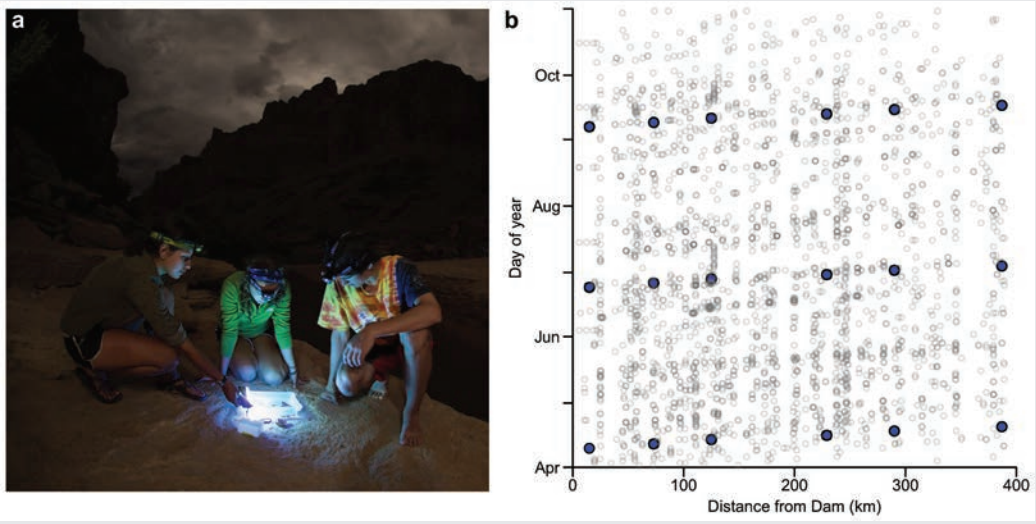

Figure 4. Citizen science in the Grand Canyon. Professional river guides, private boaters, educational groups, and other citizen scientists rafting the Colorado River in the Grand Canyon deployed light traps each night in camp between 2012 and 2014 (a); a Grand Canyon Youth river trip pictured (photo courtesy Freshwaters Illustrated/Dave Herasimtschuk), ultimately producing a data set of more than 2500 adult aquatic-insect samples (b). The spatial and temporal coverage of the citizen-science-derived data set (open black circles) far exceeds the scope of invertebrate sample data sets that can be collected using river trips staffed by professional scientists (e.g., blue filled circles, which represent the invertebrate sampling effort described in Cross et al. 2013). Abbreviation: km, kilometers.

Table 1. ΔBIC table comparing various univariate models for the three dominant insect taxa collected in the Grand Canyon light trap samples.

Model	Microcaddisflies	Blackflies	Midges
Base model (temporal and spatial random effects)	52.9	11.9	27.4
River slope	60.7	15.5	29.0
Distance from dam	26.2	**0.0**	32.2
Distance from tributaries	**0.0**	17.6	30.8
Hydropeaking waves	60.5	16.2	**0.0**

Note: The best-performing model for each taxa is underlined and bold. The multivariate models containing combinations of these variables are included in table S1; the univariate models listed here highlight the main driver of abundance for each taxon.

of a 250-milliter bottle pre-filled with 95% ethanol into the plastic container and turned on the light. After one hour, lights were turned off, and the contents were poured back into the 250-milliliter bottle for storage.

Three taxonomic groups were collected in sufficient numbers by citizen scientists to allow analysis: microcaddisflies in the family Hydroptilidae, blackflies (*Simulium arcticum*), and midges in the family Chironomidae. The abundance data for these taxa were fit to a series of mixed-effects models representing different hypothesized controls on spatial patterns. We had anticipated *a priori* that there would be a high degree of heterogeneity in these count data and that many samples would contain very few or no individuals; therefore, we used a negative binomial distribution for all models. Preliminary information content analysis indicated that a base model including random effects for both sample month of year (i.e., time) and sample location within the 12 distinct geomorphic reaches within the Grand Canyon (i.e., space; Schmidt and Graf 1990) was strongly preferred over other candidate base models containing only one of these random effects. Therefore, the base model with both random effects was used in all subsequent analysis. We then fit different models representing competing hypotheses for each taxonomic group, each consisting of the base model plus fixed effects for river surface slope, river kilometer, distance from a tributary, and hydropeaking wave phase, considered either alone or in combination. The river surface slope variable essentially differentiates rapids and other high-energy environments from low-energy environments such as pools, reflecting numerous empirical studies from the Grand Canyon that have found higher invertebrate abundance in higher-energy habitats (Cross et al. 2013). Information on slope is derived from a comprehensive LIDAR data set representing over 2700 individuals measurements throughout the Grand Canyon (Magirl et al. 2005). Similarly, the river-kilometer variable functions as a proxy for environmental variables that vary as a function of distance from the dam, such as water temperature and turbidity. The model with distance from a tributary was considered on the basis of the possibility that taxa reared in tributaries may disperse as adults and appear in light traps set along the mainstem Colorado River, potentially inflating abundance estimates near these confluences. This model was based on the absolute distance between the trap and the nearest tributary with a baseflow of more than 1 cubic meter per second. Finally, the model with hydropeaking wave phase accounted for the difference in discharge at dusk (4 p.m.) relative to the daily minimum discharge for a given sample location; note that the low light conditions of dusk occur early in the Grand Canyon owing to shading by canyon walls (Yard et al. 2005). This variable reflected the likelihood that eggs laid along shorelines at dusk would be subsequently dewatered and subject to desiccation. Models were fit in R (version x64 3.1.2) using the glmmADMB package and compared using the Bayesian information criterion (BIC). Models with $\Delta BIC > 4$ have very little statistical support with respect to the best model (Burnham and Anderson 2002).

Spatial variation in aquatic-insect abundance throughout the Grand Canyon closely matched predictions from our life history–hydrodynamic model, with variation among taxa being primarily related to egg-laying strategy. For instance, river-edge egg-laying specialists were exceedingly rare throughout the Grand Canyon, with only microcaddisflies—and no mayflies or stoneflies—present in sufficient abundance to analyze statistically (table 1, supplemental table S1, supplemental figure S1). Benthic larval surveys conducted over the past 30 years have also noted that EPT taxa are conspicuously absent from the Grand Canyon (Stevens et al. 1997, Cross et al. 2013), indicating that the scarcity of EPT taxa in light trap samples is not an artifact of our sampling methods. The abundance of microcaddisflies was generally low throughout the Grand Canyon and declined precipitously with distance from tributaries. As such, the distance from the tributary variable was by far the most important in improving the performance of microcaddisfly statistical models (table 1). Light traps that were proximate to tributaries (i.e., less than 1 km) sometimes captured thousands of microcaddisflies, whereas traps that were distant from tributaries (i.e., more than 20 km) never caught more than 300 microcaddisflies. This suggests that microcaddisflies are not well established in the mainstem Colorado River and that the majority of adult microcaddisflies captured in light traps actually dispersed from tributaries that do support diverse aquatic-insect populations (Oberlin et al. 1999). Therefore, citizen-science data indicate that taxa with river-edge egg-laying behaviors have been largely extirpated from the Grand Canyon and that extant

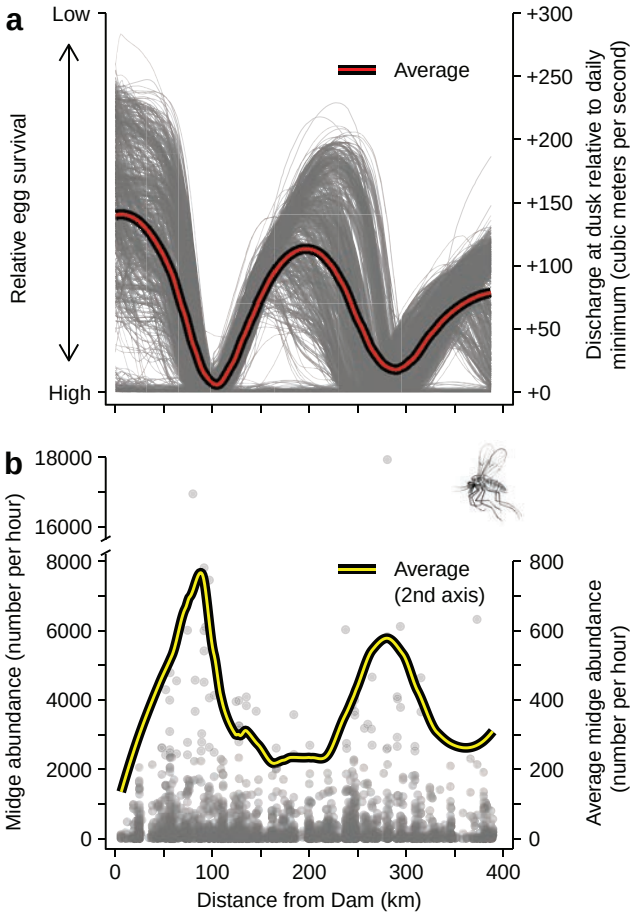

Figure 5. Spatial periodicity in insect abundance along a river continuum. Hydropeaking waves released from the Glen Canyon Dam propagate downstream through the Colorado River in the Grand Canyon, and the survival of insect eggs will be highest at locations where daily flow minima occur at dusk, approximately 100 and 275 kilometers (km) downstream from the Dam (a). Midge abundance exhibits spatial periodicity because of variability in egg survival, with average abundance more than three times greater at locations where the daily flow minima was in phase with peak egg-laying activity (b).

populations of microcaddisflies are strongly tied to the presence of individuals originating from tributary streams.

The open-water generalist blackfly *Simulium arcticum* was present throughout the Grand Canyon, and as predicted, there was not statistical support for a hydropeaking effect or any association with tributaries (table 1, table S1, figure S1). The best-supported model included a fixed effect for distance from the dam with a negative coefficient, indicating a general downstream decline in blackfly abundance. Prior investigations of invertebrate feeding habits in the Grand Canyon demonstrate that the quality of suspended organic matter consumed by filter feeding blackflies declines with distance downstream (Wellard Kelly et al. 2013), and it therefore seems likely that blackfly abundance is reflective of this gradient.

Also as predicted, midges, as intermediate strategists, exhibited strong spatial periodicity in abundance that was related to the timing of hydropeaking waves; the best overall model was univariate and included only the fixed effect related to the timing of hydropeaking waves (figure 5, table 1, table S1). In fact, locations where the daily flow minimum occurred at dusk when most midges lay their eggs (Pinder 1995) had a threefold greater abundance relative to locations where the timing of midge egg laying was out of phase with daily tides (figure 5). Therefore, empirical citizen-science data from the 400-km-long Grand Canyon segment of the Colorado River are consistent with the hypothesis that hydropeaking waves control the abundance and diversity of aquatic insects via egg mortality, and these effects are contingent on the egg-laying strategies of individual taxa.

Hydropeaking as a lever on insect diversity throughout the American West

In addition, we tested predictions of our life history–hydrodynamic model by comparing insect diversity among large, dammed rivers in the Western United States that vary in the degree of hydropeaking. For this test, we quantified the degree of hydropeaking across rivers using a hydropeaking index: the daily coefficient of variation in discharge averaged over 5 or more years (Dibble et al. 2015). We obtained subdaily (15–, 30–, and 60-minute) discharge data and available raw benthic invertebrate data from government agency databases, hydroelectricity companies, private consulting firms, universities, and individual scientists (see supplemental table S2). We used EPT percent abundance—computed as the mean of all available benthic samples across years—as our metric for assessing insect diversity. EPT percent abundance is widely used in river bioassessment investigations (Carlisle et al. 2013), and our use of it in this analysis is in line with earlier discussion about the propensity of these taxa to cement eggs on shallow substrates that are vulnerable to hydropeaking desiccation (Statzner and Beche 2010). To ensure that the data set contained only high-quality data that were comparable in terms of collection methods, sampling effort, and spatial context, the suite of available raw data was subset to include only benthic data (i.e., no water column drift samples), only dams with at least three discrete samples, and only samples collected within 50 km downstream of the dam. This resulted in a final data set of 1267 samples across 16 dams, 14 rivers, and 9 states throughout the Western United States (see table S2).

We found that aquatic-insect diversity was strongly and negatively related to the degree of hydropeaking across the 16 rivers for which adequate data were available (figure 6). Notably, this decline in diversity proceeded according to a logistic function (supplemental table S3), such that there was little association between insect diversity and hydropeaking index values less than 0.10. This indicates that diverse assemblages of aquatic insects can still persist in heavily altered, dammed rivers, so long as they lack large, artificial tides. At hydropeaking index values greater than

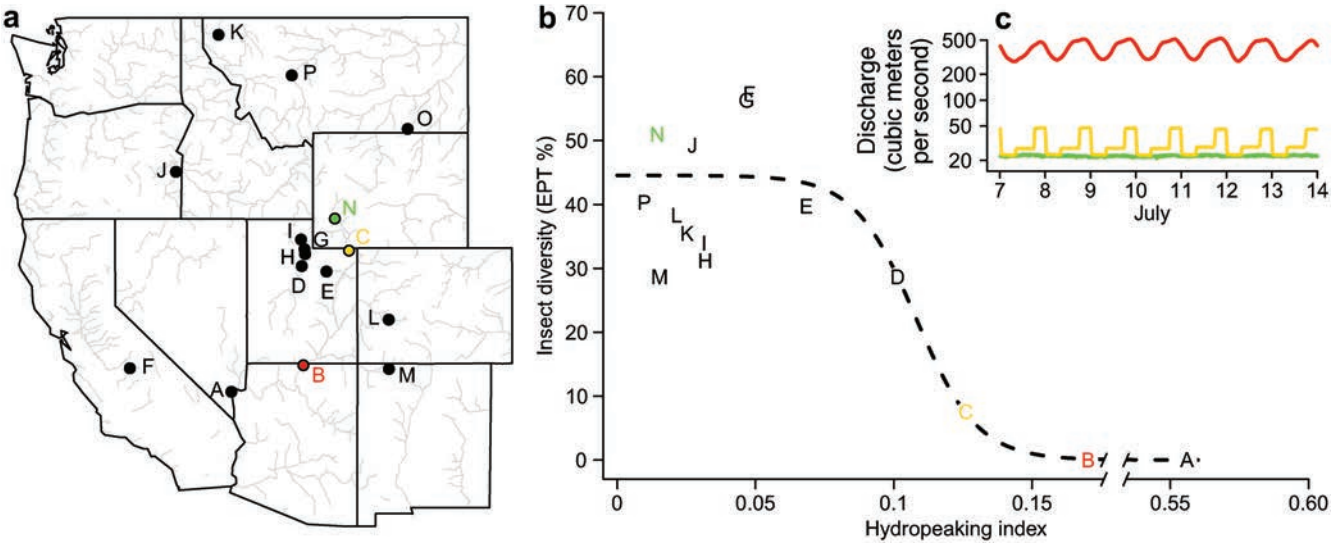

Figure 6. Hydropeaking is a lever on aquatic-insect diversity. We gathered available invertebrate data from dammed rivers throughout the Western United States (a). Insect diversity was strongly and negatively related to the degree of hydropeaking across the 16 rivers for which adequate data were available (b); the relative abundance of insect orders Ephemeroptera (mayflies), Plecoptera (stoneflies), and Trichoptera (caddisflies; EPT percent, y-axis) is a widely used aquatic-insect diversity metric. Inset (c) shows the discharge over a week in July 2013 for three well-studied river segments: the Green River below the Fontenelle Dam (green, low hydropeaking index value), the Green River below the Flaming Gorge Dam (yellow, moderate hydropeaking index value), and the Colorado River below the Glen Canyon Dam (red, high hydropeaking index value; note the log y-axis). Key to dams and rivers: A, the Hoover Dam, Colorado River; B, the Glen Canyon Dam, Colorado River; C, the Flaming Gorge Dam, Green River; D, the Deer Creek Dam, Lower Provo River; E, the Starvation Dam, Strawberry River; F, the Pine Flat Dam, Kings River; G, the Echo Dam, Weber River; H, the Wanship Dam, Weber River; I, the Causey Dam, S. Fork Ogden River; J, the Owyhee Dam, Owyhee River; K, the Libby Dam, Kootenai River; L, the Crystal Dam, Gunnison River; M, the Navajo Dam, San Juan River; N, the Fontenelle Dam, Green River; O, the Tongue River Dam, Tongue River; (p) the Holter Dam, Missouri River. See supplemental tables S2 and S3 for details.

0.10, however, insect diversity declined rapidly and eventually approached zero. In fact, downstream of both the Hoover and Glen Canyon Dams, which had the two largest hydropeaking values in our data set, few to no mayflies, stoneflies, or caddisflies were present. We also compared candidate models containing other variables that might affect insect diversity downstream of dams for which data could be compiled: dam height (a proxy for downstream water quality including temperature) and channel width (a proxy for ecosystem size). The univariate model containing only the hydropeaking index performed better than univariate or multivariate models containing these other variables. Therefore, strong agreement between predictions of our life history–hydrodynamic model and two large validation data sets implicate hydropeaking as a primary factor limiting aquatic-insect diversity and abundance in dammed rivers.

Hydropeaking and the specter of multiple stressors

It is widely recognized that flow, temperature, and sediment alterations associated with river regulation can lead to invertebrate assemblages that are ecologically unhealthy (Arthington et al. 2006). Specifically, insect diversity and richness are often low downstream of dams, and invertebrate assemblages are often dominated by noninsects such as worms, snails, and amphipod crustaceans (Vinson 2001, Cross et al. 2011, Robinson 2012). However, the virtual absence of mayflies, stoneflies, and caddisflies in the Colorado River downstream of the Glen Canyon and Hoover Dams is unusual even relative to other dammed rivers in the region (figure 7). One possible explanation for the low diversity of aquatic insects in the mainstem Colorado River may be that invertebrate assemblages have never been diverse, even before the construction of these dams. The physical template of the unregulated Colorado River did have a dramatic disturbance regime with many distinctive characteristics that may have made life difficult for aquatic insects (Resh et al. 1988), including large snowmelt floods, extremely high suspended sediment concentrations, and low water clarity (Schmidt and Grams 2011). However, the Green and Colorado Rivers located near or within the Cataract Canyon, approximately 200 km upriver of the Glen Canyon Dam, maintain similar characteristics to the unimpounded Colorado River, and the invertebrate assemblage of these reaches is dominated by EPT taxa, including 16 genera of mayflies, 7 genera of stoneflies, and 7 genera of caddisflies (Haden et al. 2003). Tributaries in the Grand Canyon

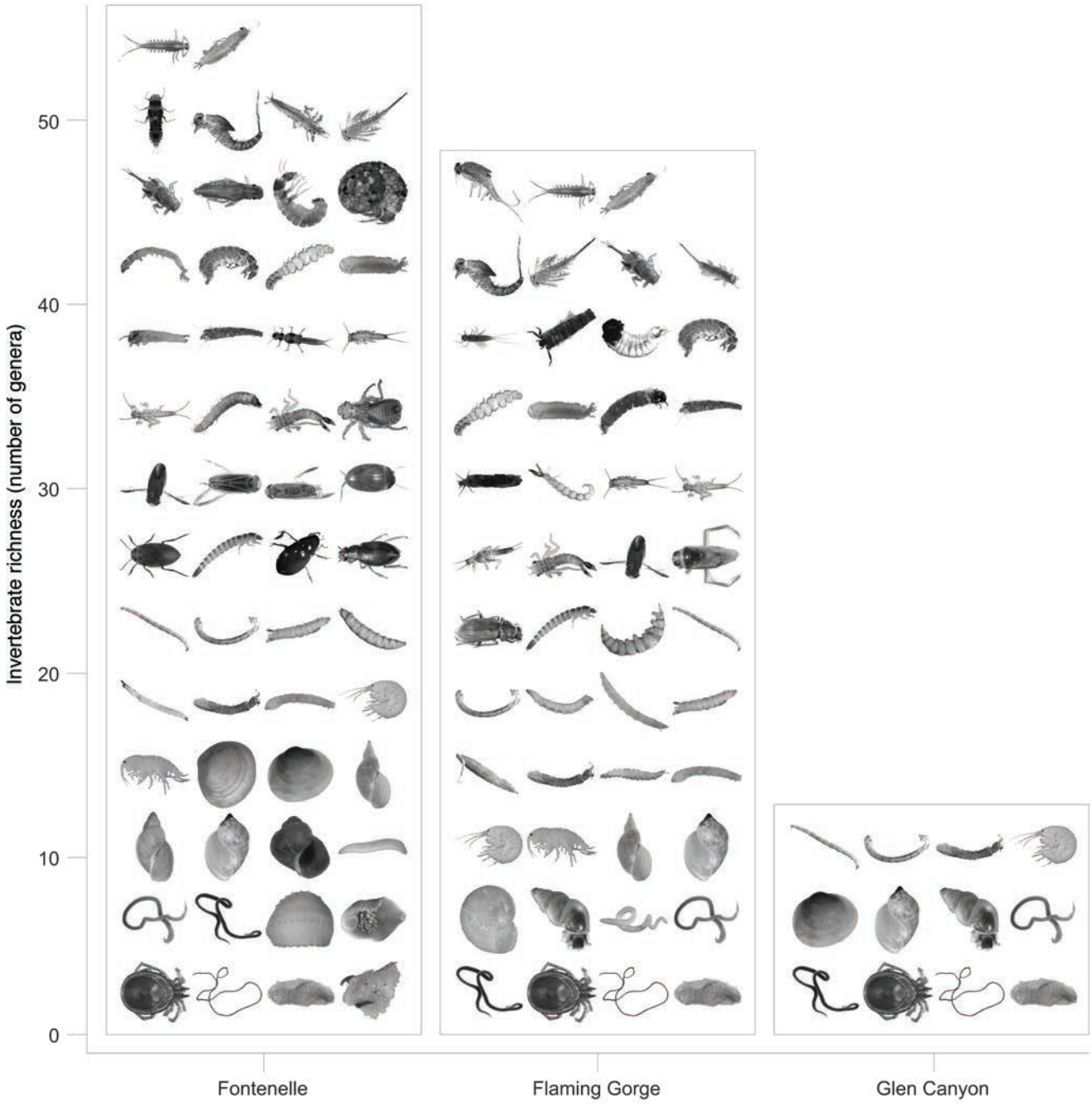

Figure 7. Noninsects dominate below hydropeaking dams. A photo collage showing genus-level invertebrate richness for three well-studied Western US rivers. The Green River below the Fontenelle Dam (left) has a low hydropeaking index value, and invertebrate assemblages comprise 54 unique genera, including many insects. The Green River below the Flaming Gorge Dam (middle) has a moderate hydropeaking index value and contains 47 unique invertebrate genera. The Colorado River below the Glen Canyon Dam (right) has a high hydropeaking index value and supports only 12 unique invertebrate genera, most of which are noninsects. See supplemental table S4 for a list of genera.

segment of the Colorado River between the Glen Canyon and Hoover Dams also support diverse invertebrate assemblages that include many species of mayflies, stoneflies, and caddisflies (Oberlin et al. 1999, Whiting et al. 2014). It therefore seems probable that EPT taxa were extirpated from these regulated segments of the mainstem Colorado River and that some stressors exist that prevent these insect groups from recolonizing the river.

Decreases in river temperature due to cold, stenothermic releases from large dams are often considered to be

the dominant driver of invertebrate community assembly in tailwaters (Olden and Naiman 2010), including for the Colorado River ecosystem downstream of the Glen Canyon Dam (Stevens et al. 1997). However, this thermal-alteration hypothesis alone cannot adequately explain why taxa from cool-water tributaries do not colonize these hydropeaking river segments. In the Colorado River in the Grand Canyon, for example, the Tapeats Creek inflow closely approximates temperatures in the mainstem (see supplemental figure S2). In spite of this thermal similarity, the 11 EPT taxa present in the Tapeats Creek (Oberlin et al. 1999) have not colonized the mainstem in the decades since completion of the Glen Canyon Dam. However, the Tapeats Creek also happens to be located at river kilometer 240, situating it at a segment of the mainstem river where daily flows are elevated at dusk (figure 5), thereby making it an unlikely source of colonists from the perspective of hydropeaking wave-induced egg mortality.

Using multiple lines of evidence, we have demonstrated that hydropeaking represents a significant stressor that is capable of constraining both the abundance and diversity of aquatic insects via egg mortality. Although interactions among stressors have undoubtedly played a role in extirpating aquatic insects from these segments (e.g., flow and temperature; Olden and Naiman 2010, Statzner and Beche 2010), managers have limited ability to mitigate many stressors. For example, the high cost (more than $200 million) and risks (i.e., invasion by warm-water nonnatives fishes) associated with the installation of a temperature-control device on the Glen Canyon Dam render the restoration of Colorado River temperature regimes improbable. Each of the stressors that large dams impose on rivers likely represents an environmental filter that limits invertebrate populations to some extent (Poff 1997, Statzner and Beche 2010), and cumulatively, all of the stressors that the Glen Canyon and Hoover Dams impose on the Colorado River are responsible for the extremely low insect diversity and productivity conditions we observed. Nonetheless, identifying the specific life-history bottleneck that hydropeaking imposes on aquatic insects represents an important step toward understanding how to potentially improve the health of invertebrate assemblages downstream of hydropeaking dams along the Colorado River and throughout the world.

Ecosystem consequences of biodiversity loss and a path forward

Although some may argue about the extent to which aquatic insects have value or importance in their own right, in practical terms, unhealthy aquatic invertebrate assemblages do have tangible negative impacts on wildlife populations that are universally valued by society (figure 8). For instance, recent food-web and bioenergetics studies demonstrate that in the popular Lees Ferry sport fishery downstream of the Glen Canyon Dam, the maximum size and growth of rainbow trout are limited by the abundance and overall small size of their invertebrate prey (Cross et al. 2011, Dodrill et al. 2016). In addition, the simple food-web architecture in Lees Ferry results in rainbow trout populations that are inherently unstable and not resistant to controlled flood experiments that are released from the Dam (Cross et al. 2013). Farther downstream in the Grand Canyon, food-web studies indicate that the abundance and distribution of native fishes, including endangered humpback chub (*Gila cypha*), are also limited by the availability of insect prey; native fish populations consume virtually all of the available annual midge and blackfly production (Cross et al. 2013).

River managers are increasingly conducting environmental-flow experiments that mimic key aspects of natural flow regimes to rehabilitate river ecosystems or achieve specific ecological outcomes (Acreman et al. 2014, Olden et al. 2014). Incorporating knowledge of life stage–specific requirements for fish is an axiomatic component of such environmental flows. For instance, controlled floods are released from many dams to clean gravels of fine sediment and improve spawning habitat for salmonids (Olden et al. 2014). Similarly, river managers are designing environmental flows that enhance the flow conditions experienced by insect larvae. However, because the importance of recruitment dynamics to insect populations has only recently been demonstrated (Encalada and Peckarsky 2012, Lancaster and Downes 2014, Macqueen and Downes 2015), the flow conditions necessary to sustain other life stages have not yet been considered. Furthermore, implementing environmental flows is challenging in highly managed rivers because of the juxtaposition of uncertain environmental benefits against the readily quantified economic losses associated with reduced hydroelectricity generation (Jacobson and Galat 2008).

Our study informs the design of cost-effective environmental flows that should enhance biodiversity and ecosystem function downstream of hydropower dams on the Colorado River and elsewhere. Specifically, our study suggests that reducing hourly discharge variation during periods of peak aquatic-insect egg laying should alleviate the life-history bottleneck that arises from hydropeaking operations. Aquatic insects can be extremely fecund, with a single female laying hundreds to thousands of eggs (Merritt et al. 2008, Statzner and Beche 2010). Therefore, alleviating the life-history bottleneck that hydropeaking imposes on aquatic insects may not require long blocks of stable flow releases that completely preclude hydropeaking. For example, hydropeaking is less lucrative on weekends when electricity demands are low (Førsund 2015), so a cost-effective environmental flow could involve releasing stable and low flows every weekend during periods of peak aquatic-insect egg laying. Releasing low flows every weekend would ensure that eggs laid on weekends remained wetted and were never subject to desiccation prior to hatching, which typically occurs after days to weeks of incubation (Merritt et al. 2008, Statzner and Beche 2010). This type of environmental flow would minimally affect hydroelectricity revenues (USBR 2016) while substantially improving the quality of substrates available for aquatic-insect egg laying and rearing.

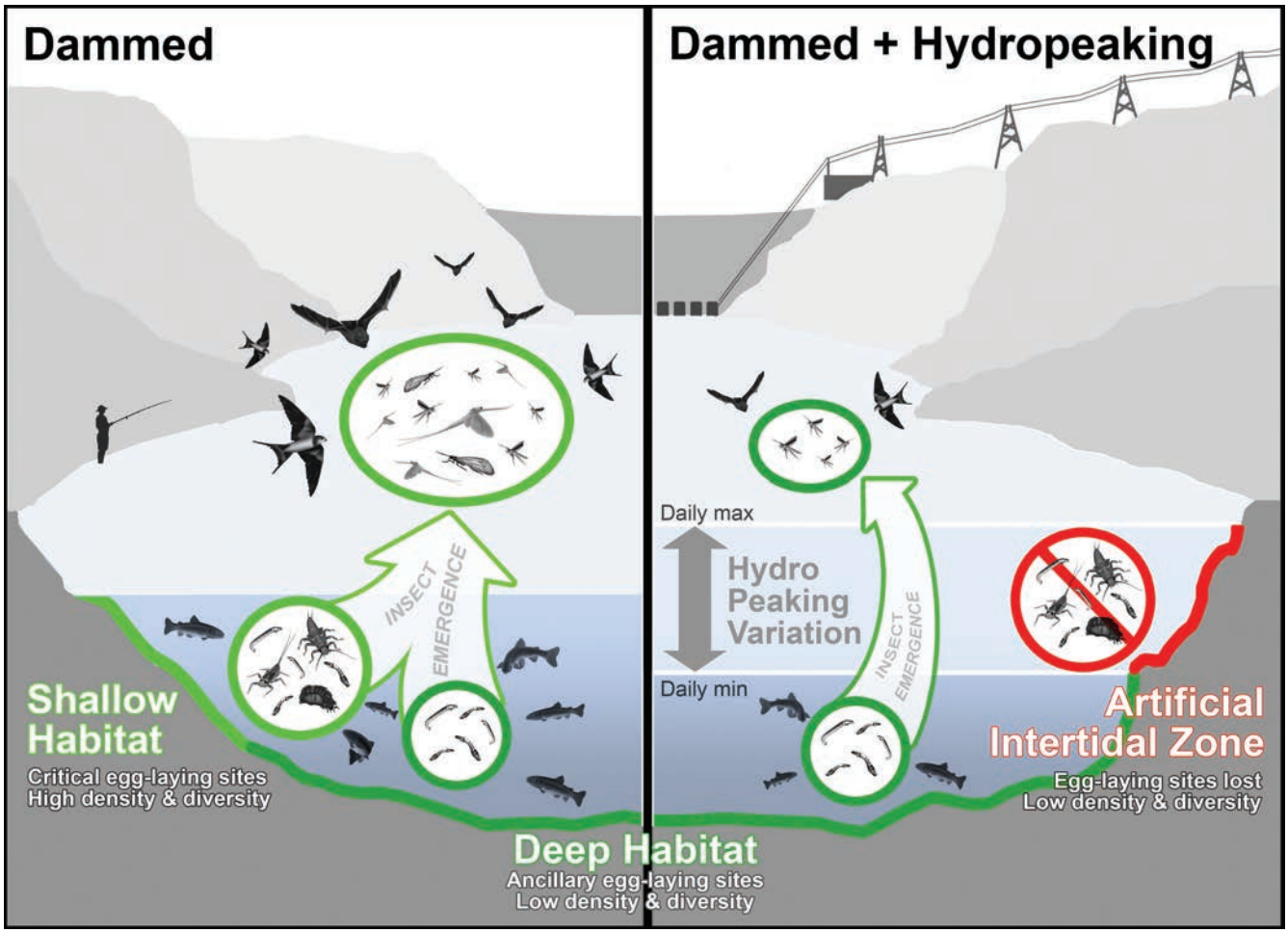

Figure 8. Aquatic insects play an essential role in river and riparian food webs. Aquatic insects are ubiquitous in freshwaters and are the primary prey for myriad species of wildlife living in and along rivers. These insects have complex life cycles that include a terrestrial winged adult life stage, whereas egg, larval, and pupal stages are aquatic. Ecologically important insect groups such as mayflies, stoneflies, and caddisflies cement their eggs along river-edge habitats, making them especially sensitive to dam water management practices such as hydropeaking that affect these edge habitats.

Environmental flows such as this may allow highly managed river ecosystems to continue meeting societal needs for renewable hydroelectricity while ensuring the sustainable provisioning of critical ecosystem services that are provided by the world's rivers.

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Supplemental material

The supplemental material is available online at *http://bioscience.oxfordjournals.org/lookup/suppl/doi:10.1093/biosci/biw059/-/DC1*. Data associated with this article are available at http://dx.doi.org/10.5066/F7WM1BH4.

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Theodore A. Kennedy (tkennedy@usgs.gov), Jeffrey D. Muehlbauer, Charles B. Yackulic, Kimberly L. Dibble, Eric W. Kortenhoeven, and Anya N. Metcalfe are affiliated with the US Geological Survey, Southwest Biological Science Center, Grand Canyon Monitoring and Research Center, in Flagstaff, Arizona. David A. Lytle is with the Department of Integrative Biology at Oregon State University, in Corvallis. Scott W. Miller is affiliated with the Department of Watershed Sciences at Utah State University, in Logan. Colden V. Baxter is with the Department of Biology at Idaho State University, in Pocatello.