

Relationship between River Water Flow Rate, Periphyton Abundance and Macroinvertebrate Communities

Owen Choy¹, Grace Constantian², June Griffin³, Chloe Pak³

¹University of California, Santa Barbara; ²University of California, San Diego;

³University of California, Irvine

ABSTRACT

Periphyton, which includes aquatic primary producers, comprises the crucial foundation of freshwater river and stream food webs. We conducted an observational study in the South Fork Eel River, which is part of federally protected coniferous coastal range forests in northwestern California. We studied how water flow rate could impact periphyton abundance, and how both water flow rate and periphyton abundance could impact macroinvertebrate density and community composition. Water flow rates as well as periphyton abundance and macroinvertebrate larvae were quantified. We predicted that with greater flow rates, periphyton abundance would increase and macroinvertebrate populations would be denser and more diverse. We found that as flow rates increased, periphyton abundance decreased. Macroinvertebrate densities and diversity increased with flow rate, and decreased with higher periphyton abundance. Our findings contribute to the understanding of trophic relationships and community interactions within running freshwater ecosystems, which are a dynamic and critical habitat facing increasing anthropogenic and climate pressure.

Keywords: periphyton, Cladophora glomerata, epiphytic diatoms, freshwater river ecosystems, macroinvertebrate density

INTRODUCTION

1.1 Riverine Food Webs

Although rivers cover less than 1% of the earth's surface, they harbor extraordinary biodiversity and are essential for ecosystem services, such as drinking water and energy production (Vörösmarty et al. 2010). At the foundation of these critical ecosystems are photosynthetic primary producers, such as algae and diatoms, which support the

highest reaches of the food web (Nakano and Murakami 2001). The assemblage of these photosynthetic producers (algae, diatoms, cyanobacteria), as well as detritus, fungi, and microbes that proliferate on benthic substrates is referred to as periphyton (Larned 2010). Studying the conditions in which these periphytic species grow is critical to understanding the ecosystem dynamics of species which depend on them.

Periphyton directly supports herbivorous and detritivorous animals—many of which are aquatic macroinvertebrates—by providing habitat, oxygen, nutrients and food (Bergey 1992, Larned 2010). Aquatic algae-feeding insect larvae are a critical food source for aquatic predators such as frogs, crustaceans, and fish (Voshell 2002). Additionally, studies have found that the emergent adults of aquatic insect larvae can ultimately comprise 25–100% of the energy or carbon obtained by terrestrial fauna such as bats, birds, lizards, and spiders (Baxter et al. 2005, Jackson et al. 2020). In their close association with periphytic species, aquatic macroinvertebrates act as a crucial link between primary producers and higher trophic levels. Thus, the study of periphyton and macroinvertebrates within and across habitats is critical to understanding aquatic food webs and aquatic ecosystems.

This essential habitat has been under threat by a variety of climate change-related and anthropogenic stressors in recent years. Populations of freshwater species have declined by an average of 83% since 1970, a steeper drop compared to terrestrial and marine species (Grooten and Almond 2018). Climate change, which is predicted to increase the variability and extremity of precipitation, can intensify drought conditions and contribute to a decline in freshwater biodiversity (Pendergrass et al. 2017, Zhang et al. 2021). Anthropogenic stressors, such as water diversion, agriculture, and urbanization, can deposit sediment and nutrient runoff into these systems, which is known to greatly diminish habitat quality for macroinvertebrates (Wagner 1989, Wood and Armitage 1997, Wang et al. 2007, Wagenhoff et al. 2012). Understanding the

function of trophic interactions in healthy rivers is critical for the proper management and protection of this vital ecosystem as more rivers become threatened by human activity.

1.2 Water Availability and Flow

The largest, most variable abiotic factor in freshwater ecosystems is water availability (Naiman et al. 2008). In years with less precipitation, river flow declines and can separate into stagnant pools (Power et al. 2015). Greater availability of water in wetter years, as experienced across the State of California in 2023, results in faster and higher flowing water (Blöschl et al. 2015). With factors like drought and abnormal precipitation patterns magnified by climate change, studying the impact of varying water flow rates on river ecosystems is crucial. Water diversions can also decrease the amount of water flowing through a river. Some algal species (*Cladophora* spp.) thrive in rapidly moving water because the current cleans the cell surface of the algae, increasing its ability to exchange materials like nutrients with its environment (Whitford 1960). Faster-flowing water increases nutrient availability which supports periphyton growth (Whitton 1970), and consequently amplifies the amount of food available to support macroinvertebrate larvae. Benthic macroinvertebrates also increase in abundance and richness in greater water velocities, likely due to the increase in nutrient flow for food sources (Schoen et al. 2013) or oxygen availability (Trinci et al. 2017). However, an excess of nutrients, which can be caused by agricultural runoff or other factors, could lead to harmful algal blooms, eutrophication, and the

proliferation of harmful cyanobacteria (Power et al. 2015, Wurtsbaugh et al. 2019). This is why it is crucial to understand how conditions like water flow could support or impair the food web through the growth of primary producers. While the effects of water speed on periphyton and macroinvertebrates has been well studied (Gowns and Gowns 2001), as well as the trophic relationship between periphyton and macroinvertebrates, studies that combine these variables and can compare whether water speed or food abundance is a driving factor in macroinvertebrate growth have yet to be conducted. Many studies also focus on macroinvertebrate abundance instead of density. Our study aims to fill these gaps by exploring the effect of both water flow rates and periphyton abundance on macroinvertebrate density.

1.3 Seasonality in Mediterranean Ecosystems

In regions that experience distinct seasonality, river ecosystems have seasonal flooding and drying events on a yearly basis (Avital, G. and Resh, V.H. 1999). A prime example is Mediterranean seasonality, where the majority of precipitation occurs during late fall to winter (October-March) and summers are warm and dry with little to no rainfall (Power et al. 2015, Dralle et al. 2016). For spring-fed waterways in these regions, the greatest volume of water flows in winter when precipitation runoff contributes to scouring bankfull (i.e., maximum width) floods (Bowles, David E. 2022). In summer, waterways experience the lowest flow, referred to as base flow (Johnson 1979, Ács and Kiss 1993). For the river ecosystem, this means that aquatic

vegetation and invertebrates are washed away by floods during the winter season but the highest level of productivity occurs in the summer because algae and invertebrates are able to proliferate under prime conditions without being swept away (Power et al. 1988, Sculley et al. 2017). Summers also have increased temperatures, which boosts aquatic primary productivity, the abundance of macroinvertebrates, and creates advantageous conditions for top predators in stream systems (Hannesdóttir et al. 2013).

However, significant variability in precipitation and flooding between years produces substantial variation in summer algal growth and in consumer composition (Sculley et al. 2017). Without scouring floods in the winter, macroinvertebrate grazers that feed on algae are not swept downstream and are allowed to proliferate. This causes a reduced abundance of algae in the following summer, since armored macroinvertebrate grazers (such as caddisfly larvae) are protected from significant predation pressure and consume algae before it can reach substantial abundance (Power et al. 2009). Moreover, in periods of significant drought, extremely low stream flow increases susceptibility in streams to pool isolation and warming, which can contribute to a decline in primary consumers and cause waterways to be dominated by algal or cyanobacterial blooms (Power et al. 2015). The differences in water availability and conditions are thus an important overarching factor in determining the abundance of producers and consumers that should be studied further.

1.4 The Eel River

The Eel River, located in northern California, USA is an ideal system for studying dynamic freshwater food webs because of its pristine water quality and its susceptibility to changes in water availability. The river and surrounding coniferous coastal range forest have been untouched by anthropogenic disturbances such as logging or heavy development since the late 1930s (Johnson 1979). 640 kilometers of the Eel have been protected federally and under state law since 1981 and 1972, respectively, to prevent dam development and to ensure optimal water and environmental standards (National Wild and Scenic Rivers System n.d.). The Eel is an ideal natural reference system for the conservation of rivers that are negatively affected by human impact. For example, understanding how the natural state of the Eel is affected by water flow rates or the relationship between different trophic levels can be used as a benchmark for other rivers that are experiencing water diversion or agricultural runoff. In addition, the Mediterranean seasonality of the Eel causes dry summers with low base flow and wet winters with scouring floods, making it a prime representation of river ecosystems with high vulnerability to fluctuating water availability and its variable effect on periphytic abundance. We hope to better understand how variations in river water availability and periphyton abundance affect the Eel ecosystem to apply to the conservation of other freshwater streams.

1.5 Questions and Hypothesis

In this study, we investigated the relationship between water flow rates and

the composition of primary producers and periphyton-eating macroinvertebrates. Specifically, we asked (1) if water flow rate affects periphyton abundance; and (2) if water flow rate and periphyton abundance influence macroinvertebrate density and community composition. We predicted that a greater flow rate would increase periphyton abundance because flowing water increases nutrient availability and encourages periphytic growth (Whitton 1970). We also predicted that a greater flow rate would increase macroinvertebrate density, which support the findings of (Schoen et al. 2013), which demonstrated that the abundance and richness of benthic macroinvertebrates increased with greater water velocity, likely due to the increase in nutrient flow. Further, we expect that greater periphyton abundance would increase macroinvertebrate density because periphyton, namely diatoms and green algae, are food sources for invertebrate grazers (Dodds 1991) and provide habitat (Power et al. 2013). Finally, we expect to find greater diversity of macroinvertebrates in areas with higher flow rate and greater periphytic abundance because of increased nutrient availability and microhabitat availability that support a wider range of taxa.

METHODS

2.1 Study System

Data collection took place from 1 August to 5 August 2023 between the hours of 10am to 3pm at the South Fork Eel River, a 169-kilometer stretch of the Eel River located in the coastal range forests of northern California (39°44'29.0"N 123°38'02.1"W) (US Geological Survey

1981). The Eel is a relatively short, steep river that is largely bedded with gravel and cobble substrate (Power et al. 2015). The study site is located in the Angelo Coast Range Reserve, a 3258-hectare plot of land managed by the University of California Natural Reserve System that has been protected from major human disturbance since the late 1930s (Johnson 1979). The Eel River hosts a variety of organisms including coho salmon, steelhead trout, California roach, Pacific lamprey, yellow-legged frogs, Western toads, Pacific giant salamanders, native mussels, aquatic garter snakes, river otters, a wide range of aquatic and flying insects, and several types of algae (Cladophora, Desmidium, Oedogonium, Mougoetia, and Spirogyra), diatoms (Achnanthes, Cocconeis, Epithemia, Gomphonema, and Rhoicosphenia), and cyanobacteria (Anabaena, Calothrix, Cylindrocapsa, and Nostoc) (Power et al. 2009, Angelo Coast Range Reserve n.d.). The largely coastal conifer forest area is a part of the greater Eel River Watershed, which receives an average of 215.6 centimeters of precipitation annually (Angelo Coast Range Reserve n.d.). The region has a Mediterranean climate with cold, wet winters (lows below freezing) and warm, dry summers (August highs average 31°C). The pristine condition of the Eel, its vulnerability to climate change, and the summer season of the study makes this an ideal system for studying freshwater food webs.

2.2 Species

This study focused on periphyton species that are a food source to the macroinvertebrates that inhabit them (Larned 2010, Power et al. 2015). We

examined and collected samples of the dominant green algal species, Cladophora glomerata, along with its associated epiphytic diatoms, Epithemia turgida and Epithemia sorex, that surround and cling to the green algae (Power et al. 2009). Within the periphyton samples, the macroinvertebrates we identified were caddisflies (Trichoptera), mayflies (Ephemeroptera), midges (Diptera: Chironomidae), black flies (Diptera: Simuliidae), and aquatic caterpillars (Lepidoptera: Crambidae: Petrophila spp.) (Pneh 2018). All of these macroinvertebrates are herbivorous and specifically consume diatoms, green algae or both (Voshell 2002).

2.3 Periphyton Collection

Plots were chosen using a 0.5-by-0.5-meter quadrat along the South Fork Eel River starting in a selected location with visible periphyton. Each plot was systematically placed 2 meters into the stream from the eastern bank of the river and distanced 4.5 meters apart. We moved upstream as we collected data to minimize downstream impact on sampling. To determine periphytic abundance at each plot, we measured the percent cover of periphyton and determined its thickness. Periphyton percent cover (PPC) was calculated using the point intercept method across 8 points in the quadrat, each distanced 10 centimeters apart. Periphyton thickness was measured and categorized as ≤ 0.5 centimeters or > 0.5 centimeters for the plot after being averaged between the 8 points. Together, PPC and periphyton thickness were the variables measured to describe periphyton abundance.

The flow rate of the river was measured by timing the number of seconds it took a floating oblong leaf (of no more than 6 centimeters along its major axis) to travel 2 meters downstream. The starting point of the leaf was the lower left hand corner of the quadrat when facing downstream. Areas of the river that had effectively no surface flow or were slow enough to be affected by a light breeze were designated as “still.” When a moderate or strong breeze had a visible effect on the surface flow of the river, sampling was paused until the breeze subsided.

To determine the composition and density of macroinvertebrates in the periphyton, periphyton samples were collected by hand and contained in 50-milliliter Falcon™ centrifuge tubes. No more than one sample was taken per plot. The volume of each sample was approximately 5 milliliters after being lightly compressed within the tube with minimal water. Plots with periphyton thickness less than 0.5 centimeters in thickness or unable to fill 5 milliliters were collected to a smaller fraction of this volume (macroinvertebrate density accounted for this difference).

2.4 Sample Analyses

All of the periphyton samples collected from the field were processed within 24 hours of collection. To sort and identify the macroinvertebrates within each periphyton sample, the contents of the tube were emptied into a glass petri dish and examined with a dissecting microscope under 20x magnification. Fine point 4.5” forceps and 4.5” scissors (DR Instruments Precision Plus Dissection Kit) were used to sort through the sample to find

macroinvertebrates. Macroinvertebrates were separated into a separate glass petri dish using a glass eyedropper (DR Instruments Precision Plus Dissection Kit). The macroinvertebrates were then identified and quantified using a dissecting microscope under 20x magnification. Identified macroinvertebrates that are known not to consume periphyton, or those that were unidentifiable or very uncommon (1-2 instances) across the samples were excluded from further analysis. The number of macroinvertebrates within periphyton samples that were a fraction of the 5-milliliter volume were proportionally scaled up to match the volume of the other samples.

2.5 Statistical Analyses

We performed our statistical analyses using JMP statistical software v17 (SAS Institute inc. Cary, NC, 1989–2023). To analyze the impact of water flow rate on periphyton percent cover (PPC), we conducted a t-test to determine the difference in PPC between still and moving water, as well as a linear regression to analyze the effect of flow rate of moving water on PPC. To analyze the correlation between water flow rate on periphyton thickness, a chi-squared test was performed to compare the difference in periphyton thickness ($\leq 0.5\text{cm}$ or $>0.5\text{cm}$) between still and moving water. We also conducted a logistic regression to assess the impact of flow rate on whether periphyton thickness was more likely to be $\leq 0.5\text{cm}$ or $>0.5\text{cm}$. Two t-tests were performed to examine the difference between still and moving water and the difference between $\leq 0.5\text{cm}$ periphyton thickness and $>0.5\text{cm}$ periphyton thickness on macroinvertebrate

density. We conducted two linear regressions to assess the effects of flow rate and PPC on macroinvertebrate density. Finally, we ran two discriminant analyses to analyze the differences in macroinvertebrate community composition between still and moving water as well as between $\leq 0.5\text{cm}$ periphyton thickness and $> 0.5\text{cm}$ periphyton thickness.

RESULTS

3.1 Impact of Water Conditions on Periphyton Abundance

PPC showed no differences between still and moving water ($N_{\text{still}} = 18$, $N_{\text{moving}} = 36$, $t = 1.20$, $p = 0.24$). As flow rate increased within moving water, PPC decreased ($N = 36$, $R^2 = 0.31$, $p = 0.0004$). We also found that there were more instances of $> 0.5\text{cm}$ thick periphyton in still water than in moving water ($N = 54$, $\chi^2 = 17.03$, $p = 0.0001$). There is no effect of flow rate in moving water on periphyton thickness ($N = 36$, $R^2 = 0.03$, $p = 0.55$).

3.2 Impact of Water Conditions and Periphyton Abundance on Macroinvertebrate Density

Macroinvertebrate density was greater in moving water than in still water ($N_{\text{still}} = 7$, $N_{\text{moving}} = 25$, $t = 3.00$, $p = 0.01$). There was no effect of flow rate in moving water on macroinvertebrate density ($N = 25$, $R^2 = 0.11$, $p = 0.11$). We also found that as PPC increases, macroinvertebrate density decreases ($N = 32$, $R^2 = 0.12$, $p = 0.05$). Finally, $\leq 0.5\text{cm}$ thick periphyton had greater macroinvertebrate density than $> 0.5\text{cm}$

thick periphyton ($N_{\leq 0.5\text{cm}} = 23$, $N_{> 0.5\text{cm}} = 10$, $t = -3.38$, $p = 0.0016$).

3.3 Impact of Water Conditions and Periphyton Abundance on Macroinvertebrate Community Composition

Overall, we found that macroinvertebrates of all quantified groups were more dense in moving water than in still water, while black flies and aquatic caterpillars were only present in moving water (Fig. 1). The most common taxa were the caddisflies and midges. This difference between macroinvertebrate communities in still versus moving water was able to be predicted correctly by a computer algorithm 74.2% of the time. We also found that all measured macroinvertebrate taxa were more dense in $\leq 0.5\text{cm}$ thick periphyton than in $> 0.5\text{cm}$ thick periphyton, with black flies and aquatic caterpillars only being present in $\leq 0.5\text{cm}$ (Fig. 2). The most common taxa were also the caddisflies and midges. This difference between macroinvertebrate communities in $\leq 0.5\text{cm}$ thick periphyton versus $> 0.5\text{cm}$ thick periphyton was able to be predicted by a computer algorithm correctly 80.6% of the time.

DISCUSSION

In general, periphyton abundance was greater in still or slow-moving waters, which does not support our initial predictions that periphyton abundance would increase with greater water flow. An explanation for a greater periphyton abundance in still or slower moving waters is that constant disturbance from fast-moving waters hinders vertical periphyton growth by

flushing away epiphytes and inhibiting light, making these areas less likely to be occupied (Wang 1974, Widdows and Navarro 2007). While flowing water carries nutrients (Whitton 1970), too much flowing water nullifies any benefit that periphyton might receive since too much flow hinders vertical growth.

We found that macroinvertebrate density was greater in moving water than in still water, in the moving water there was no impact of flow rate. This partially supports our hypothesis that macroinvertebrate density would increase with greater water flow. More macroinvertebrates were found in periphyton that grew in moving water compared to still water, but the quantity of macroinvertebrates did not change with faster flow rates. These results partially contradict the findings of Courtwright and May (2013), which found that water flow was a major factor contributing to macroinvertebrate abundance, and that increased water flow conferred increased macroinvertebrate abundance. Our findings could be a result of the different size and structure of their study system (tributaries of Dry River, Union Springs, and Dry Run; Virginia, USA) compared to the Eel River. These waterways are relatively shallow, with mean bankfull widths of 5-6m, whereas the Eel River can reach bankfull widths of 30m (Polis et al. 2004). Observationally, we saw that still waters were generally deeper or directly connected to deeper parts of the river, which offers more nutrient and oxygen circulation and access. In other words, no areas surveyed were prone to stagnation, intermittent pauses in flow, or pool isolation, which occurred in their study system. This highlights the contrasting

community dynamics of invertebrate communities in freshwater systems of different sizes and structures.

Interestingly, we saw that as periphyton abundance increased, macroinvertebrate density decreased. This does not support our hypothesis that greater periphyton abundance would increase macroinvertebrate density. This could possibly result from periphyton thickness being thinner in faster-flowing water, which could provide greater circulation of oxygen or other nutrients to invertebrates. The close correlation between fast moving waters and thin algae makes the two qualities covarying, creating a microhabitat in which macroinvertebrate density increases. As our study did not separate water flow rate and periphyton abundance, a future study could use a lab environment to examine if the same macroinvertebrate density patterns appear when these variables are disentangled. Finally, we found that macroinvertebrates of all quantified groups were more dense in moving water than in still water and in $\leq 0.5\text{cm}$ thick periphyton than in $>0.5\text{cm}$ thick periphyton, with black flies and aquatic caterpillars only being present in moving water. This supports our hypothesis that water flow and periphyton abundance affect macroinvertebrate community composition. These results partially support our hypothesis as we found greater diversity in macroinvertebrate communities in greater flow rates, but not with a higher periphyton abundance. In a study done on grazing caddisfly larvae, *Micrasema quadriloba*, it was found that in certain stages of their development the distribution of the larvae was dependent on water flow and not the abundance of periphyton

(Katano et al. 2005). While we were unable to identify the stage of development the macroinvertebrate were in in our study, this is a potential reason why we saw more macroinvertebrates in the moving water despite there being less periphyton. Future studies should consider more specific larval stages of macroinvertebrates to incorporate which environmental conditions carry the most weight at the time of the study.

In a study done on grazing caddisfly larvae, *Micrasema quadriloba*, it was found that in certain staging of their development the distribution of the larvae was dependent on water flow and not the abundance of periphyton (Katano et al. 2005). While we were unable to identify the stage of development the macroinvertebrate were in in our study, this is a potential reason why we saw more macroinvertebrates in the moving water despite there being less periphyton. Future studies should consider more specific larval stages of macroinvertebrates to incorporate which environmental conditions carry the most weight at the time of the study.

Our results support previous findings that factors contributing to variability in precipitation and flooding can influence the abundance of primary producers and macroinvertebrates, which can have other bottom-up effects in river ecosystems (Power et al. 2015). Year-to-year variability in precipitation and flooding can produce drastic water flow variability in streams (DiMarco and Savitz 2020). This suggests that human disturbance in rivers that affect water flow—such as the addition of dams and stream diversion—can largely impact the ecosystem. The increasing variability of precipitation due to climate change can

likely have a similar effect (Gao and Giorgi 2008, García-Ruiz et al. 2011, Dralle and Thompson 2016). Power et al. (2015) examined the aquatic community within the Eel and demonstrated how flow variability can affect the biological conditions of the Eel ecosystem. High water flow that is maintained in the summer creates favorable conditions for salmonids by supplying essential nutrients, energy, and more habitat. Increased periphytic growth can increase the surface area available for invertebrate, microbial, and diatomic inhabitants later in the dry season as well. However, if summer base flow is too low, it can cause algal blooms to stagnate and decompose, increasing the temperature and pH of the water (Power 1990) and releasing nutrients (Paerl and Otten 2013). This creates prime conditions for the growth of potentially neurotoxic cyanobacteria that are harmful to the ecosystem (Power et al. 2015). The sensitivity of the river ecosystem due to variability in stream flow and the existence of alternative stable states that can either be beneficial or detrimental make the preservation and close monitoring of this ecosystem highly critical.

The protection of freshwater systems have been lagging, especially compared to marine systems (Saunders et al. 2002, Kingsford and Nevill 2005, Suski and Cooke 2007). Protected areas that contain streams have focused on terrestrial reserves and freshwater species and habitats, but fail to fully protect the entire water system from sediment deposition, land disturbance, or altered hydrologies (Saunders et al. 2002). Unprotected upstream disturbance from activities such as dam development or water diversion can negatively impact downstream protected areas, reversing

their intended benefit. In order to ensure the longevity of sensitive river ecosystems, protected areas that focus on water availability, regimes and water quality throughout the entire hydrologic system must be established (Valle Ferreira 2000, Poiani et al. 2000, Kingsford et al. 2011). Other directions of future research would be to conduct this study in freshwater ecosystems that are experiencing direct anthropogenic influence (especially in situations of water diversion and drought). A long-term version of this study could look at the impacts of climate change on these freshwater ecosystems and track changes in water flow, periphyton abundance, and macroinvertebrate communities as we have at the Eel river. In addition to the methods from this study, we emphasize that the interactive effects between water flow and periphyton abundance should be explored in greater detail as they relate to macroinvertebrate populations. This study displayed the interconnectedness of water flow, periphyton, and macroinvertebrates, and disentangling these variables would allow us to better understand the foundation of freshwater food webs.

ACKNOWLEDGMENTS

This work was performed at the Donald and Sylvia McLaughlin Natural Reserve DOI: [10.21973/N3W08D](https://doi.org/10.21973/N3W08D) This reserve is part of University of California Natural Reserve System. Special thanks to Dr. Timothy Miller, Dr. Renske Kirchholtes, and Ph.D student and CEC TA Lydia Dean for their invaluable guidance and support throughout the duration of this project. Additional thanks to Angelo Coast Range Reserve director Peter Steel for allowing us to conduct research in the beautiful and inspiring Eel River.

REFERENCES

- Ács, É., and K. T. Kiss. 1993. Effects of the water discharge on periphyton abundance and diversity in a large river (River Danube, Hungary). *Hydrobiologia* 249:125–133.
- Angelo Coast Range Reserve. (n.d.). Natural History. <https://angelo.berkeley.edu/about-angelo/natural-history/>.
- Avital, G. and Resh, V.H. 1999. Streams in Mediterranean climate regions: Abiotic influences and biotic responses to predictable seasonal events - *ProQuest. Annual Review of Ecology and Systematics* 30:51.
- Baxter, C. V., K. D. Fausch, and W. Carl Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology* 50:201–220.
- Bergey, E. A. 1992. Biotic and abiotic influences on benthic algal populations in California coast range streams. Ph.D., University of California, Berkeley, United States -- California.
- Blöschl, G., L. Gaál, J. Hall, A. Kiss, J. Komma, T. Nester, J. Parajka, R. A. P. Perdigão, L. Plavcová, M. Rogger, J. L. Salinas, and A. Viglione. 2015. Increasing river floods: Fiction or reality? *WIREs Water* 2:329–344.
- Bowles, David E. 2022. Resiliency and recovery of aquatic vegetation following scouring floods in two first-Magnitude Springs, Missouri, USA. *Hydrobiology* 1:164–182.
- Courtwright, J., and C. L. May. 2013. Importance of terrestrial subsidies for native brook trout in Appalachian

- intermittent streams. *Freshwater Biology* 58:2423–2438.
- DiMarco, D., and R. Savitz. 2020. How a river's length and discharge relate to the precipitation in its basin. *Sustainable Water Resources Management* 6:106.
- Dodds, W. K. 1991. Community interactions between the filamentous alga *Cladophora glomerata* (L.) Kuetzing, its epiphytes, and epiphyte grazers. *Oecologia* 85:572–580.
- Dralle, D. N., N. J. Karst, and S. E. Thompson. 2016. Dry season streamflow persistence in seasonal climates. *Water Resources Research* 52:90–107.
- Dralle, D. N., and S. E. Thompson. 2016. A minimal probabilistic model for soil moisture in seasonally dry climates. *Water Resources Research* 52:1507–1517.
- Gao, X., and F. Giorgi. 2008. Increased aridity in the Mediterranean region under greenhouse gas forcing estimated from high resolution simulations with a regional climate model. *Global and Planetary Change* 62:195–209.
- García-Ruiz, J. M., J. I. López-Moreno, S. M. Vicente-Serrano, T. Lasanta-Martínez, and S. Beguería. 2011. Mediterranean water resources in a global change scenario. *Earth-Science Reviews* 105:121–139.
- Grooten, M., and R. E. A. Almond. 2018. Living planet report - 2018: aiming higher. Living planet report - 2018: aiming higher.
- Growns, I. O., and J. E. Growns. 2001. Ecological effects of flow regulation on macroinvertebrate and periphytic diatom assemblages in the Hawkesbury–Nepean River, Australia. *Regulated Rivers: Research & Management* 17:275–293.
- Hannesdóttir, E. R., G. M. Gíslason, J. S. Ólafsson, Ó. P. Ólafsson, and E. J. O'Gorman. 2013. Chapter Five - Increased stream productivity with warming supports higher trophic levels. Pages 285–342 in G. Woodward and E. J. O'Gorman, editors. *Advances in Ecological Research*. Academic Press.
- Jackson, B. K., S. L. Stock, L. S. Harris, J. M. Szwczak, L. N. Schofield, and M. A. Desrosiers. 2020. River food chains lead to riparian bats and birds in two mid-order rivers. *Ecosphere* 11:e03148.
- Johnson, S. 1979, May. The Land Use History of The Coast Range Preserve, Mendocino County, California.
- Katano, I., H. Mitsuhashi, Y. Isobe, H. Sato, and T. Oishi. 2005. Reach-Scale Distribution Dynamics of a Grazing Stream Insect, *Micrasema quadriloba* Martynov (Brachycentridae, Trichoptera), in Relation to Current Velocity and Periphyton Abundance. *Zoological Science* 22:853–860.
- Kingsford, R. T., H. C. Biggs, and S. R. Pollard. 2011. Strategic adaptive management in freshwater protected areas and their rivers. *Biological Conservation* 144:1194–1203.
- Kingsford, R. T., and J. Nevill. 2005. Scientists urge expansion of freshwater protected areas. *Ecological Management & Restoration* 6:161–162.
- Larned, S. T. 2010. A prospectus for periphyton: recent and future ecological research. *Journal of the*

- North American Benthological Society 29:182–206.
- Naiman, R. J., J. J. Latterell, N. E. Pettit, and J. D. Olden. 2008. Flow variability and the biophysical vitality of river systems. *Comptes Rendus Geoscience* 340:629–643.
- Nakano, S., and M. Murakami. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences of the United States of America* 98:166–170.
- National Wild and Scenic Rivers System. (n.d.). Eel River. <https://www.rivers.gov/rivers/river/eel>.
- Paerl, H. W., and T. G. Otten. 2013. Harmful cyanobacterial blooms: Causes, consequences, and controls. *Microbial Ecology* 65:995–1010.
- Pendergrass, A. G., R. Knutti, F. Lehner, C. Deser, and B. M. Sanderson. 2017. Precipitation variability increases in a warmer climate. *Scientific Reports* 7:17966.
- Pneh, S. 2018. The Bug Guide for the Angelo Coast Range Reserve (and beyond).
- Poiani, K. A., B. D. Richter, M. G. Anderson, and H. E. Richter. 2000. Biodiversity conservation at multiple scales: Functional sites, landscapes, and networks. *Bioscience* 50:133–146.
- Polis, G. A., M. E. Power, and G. R. Huxel, editors. 2004. Food webs at the landscape level. University of Chicago Press, Chicago, IL.
- Power, M. E. 1990. Benthic Turfs vs Floating Mats of Algae in River Food Webs. *Oikos* 58:67–79.
- Power, M. E., K. Bouma-Gregson, Patrick Higgins, and S. M. Carlson. 2015. The Thirsty Eel: Summer and Winter Flow Thresholds that Tilt the Eel River of Northwestern California from Salmon-Supporting to Cyanobacterially Degraded States. *Copeia* 2015:200–211.
- Power, M. E., J. R. Holomuzki, and R. L. Lowe. 2013. Food webs in Mediterranean rivers. *Hydrobiologia* 719:119–136.
- Power, M. E., R. J. Stout, C. E. Cushing, P. P. Harper, F. R. Hauer, W. J. Matthews, P. B. Moyle, and B. Statzner. 1988. Biotic and abiotic controls in river and stream communities. *Journal of the North American Benthological Society* 7:456–479.
- Power, M., R. Lowe, P. Furey, J. Welter, M. Limm, J. Finlay, C. Bode, S. Chang, M. Goodrich, and J. Sculley. 2009. Algal mats and insect emergence in rivers under Mediterranean climates: towards photogrammetric surveillance. *Freshwater Biology* 54:2101–2115.
- Saunders, D. L., J. J. Meeuwig, and A. C. J. Vincent. 2002. Freshwater protected areas: Strategies for conservation. *Conservation Biology* 16:30–41.
- Schoen, J., E. Merten, and T. Wellnitz. 2013. Current velocity as a factor in determining macroinvertebrate assemblages on wood surfaces. *Journal of Freshwater Ecology* 28:271–275.
- Sculley, J. B., R. L. Lowe, C. A. Nittrouer, T. M. Drexler, and M. E. Power. 2017. Eighty years of food-web response to interannual variation in discharge recorded in river diatom frustules from an ocean sediment core. *Proceedings of the National Academy of Sciences* 114:10155–10159.

- Suski, C. D., and S. J. Cooke. 2007. Conservation of aquatic resources through the use of freshwater protected areas: Opportunities and challenges. *Biodiversity and Conservation* 16:2015–2029.
- Trinci, G., G. L. Harvey, A. J. Henshaw, W. Bertoldi, and F. Hölker. 2017. Life in turbulent flows: interactions between hydrodynamics and aquatic organisms in rivers. *WIREs Water* 4:e1213.
- US Geological Survey. 1981. Geographic names information system. <https://edits.nationalmap.gov/apps/gaz-domestic/public/summary/253918>.
- Valle Ferreira, L. 2000. Effects of flooding duration on species richness, floristic composition and forest structure in river margin habitat in Amazonian blackwater floodplain forests: implications for future design of protected areas. *Biodiversity & Conservation* 9:1–14.
- Vörösmarty, C. J., P. B. McIntyre, M. O. Gessner, D. Dudgeon, A. Prusevich, P. Green, S. Glidden, S. E. Bunn, C. A. Sullivan, C. R. Liermann, and P. M. Davies. 2010. Global threats to human water security and river biodiversity. *Nature* 467:555–561.
- Voshell, J. R. 2002. A guide to common freshwater invertebrates of North America. McDonald & Woodward Pub, Blacksburg, Va.
- Wagenhoff, A., C. R. Townsend, and C. D. Matthaei. 2012. Macroinvertebrate responses along broad stressor gradients of deposited fine sediment and dissolved nutrients: a stream mesocosm experiment. *Journal of Applied Ecology* 49:892–902.
- Wagner, R. 1989. THE INFLUENCE OF ARTIFICIAL STREAM BOTTOM SILTATION ON EPHEMEROPTERA IN EMERGENCE TRAPS-Web of Science Core Collection. <https://www.webofscience.com/wos/woscc/full-record/WOS:A1989U052000006?SID=USW2EC0C73ZcaQt2OSAeQnlkIE7Li>.
- Wang, L., D. M. Robertson, and P. J. Garrison. 2007. Linkages between nutrients and assemblages of macroinvertebrates and fish in wadeable streams: implication to nutrient criteria development. *Environmental Management* 39:194–212.
- Wang, W.-C. 1974. Effect of turbidity on algal growth.
- Whitford, L. A. 1960. The Current Effect and Growth of Fresh-Water Algae. *Transactions of the American Microscopical Society* 79:302–309.
- Whitton, B. A. 1970. Biology of Cladophora in freshwaters. *Water Research* 4:457–476.
- Widdows, J., and J. M. Navarro. 2007. Influence of current speed on clearance rate, algal cell depletion in the water column and resuspension of biodeposits of cockles (*Cerastoderma edule*). *Journal of Experimental Marine Biology and Ecology* 343:44–51.
- Wood, P. J., and P. D. Armitage. 1997. Biological effects of fine sediment in the lotic environment. *Environmental Management* 21:203–217.
- Wurtsbaugh, W. A., H. W. Paerl, and W. K. Dodds. 2019. Nutrients, eutrophication and harmful algal

blooms along the freshwater to marine continuum. WIREs Water 6:e1373.

Zhang, W., K. Furtado, P. Wu, Tianjun Zhou, R. Chadwick, C. Marzin, J. Rostron, and D. Sexton. 2021. Increasing

precipitation variability on daily-to-multiyear time scales in a warmer world.

<https://www.science.org/doi/10.1126/sciadv.abf8021>.

5. Tables and Figures

Figure 1. Macroinvertebrate Community Composition Differences Between Still and Moving Water.

Higher numbers of each macroinvertebrate taxa as well as a higher number of total taxa were found in samples from moving water compared to still water. Periphyton samples (including *Cladophora glomerata*, *Epithemia turgida*, and *Epithemia sorex*) from the Eel River in Mendocino County, CA were collected from 1 August to 5 August 2023 and examined for macroinvertebrates. Only periphyton-consuming macroinvertebrates were counted. Taxa included caddisflies (Trichoptera), Mayflies (Ephemeroptera), midges (Diptera: Chironomidae), black flies (Diptera: Simuliidae), and aquatic caterpillars (Lepidoptera: Crambidae: *Petrophila* spp.). Caddisflies and midges were the most common taxa. As all samples were scaled to the same volume, larger number of individuals per taxa translates to a higher density per taxa in moving water. The additional presence of black flies and aquatic caterpillars in moving water translates to a higher diversity of macroinvertebrates in moving water.

Figure 2. Macroinvertebrate Community Composition Differences Between >0.5cm Thick Periphyton and ≤0.5cm Thick Periphyton.

Higher numbers of each macroinvertebrate taxa as well as a higher number of total taxa were found in samples from >0.5cm periphyton thickness compared to ≤0.5cm periphyton thickness. Periphyton samples (including *Cladophora glomerata*, *Epithemia turgida*, and *Epithemia sorex*) from the Eel River in Mendocino County, CA were collected from 1 August to 5 August 2023 and examined for macroinvertebrates. Only periphyton-consuming macroinvertebrates were counted. Taxa included caddisflies (Trichoptera), Mayflies (Ephemeroptera), midges (Diptera: Chironomidae), black flies (Diptera: Simuliidae), and aquatic caterpillars (Lepidoptera: Crambidae: *Petrophila* spp.). Caddisflies and midges were the most common taxa. As all samples were scaled to the same volume, the larger number of individuals per taxa translates to a higher density per taxa in moving water. The additional presence of black flies and aquatic caterpillars in >0.5cm thick periphyton translates to a higher diversity of macroinvertebrates in >0.5cm thick periphyton.