



Managing climate refugia for freshwater fishes under an expanding human footprint

Joseph L Ebersole^{1*}, Rebecca M Quiñones², Shaun Clements³, and Benjamin H Letcher⁴

Within the context of climate adaptation, the concept of climate refugia has emerged as a framework for addressing future threats to freshwater fish populations. We evaluated recent climate-refugia management associated with water use and landscape modification by comparing efforts in the US states of Oregon and Massachusetts, for which there are contrasting resource use patterns. Using these examples, we discuss tools and principles that can be applied more broadly. Although many early efforts to identify climate refugia have focused on water temperature, substantial gains in evaluating other factors and processes regulating climate refugia (eg stream flow, groundwater availability) are facilitating refined mapping of refugia and assessment of their ecological value. Major challenges remain for incorporating climate refugia into water-quality standards, evaluating trade-offs among policy options, addressing multiple species' needs, and planning for uncertainty. However, with a procedurally transparent and conceptually sound framework to build upon, recent efforts have revealed a promising path forward.

Front Ecol Environ 2020; 18(5): 271–280, doi:10.1002/fee.2206

Anthropogenic climate change is influencing freshwater ecosystems in several ways, for example by increasing water temperatures, changing water flow timing and magnitude, and altering biogeochemical cycling (Poff *et al.* 2002; Milly *et al.* 2005; Palmer *et al.* 2009). These impacts affect aquatic organisms both in relatively undisturbed habitats and in areas previously modified by human activity (Ficke *et al.* 2007). Although some species will benefit from predicted

changes, species with specialized habitat requirements, narrow physical tolerances, weak adaptive capacity, and limited dispersal capability are more vulnerable to alterations in environmental conditions (Figure 1; Lynch *et al.* 2016; Walters *et al.* 2018).

Understanding and predicting the response of aquatic ecosystems to a changing climate is complicated by spatial and temporal variation in vulnerability (Foden *et al.* 2013). Certain aquatic habitats and associated biota are already responding to climate change. This is particularly true where exposure (extent of environmental change) is greatest, sensitivity (extent of species' response to change) is highest, and resilience and adaptive capacity (species' ability to adapt via evolution or behavior) are lowest (Foden *et al.* 2013). Changes are expected to occur more slowly in climate refugia (areas where natural and managed physical or biological processes and structures buffer external climate forcing factors), enabling species to persist (Morelli *et al.* 2016). We describe current efforts to identify and assess potential climate refugia, drawing from examples in Oregon and Massachusetts, where innovative research and management are being combined to help inform climate-refugia management for freshwater fishes. Fish conservation efforts in these two states – despite their differing biophysical contexts and land-use histories – offer insights into managing refugia in the face of the globally pervasive challenges posed by human water use and modification of aquatic habitats. From these examples, we summarize key lessons to help guide future applications of climate-refugia science to freshwater fish management.

In a nutshell:

- Protection of freshwater fishes in the face of anthropogenic climate change and human resource use is spurring the development of innovative resource management strategies
- Identifying and managing climate refugia is one conservation approach that helps not only to protect vulnerable freshwater fishes and their habitats but also to deliver ecosystem services
- We describe approaches for identifying refugia at multiple spatial and temporal scales, in addition to management strategies that reduce climate exposure and sensitivity as well as maintain spatial connectivity within watersheds to better ensure fish population persistence
- Alignment of stakeholder objectives and actions is helping to remove institutional barriers and promote long-term success in conservation outcomes

■ Beyond temperature: identifying climate refugia for vulnerable fishes

Cold-water fishes are among the most vulnerable of all taxa to climate change. In many regions, these populations are

¹Pacific Ecological Systems Division, Office of Research and Development, US Environmental Protection Agency, Corvallis, OR *(ebersole.joe@epa.gov); ²Massachusetts Division of Fisheries and Wildlife, Westborough, MA; ³Oregon Department of Fish and Wildlife, Salem, OR; ⁴Conte Anadromous Fish Laboratory, US Geological Survey, Turners Falls, MA

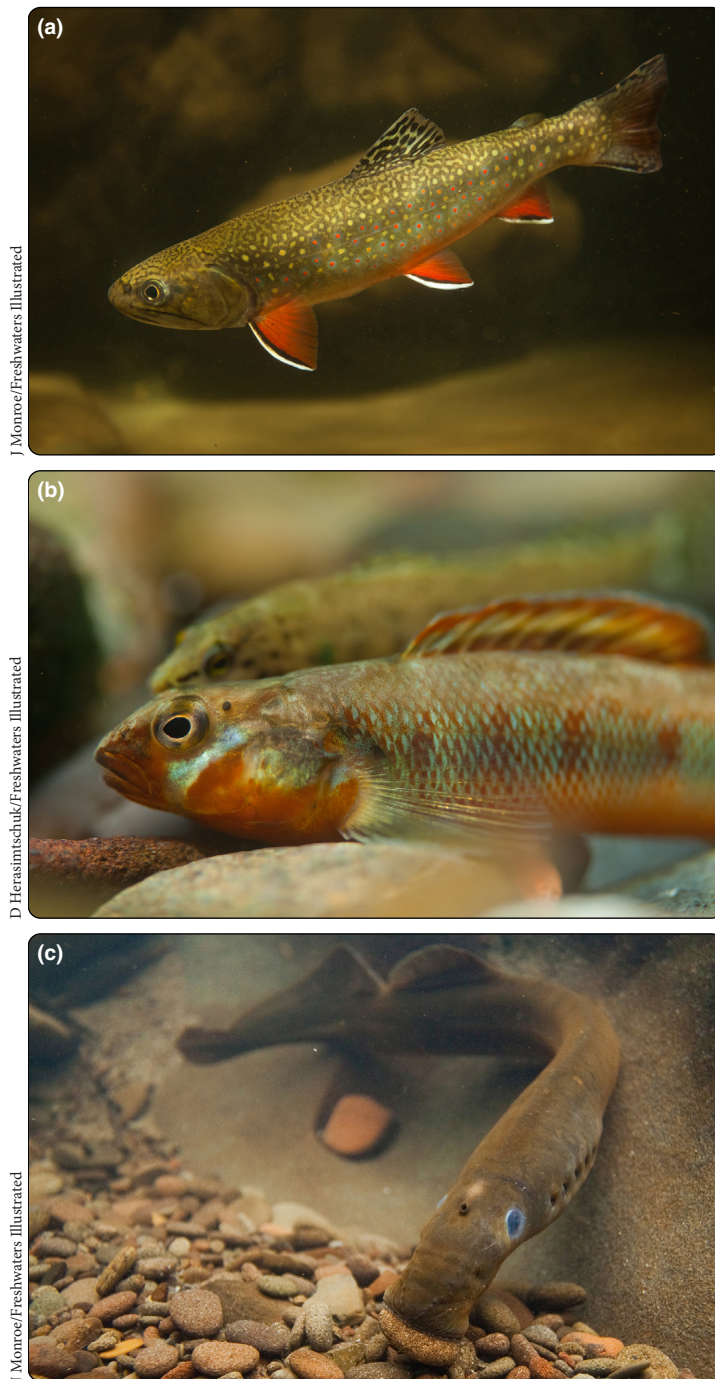


Figure 1. Freshwater taxa increasingly dependent on climate refugia include stenothermal (tolerant of only a narrow temperature range) cold-water species threatened by warming, such as (a) brook trout (*Salvelinus fontinalis*); benthic specialists threatened by flood scour and siltation, such as (b) gilt darter (*Percina evides*); and species threatened by habitat fragmentation, stream dewatering, and predation by non-native species, such as (c) Pacific lamprey (*Entosphenus tridentatus*).

progressively becoming more restricted to or dependent on persistent cold-water habitats associated with headwater forested stream networks, and/or habitats supported by groundwater or seasonal snowmelt (Figure 2). Because these habitats

and their associated fish populations are among those already affected by and under growing threat from climate change and human use, the management of climate refugia as a conservation strategy is increasingly being applied to these systems (Isaak *et al.* 2015). Temperature change is not the only stressor, however, and as such fishes other than cold-water species are also vulnerable to climate change (Moyle *et al.* 2013). For sensitive freshwater fishes, climate change is likely to enhance exposure to multiple interacting stressors (Staudt *et al.* 2013). To maintain viability, fish populations will require a suite of resources – including food, protective cover from predators, suitable water quality, appropriate flow regimes, spawning substrates, and sufficient capacity to deal with parasites and diseases, among others – to successfully complete their life histories. Exposure to all climate-induced stressors, including water temperature, must be minimized for climate refugia to be effective for vulnerable fishes. In addition, climate refugia will be most effective where habitat networks enable the expression of phenotypic and behavioral plasticity (Beever *et al.* 2017). For mobile fish species, adaptive opportunities will be greatest in stream, river, and lake networks with spatial arrangements that allow effective connectivity among seasonal habitats (Fullerton *et al.* 2017), and from which range shifts into newly suitable habitats are feasible (Rahel *et al.* 2008). Improving our ability to identify and manage current and potential refugia for freshwater fishes will require consideration of these and other factors. In the following examples, we present advances in climate-refugia science and management for cold-water fishes in two US states, and describe lessons learned for climate-refugia management more broadly.

Modeling refugia for cold-water species

Land uses in Massachusetts have altered freshwater habitats for centuries; for instance, deforestation for agriculture is thought to have greatly impacted many freshwater ecosystems by the 1850s (Moore *et al.* 1997). More recent land-use changes, particularly those associated with dam construction and road building, have resulted in many rivers and streams seasonally exceeding temperature tolerances for cold-water species like eastern brook trout (*Salvelinus fontinalis*) (Hall *et al.* 2002; Hudy *et al.* 2008). Although more than 80% of all flowing waters in the state likely once supported cold-water habitats, an evaluation of 134 watersheds revealed that less than 50% of historical cold-water habitats remain in the majority (78%) of these watersheds (Hudy *et al.* 2008).

Stream conditions have concurrently been affected by changes in climate and in land use. Annual average air temperatures in the northeastern US have increased by approximately 0.26°C per decade since 1970 (NECASC 2018), further contracting cold-water habitat. Moreover, there has been a roughly 70% increase in the number of extreme precipitation events since 1958 (Melillo *et al.* 2014), especially in winter (Blum *et al.* 2018). These events increase soil erosion and sediment delivery

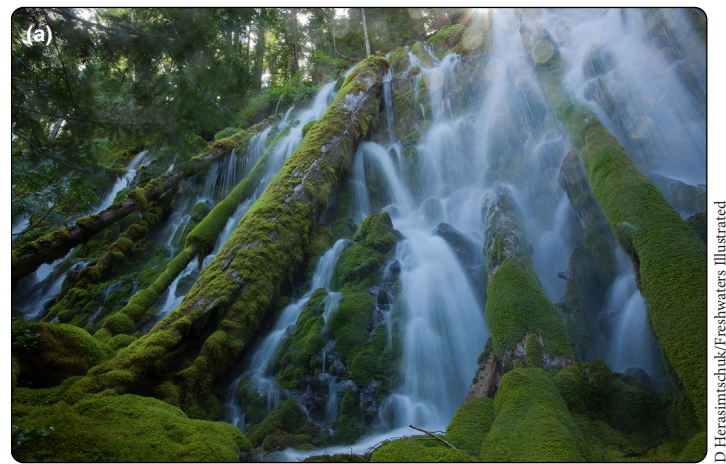
to streams, which in turn reduces survival of young age classes and limits adult migration among some salmonid species (reviewed in Groot and Margolis [2003]). Earlier snowmelt and more frequent winter rain have resulted in earlier (7–14 days) and higher peak flows in New England rivers and streams (Hodgkins *et al.* 2003; Hayhoe *et al.* 2007). As the magnitude of peak flows increases so too do the streamflow velocities that scour river channels, affecting the survival of cold-water species that depend on stream substrate at some point in their life histories (eg brook trout, spring salamander [*Gyrinophilus porphyriticus*], freshwater pearl mussel [*Margaritifera margaritifera*]; Hastie *et al.* 2003; Lowe 2012; Goode *et al.* 2013).

Because cold-water species are among the most sensitive of all taxa to climate change (MCCS and MassWildlife 2010), Massachusetts has initiated a process to identify key refugia features as a first step in their conservation (Morelli *et al.* 2016). Using data from an extensive fish survey effort (>10,000 surveys conducted since 1980), potential refugia were identified based on the presence of cold-water species during summer surveys. Surveys conducted in 2016 – the worst drought year recorded in the state since 1965 – also identified locations where cold-water species can persist under drought conditions (WebPanel 1). These data were incorporated into existing models (see ice.ecosheds.org for details on model development and specified uncertainty) to evaluate the effects of land use (eg agriculture, forest cover) and watershed characteristics (eg geology) on the resiliency of refugia under three warming scenarios. Preliminary results suggest that the number of sites across the state with >50% occurrence probability for cold-water species may decrease by 42–77% over the next 50 years in a warming (2–4°C) climate (Figure 3).

This effort identifies the potential future network of refugia, as well as the relative longevity of each potential refuge. Future efforts could incorporate data from recent climate projections (NECASC 2018), predicted flood stages, groundwater inputs, large-river temperature models, and water management (eg water withdrawals, stormwater inputs). Information on the environmental tolerances of additional cold-water species could be incorporated to evaluate the suitability of brook trout as an umbrella species – a species whose management will help to conserve other species using the same habitat. Our results suggest that brook trout models may represent some species (eg slimy sculpin [*Cottus cognatus*]) well, but not others (eg American brook lamprey [*Lethenteron appendix*]). While models are the only practical approach for identifying locations that may serve as refugia, scientists must clearly communicate the precision of and confidence in such models to decision makers, given the adverse economic and biological consequences of misidentifying locations.

Interactions between contemporary climate change and historical legacies

The spatial arrangement and availability of seasonal habitats, including foraging and spawning locations, will be critical



D Herasimtschuk/Freshwaters Illustrated



KN Edmonds



Figure 2. In temperate-latitude settings, climate refugia for freshwater fishes have been identified in (a) groundwater- or snowmelt-dominated systems (McKenzie River, Oregon); (b) forested watersheds with topographic complexity (Great Smoky Mountains, North Carolina); and (c) alluvial aquifer connectivity and floodplain structural complexity (Upper Talarik Creek, Alaska). Processes (eg groundwater availability, seasonal snowmelt) are often interdependent, and freshwater systems associated with various landforms (eg mountains, alluvial plains) may be influenced by different processes to varying degrees.

for climate refugia to provide the full suite of resources necessary to better ensure population persistence. Furthermore, refuges (Panel 1) that provide seasonal shelter from episodic

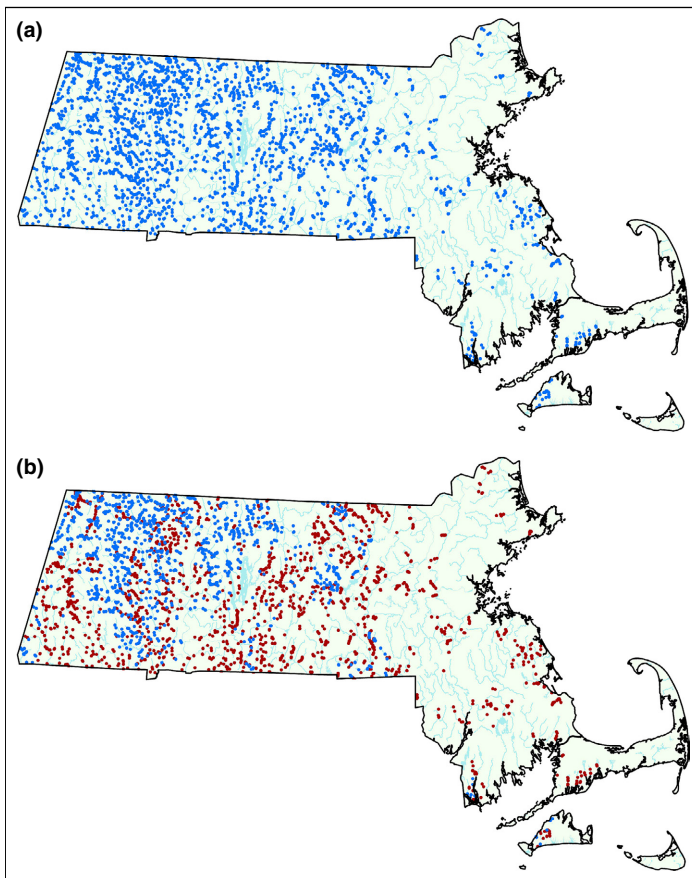


Figure 3. Distribution of cold-water refuges (blue circles) under (a) current conditions and (b) a modeled warming scenario of a 4°C increase in average July air temperatures. Red circles indicate existing cold-water refuges likely to lose cold-water habitat in summer months. Reductions in cold-water habitats associated with the 4°C warming scenario may occur by the 2070s (Bradley *et al.* 2018). Data from the Massachusetts Division of Fisheries and Wildlife and ice.ecosheds.org.

disturbances like floods and droughts, or that help segregate fish populations from stressors such as disease and invasive species, will enhance the refugial function of stream networks (Figure 4). Yet the combined effects of land- and water-use legacies with climate change have altered, disconnected, or

otherwise reduced refugial function in many freshwater habitats by increasing exposure, enhancing sensitivity, and reducing the adaptive capacity of vulnerable populations (Figure 5, a and b; Sedell *et al.* 1990).

Fundamentally, refugia for freshwater fish require the presence of water. This is well illustrated by river systems in mediterranean climate regions, where water in isolated refugia during seasonal droughts defines the distribution and population dynamics of fishes (reviewed by Filipe *et al.* [2013]). In many areas, however, natural drought is being exacerbated by water overallocations (WebPanel 2; Lall *et al.* 2018). In addition, impacts associated with water availability and low summer streamflows, along with warmer water temperatures (Arismendi *et al.* 2013), are compounded by land-use legacies that have altered freshwater habitats (Steel *et al.* 2016). In the US Pacific Northwest, for example, the lowland coastal rivers where coho salmon (*Oncorhynchus kisutch*) were once abundant are currently too warm to support salmonids in the summer months due largely to conversion of wetlands to agriculture, and to constraints imposed by the presence of roads and levees (Beechie *et al.* 1994). In response, centers of coho salmon reproduction have shifted to smaller streams on forested lands higher in the watersheds, areas that may be less conducive to salmon production and that have also been substantially altered by past forestry activities that resulted in simplified stream channels (Steel *et al.* 2016). In the eastern US, brook trout have been similarly pushed into headwater systems and away from more productive downstream rivers (Petty *et al.* 2014). The dendritic (branched, tree-like) nature of watersheds means that headwater constriction of suitable habitats will inherently fragment populations as they are pushed into tributary branches by downstream warming and habitat alteration. Habitat loss will be compounded as those same headwater habitats lose streamflow due to the increasing probability of more frequent summer droughts. Moreover, land uses that have exacerbated the adverse effects of floods and sedimentation additionally restrict fish populations to hydrologically intact refugia. Facing such constraints, efforts to identify “anchor habitats” potentially serving as refugia for Pacific Northwest salmon (Pinsky *et al.* 2009) and eastern brook trout (ice.ecosheds.org) are focusing

Panel 1. Refuges and refugia

Highly mobile species such as salmon or migratory songbirds require the presence of habitats and resources at specific locations at the appropriate times. Relatively small portions of a mobile species' overall range can be disproportionately critical for providing resources at essential times; examples include nesting habitats for sea turtles, seasonal wetlands for migratory waterfowl, or short-term refuge habitats from drought or extremes in temperature. Consequently, climate-change refugia for such species may be more generally defined as the suite of habitats and resources required over a species' life cycle that are relatively buffered from contemporary climate change and that allow the species to persist over longer time scales (see glossary in Morelli *et al.*'s [2020] WebPanel 1). Cold-water

fishes reliant on headwater refugia for reproduction and rearing may be temporarily dependent on thermal refuges at cold-water tributary mouths as they move through thermally stressful river corridors during seasonal migrations (Keefer *et al.* 2009). Similarly, seasonal refuges from floods and droughts provided by low-velocity tributaries or perennial stream segments, respectively, can be critical for persistence of flow-sensitive species in hydrologically variable streams (Figure 4). Therefore, small temporary shelters from exposure or disturbance that act as refuges, while insufficient alone at supporting population persistence in the face of climate change, may play vital supplemental roles in supporting overall climate refugia for mobile species.

on those watersheds with spatial connectivity among intact watershed components that provide the full suite of resources required for year-round population persistence.

■ Actionable refugia: challenges and opportunities for refugia management

After potential refugia have been identified, mapped, and validated, managers are faced with the difficult process of evaluating and prioritizing refugial features for specific actions (Morelli *et al.* 2016). Needs and considerations beyond those associated with the species targeted by refugial planning will come into play, including logistical constraints imposed by land ownership, valuation of trade-offs, and relative certainty in scientists' ability to predict refugium longevity. It will also be important to anticipate appropriate ways to manage for transitions and connectivity among refugia, assuming that environmental conditions will exceed species' envelopes within transitional refugia given sufficient time and rate of change (Morelli *et al.* 2020). Effective planning will require informed modeling to identify workable solutions to meet diverse needs under far-from-optimal conditions. In the following sections we describe several examples that highlight management approaches currently in operation.

Opportunities under constraint: making the best of a bad situation

Faced with the realities of an ever-increasing human footprint (Steffen *et al.* 2015), resource managers who are planning refugia for vulnerable fishes must capitalize on opportunities (Williams *et al.* 2015). Climate adaptation, to the degree it is considered by local and regional governments, often prioritizes human infrastructure and the needs of agriculture, energy, and transportation over species conservation, further imperiling biodiversity through indirect means (Turner *et al.* 2010). In many cases, climate adaptation planning for biodiversity may be an afterthought, if it is considered by regional authorities pressed by human economic demands. This could reflect in part insufficient communication that intact and functioning freshwater systems provide humans with various benefits including clean water, food, and flood control (Baron *et al.* 2002). In such a context, efforts to conserve climate refugia could benefit not only from adaptation strategies that address both human and environmental needs, but also from creative and effective communication strategies that inform decision makers and members of the public about the ecosystem goods and services associated with protected refugia.

Staying out of hot water: using real-time data to provide refugia for fish

During the past decade, high water temperatures have resulted in fish kills in several river systems. For example, in summer 2009, reduced flows in Fifteenmile Creek, a tributary of the Columbia River, increased temperatures beyond the lethal range

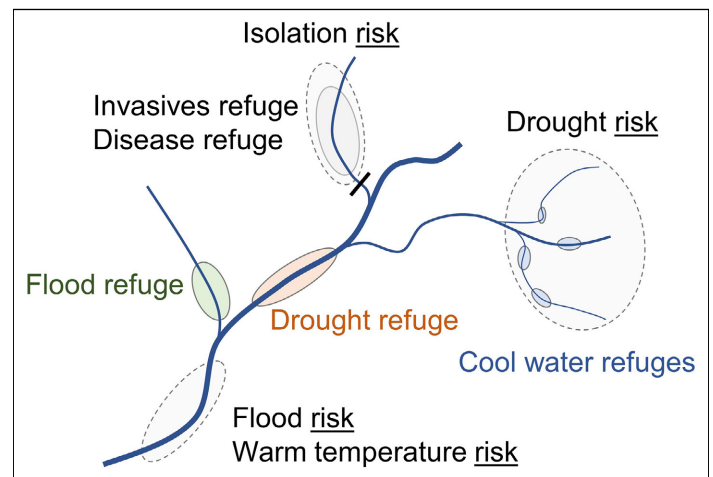


Figure 4. Refuge habitats (solid ellipses) for cold-water fishes provide short-term shelter from risks (dashed ellipses), but are also critical for long-term species persistence within the stream network that, as a whole, constitutes a climate refugium. Areas of risk can encompass refuge habitats of similar or contrasting risk within them (eg cold-water refuges nested within the drought-risk portion of the stream network). In addition, a refuge from invasives created by the presence of a barrier (black bar) that prevents invasion by predators or diseases can also potentially be encompassed by an isolation risk if the isolated population is too small to persist in the face of stochastic (random) disturbance events within the watershed.

for steelhead trout (*Oncorhynchus mykiss*), a US Endangered Species Act (ESA)-listed species, resulting in mortality of thousands of juveniles. This event prompted local farmers, state agencies, non-profit organizations, and the local Watershed Council to explore options for improving water quality and quantity while maintaining agricultural productivity. The outcome was adoption of the Fifteenmile Action to Stabilize Temperature (FAST), a program intended to balance the needs of fish and farmers. Under FAST, the State uses a predictive model that combines weather and streamflow data to forecast water temperatures; when the model projects that stream temperatures will exceed the threshold for steelhead survival, an automatic call to irrigators is triggered, indicating the need to reduce water withdrawals. Participation in the program is voluntary and irrigators are compensated. Modeling by the State suggests that reducing withdrawals lowers stream temperatures by at least 0.9°C. In 2015, Oregon experienced one of its worst droughts, with numerous fish kills occurring throughout the state (OEM and OWRD 2016) but there were no documented fish kills in Fifteenmile Creek – at the time subject to FAST – despite two drought alerts spanning a total of 16 days.

Meeting needs for humans and fish: water capture, storage, and release

Maintaining climate refugia for aquatic species will require water – specifically, clean and cold water. As illustrated above, water availability will likely be a serious constraint for climate-effective planning. Perception of water crises is often

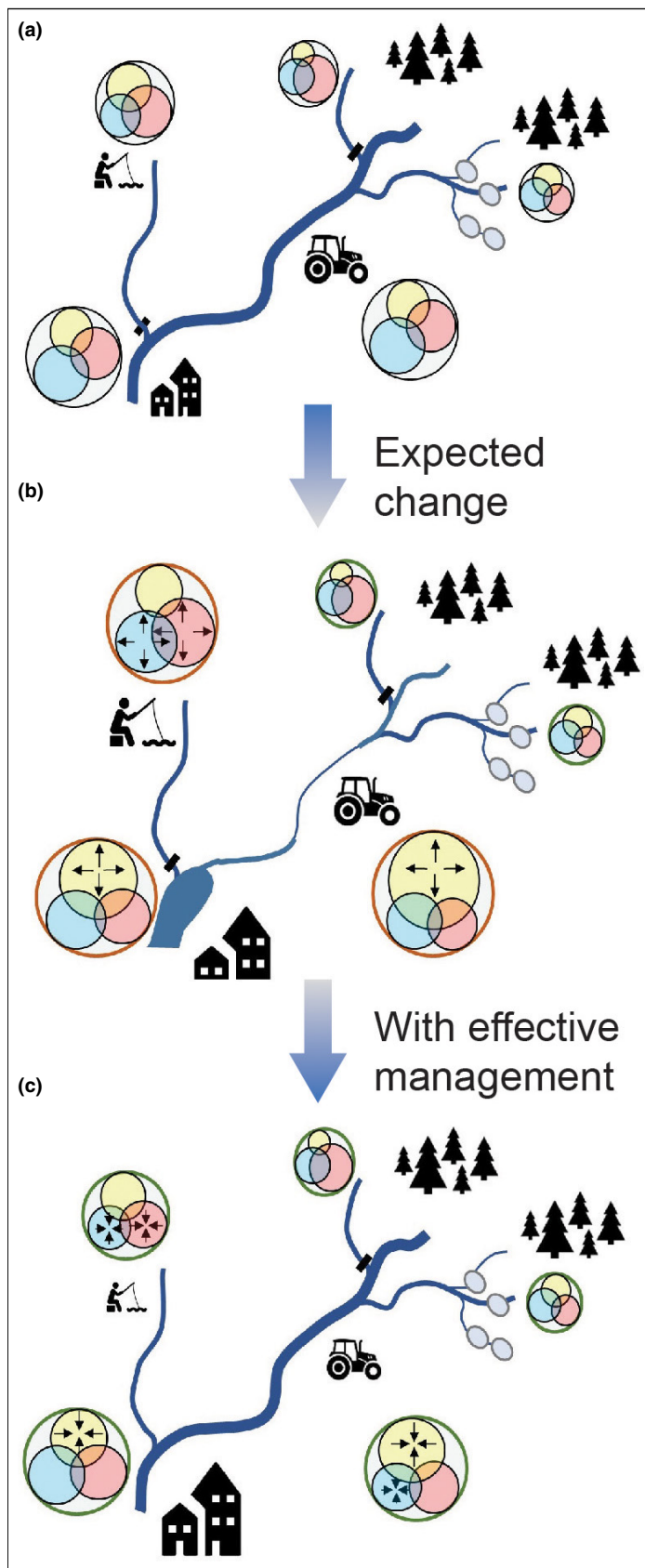


Figure 5. Refugia management involves first (a) assessing current ecosystem services, fish population status, and associated human impacts; and then (b) identifying overall climate-change vulnerability (large outer circles), here represented by the sum of the three vulnerability elements *exposure* (yellow circles), *sensitivity* (blue circles), and *adaptive capacity* (pink circles) (adapted from Kovach *et al.* [2019]). Vulnerability element circles increase in size with greater exposure, with enhanced sensitivity, or with *reduced* adaptive capacity, resulting in greater overall vulnerability (represented by larger outer circle). Potential refugia (vulnerability circles with an orange outline) are those that could function as refugia if there were a change in management strategy; current refugia (vulnerability circles with a green outline) are those that may require protection to continue functioning as refugia. (c) Refugial management incorporates an understanding of existing and potential land/water/fish management trade-offs to develop actions that reduce exposure or sensitivity while maintaining adaptive capacity in key areas and at key times.

contributing to isolation and fragmentation, which has led to the ESA listing of numerous migratory fish populations (NRC 1996). Despite the associated environmental impacts, calls for engineering approaches to address water crises will continue, and will require assessment of trade-offs (Poff *et al.* 2003). Reservoirs or aquifer storage add capacity to hold water during periods of high runoff for release during times of need, providing control over the timing and quantity of water delivery to downstream users. These regulated flows can be used to meet human or ecological needs (Adams *et al.* 2017). Some of the ecological impacts of water storage projects can be foreseen and mitigated, but careful monitoring to evaluate success and detect the emergence of unanticipated, adverse effects will be essential. For example, because water thermally stratifies within deep reservoirs (producing a bottom layer of cold water), releases from dams with selective withdrawal capability can influence temperatures for the potential benefit of downstream species (WebPanel 3), but can also interrupt flows of sediment and alter water chemistry (Poff *et al.* 2003). Water releases from smaller, run-of-river dams and reservoirs can often operate with relatively minor water storage and flow diversion, but may substantially increase downstream temperatures. Cold-water fishes in systems with smaller reservoirs could benefit from dam removal to provide better access to climate refugia and to further improve instream flow and sediment conditions (Stanley and Doyle 2003).

While construction and development of storage reservoirs is frequently promoted in response to water needs, managers are increasingly incorporating natural infrastructure and the ecosystem services provided by watersheds into management strategies. Managing forests or wetlands for clean water can be sustainable and economically viable, provide a host of additional benefits (eg flood control), and minimize some of the negative consequences of hard infrastructure approaches to water regulation. Similarly, headwater meadows and beaver (*Castor canadensis*)-pond complexes can provide valuable natural-infrastructure water storage services (Tague *et al.* 2008). Re-establishment of beaver populations is increasingly being used to restore wet-meadow hydrologic function (Beechie *et al.* 2013).

accompanied by pleas for additional reservoir storage. The well-known adverse ecological effects of dams on fish populations can be extreme, resulting in species extirpation or

Ecosystem models that link societal benefits to forest management options are being used to inform community forest management for timber production and streamflow for salmon (WebPanel 4). Such efforts to “put nature to work” are recognizing and highlighting the important ecosystem services that watersheds provide across the landscape on a daily basis.

■ Aligning management and overcoming institutional constraints

Effective application of climate refugia for freshwater fishes requires an expanded view that (1) considers exposure beyond temperature, incorporates sensitivity and adaptive capacity, and includes human use and resource management into the mapping of refugia; (2) seeks to reduce institutional misalignment; and (3) takes into account the past and present institutional settings of water and resource allocation, and seeks to improve the flexibility of these frameworks to adapt to current realities.

Identifying current and potential refugia is a key step for informing management, but ideally this involves more than simply mapping locations based on certain single-species criteria (eg water temperature for salmonids). During this process, we suggest that researchers and managers attempt to address several key questions, such as: what and where are the relevant ecosystem services in the basin? What other demands exist for those services? What are the management processes and legal/institutional constraints that influence the delivery of those services (exposure), increase sensitivity, or reduce adaptive capacity (Figure 5a)? How will climate change impact service delivery and/or demand? And, what are the exposure thresholds for the most sensitive (representative) species (Figure 5b)? Beyond identifying refugial locations for the most climate-sensitive species, managers – by answering these questions – will be better equipped not only to understand what changes are needed basinwide to reduce exposure and sensitivity and to simultaneously maintain adaptive capacity (Figure 5c), but also to uncover the complexity of riverscapes as socioecological systems and identify critical human dimensions that need to be addressed (Dunham *et al.* 2018).

Ultimately, success will depend upon reconciling potentially misaligned management objectives between the institutions that manage land, water, and fish. Management decisions for these resources occur at various levels, involving landowners; water-right holders; federal, tribal, state, and local government regulators; and government and non-governmental organizations that engage in voluntary protection or restoration of habitat. The general lack of coordination

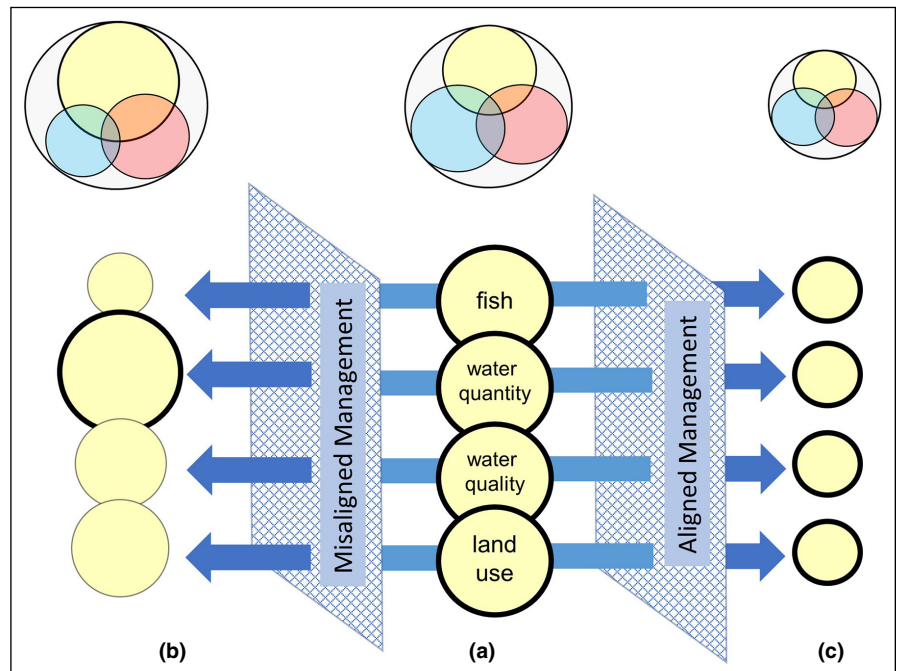


Figure 6. Aligning stakeholder goals is key to successful refugia management. (a) Each vulnerability element (exposure, sensitivity, and adaptive capacity; see Figure 5) is influenced by fish, water quality, water quantity, and land-use management sub-elements; the relative size of each element reflects the largest sub-element (bold circles). (b) Illustrates a case where the institutions managing each exposure sub-element do not share the same goals for refugia, and exposure is increased due to failure to address sources of water quantity limitation such as water withdrawals. (c) Illustrates a case where there is institutional alignment and a common goal of creating and managing for refugial services; in this instance, exposure is reduced across all sub-elements, thereby reducing overall vulnerability.

that may exist across this diffuse multi-regulator/stakeholder structure may impede the implementation of a strategic approach to protecting or restoring climate refugia. Because different governmental agencies often have different (and occasionally incompatible) objectives for managing resources, this may result in conflicting and unbalanced outcomes as well as suboptimal resource use. By aligning objectives within a given geographical area, agencies could then help to manage resources with competing uses in a consistent and optimal manner (Figure 6). By designating the underlying objectives for resource use in an area, the various agencies – now institutionally aligned – may be better positioned to apply their authorities/incentives toward fulfilling those objectives, and in so doing help to rectify many issues related to increased demand for natural resources.

Adapting past frameworks to meet today's challenges

It may be important to consider how the applicable laws and agency jurisdiction governing land use and water rights affect the ability to manage refugia. This ability may depend on (1) the historical context that gave rise to the laws and policies governing land and water use: for example, the riparian water doctrine that governs water rights in many eastern US states has origins dating back to Ancient Roman times and

is based on English common law, whereas the prior appropriation doctrine for water rights practiced in many western states has origins in the California Gold Rush during which the first person to post a sign held the rights (Johnson and DuMars 1989); (2) the flexibility of the frameworks and policies to reflect current conditions; and (3) the institutional capacity to review and revise laws, policies, and/or incentive frameworks (Dunham *et al.* 2018). A formal review of these factors may be needed to determine whether effective management of refugia will be possible. Each jurisdiction may need to tailor solutions that capitalize on opportunities given unique social, legal, and administrative constraints (eg individual agency mandates). Where current laws and associated administrative processes are inadequate to achieve protection of refugia, consideration could be given toward revising policy approaches. When implementing changes to existing legal frameworks, there are several common themes that have emerged across jurisdictions that may improve the likelihood of successfully protecting refugia, including (1) a means to designate areas for protection and/or management as refugia; (2) a means to incentivize management of land and water for refugial services, or otherwise avoid constraining private land property rights and water rights; (3) ensuring that groundwater and surface water are managed together, and that land and water are managed together; (4) allowing for the creation of environmental water rights (ie the right to leave water in-river); and (5) ensuring water use is measured and reported. Beyond the legal frameworks, administrative processes may need to identify the resource uses that may affect refugia and policies to address potential conflicts. Included in these policies are guidelines that facilitate buffering, optimize connectivity, maintain or enhance adaptive capacity, and incentivize use of innovative management tools to accomplish goals.

■ Conclusions

Tomorrow's climate refugia managers will face daunting challenges given (1) an expanding human footprint and (2) the social and institutional barriers that may prevent progress toward creation of integrated refugia networks. Formal mechanisms to balance demands and determine appropriate allocation of natural resources for climate refugia management could be useful at many levels of governance. Integrated refugia networks may be an effective option for vulnerable populations/species in jurisdictions where there is adequate support for changes. As the impacts of climate change become more pronounced on all sectors, there may be increased social pressure to address these barriers, which may provide opportunities for managers to gain further support for change.

■ Acknowledgements

Publication of this Special Issue was funded by the US Department of the Interior National, Northeast, and

Northwest Climate Adaptation Science Centers. We acknowledge the continued contribution of the Climate Refugia Coalition to advancing the science of climate-change refugia. We thank C Barrows, J Markwiese, E Grant, J Vaughn, A Pakenham-Stevenson, and T Stahl for helpful comments on earlier drafts, and Jacob Ebersole for assistance with graphics. The views expressed in this article are those of the authors and do not necessarily represent the views or policies of the US Environmental Protection Agency (EPA) or the Oregon Department of Fish and Wildlife. Any mention of trade names, products, or services is for descriptive purposes and does not imply an endorsement by the US Government or the US EPA.

■ References

- Adams LE, Lund JR, Moyle PB, *et al.* 2017. Environmental hedging: a theory and method for reconciling reservoir operations for downstream ecology and water supply. *Water Resour Res* **53**: 7816–31.
- Arismendi I, Safeeq M, Johnson SL, *et al.* 2013. Increasing synchrony of high temperature and low flow in western North American streams: double trouble for coldwater biota? *Hydrobiologia* **712**: 61–70.
- Baron JS, Poff NL, Angermeier PL, *et al.* 2002. Meeting ecological and societal needs for freshwater. *Ecol Appl* **12**: 1247–60.
- Beechie TJ, Beamer E, and Wasserman L. 1994. Estimating coho salmon rearing habitat and smolt production losses in a large river basin, and implications for habitat restoration. *N Am J Fish Manage* **14**: 797–811.
- Beechie T, Imaki H, Greene J, *et al.* 2013. Restoring salmon habitat for a changing climate. *River Res Appl* **29**: 939–60.
- Beever EA, Hall LE, Varner J, *et al.* 2017. Behavioral flexibility as a mechanism for coping with climate change. *Front Ecol Environ* **15**: 299–308.
- Blum AG, Kanno Y, and Letcher BH. 2018. Seasonal streamflow extremes are key drivers of brook trout young-of-the-year abundance. *Ecosphere* **9**: e02356.
- Bradley R, Karmalkar A, and Woods K. 2018. How will global warming of 2°C affect Massachusetts? Observed and projected changes in climate and their impacts. Amherst, MA: Climate System Research Center, University of Massachusetts Amherst.
- Dunham JB, Angermeier PL, Crausbay SD, *et al.* 2018. Rivers are social-ecological systems: time to integrate human dimensions into riverscape ecology and management. *WIREs Water* **5**: e1291.
- Ficke AD, Myrick CA, and Hansen LJ. 2007. Potential impacts of global climate change on freshwater fisheries. *Rev Fish Biol Fisher* **17**: 581–613.
- Filipe AF, Lawrence JE, and Bonada N. 2013. Vulnerability of stream biota to climate change in mediterranean climate regions: a synthesis of ecological responses and conservation challenges. *Hydrobiologia* **719**: 331–51.
- Foden WB, Butchart SHM, Stuart SN, *et al.* 2013. Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. *PLoS ONE* **8**: e65427.

- Fullerton AH, Burke BJ, Lawler JJ, *et al.* 2017. Simulated juvenile salmon growth and phenology respond to altered thermal regimes and stream network shape. *Ecosphere* **8**: e02052.
- Goode JR, Buffington JM, Tonina D, *et al.* 2013. Potential effects of climate change on streambed scour and risks to salmonid survival in snow-dominated mountain basins. *Hydrol Process* **27**: 750–65.
- Groot C and Margolis L (Eds). 2003. Pacific salmon life histories. Vancouver, Canada: UBC Press.
- Hall B, Motzkin G, Foster DR, *et al.* 2002. Three hundred years of forest and land-use change in Massachusetts, USA. *J Biogeogr* **29**: 1319–35.
- Hastie LC, Cosgrove PJ, Ellis N, *et al.* 2003. The threat of climate change to freshwater pearl mussel populations. *AMBIO* **32**: 40–47.
- Hayhoe K, Wake CP, Huntington TG, *et al.* 2007. Past and future changes in climate and hydrological indicators in the US Northeast. *Clim Dynam* **28**: 381–407.
- Hodgkins G, Dudley R, and Huntington T. 2003. Changes in the timing of high river flows in New England over the 20th century. *J Hydrol* **278**: 244–52.
- Hudy M, Thieling TM, Gillespie N, *et al.* 2008. Distribution, status, and land use characteristics of subwatersheds within the native range of brook trout in the eastern United States. *N Am J Fish Manage* **28**: 1069–85.
- Isaak DJ, Young MK, Nagel DE, *et al.* 2015. The cold-water climate shield: delineating refugia for preserving salmonid fishes through the 21st century. *Glob Change Biol* **21**: 2540–53.
- Johnson NK and DuMars CT. 1989. A survey of the evolution of western water law in response to changing economic and public interest demands. *Nat Resources J* **29**: 347–87.
- Keefer ML, Peery CA, and High B. 2009. Behavioral thermoregulation and associated mortality trade-offs in migrating adult steelhead (*Oncorhynchus mykiss*): variability among sympatric populations. *Can J Fish Aquat Sci* **66**: 1734–47.
- Kovach RP, Dunham JB, Al-Chokhachy R, *et al.* 2019. An integrated framework for ecological drought across riverscapes of North America. *BioScience* **69**: 418–31.
- Lall UT, Johnson P, Colohan A, *et al.* 2018. Water. In: Reidmiller DR, Avery CW, Easterling DR, *et al.* (Eds). Impacts, risks, and adaptation in the United States: Fourth National Climate Assessment, vol II. Washington, DC: US Global Change Research Program.
- Lowe WH. 2012. Climate change is linked to long-term decline in a stream salamander. *Biol Conserv* **145**: 48–53.
- Lynch AJ, Myers BJE, Chu C, *et al.* 2016. Climate change effects on North American inland fish populations and assemblages. *Fisheries* **41**: 346–61.
- MCCS (Manomet Center for Conservation Sciences) and MassWildlife (Massachusetts Division of Fisheries and Wildlife). 2010. Climate change and Massachusetts fish and wildlife: habitat and species vulnerability, vol 2. Plymouth, MA: MCCS.
- Melillo JM, Richmond TC, and Yohe GW (Eds). 2014. Highlights of climate change impacts in the United States: the Third National Climate Assessment. Washington, DC: US Global Change Research Program.
- Milly PCD, Dunne KA, and Vecchia AV. 2005. Global pattern of trends in streamflow and water availability in a changing climate. *Nature* **438**: 347–50.
- Moore MV, Pace ML, Mather JR, *et al.* 1997. Potential effects of climate change on freshwater ecosystems of the New England/Mid-Atlantic region. *Hydrol Process* **11**: 925–47.
- Morelli TL, Barrows CW, Ramirez AR, *et al.* 2020. Climate-change refugia: biodiversity in the slow lane. *Front Ecol Environ* **18**: 228–34.
- Morelli TL, Daly C, Dobrowski SZ, *et al.* 2016. Managing climate change refugia for climate adaptation. *PLoS ONE* **11**: e0159909.
- Moyle PB, Kiernan JD, Crain PK, *et al.* 2013. Climate change vulnerability of native and alien freshwater fishes of California: a systematic assessment approach. *PLoS ONE* **8**: e63883.
- NECASC (Northeast Climate Adaptation Science Center). 2018. Massachusetts climate change projections. Amherst, MA: NECASC, University of Massachusetts Amherst.
- NRC (National Research Council). 1996. Upstream: salmon and society in the Pacific Northwest. Washington, DC: National Academies Press.
- OEM (Oregon Office of Emergency Management) and OWRD (Oregon Water Resources Department). 2016. Drought annex: State of Oregon emergency operations plan. Salem, OR: OEM and OWRD.
- Palmer MA, Lettenmaier DP, Poff NL, *et al.* 2009. Climate change and river ecosystems: protection and adaptation options. *Environ Manage* **44**: 1053–68.
- Petty JT, Thorne D, Huntsman BM, *et al.* 2014. The temperature–productivity squeeze: constraints on brook trout growth along an Appalachian river continuum. *Hydrobiologia* **727**: 151–66.
- Pinsky ML, Springmeyer DB, Goslin MN, *et al.* 2009. Range-wide selection of catchments for Pacific salmon conservation. *Conserv Biol* **23**: 680–91.
- Poff NL, Brinson MM, and Day Jr JW. 2002. Aquatic ecosystems and global climate change – potential impacts on inland freshwater and coastal wetland ecosystems in the United States. Washington, DC: Pew Center.
- Poff NL, Allan JD, Palmer MA, *et al.* 2003. River flows and water wars: emerging science for environmental decision making. *Front Ecol Environ* **1**: 298–306.
- Rahel FJ, Bierwagen B, and Taniguchi Y. 2008. Managing aquatic species of conservation concern in the face of climate change and invasive species. *Conserv Biol* **22**: 551–61.
- Sedell JR, Reeves GH, Hauer FR, *et al.* 1990. Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. *Environ Manage* **14**: 711–24.
- Stanley EH and Doyle MW. 2003. Trading off: the ecological effects of dam removal. *Front Ecol Environ* **1**: 15–22.
- Staudt A, Leidner AK, Howard J, *et al.* 2013. The added complications of climate change: understanding and managing biodiversity and ecosystems. *Front Ecol Environ* **11**: 494–501.
- Steel EA, Muldoon A, Flitcroft RL, *et al.* 2016. Current landscapes and legacies of land-use past: understanding the distribution of juvenile coho salmon (*Oncorhynchus kisutch*) and their habitats along the Oregon Coast, USA. *Can J Fish Aquat Sci* **74**: 546–61.
- Steffen W, Broadgate W, Deutsch L, *et al.* 2015. The trajectory of the Anthropocene: the great acceleration. *Anthropocene Rev* **2**: 81–98.
- Tague C, Valentine S, and Kotchen M. 2008. Effect of geomorphic channel restoration on streamflow and groundwater in a snowmelt-dominated watershed. *Water Resour Res* **44**: W10415.

- Turner WR, Bradley BA, Estes LD, *et al.* 2010. Climate change: helping nature survive the human response. *Conserv Lett* **3**: 304–12.
- Walters AW, Mandeville CP, and Rahel FJ. 2018. The interaction of exposure and warming tolerance determines fish species vulnerability to warming stream temperatures. *Biol Lett-UK* **14**: 20180342.
- Williams J, Isaak D, Imhof J, *et al.* 2015. Cold-water fishes and climate change in North America. *Ref Mod Earth Syst Environ Sci*; doi.org/10.1016/B978-0-12-409548-9.09505-1.

■ Supporting Information

Additional, web-only material may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/fee.2206/supinfo>

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.



The gleam of a Grim Reaper

Crab spiders ambush pollinating insects by settling on flowers and lying motionless in wait. Although it is generally believed that the spiders use camouflage by matching coloration against floral backgrounds, bees that have co-evolved with such spiders can potentially detect the presence of crab spiders, and therefore avoid them. In this evolutionary arms race, some crab spiders have probably evolved to manipulate flower signals. In fact, some crab spiders are known to reflect brightly in the ultraviolet (UV) spectrum and make the flowers more attractive for pollinators (*Nature* 2003; doi.org/10.1038/421334a). Here, we observed the conspicuous fluorescence of a crab spider

(*Misumenops tricuspidatus*) under UV light as it sat on an *Erigeron annuus* flower.

Fluorescent pigments glow by absorbing UV light and re-emitting it at longer wavelengths. Some animals use not only UV reflectance but also UV-induced fluorescence as a communication signal. Because many insects are particularly sensitive to wavelengths in the green and blue spectrum within which the crab spider fluoresces, flowers harboring the spider probably attract more pollinators because of the fluorescence signal. If this is the case, crab spiders can use a “double trick” (ie UV reflectance and UV-induced fluorescence) to assist in prey capture. It is worth investigating whether fluorescence in crab spiders functions as a signal to attract prey, or is simply a by-product of pigment molecules.

Kenji Suetsugu¹ and Takuya Morihisa²
¹Kobe University, Hyogo, Japan; ²Shimane, Japan
 doi:10.1002/fee.2212

