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The use of umbrella fish species to provide a more comprehensive approach for freshwater conservation management

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Abstract

1) Where freshwater species populations are in decline, conservation management requires rapid, cost-effective approaches to develop recommendations, particularly at broad geographical scales or where species-specific information is lacking. The umbrella species approach, typically applied to terrestrial taxa, is one potentially useful option to inform large-scale freshwater management efforts.

2) A quantitative, integrated approach is proposed for selecting suites of umbrella fish species over diverse spatial scales using a combination of species ranges, life-history traits, and species vulnerability scores. The approach also uses expert opinion to validate methods and results.

3) This approach was applied to native fishes in California and results for two river basins are explored in the context of instream flow management. These examples illustrate how the results could help address two common instream flow management challenges in California: (i) the lack of information related to species-specific flow requirements in basins with many species, and (ii) the need to move beyond a single species approach to flow management. In addition, the results indicate that the protection of native fishes in California would provide co-benefits for other aquatic and riparian taxa.

4) A key benefit of this approach is that the data used to select suites of umbrella species (e.g. species ranges, life-history traits, climate vulnerabilities) are widely available at varying degrees of specificity for most freshwater fishes. Therefore, this flexible approach could be applied in other regions to aid managers in making freshwater conservation decisions, such as for instream flow strategies, in an efficient and cost-effective manner.

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Keywords

biodiversity, fish, habitat management, indicator species, river, stream, environmental flows, instream flows

1. INTRODUCTION

Globally, freshwater species are experiencing population declines that outpace those in most terrestrial and marine systems (Reid et al., 2019; Tickner et al., 2020). Given this scale of loss, protecting and managing freshwater species at broad spatial scales over diverse environmental conditions is necessary, albeit challenging. In river systems in particular, determining streamflow requirements (i.e. instream flows) for fish communities while also allowing for human water use is often time- and data-intensive. As a result of these challenges, rapid and cost-effective approaches to developing freshwater conservation management priorities and recommendations, such as instream flow strategies that support entire fish communities across large geographical scales, would be beneficial.

One such approach that could address this challenge for freshwater fish conservation is the use of umbrella species, where conservation focus on a single species provides a protective 'umbrella' to numerous co-occurring species (Fleishman, Murphy & Brussard, 2000; Roberge & Angelstam, 2004; Branton & Richardson, 2014). This concept can guide management recommendations when detailed information on other species at a particular location is unavailable, or when it is too costly or time consuming to collect data on co-occurring species individually (Fleishman, Murphy & Brussard, 2000; Fleishman, Blair & Murphy, 2001). However, despite being described extensively, the umbrella species concept has rarely been implemented in practice, has achieved varying degrees of success when implemented, and has been subject to criticism (Bifolchi & Lodé, 2005). For example, although some studies have found the approach to be useful (Fleishman, Blair & Murphy, 2001), others have found mixed results (Caro, 2003; Bifolchi & Lodé, 2005). Furthermore, this concept has rarely been explored or implemented in freshwater systems (Wenger, 2008; Branton & Richardson, 2014).

Despite these challenges, some studies indicate that the selection of a suite of umbrella species or taxa, rather than a single species, may be particularly effective as a conservation strategy, especially at large spatial scales (Sanderson et al., 2002; Roberge & Angelstam, 2004; Khosravi & Hemami, 2019; Magg, Ballenthien & Braunisch, 2019). Criteria used to select umbrella species have included spatial area requirements, ecological function, and vulnerability (e.g. climate vulnerability) (Coppolillo et al., 2004; Roberge & Angelstam, 2004). A growing body of literature indicates that umbrella species can protect target groups if they are selected using relevant, quantitative, and uniform criteria (Carroll, Noss & Paquet, 2001; Favreau et al., 2006; Branton & Richardson, 2014; Li & Pimm, 2016; Maslo et al., 2016). For example, Coppilillo et al. (2004) scored terrestrial species in two distinct biogeographical areas to determine optimal umbrella species, using five criteria categories (area, heterogeneity, vulnerability, ecological functionality, and socio-economic significance). However, in most cases, these criteria have rarely been used in the conservation planning process and have instead been used retrospectively to evaluate the benefits associated with the protection of imperilled species (Fleishman, Murphy & Brussard, 2000; Maslo et al., 2016). Umbrella species have also been frequently selected because of their listing status, which can trigger regulatory action and conservation protections (Maslo et al., 2016), rather than their ability to represent other co-occurring species. As a result, criteria used for the selection of umbrella species has been inconsistent and often subjective, leading to uncertainty in their application and effectiveness.

This paper describes an approach for selecting a suite of umbrella fish species, which can be applied over large and physically diverse spatial scales and can directly inform freshwater conservation and associated streamflow management. Data types commonly available for freshwater fishes (e.g. species ranges, life-history traits, vulnerabilities) were used to select a suite of umbrella species that can address specific management concerns related to the identification of streamflow targets (i.e. instream flows), and a range of experts were invited to validate the methods and results.

This approach was applied across the state of California, which contains a diverse assemblage of native fishes (Quiñones & Moyle, 2015), 79% of which are endemic (Grantham et al., 2017). A key management concern and conservation strategy in California's river systems is the development of instream flow regimes that provide sufficient quantity of flow at the appropriate times of year to support native species. Historically, the development of these recommendations has been limited by data availability, time, and monetary resources, and management efforts have typically defaulted to an approach focused on the instream flow needs for a single sensitive or endangered species (Poff, 2009). In addition, streamflow management has been fragmented, efforts have lacked regional coordination, and recommendations have been developed on a stream-by-stream or species-by-species basis. Recent work (e.g. Grantham et al., 2017) highlights the need for statewide, coordinated efforts to address freshwater fish conservation. The applicability of this approach for streamflow management is then assessed for two river basins in California with differing management concerns. The potential for wider application of the method for other geographical regions is also discussed.

2. METHODS

2.1 Overview

Objective criteria for selecting a relevant suite of umbrella fish species were developed, using three types of data: species range maps, life-history traits, and climate vulnerability scores. To select a suite of umbrella species, a spatial clustering analysis on species range data was performed to divide regions into smaller-scale assemblages appropriate for management efforts at the river basin or sub-river basin scale. Within each region, species life history, habitat preference, and physiological tolerance traits were used to group species with similar characteristics using hierarchical clustering. Each species was then scored according to their vulnerability to climate change (highly vulnerable = 1, least vulnerable = 4) and data availability (well-studied species = 1, little known about species = 4) in order to select an umbrella species for each trait-based group. Together, the spatial and trait-based clustering produced a compilation of suites of umbrella species representative of fish assemblages within each region of the state (Figure 1).

2.2 Spatial clustering to determine regional species assemblages

2.2.1 Species ranges

To determine regional fish assemblages across California, native fish distribution data were obtained from the PISCES database (Santos et al., 2014) at the United States Geologic Survey (USGS) hydrologic unit code (HUC) 12 scale. Only current species ranges were included; historical ranges and areas where translocations have occurred were excluded. To select species for analysis, the flow sensitive species list developed by Grantham, Viers & Moyle (2014) was expanded, as conservation measures for fish in California are largely related to instream flow management. The selected species were defined by having a component of their life history susceptible to altered flow regimes (Grantham, Viers & Moyle, 2014). The list of species used in the analysis is provided in Appendix A. The term 'species' hereafter refers to species or subspecies, whichever was the finest taxonomic resolution available for the analysis.

2.2.2 Developing geographical boundaries for spatial clustering

California was divided into four geographical regions each with distinct climates and topographies for spatial clustering. These regional divisions were used to prevent areas with high species richness from dominating the cluster analysis described below. Regions were created by combining HUC 4-level basin units, so that river basins remained connected within general geographical regions (Figure 2). All HUC 12-level basin units not containing native fishes or generally depauperate native fish assemblages (fewer than three species present) were excluded from clustering because streamflow management in these areas is typically single-species focused. Areas excluded from analysis included the highest elevations of the Sierra Nevada range, portions of the Modoc plateau in north-eastern California, portions of the southern east slope of the coast range, and the south-eastern desert region of the state. HUC 12 units in the immediate vicinity of the San Francisco Bay and the legal Sacramento/San Joaquin Delta were also excluded, because this area has unique management considerations as a result of its highly managed and degraded nature, and is subject to specific regulatory processes (Alexander et al., 2018). The regions described here were used solely as the input boundaries for spatial clustering and are at too large a scale for management recommendations or actions.

2.2.3 Species-level spatial clustering within geographical regions

To generate species-level clusters within each geographical region, a spatial k-means clustering approach was applied, which created geographically contiguous clusters based on species ranges. Specifically, the Grouping Analysis tool in ArcGIS 10.5.1 was used, which uses a minimum spanning tree approach (Assunção et al., 2006) to identify fish assemblages within the four geographical regions of California. Spatial input data for HUC12s in each region was provided, which included attributes indicating presence or absence of each species. Presence was aggregated to species level, so that a species was included as ‘present’ in a HUC12 if any sub-species, distinct population segment, or ecologically significant unit (ESU) was present, according to PISCES. HUC12s where species of interest were absent were excluded. A range of cluster sets were evaluated (between 2-8) for each region, and an initial set of clusters was selected based on species groupings that were contiguous, and also optimized the number of species for streamflow management purposes (i.e. clusters with one or two species were not selected). These spatial groupings were defined as 'regional fish assemblages' and are at a scale appropriate for management recommendations.

2.3 Trait-based hierarchical clustering to determine suites of umbrella species

2.3.1 Species life-history traits data

Life-history trait data were obtained from the FishTraits database (Frimpong & Angermeier, 2009). FishTraits contained more than 100 trophic ecology, life history, habitat association, and tolerance traits for 731 native fishes in the United States. For California, the database contained information for ~70% of the species used in the analysis. For the remaining species not covered by FishTraits, information from Moyle (2002) was used to identify these traits manually. All traits in the database were used in the hierarchical clustering except those related to geographical range (e.g. latitudinal and longitudinal coordinates of species ranges) and conservation status (e.g. listing status, reason for listing), as this information was not appropriate for determining life-history similarity between species. Furthermore, geographical ranges were accounted for in the spatial clustering analysis, and vulnerabilities were taken into account during the scoring and selection process described below. A complete list of traits in the database is available in Frimpong & Angermeier (2009).

2.3.2 Hierarchical clustering on species traits data

A hierarchical cluster analysis was performed in R version 3.5.1 and RStudio version 1.1.463 using the hclust function in the stats package (R Core Team, 2018). This agglomerative clustering algorithm groups objects using a distance matrix and produces a hierarchy of clusters based on similarity within and across groups. The method was selected because the number of clusters did not need to be defined before the analysis (as required by similar clustering methods, e.g. k-means). Clustering was performed on species traits for all species within each geographical region using the complete linkage method (R Core Team, 2018). This allowed the identification of discrete groups of species within each region that shared the most similar life-history traits.

2.4 Umbrella species selection

To select suitable candidates as umbrella species within each trait-based group from the hierarchical clustering, species were scored using information about their vulnerability to climate change and the amount of data associated with each species. Climate change vulnerability was selected for scoring here to serve as a proxy of overall vulnerability or sensitivity. To determine vulnerabilities, scores developed by Moyle et al. (2013) were used. Moyle et al. (2013) scored all native fishes in California using a scaled suite of 10 vulnerability metrics, including metrics related to physiological tolerance, vulnerability to extreme weather events, and ability to shift habitat ranges. In order to assess data availability associated with species in the analysis, scores from Moyle, Katz & Quiñones (2011) were also used, which contained criteria related to how well-studied individual species were. Together, these criteria were used to select species vulnerable or sensitive to climate change, and also to select species sufficiently studied that could inform management efforts. Candidates for umbrella species were identified as those that were both highly vulnerable to climate change and relatively well studied (e.g. significant data associated with the species and/or their response to environmental stressors). Scores for each trait-based group of species within each region were tabulated to select final suites of umbrella species. Suites of species were selected to encapsulate the diverse needs of several vulnerable or sensitive species. This process allowed the selection of the most vulnerable and well-studied species from each trait-based group, providing a suite of umbrella species with diverse traits.

2.4.1 Expert opinion

Nine experts in California fish biology and freshwater species management were asked to evaluate the methods used and results obtained. Experts were senior level scientists from academic institutions, non-profit organizations, and local, state, and federal government agencies throughout California. Each was asked to provide opinion independent of their professional affiliation. They were asked to give feedback on the spatial clustering methodology and results, and to address the following questions:

- Do the fish species within these regional assemblages and the assemblage boundaries align with the known ecology of the species and from a conservation management perspective?
- Do the number of assemblages for each region align with the known ecology of the species and from a conservation management perspective? Should there be more or fewer assemblages in a given region?
- Are any species missing from a given assemblage?
- Are there any fish species susceptible to changes in flow that were not included in the list of species used in spatial clustering?

For the first iteration of spatial clustering, all flow-sensitive species identified by Grantham, Viers & Moyle (2014) were included. Based on the experts' responses, this list of species was expanded to include additional native species susceptible to changes in stream flow; this nearly doubled the number of species assessed (total species = 118; see Appendix A for complete list). Based on expert response and knowledge, the ranges for Santa Ana speckled dace (*Rhinichthys osculus*), Santa Ana sucker (*Catostomus santaanae*), Pacific lamprey (*Entosphenus tridentatus*), coastal threespine stickleback (*Gasterosteus aculeatus*), and mountain whitefish (*Prosopium williamsoni*) were updated. Clustering analysis was then re-run, and the results were disseminated to the same experts for final review and concurrence. Although expert-based approaches are prone to biases, the use of expert knowledge here was to evaluate the methodology and results critically rather than to provide recommendations on specific species to be used as umbrellas, thereby minimizing the introduction of bias.

2.5 Application of results to streamflow management in two California basins

To demonstrate the applicability of the method to inform freshwater conservation and management concerns, life history needs of all umbrella species identified in California were related to seasonal flow components (after Yarnell et al., 2016) through a literature review and consultation with the fish biology experts. The results from two river basins are presented to illustrate how the data could be used to address different conservation challenges related to streamflow management for native fish species.

The Eel River in the North Coast region of California contains a diverse assemblage of native fishes including several species of salmonids (Salmonidae), roach (Cyprinidae), and sculpin (Cottidae), as well as lamprey (Petromyzontidae), green sturgeon (*Acipenser medirostris*), and pikeminnow (*Ptychocheilus grandis*) (Santos et al., 2014). Owing to expected shifts in hydrological conditions resulting from climate change and the effect of numerous water diversions in the area to support cannabis cultivation, conservation management is focused on developing instream flow regimes that support the needs of native fishes. However, specific data detailing flow requirements for each species in the basin are not currently available. Understanding flow requirements for a suite of umbrella species, rather than the full assemblage, therefore potentially provides an alternative approach for developing instream flow recommendations in the Eel River and other North Coast River basins.

The American River in California's Central Valley region contains a variety of native fish species, including various salmonids (Salmonidae), hardhead (*Mylopharodon conocephalus*), Sacramento pikeminnow (*Ptychocheilus grandis*), sculpin (Cottidae), and Sacramento sucker (*Catostomus occidentalis*) (Santos et al., 2014). Most major rivers in the Central Valley are regulated by dams (Grantham, Viers & Moyle, 2014), and historically, flow releases for the environment have typically focused on the needs of a single anadromous species that is absent from these streams during parts of the year (Zarri et al., 2019), consequently overlooking the flow requirements of resident species. Understanding the flow needs of both resident and anadromous species using a suite of umbrella species could support management efforts by informing the development of flow regimes that satisfy the needs of a more diverse array of species.

3. RESULTS

3.1 Spatial clustering

Spatial k-means clustering identified a total of 16 regional fish assemblages throughout California (Figure 3). The Central Valley/west slope Sierra Nevada region contained four assemblages, the Great Basin region contained three assemblages, the North Coast region contained six assemblages, and the South Coast region contained three assemblages (Figure 3). Appendix B includes tables of the species that comprise each fish assemblage within each region.

3.2 Hierarchical trait-based clustering

The final number of trait-based species groups for each region, determined via hierarchical clustering analysis and validated via expert opinion were: Central Valley/west slope Sierra Nevada, k = nine groups, Great Basin, k = five groups, North Coast, k = eight groups, and South Coast, k = six groups. These results are shown as dendrograms in Figure 4. Each group represents species with similar traits, and the final number of groups were selected to capture distinct trophic ecology, life history, habitat association, and tolerance differences between species groups.

3.3 Umbrella species selection

Of 118 native fish species across California, 49 umbrella species were identified. These included a suite of 20 umbrella species for the Central Valley, six species for the Great Basin, 19 species for the North Coast, and 14 species for the South Coast (Table 1). Scores for each species are available in Appendix C. Eleven species served as umbrella species for more than one region. For example, Sacramento sucker serves as an umbrella species for both the Central Valley and North Coast regions. Some trait-based groups included more than one umbrella species owing to several species receiving equal scores. Expert opinion and consensus resulted in several additional species included as potential umbrella candidates to adequately capture diverse life histories of similar species within assemblages. For example, both a resident and anadromous salmonid umbrella species was included in group four associated with the North Coast (Figure 4).

3.4 Application of results to streamflow management in two California river basins

The Eel River basin, the largest river basin in the North Coast and located within North Coast Assemblage 1, contains a suite of 10 umbrella species: coastrange sculpin (*Cottus aleuticus*), Central Coast Coho salmon (*Oncorhynchus kisutch*), hardhead (*Mylopharodon conocephalus*), Northern tidewater goby (*Eucyclogobius newberryi*), prickly sculpin (*Cottus asper*), Sacramento pikeminnow (*Ptychocheilus grandis*), coastal threespine stickleback (*Gasterosteus aculeatus*), coastal rainbow trout (*Oncorhynchus mykiss*), western brook lamprey (*Lampetra richardsoni*), white sturgeon (*Acipenser transmontanus*), and northern coastal roach (*Hesperoleucus venustus navarroensis*). In respect of streamflow requirements, all the Eel River umbrella species require either adequate dry-season baseflow, peak magnitude flows, or both seasonal flow components for life-history success. Two species also require spring recession flows for spawning (Sacramento pikeminnow and hardhead), whereas coastrange sculpin need adequate magnitude and duration of wet-season baseflow.

The American River, located within Central Valley Assemblage 2, contained a suite of 11 umbrella species, including fall- and spring-run Chinook salmon (*Oncorhynchus tshawytscha*), hardhead (*Mylopharodon conocephalus*), hitch (*Lavinia exilicauda),* riffle sculpin (*Cottus gulosus*), Sacramento pikeminnow (*Ptychocheilus grandis*), Sacramento splittail (*Pogonichthys* *macrolepidotus*), Sacramento speckled dace (*Rhinichthys osculus*), Sacramento sucker (*Catostomus occidentalis*), inland threespine stickleback (*Gasterosteus aculeatus*), and white sturgeon (*Acipenser transmontanus*). Fall-run Chinook salmon, a federally listed species whose flow requirements have been used to drive streamflow management in many Central Valley streams, have specific flow requirements during fall (= 'autumn'), winter, and spring months, but are typically absent from Central Valley streams during early and mid-summer owing to their migratory behaviour. Thus, fall-run Chinook salmon require adequate winter baseflow, fall pulse flows, and spring recession flows. However, the remaining umbrella species require at least three of the five seasonal flow components each, resulting in a cumulative requirement of all five seasonal flow components to support the suite of umbrellas species in the American River.

4. DISCUSSION

As freshwater biodiversity declines, uniform and rapid approaches are needed to inform conservation management actions across diverse and broad geographical areas. This study provides an alternative approach to managing freshwater fish assemblages (and co-occurring taxa) using suites of umbrella species identified from readily available data, including species ranges and vulnerability scores. As with any approach or study reliant on species range data, it is assumed that present species distribution is accurately represented. In this approach, species range data are at the sub-basin level (USGS HUC 12 units), rather than at the individual stream scale. As data at a fine resolution were not available, conservation managers in California wishing to use the results of this analysis in management decisions should pair umbrella species and species ranges with site-specific, on-the-ground knowledge of species presence and ranges when possible. Similarly, the approach used climate vulnerability to represent overall species vulnerability when scoring and selecting umbrella species. As general species vulnerability scores were not available for all species used in the analysis, climate vulnerability was used as a proxy. Furthermore, a frequent criticism of the umbrella species approach is that the requirements or vulnerabilities of a single species are unlikely to encapsulate adequately those of other co-occurring species within a given area, particularly over large spatial scales (Hess & King, 2002; Roberge & Angelstam, 2004). Although the selection of a single, vulnerable species as an umbrella may not necessarily protect others because of any specific life-history or habitat requirements, the protection of a suite of vulnerable species – and their seasonal flow and habitat needs – may provide better protection for a wider community of riverine species, including benthic macroinvertebrates, amphibians, and riparian vegetation.

This approach relies on expert opinion to validate datasets, methods, and results. Although the use of expert opinion in the selection of umbrella and other surrogate species can be valuable, particularly given limited information and data gaps (Beazley, Baldwin & Reining, 2010; Moody & Grand, 2012), it can also be prone to taxonomic and regional biases and has been criticized for being irreproducible (Burgman et al., 2011; Magg, Ballenthien & Braunisch, 2019). Despite this, conservation management decisions are typically informed to some extent by expert knowledge (Martin et al., 2012). In this study, experts were involved throughout the process, which served as an informal peer review from those involved in practical freshwater conservation management in California. Rather than presenting a final product and recommending its use to inform management actions, as is typically the case, this method incorporated the use of expert knowledge in the development of the approach as well as in the analysis of the results. This expert involvement not only strengthened the methodology and results of the systematic approach to selecting umbrella species, but also provided an opportunity to include practitioners involved in management to provide input, thereby improving the chances of the application of the results of the analysis in management decisions.

4.1 Application of results to streamflow management

Determining suites of umbrella species for all native fishes across California (>42 x 10^6 ha) has potential application for streamflow management actions at the sub-regional scale. California is geographically and topographically varied, with a Mediterranean climate that produces strong seasonality in streamflow. Natural resource agencies in California responsible for maintaining streamflow for native fishes (e.g. the State Water Resources Control Board, the Department of Fish and Wildlife) could use results from this study to guide selection of important seasonal flow components of the annual hydrograph (e.g. summer baseflow or fall pulse flows) within instream flow recommendations as part of a multiple-species approach to flow management, rather than focus on an individual species or a minimum flow threshold. Such flow components are fundamental to native fish life history (Lytle & Poff, 2004; Yarnell et al., 2020), and thus inclusion of these seasonal flow components may help restore native fish assemblages in rivers with modified flow regimes (Kiernan, Moyle & Crain, 2012).

In areas with particularly high species diversity, such as the Eel River on the North Coast, where flow requirements of individual fish species are either unknown or too time- and resource-intensive to obtain, this approach could provide managers with a tool for evaluating the flow requirements of the full fish assemblage by focusing on the flow requirements of the umbrella species. For fisheries managers interested in supporting the full regional fish assemblage throughout the Eel River basin, flow recommendations should include priorities for adequate magnitude dry-season baseflow and peak magnitude flows in winter, both of which are needed by all umbrella species. For those sub-basins with Sacramento pikeminnow, hardhead, or coastrange sculpin, managers should also preserve adequate spring recession flow and wet-season baseflow, respectively. Ensuring that the flow requirements of the umbrella species present in a sub-basin are met is likely to ensure that flows are adequate for the full fish assemblage present.

In much of California, including the Central Valley, restoration of flow regimes has focused historically on single species (typically anadromous species from the family Salmonidae) or a discrete life stage of a single species (e.g. adult spawning), with the assumption that sufficient flows for that species will improve the conservation of co-occurring native fishes. Under this single species management paradigm, the summer baseflow period might be ignored to the detriment of several resident species, such as riffle sculpin (*Cottus gulosus*) and pikeminnow (*Ptychocheilus grandis*), which require sufficient summer flows during California's hot and dry summers. In addition, high spring flows trigger spawning for several native fishes, including many of the umbrella species identified in the regional fish assemblage in the American River (e.g. riffle sculpin, pikeminnow, hardhead), while also initiating floodplain connectivity for spawning by Sacramento splittail (*Pogonichthys macrolepidotus*). Managing for the full assemblage of fish species in Central Valley streams would also provide co-benefits to other aquatic and riparian species dependent on seasonal variability in flows, including the foothill yellow-legged frog *(Rana bolyii)* and cottonwood (*Populus* spp.) (Yarnell, Viers & Mount, 2010). In short, to support the full regional fish assemblage in the American River, flow recommendations should be focused on the needs of the suite of umbrella fish species, rather than the needs of a single-fish species, and include all five seasonal flow components. The method presented here thus moves beyond single species management and, importantly, necessitates the use of multiple species for streamflow management purposes, ensuring that flow needs of all native species are considered in streamflow management.

5. CONCLUSION

Although the method presented here was applied to freshwater fishes throughout California, its application is not limited to a single geographical region. Owing to the types of data applied in this approach (e.g. species ranges, life history information, vulnerabilities), the method is applicable to other freshwater fishes across other biogeographical areas. In summary, this method provides a straightforward and rapid means of selecting a suite of umbrella fish species upon which to base conservation management recommendations and conduct additional, quantitative analyses that can inform the needs of umbrella species under a changing climate. The test of whether the results from this method provide a practical alternative to the present single-species bias in freshwater conservation management will be whether the responsible authorities embrace the approach and what subsequent effects may occur. A holistic approach to conservation management of native fish assemblages requires consideration of all species and the focus on a suite of umbrella fish species is a cost effective and efficient means to support declining freshwater communities.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

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Tables

Table 1. Suites of umbrella species for each assemblage, within each region.

Region	Assemblage	Suite of Umbrella Species
Central Valley	1	Hardhead, Pit sculpin, riffle sculpin, rough sculpin, Sacramento pikeminnow, Sacramento speckled dace, Sacramento sucker
	2	Central Valley fall chinook salmon, Central Valley spring chinook salmon, hardhead, Clear Lake hitch, riffle sculpin, Sacramento pikeminnow, Sacramento splittail, Sacramento speckled dace, Sacramento sucker, inland threespine stickleback, white sturgeon
	3	Central Valley fall chinook salmon, Central Valley spring chinook salmon, hardhead, Kern brook lamprey, Red Hills roach, riffle sculpin, Sacramento pikeminnow, Sacramento splittail, Sacramento speckled dace, Sacramento sucker, Little Kern golden trout, inland threespine stickleback, white sturgeon, Red Hills roach
	4	Hardhead, Modoc sucker, Pit sculpin, Sacramento pikeminnow, Sacramento speckled dace, Sacramento sucker, Goose Lake tui chub
Great Basin	1	Lahontan speckled dace, Cow Head tui chub
	2	Paiute sculpin, Lahontan speckled dace, Tahoe sucker
	3	Paiute cutthroat trout, Paiute sculpin, Lahontan speckled dace, Tahoe sucker
North Coast	1	Coastrange sculpin, Central Coast coho salmon, hardhead, northern tidewater goby, prickly sculpin, Sacramento pikeminnow, coastal threespine stickleback, coastal rainbow trout, western brook lamprey, white sturgeon, northern coastal roach
	2	Lost River sucker, Klamath speckled dace, coastal rainbow trout
	3	Coastrange sculpin, Southern Oregon Northern California Coast coho salmon, northern tidewater goby, prickly sculpin, Klamath speckled dace, coastal threespine stickleback, coastal rainbow trout, western brook lamprey, white sturgeon
	4	Coastrange sculpin, Central Coast coho salmon, hardhead, northern tidewater goby, prickly sculpin, Sacramento pikeminnow, Sacramento splittail, Coastal threespine stickleback, Coastal rainbow trout, Western brook lamprey, White sturgeon
	5	Coastrange sculpin, Southern Oregon Northern California Coast coho salmon, northern tidewater goby, prickly sculpin, Klamath speckled dace, coastal threespine stickleback, coastal rainbow trout, western brook lamprey, white sturgeon
	6	Coastrange sculpin, Southern Oregon Northern California Coast coho salmon, prickly sculpin, Klamath speckled dace, coastal threespine stickleback, coastal rainbow trout, western brook lamprey, white sturgeon
South Coast	1	Riffle sculpin, Sacramento pikeminnow, unarmored threespine stickleback, Southern California steelhead, Monterey hitch, Monterey sucker

	2	California killifish, coastrange sculpin, Monterey hitch, southern tidewater goby, riffle sculpin, Sacramento pikeminnow, threespine stickleback, Southern California steelhead, Monterey sucker
	3	Arroyo chub, California killifish, lamprey, northern tidewater goby, prickly sculpin, Santa Ana sucker, speckled dace, threespine stickleback, Southern California steelhead

Figure Legends

Figure 1. Overview of methodology used to select suite of umbrella species.

Figure 2. Four regions used in spatial clustering analysis: (i) Central Valley/west slope Sierra Nevada, (ii) North Coast, (iii) South Coast, and (iv) Great Basin. Some parts of the state were excluded from this analysis. These areas were manually excluded either because they do not contain native fishes, or because they have unique management considerations where species are typically managed individually (e.g. desert, San Francisco Bay, Sacramento/San Joaquin Delta).

Figure 3. Regional fish assemblages determined by spatial k-means clustering (k=16 total assemblages). Shading indicates region, outlines within each region indicate assemblage boundaries. Central Valley/west slope Sierra Nevada = 4 assemblages, Great Basin = 3, North Coast = 6, and South Coast = 3.

Figure 4. Trait-based cluster dendrogram for each of the four regions: (a) North Coast, (b) Central Valley, (c) Great Basin, (d) South Coast. Dashed lines indicate group boundaries.

Appendix A. Species Used in Clustering

Species used in clustering, adapted from Grantham, Viers & Moyle (2014). While clustering was done at the species level, the table below clarifies the subspecies included under a given common name.

Family	Scientific Name	Common Name	Subspecies Included in Clustering
Acipenseridae	*Acipenser medirostris*	Green sturgeon	Northern green sturgeon, southern green sturgeon
Acipenseridae	*Acipenser transmontanus*	White sturgeon	
Catostomidae	*Catostomus fumeiventris*	Owens sucker	
Catostomidae	*Catostomus latipinnis*	Flannelmouth sucker	
Catostomidae	*Catostomus luxatus*	Lost River sucker	
Catostomidae	*Catostomus microps*	Modoc sucker	
Catostomidae	*Catostomus occidentalis*	Sucker	Humboldt sucker, Goose Lake sucker, Monterey sucker, Sacramento sucker
Catostomidae	*Catostomus rimiculus*	Klamath smallscale sucker	
Catostomidae	*Catostomus santaanae*	Santa Ana sucker	
Catostomidae	*Catostomus snyderi*	Klamath largescale sucker	
Catostomidae	*Catostomus tahoensis*	Tahoe sucker	
Catostomidae	*Chasmistes brevirostris*	Shortnose sucker	
Catostomidae	*Pantosteus lahontan*	Lahontan mountain sucker	
Catostomidae	*Xyrauchen texanus*	Razorback sucker	
Centrarchidae	*Archoplites interruptus*	Sacramento perch	

Cottidae	*Cottus aleuticus*	Coastrange sculpin	
Cottidae	*Cottus asper*	Prickly sculpin	Clear Lake prickly sculpin, prickly sculpin
Cottidae	*Cottus asperrimus*	Rough sculpin	
Cottidae	*Cottus beldingi*	Paiute sculpin	
Cottidae	*Cottus gulosus*	Riffle sculpin	
Cottidae	*Cottus klamathensis*	Marbled sculpin	Upper Klamath marbled sculpin, bigeye marbled sculpin, Lower Klamath marbled sculpin
Cottidae	*Cottus perplexus*	Reticulate sculpin	
Cottidae	*Cottus pitensis*	Pit sculpin	
Cyprinidae	*Hesperoleucus mitrulus*	Roach (mitrulus)	Northern roach
Cyprinidae	*Hesperoleucus parvipinnus*	Roach (parvipinnus)	Gualala roach
Cyprinidae	*Hesperoleucus symmetricus*	Roach (symmetricus)	Kaweah roach, California roach, Red Hills roach
Cyprinidae	*Hesperoleucus symmetricus* x *venustus*	Roach (symmetricus x venustus)	Clear Lake roach
Cyprinidae	*Hesperoleucus venustus*	Roach (venustus)	Southern coastal roach, Northern coastal roach
Cyprinidae	*Lavinia exilicauda chi*	Hitch	Clear Lake hitch, Sacramento hitch, Monterey hitch
Cyprinidae	*Mylopharodon conocephalus*	Hardhead	
Cyprinidae	*Pogonichthys macrolepidotus*	Sacramento splittail	
Cyprinodontidae	*Cyprinodon macularius*	Desert pupfish	
Cyprinodontidae	*Cyprinodon nevadensis*	Pupfish	Amargosa River pupfish, Shoshone pupfish
Cyprinodontidae	*Cyprinodon radiosus*	Owens pupfish	
Cyprinodontidae	*Cyprinodon salinus*	Salt Creek pupfish	
Embiotocidae	*Hysterocarpus traskii*	Tule perch	Russian River Tule perch, Sacramento tule perch

Fundulidae	*Fundulus parvipinnis*	California killifish	
Gasterosteidae	*Gasterosteus aculeatus*	Threespine stickleback	Coastal threespine stickleback, inland threespine stickleback, unarmored threespine stickleback, Shay Creek stickleback
Leuciscidae	*Gila coerulea*	Blue chub	
Leuciscidae	*Gila orcutti*	Arroyo chub	
Leuciscidae	*Ptychocheilus grandis*	Sacramento pikeminnow	
Leuciscidae	*Rhinichthys osculus*	Speckled dace	Klamath speckled dace, Amargosa Canyon speckled dace, Lahontan speckled dace, Long Valley speckled dace, Owens speckled dace, Santa Ana speckled dace
Leuciscidae	*Richardsonius egregius*	Lahontan redside	
Leuciscidae	*Siphatales bicolor bicolor*	Tui chub (bicolor)	Klamath tui chub, Lahontan stream tui chub, Owens tui chub
Leuciscidae	*Siphatales mohavensis*	Mojave tui chub	
Leuciscidae	*Siphatales thalassinus*	Tui chub (thalassinus)	Goose Lake tui chub, Cow Head tui chub, Pit River tui chub
Osmeridae	*Hypomesus pacificus*	Delta smelt	
Osmeridae	*Spirinchus thaleichthys*	Longfin smelt	
Osmeridae	*Thaleichthys pacificus*	Eulachon	
Oxudercidae	*Eucyclogobius kristinae*	Southern tidewater goby	
Oxudercidae	*Eucyclogobius newberryi*	Northern tidewater goby	
Petromyzontidae	*Entosphenus folletti*	Northern California brook lamprey	
Petromyzontidae	*Entosphenus similis*	Klamath River lamprey	

Petromyzontidae	*Entosphenus tridentata*	Goose Lake lamprey	Goose Lake lamprey, Pacific Lamprey
Petromyzontidae	*Lampetra ayersi*	River lamprey	
Petromyzontidae	*Lampetra hubbsi*	Kern brook lamprey	
Petromyzontidae	*Lampetra lethophaga*	Pit-Klamath brook lamprey	
Petromyzontidae	*Lampetra richardsoni*	Western brook lamprey	
Salmonidae	*Oncorhynchus clarki*	Cutthroat trout	Coastal cutthroat trout, Lahontan cutthroat trout, Paiute cutthroat trout
Salmonidae	*Oncorhynchus gorbuscha*	Pink salmon	
Salmonidae	*Oncorhynchus keta*	Chum salmon	
Salmonidae	*Oncorhynchus kisutch*	Coho salmon	Central Coast coho salmon, Southern Oregon Northern California coast coho salmon
Salmonidae	*Oncorhynchus mykiss*	Golden trout, Redband trout, Rainbow trout, steelhead	California golden trout, Eagle Lake rainbow trout, Kern River rainbow trout, coastal rainbow trout, McCloud River redband trout, Little Kern golden trout, Central California coast winter steelhead, Central Valley steelhead, Goose Lake redband trout, Klamath Mountains Province summer steelhead, Klamath Mountains Province winter steelhead, Northern California coast summer steelhead, Northern California coast winter steelhead, South Central California coast steeelhead, Southern California steelhead

Salmonidae	*Oncorhynchus tshawytscha*	Chinook salmon	California Coast fall chinook salmon, Central Valley fall chinook salmon, Central Valley late fall chinook salmon, Central Valley spring chinook salmon, Central Valley winter chinook salmon, Southern Oregon Northern California coast fall chinook salmon, Upper Klamath-Trinity fall chinook salmon, Upper Klamath-Trinity spring chinook salmon
Salmonidae	*Prosopium williamsoni*	Mountain whitefish	

Appendix B. Tabular results of clustering analysis

Tabular results of final clustering analysis, by geographical region. A "+" indicates species presence in a given assemblage within the region.

Central Valley

Species	Assemblage 1	Assemblage 2	Assemblage 3	Assemblage 4
Chinook salmon		+	+	
Delta smelt		+		
Green sturgeon		+	+	
Hardhead	+	+	+	+
Hitch		+	+	
Kern brook lamprey			+	
Lamprey		+	+	+
Marbled sculpin	+			+
Modoc sucker				+
Pit Klamath brook lamprey	+			+
Pit sculpin	+			+
Prickly sculpin	+	+	+	
Riffle sculpin	+	+	+	
River lamprey		+		
Roach (mitrulus)	+			+
Roach (symmetricus x venustus)		+		
Roach (symmetricus)	+	+	+	+
Roach (venustus)		+		
Rough sculpin	+			
Sacramento pikeminnow	+	+	+	+
Sacramento splittail		+	+	
Speckled dace	+	+	+	+
Sucker	+	+	+	+
Threespine stickleback		+	+	
Trout (mykiss)	+	+	+	+
Tui chub (thalassinus)	+			+
Tule perch	+	+	+	
Western brook lamprey		+		
White sturgeon		+	+	

Great Basin

Species	Assemblage 1	Assemblage 2	Assemblage 3
Cutthroat trout			+

Lahontan mountain sucker		+	+
Lahontan redside	+	+	+
Mountain whitefish			+
Paiute sculpin		+	+
Speckled dace	+	+	+
Tahoe sucker		+	+
Trout (mykiss)		+	
Tui chub (thalassinus)	+		
Tui chub (bicolor)		+	+

North Coast

Species	**Group 1**	**Group 2**	**Group 3**	**Group 4**	**Group 5**	**Group 6**
Blue chub		+				
Chinook salmon	+		+	+	+	+
Chum salmon	+		+	+	+	
Coastrange sculpin	+		+	+	+	+
Coho salmon	+		+	+	+	+
Cutthroat trout	+		+		+	
Delta smelt				+		
Eulachon	+		+		+	
Green sturgeon	+		+	+	+	+
Hardhead	+			+		
Hitch				+		
Klamath largescale sucker		+				
Klamath River lamprey		+	+		+	+
Klamath smallscale sucker			+		+	+
Lamprey	+	+	+	+	+	+
Longfin smelt	+			+	+	
Lost River sucker		+				
Marbled sculpin		+			+	+
Northern California brook lamprey		+				
Northern tidewater goby	+		+	+	+	
Pink salmon	+			+	+	
Pit Klamath brook lamprey		+				
Prickly sculpin	+		+	+	+	+
Reticulate sculpin			+			
Riffle sculpin	+			+		
River lamprey	+		+	+	+	

Roach (parvipinnus)	+					
Roach (venustus)	+			+		
Sacramento pikeminnow	+			+		
Sacramento splittail				+		
Shortnose sucker		+				
Speckled dace		+	+		+	+
Sucker	+			+		
Threespine stickleback	+		+	+	+	+
Trout (mykiss)	+	+	+	+	+	+
Tui chub (bicolor)		+				
Tule perch				+		
Western brook lamprey	+		+	+	+	+
White sturgeon	+		+	+	+	+

South Coast

Species	**Assemblage 1**	**Assemblage 2**	**Assemblage 3**
Arroyo chub	+		
California killifish	+		+
Coastrange sculpin			+
Hitch		+	+
Lamprey	+	+	+
Northern tidewater goby	+		+
Pink salmon			+
Prickly sculpin	+	+	+
Riffle sculpin		+	+
Roach (venustus)		+	+
Sacramento pikeminnow		+	+
Santa Ana sucker	+		
Speckled dace	+	+	+
Sucker		+	+
Threespine stickleback	+	+	+
Trout (mykiss)	+	+	+

Appendix C. Species scoring

Species scores for each region, where 'Common Name' refers to the species common name on the dendrogram. †

† Climate scores range from 1-4, where 1 is the most vulnerable to climate change and 4 is least vulnerable. Data availability scores range from 1-4, where 1 is a well-studied species, and 4 is a species with few data associated with it. Note: the inverse of data availability scores from Moyle 2013 were taken, so that during scoring the lowest scores represented the most vulnerable and best studied species.

Region	Common Name	Scientific Name	Climate Change[a]	Data Availability[b]	Final Score
Central Valley	California golden trout	*Oncorhynchus mykiss aguabonita*	1	1	2
	Little Kern golden trout	*Oncorhynchus mykiss whitei*	1	1	2
	Central Valley Spring chinook salmon	*Oncorhynchus tshawytscha*	1	1	2
	Central Valley fall chinook salmon	*Oncorhynchus tshawytscha*	1	1	2
	Modoc sucker	*Catostomus microps*	1	1	2
	White sturgeon	*Acipenser transmontanus*	2	1	3
	Red Hills roach	*Hesperoleucus symmetricus serpentinus*	1	2	3
	Clear Lake hitch	*Lavinia exilicauda chi*	1	2	3
	Hardhead	*Mylopharodon conocephalus*	1	2	3
	Rough sculpin	*Cottus asperrimus*	2	1	3
	Riffle sculpin	*Cottus gulosus*	2	1	3
	Pit sculpin	*Cottus pitensis*	2	1	3
	Inland threespine stickleback	*Gasterosteus aculeatus microcephalus*	2	1	3
	Sacramento splittail	*Pogonichthys macrolepidotus*	1	2	3
	Sacramento pikeminnow	*Ptychocheilus grandis*	3	1	4
	Goose Lake tui chub	*Siphatales thalassinus thalassinus*	2	2	4
	Kern Brook lamprey	*Lampetra hubbsi*	1	3	4
	Clear Lake prickly sculpin	*Cottus asper subspecies*	2	2	4
	Sacramento sucker	*Catostomus occidentalis*	3	1	4
	Sacramento tule perch	*Hysterocarpus traskii*	2	2	4
	Sacramento speckled dace	*Rhinichthys osculus subspecies*	2	3	5
Great Basin	Paiute cutthroat trout	*Oncorhynchus clarki*	1	1	2
	Cow Head tui chub	*Siphatales thalassinus*	1	1	2
	Paiute sculpin	*Cottus beldingi*	2	1	3
	Tahoe sucker	*Catostomus tahoensis*	3	1	4
	Lahontan speckled dace	*Rhinichthys osculus*	3	2	5
	Sacramento speckled dace	*Rhinichthys osculus*	2	3	5
North Coast	Central Coast coho salmon	*Oncorhynchus kisutch*	1	1	2
	Southern Oregon Northern California Coast coho salmon	*Oncorhynchus kisutch*	1	1	2
	Inland threespine stickleback	*Gasterosteus aculeatus microcephalus*	2	1	3

	Hardhead	*Mylopharodon conocephalus*	1	2	3
	Lost River sucker	*Catostomus luxatus*	2	1	3
	Coastrange sculpin	*Cottus aleuticus*	2	1	3
	Coastal rainbow trout	*Oncorhynchus mykiss irideus*	2	1	3
	Upper Klamath-Trinity Spring chinook salmon	*Oncorhynchus tshawytscha*	1	2	3
	White sturgeon	*Acipenser transmontanus*	2	1	3
	Sacramento splittail	*Pogonichthys macrolepidotus*	1	2	3
	Northern tidewater goby	*Eucyclogobius newberryi*	2	1	3
	Coastal threespine stickleback	*Gasterosteus aculeatus*	3	1	4
	Sacramento pikeminnow	*Ptychocheilus grandis*	3	1	4
	Southern green sturgeon	*Acipenser medirostris*	3	1	4
	Sacramento tule perch	*Hysterocarpus traskii*	2	2	4
	Prickly sculpin	*Cottus asper subspecies*	4	1	5
	Northern coastal roach	*Hesperoleucus venustus navarroensis*	2	3	5
	Klamath speckled dace	*Rhinichthys osculus Klamathensis*	3	2	5
	Western brook lamprey	*Lampetra richardsoni*	2	3	5
South Coast	Unarmored threespine stickleback	*Gasterosteus aculeatus williamsoni*	1	1	2
	Riffle sculpin	*Cottus gulosus*	2	1	3
	Coastrange sculpin	*Cottus aleuticus*	2	1	3
	Southern California steelhead	*Oncorhynchus mykiss*	1	2	3
	Southern tidewater goby	*Eucyclogobius kristinae*	2	1	3
	Northern tidewater goby	*Eucyclogobius newberryi*	2	1	3
	Santa Ana sucker	*Catostomus santaanae*	2	2	4
	California killifish	*Fundulus parvipinnis*	2	2	4
	Sacramento pikeminnow	*Ptychocheilus grandis*	3	1	4
	Santa Ana speckled dace	*Rhinichthys osculus subspecies*	2	2	4
	Arroyo chub	*Gila orcutti*	3	2	5
	Monterey hitch	*Lavinia exilicauda harengeus*	2	3	5
	Monterey sucker	*Catostomus occidentalis mnioltiltus*	2	3	5

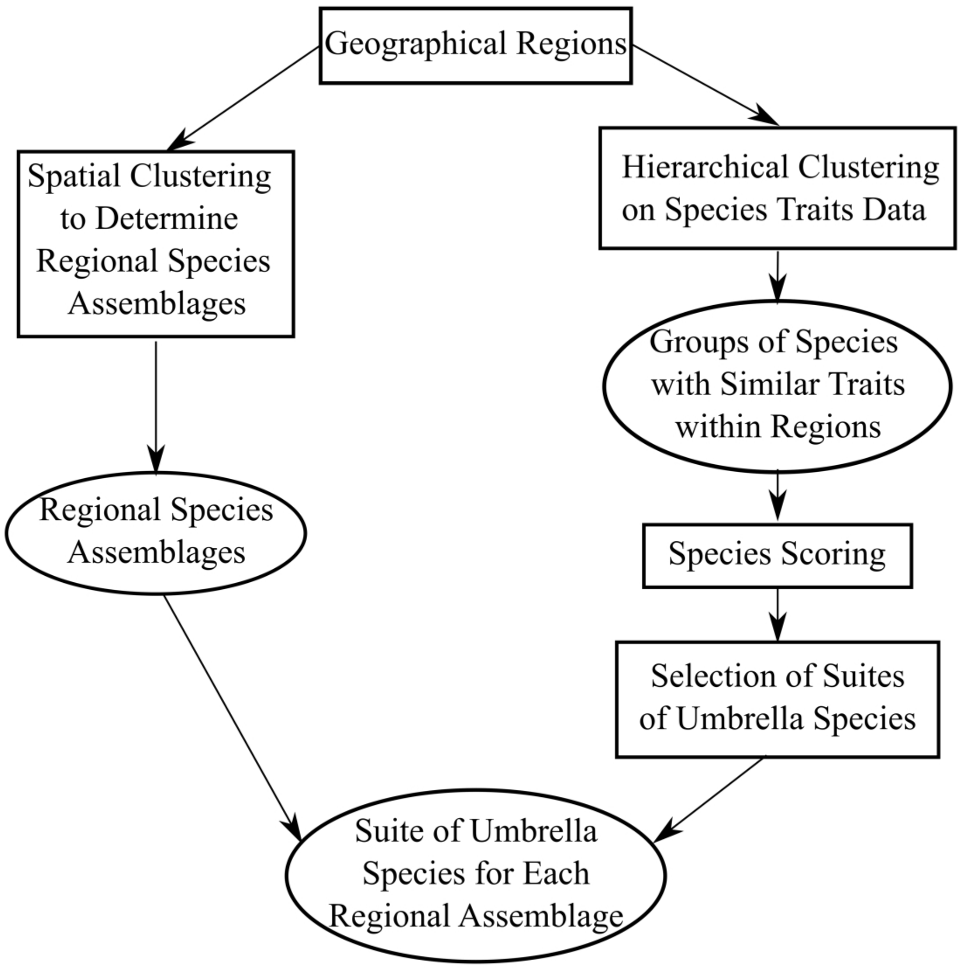

Figure 1. Overview of methodology used to select suite of umbrella species.

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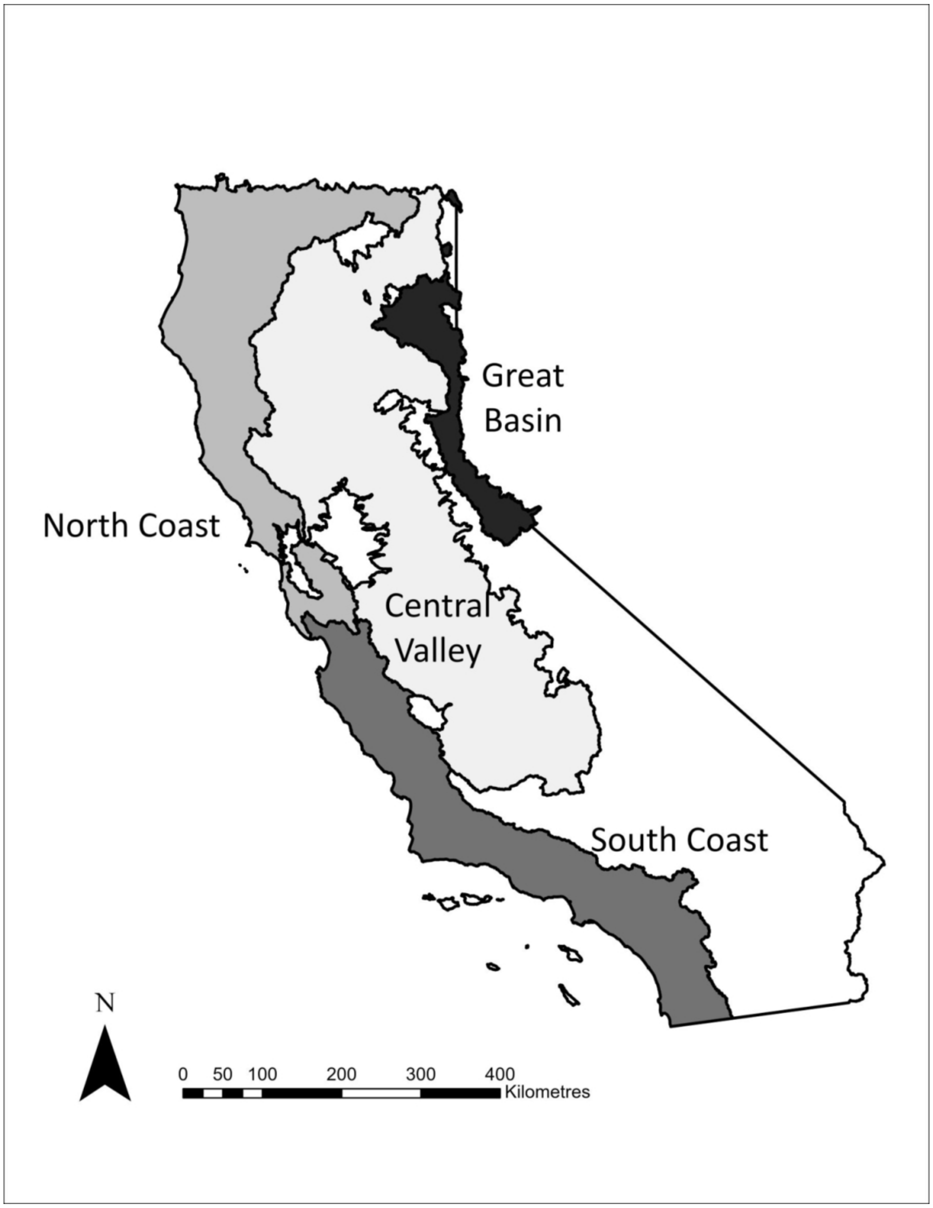

Figure 2. Four regions used in spatial clustering analysis: 1) Central Valley/west slope Sierra Nevada, 2) North Coast, 3) South Coast, and 4) Great Basin. Some parts of the state were excluded from our analysis. These areas were manually excluded because they either 1) do not contain native fishes, or 2) have unique management considerations where species are typically managed individually (e.g. desert, San Francisco Bay, Sacramento/San Joaquin Delta).

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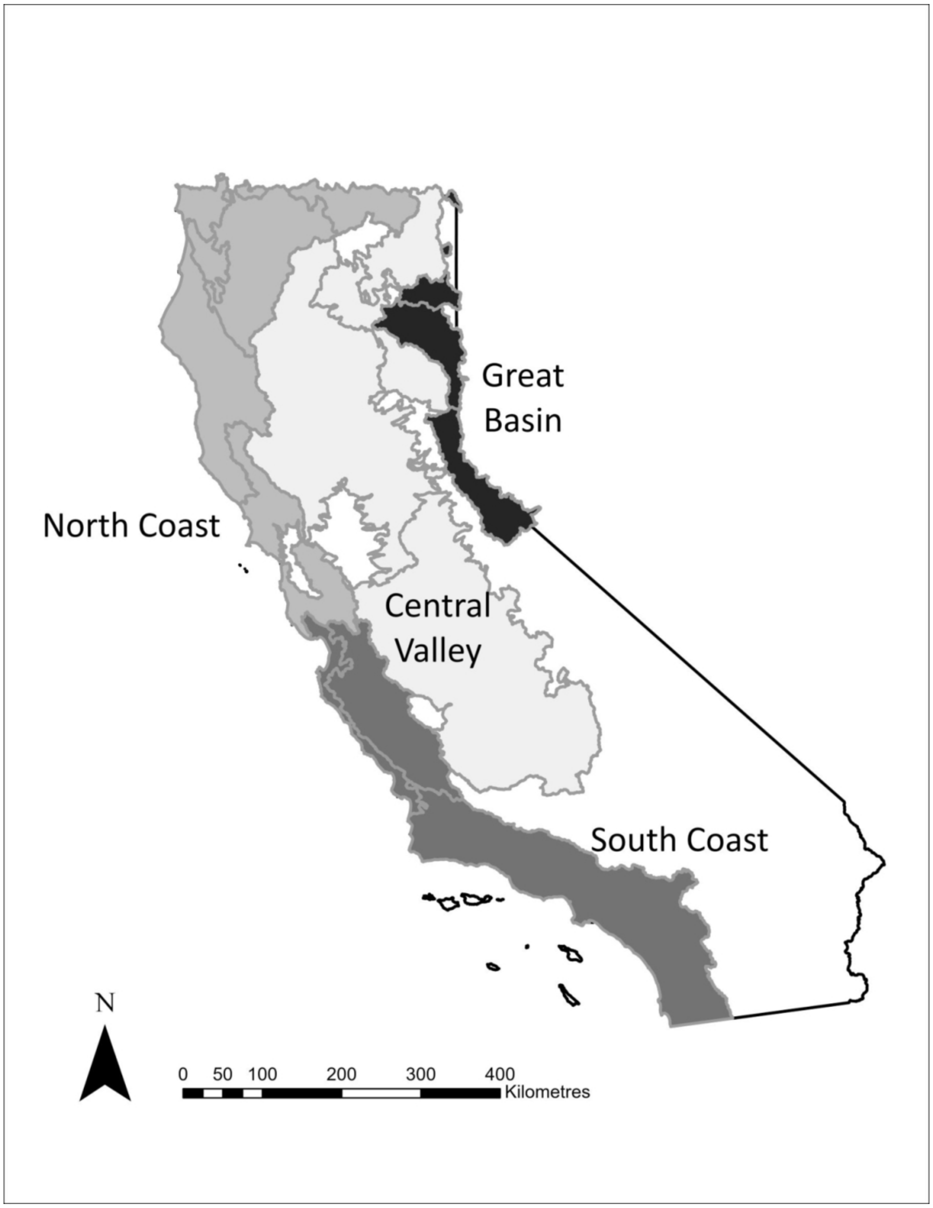

Figure 3. Regional fish assemblages determined by spatial k-means clustering (k=16 total assemblages). Shading indicates region, outlines within each region indicate assemblage boundaries. Central Valley/west slope Sierra Nevada = 4 assemblages, Great Basin = 3, North Coast = 6, and South Coast = 3.

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