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Persistence of native fishes in small streams of the urbanized San Francisco Estuary, California: acknowledging the role of urban streams in native fish conservation

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ABSTRACT

1. Urbanization is known to have pernicious consequences for native stream fishes globally. The San Francisco Estuary (SFE), California, is one of the largest, most urbanized estuaries in North America and non-native freshwater fishes are widespread in many of its catchments. Nevertheless, a diverse native and endemic freshwater fish species assemblage remains in this region.
2. Historical records (1854–2007) were reviewed and sampling conducted throughout SFE catchments to determine the distribution of stream fishes. Native stream fishes were classified by zoogeographic type, habitat preferences, physiological tolerances, and whether native fishes utilized reservoirs during their life cycle.
3. From 1993–1999, stream fishes were sampled at 270 sites distributed in 23 SFE catchments to assess the overall status and distribution of native stream fishes, and illuminate drivers of persistence.
4. In 2009, stream fishes were sampled at 65 sites within the largest estuary catchment, Alameda Creek, to further explore distributional patterns and drivers of native fish persistence.
5. Native stream fishes persist in the urbanized SFE because of several interacting factors, including the existence of extensive undeveloped landscapes in the headwaters of many catchments, the prevalence of saltwater dispersant native stream fishes, the wide physiological tolerances of native species, the presence of saltwater barriers between catchments that presumably reduces the spread of non-native fishes, and the existence of reservoirs that function as habitat for several native species. These results emerged from both the SFE-wide and the Alameda Creek analyses, suggesting they are somewhat general for this region.
6. Study results show that streams in spatially complex urban settings retain important conservation benefits to native stream fishes, despite significant perturbations and the establishment of non-native fishes.

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KEY WORDS: conservation; native fishes; persistence; San Francisco Estuary; small urban streams; TWINSPAN; urbanization

INTRODUCTION

Urbanization is known to have pervasive, deleterious effects on native stream fishes globally (Leidy and Moyle, 1998; Wang *et al.*, 2000; Brown *et al.*, 2005a; IUCN, 2010). Impacts associated with urbanization include physical alteration of the drainage network and channel geomorphology, water quality deterioration from chemical and thermal pollution, changes to the natural flow regime, introduction of non-native plants and animals, and modifications to natural ecosystem functions and processes (Paul and Meyer, 2001; Bunn and Arthington, 2002). Therefore, it is not surprising that many populations of native fishes in urban areas are extirpated, exhibit severely restricted distributions, or exist at such low population numbers that their long-term persistence is in doubt (Brown *et al.*, 2005a; Jelks *et al.*, 2008). Deleterious effects of urbanization on native fishes have been documented throughout California where most of the human population of 40 million is clustered in highly modified urban areas (Leidy, 1984, 2007; Leidy and Fiedler, 1985; Moyle, 2002; Brown *et al.*, 2005b; Marchetti *et al.*, 2006).

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The San Francisco Estuary (SFE or Estuary) is one of the most urbanized in North America with approximately seven million people living within the region, and nine million projected by 2035 (Association of Bay Area Governments, 2011). The SFE is the largest on the western coasts of North and South America in terms of surface and catchment areas (San Francisco Estuary Project, 1992), and is rich in endemic fish species and complex environmental gradients. The SFE is considered one of the most heavily invaded estuaries in the world (Cohen and Carlton, 1998). For example, there are at least 32 non-native freshwater fish species, representing 42% of all freshwater fish species now firmly established within SFE catchments (Leidy, 2007).

Approximately 90% of the annual fresh water that discharges into the Estuary comes from the Sacramento and San Joaquin rivers that combined drain over 40% of the land area of California through the Great Central Valley (Conomos *et al*., 1985). Approximately 70 smaller local catchments that encircle the Estuary contribute the remaining 10% of freshwater runoff (Porterfield *et al*., 1961). Despite the relatively smaller contribution of freshwater inflow to the SFE compared with the Sacramento–San Joaquin rivers, these catchments occur over a wide diversity of climatic, geological, and ecological conditions that together affect the composition of local assemblages of stream fishes. Many streams have been heavily affected by human activities during the last 150 years, particularly through urbanization. Complex natural environmental gradients considered within the context of human alterations to the landscape have resulted in a suite of different distributional patterns in fish species assemblages contingent on local conditions (Leidy, 2007). Understanding the various patterns of persistence of native fishes under different environmental conditions, therefore, is of considerable conservation interest.

The overarching goal of this study was to illuminate the factors that contribute to the persistence of native stream fishes in catchments flowing into the San Francisco Estuary, despite the introduction of many non-native fishes and various environmental perturbations. To do so, data was presented from: (1) a review of historical collection records from this region covering the period 1854–2007; (2) distributional data on stream fishes and their habitats collected from 270 sites in 23 catchments from 1993–1999; and (3) distributional data on stream fishes and their habitats collected in 2009 from 65 sites in the largest catchment flowing directly into SFE, Alameda Creek. From these combined data, factors that contribute to the prolonged persistence of native stream fishes in this region are quantified and elucidated. Likely reasons for the persistence of native fishes and conservation recommendations that will support the long-term persistence of native stream fishes are discussed. We believe that such recommendations may be transferable to existing urbanized and actively urbanizing catchments in California and in other Mediterranean regions of the world.

METHODS

Study area

The SFE is an inland estuary encompassing 4195 km^2 that drains to the Pacific Ocean through the narrow opening of the Golden Gate, near the city of San Francisco (Figure 1). The 68 local catchments encircling the Estuary range in area from 2.8 km^2 to 1813 km^2. The Estuary drainage area of the local catchments is about 9000 km^2, excluding the Delta, or about 6% of the total drainage area of the Sacramento–San Joaquin rivers in the Central Valley (Leidy, 2007).

The regional climate is Mediterranean with warm, dry summers (May to September) and cool, wet winters (October to April). Approximately 80% of the precipitation falls in winter. Estuary catchments near the Pacific Ocean are milder and receive more precipitation in winter and exhibit cooler air temperatures with more persistent fog in summer, than more inland locations (Conomos *et al*., 1985). Maximum annual mean daily temperature ranges from 13°C near the San Francisco Bay to 17°C in inland regions (Conomos *et al*., 1985).

Average annual discharges for streams within the Estuary range from 0.01 $m^3 s^{-1}$ to 6 $m^3 s^{-1}$ (Leidy, 2007). Annual peak flows can range from $<0.14 m^3 s^{-1}$ in the smallest catchments to 1133 $m^3 s^{-1}$ in the larger catchments (Leidy, 2007). Under conditions of unimpaired surface hydrology, streams that traverse valley alluvial deposits may be intermittent during the summer months with few surface water connections to smaller tributaries. Thus, streams typically consist of dry to nearly dry alluvial reaches, interrupted by shallow-to-deep pools underlain by bedrock. Lower stream reaches underlain by bedrock typically are perennial. Mid-to-upper reaches of tributary streams are intermittent to perennial in summer months depending on the characteristics of local aquifers. Streams may be dewatered by dams or diversions or, in some instances, may receive supplemental flows during summer months for groundwater management, for surface water transport, or as a result of urban runoff.

There are 44 major reservoirs of 6.2 ha or greater that lie within 20 Estuary catchments (California Department of Water Resources, 2011). In addition, thousands of small livestock and irrigation ponds, groundwater recharge basins and stormwater detention basins, are scattered throughout the Estuary. Catchments without major reservoirs and stream reaches upstream of reservoirs are characterized in large part by natural flow regimes.

Data sources

Historical records: 1854–2007

Historical records on the distribution of stream fishes in the Estuary were reviewed for the period 1854–2007. Distributional records were collected from published literature, unpublished reports and studies, field notes, public agency files, and fish specimens housed at universities and museums, and through interviews with individuals knowledgeable about fishes in particular streams or catchments. Criteria were developed by Leidy *et al*. (2005) to assess the relative reliability of these records to confirm the status of fishes within Estuary streams, and these records were summarized in Leidy (2007).

Distributional data collected from SFE catchments: 1993–1999

Recent distributional data for stream fishes in the SFE were collected by one of the authors (RAL) between 1993 and 1999, and include data collected from 270 sites within 23 Estuary catchments.

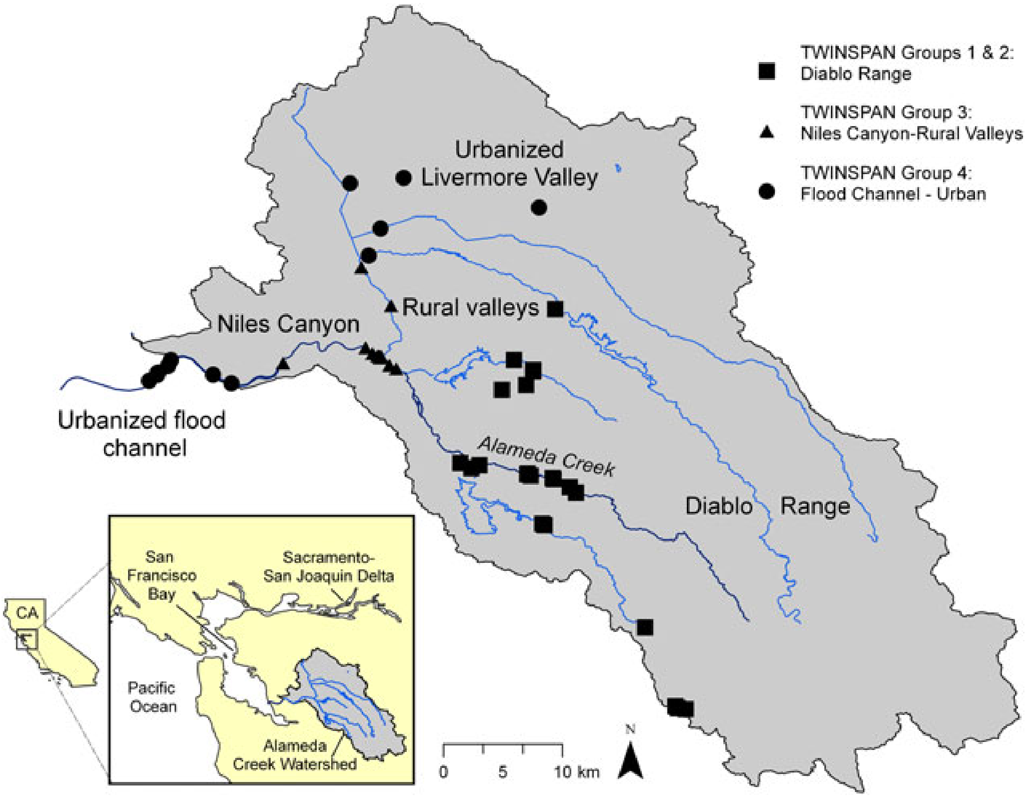

Figure 1. Study area and TWINSPAN groups, San Francisco Estuary, California.

Distributional data collected from the Alameda Creek Catchment: 2009

Between May and September 2009, stream fishes at 65 sites were sampled within the largest SFE catchment, Alameda Creek. The Alameda Creek catchment is 1813 km^2 or 20% of the total area of all SFE catchments combined (Figure 1). Approximately 80% of the headwaters of Alameda Creek are within the Diablo Mountain Range, a vast and largely undisturbed expanse of undeveloped land used primarily for ranching and passive recreation such as hiking. Alameda Creek flows through Niles Canyon, a rugged semi-natural landscape before entering the Alameda Creek flood channel that traverses a heavily urbanized plain and eventually discharges into SFE. Several tributaries contribute flow to the mainstem of Alameda Creek, most notably streams draining the urbanized Livermore Valley.

Data collection

Fish sampling

The same protocol for sampling fishes for the SFE-wide sampling (1993–1999) were used for the Alameda Creek sampling (2009). Sampling sites were stratified to maximize the diversity of habitat types (i.e. pools, runs, and riffles) in different geomorphic settings (e.g. high-elevation, high-gradient, bedrock controlled to low-elevation, low-gradient, alluvial unconsolidated substrate). Fishes were sampled primarily by single-pass electrofishing at water depths of less than 1 m. Aquatic habitats in excess of 1 m or less than 5 cm depth were typically sampled with minnow and/or beach seines or dip nets, respectively. Seining and electrofishing were conducted in a downstream to upstream direction for a minimum distance of 30 m. Isolated pools less than 30 m length characterized some sampling locations. An effort was made to sample all habitats within a sampling reach with equal effort (i.e. sampling time and area sampled); however, habitats immediately adjacent to stream banks often received more intensive sampling because these areas typically provided the most heterogeneous habitat for fishes as measured by instream and overhead riparian cover.

Collected fish were identified to species and counted. Typically, only the first 50 individuals of a species were measured (fork length, mm) and weighed (0.1 g) before release. In some instances, individual vouchers were retained and preserved in 70% isopropyl alcohol for later identification.

Environmental sampling

During both the SFE-wide sampling and Alameda Creek sampling, several physical, biological, and water quality variables were quantified. With a few exceptions (described next), slightly different methods were used for the two time periods and so the methods for the two sampling events are described separately. During both periods, stream elevation (m) was obtained from USGS 7.5′ scale topographic maps and stream order was determined after Strahler (1957). Water temperature (°C) and conductivity (μS) were recorded at the beginning of each sampling event using a handheld water quality meter (Hach C0150). For both sampling periods, the percentage of pool and riffle habitat at each site was estimated visually (Flosi and Reynolds, 1994).

For SFE-wide sampling, 16 variables were measured or estimated that were used in this analysis (Table 5), six of which are described above and 10 of which are described below. At each sample reach, three to five channel widths were measured at equally spaced transects, and were averaged to estimate the mean wetted width (m). Confinement (m) was estimated as floodplain channel width divided by bankfull width. Water depths were measured at 9–15 points along each transect to estimate mean and maximum depth (cm). At each transect, substrate composition was visually estimated using Wentworth particle-size scale independently, and confirmed collectively by two observers. Water clarity was visually assessed and assigned a rating from 1–5 (where 1=clear and 5=extremely muddy). Riparian canopy cover was visually estimated and quantified as the percentage of wetted channel covered by riparian vegetation. Instream shelter (i.e. cover) was assessed visually and rated on a scale of 0–2 (where 0=complete exposure to current and 2=complete protection).

For the 2009 Alameda Creek sampling, 17 variables were measured or estimated that were used in this analysis (Table 7), including the six described above and 11 others that are described next. Channel width (m) was measured at five equal intervals at each site, which was then averaged to estimate the mean channel width. Mean water depth (cm) was calculated from 50 random depth measurements, and maximum depth was recorded at the deepest section of each site. Water clarity (cm) was measured with a transparency turbidity tube with maximum measurable water clarity of 120cm. Percentage canopy cover was estimated using a spherical densitometer at three locations and facing four directions (12 measurements per site), and later averaged to estimate mean cover. Substrate composition was determined by randomly selecting 100 pebbles and measuring their intermediate axis (cm). This information was used to calculate the percentage of silt, sand, gravel, cobble and boulder at each site, and to calculate the associated median particle size (D-50, mm).

Data classification

Zoogeographic type and primary habitat preferences

Native fish species were classified by zoogeographic type, life history status, and primary habitat preference (Moyle and Cech, 2004). Two zoogeographic types of fishes were classified that occur in SFE catchments: (1) euryhaline marine fishes are primarily marine in distribution but may spend significant amounts of time in the freshwater reaches of coastal streams; and (2) obligatory freshwater fishes are characterized by a life history that requires spending some portion of their life cycle in fresh water (Moyle, 2002). The zoogeographic distribution patterns of obligatory freshwater fishes may be further classified as freshwater dispersant fishes that are largely unable to disperse through salt water, or saltwater dispersant fishes capable of movement through salt water (Moyle, 2002). Life history status refers to marine, anadromous, freshwater resident, estuarine resident, and amphidromous fishes. Primary habitat preferences are classified as tidal estuarine/riverine, tidal lacustrine/open bay, and the non-tidal habitats consisting of large lowland riverine, low-to-mid-elevation riverine, headwater riverine, and reservoirs/ponds.

Physiological tolerances

Physiological tolerances of native stream fishes to conditions in water quality were classified from environmental measurements taken during fish sampling in SFE streams during 1993–1999 and 2009 following definitions presented in Halliwell *et al.* (1999) and Marchetti *et al.* (2004). Tolerance categories include 'intolerant', 'moderately tolerant', 'tolerant', and 'extremely tolerant'. Intolerant fishes (e.g. rainbow trout and other salmonids) exhibit low physiological tolerance to extreme changes in water quality or impaired conditions. The moderately tolerant category includes fishes (e.g. California roach) that may persist in streams with moderately high variation in water quality. Tolerant fishes (e.g. prickly sculpin) are those capable of surviving in conditions where water quality approaches their physiological tolerance limits. Extremely tolerant refers to fishes (e.g. Sacramento blackfish) that persist under conditions in which most other fish cannot survive.

Reservoir use

Native fishes were assessed for whether they used reservoirs for some portion of their life cycles. Several SFE catchments contain reservoirs and ponds which may contribute to population persistence within a catchment, particularly when reservoirs act as a refuge during times of drought.

Data analysis

Species and sampling site data were classified using two-way indicator species analysis (TWINSPAN) for data collected in SFE catchments between 1993 and 1999 at 154 of the 270 sampling sites (PISCES Conservation Ltd, Version 4.0). A parallel analysis was performed using data collected at 44 of 65 sampling sites in Alameda Creek during 2009. The remaining sites were not included in the statistical analysis owing to spatial autocorrelation among sites or incomplete data. TWINSPAN takes species sample abundances and, using reciprocal averaging, orders the samples so that similar clusters (i.e. site groupings and species groupings) are spatially proximate to each other. Species captured at a minimum of 2% of the total sites and comprising at least 5% of the total sample abundance were used for this analysis. Euryhaline marine fishes generally were excluded from the analysis because sampling was restricted to non-tidally influenced stream environments.

RESULTS

Native fish distribution and abundance: historical and current data

From 1854–2009, and across all sources of data (historical, SFE-wide sampling, focused Alameda Creek sampling), 33 native species of fish from 11 families were recorded in SFE streams (Tables 1 and 2). One species, the thicktail chub, was documented from the historical sources but is now extinct globally. Two other species, coho salmon and tidewater goby are extirpated from SFE catchments but occur elsewhere in California streams (Table 2). Four fishes- river lamprey, western brook lamprey, eulachon, and speckled dace- are of unknown abundance within restricted geographic ranges. The remaining 26 (79%) native species vary from low to high abundances and narrow to wide geographic distributions (Table 2). Twelve (36%) of the known native fish species currently present in SFE streams are geographically widespread and have populations at moderate to high abundances. Ten (83%) of freshwater dispersant species maintain moderate to high abundances in SFE streams (Table 2).

Table 1. Status and persistence factors for native stream fishes, San Francisco Estuary, California based on historical records from 68 catchments. Zoogeographic Type: based on Moyle (2002), EM = euryhaline marine; OBF-SD = obligatory freshwater–saltwater dispersant; OBF-FD = obligatory freshwater–freshwater dispersant. Life history status: M = marine; AND = anadromous; FWR = freshwater resident; EST = estuarine resident; AMP = amphidromous. Physiological tolerance: I = intolerant; M = moderately tolerant; T = tolerant; E = extremely tolerant. Number of catchments: minimum number of catchments out of a total of 68 assessed catchments

Family	Species	Zoogeographic type	Life history status	Physiological tolerance	Headwater populations	Reservoir populations	Number of catchments (%)
Petromyzontidae (lampreys)	*Lampetra tridentata* Pacific lamprey	OBF-SD	M, AND, FWR	M	Yes	Yes	12 (18)
	Lampetra ayresii river lamprey	OBF-SD	M, AND, FWR	M	No	No	2 (3)
	Lampetra richardsoni western brook lamprey	OBF-SD	M, AND, FWR	M	Unknown	Unknown	2 (3)
Acipenseridae (sturgeons)	*Acipenser transmontanus* white sturgeon	OBF-SD	M, AND, FWR	M	No	No	5 (6)
	Acipenser medirostris green sturgeon	OBF-SD	M, AND, FWR	M	No	No	1 (1)
Cyprinidae (minnows)	*Gila crassicauda*[1] thicktail chub	OBF-SD	FWR	M	Yes	No	0
	Lavinia exilicauda[1] hitch	OBF-FD	FWR	T	No	Yes	15 (22)
	Lavinia symmetricus[1] California roach	OBF-FD	FWR	M	Yes	No	35 (51)
	Orthodon microlepidotus[1] Sacramento blackfish	OBF-FD	FWR	E	No	Yes	9 (13)
	Pogonichthys macrolepidotus[1] Sacramento splittail	OBF-FD	FWR, EST	M	No	No	3 (4)
	Mylopharodon conocephalus[1] hardhead	OBF-FD	FWR	M	No	No	2 (3)
	Ptychocheilus grandis[1] Sacramento pikeminnow	OBF-FD	FWR	T	Yes	Yes	21 (31)
	Rhinichthys osculus speckled dace	OBF-FD	FWR	M	Yes	No	1 (1)
Catostomidae (suckers)	*Catostomus occidentalis*[1] Sacramento sucker	OBF-FD	FWR	E	Yes	Yes	30 (44)
Osmeridae (smelts)	*Hypomesus transpacificus*[1] Delta smelt	OBF-SD	EST	I	No	No	1 (1)
	Spirinchus thaleichthys longfin smelt	EM	M, AND, EST	I	No	No	4 (5)
	Thaleichthys pacificus eulachon	EM	M, AND	I	No	No	1 (1)
Salmonidae (trout and salmon)	*Oncorhynchus kisutch* coho/silver salmon	OBF-SD	M, AND, FWR	I	No	No	0
	Oncorhynchus tshawytscha Chinook salmon	OBF-SD	M, AND, FWR	I	No	No	6 (7)
	Oncorhynchus keta chum salmon	OBF-SD	M, AND, FWR	I	No	No	2 (3)
	Oncorhynchus gorbuscha pink salmon	OBF-SD	M, AND, FWR	I	No	No	1 (1)
	Oncorhynchus nerka sockeye salmon/kokanee	OBF-SD	M, AND, FWR	I	No	No	1 (1)
	Oncorhynchus mykiss rainbow trout/steelhead	OBF-SD	M, AND, FWR	I	Yes	Yes	44 (65)

(*Continues*)

Table 1. (Continued)

Family	Species	Zoogeographic type	Life history status	Physiological tolerance	Headwater populations	Reservoir populations	Number of watersheds (%)
Gasterosteidae (sticklebacks)	*Gasterosteus aculeatus* threespine stickleback	OBF-SD	M, AND, EST, FWR	M	Yes	Yes	51 (75)
Cottidae (sculpins)	*Cottus asper* prickly sculpin	OBF-SD	AMP, EST, FWR	T	Yes	Yes	27 (40)
	Cottus gulosus riffle sculpin	OBF-FD	FWR	I	Yes	No	16 (24)
	Leptocottus armatus staghorn sculpin	EM	EST, AMP	T	No	No	No estimate
Centrarchidae (sunfish)	*Archoplites interruptus*[1] sacramento perch	OBF-FD	EST, FWR	M	No	Yes	1 (1)
Embiotocidae (surfperch)	*Hysterocarpus traski*[1] tule perch	OBF-SD/FD	EST, FWR	M	No	Yes	5 (7)
	Cymatogaster aggregata shiner perch	EM	EST	M	No	No	6 (7)
Gobiidae (gobies)	*Eucylogobius newberryi* tidewater goby	OBF-SD	EST	I	No	No	0
	Gillichthys mirabilis longjaw mudsucker	EM	M, EST	E	No	No	7 (10)
Pleuronectidae (righteye flounders)	*Platichthys stellatus* starry flounder	EM	M, EST	T	No	No	No estimate

[1]Fish species endemic to the Sacramento–San Joaquin zoogeographic province.

Zoogeographic diversity and life history types

Native species in SFE streams exhibit a broad range of zoogeographic types and primary habitat preferences (Tables 1 and 3). Six (18%) of the native fish species are euryhaline marine typically inhabiting the lower, tidally influenced reaches of these streams (Table 3). Twenty-six (79%) of native species are considered obligate freshwater, of which 15 species (45%) are saltwater dispersant. Saltwater dispersant fishes consist of 10 species with either anadromous or amphidromous life histories. Some formerly anadromous native species (e.g. steelhead, Pacific lamprey), in addition to Pacific ocean-stream populations, maintain adfluvial populations that use reservoirs behind dams to rear and grow before migrating into reservoir tributaries to spawn as adults.

Fish tolerance levels

Twenty-two (67%) native stream fishes are tolerant, moderately tolerant, or extremely tolerant of stressful water quality conditions (Table 1). Eight (36%) tolerant fish species are in the family Cyprinidae. Eleven (33%) native fishes are considered intolerant, and were mostly from the Salmonidae ($n=6$) and Osmeridae ($n=3$) families.

TWINSPAN site and species groups

San Francisco Estuary catchments: 1993-1999

Native and non-native species were separated in the first division, with the exception three native fishes that were associated with non-native species. In the second division, four distinct groups emerged. The first group in the second division contained two native species, rainbow trout and riffle sculpin (Table 4), and was associated with upper mainstem and tributary sites that were characterized by narrow, moderate to high gradient streams, with a high percentage of canopy cover and instream shelter (Table 5). This group was dominated by larger substrate, and had higher water clarity and lower conductance compared with other TWINSPAN groups.

The second group within the second division contained five native species -hardhead, California roach, Sacramento pikeminnow, Sacramento sucker, and tule perch- and was typically associated with middle mainstem and lower large tributary sites (Table 4). The environmental conditions of this group were intermediate between upper tributary and lower large mainstem sites, including channel width, maximum depth, and water temperature (Table 5).

The third group within the second division continued two native species- threespine stickleback and prickly sculpin- and was associated with lower small to large mainstem sites (Table 4). These sites were low gradient streams with low water clarity, low riparian canopy cover, high specific conductance, small substrate particle size, and shallow maximum water depths (Table 5).

The fourth group contained seven non-native species-common carp, rainwater killifish, mosquitofish, inland silverside, green sunfish, striped bass, and yellowfin goby- and one native species, hitch (Table 4). These species were associated with habitat conditions similar to the third group (Table 5).

Table 2. Current geographic distribution and population status of native stream fishes of the San Francisco Estuary, California

Geographic distribution (number of catchments)	Estimated population abundance (number of adults): Extirpated (0)	Low (<1000)	Moderate to High (≥1000–500,000+)	Unknown
Extirpated (0)	thicktail chub coho salmon tidewater goby			
Narrow/Restricted (≤5)		green sturgeon Delta smelt[1] chum salmon pink salmon sockeye salmon Sacramento perch	hitch hardhead splittail[1] longfin smelt[1] shiner perch starry flounder	river lamprey eulachon western brook lamprey
Intermediate to Widespread (≥6)		white sturgeon Chinook salmon rainbow trout/steelhead[1] tule perch[2]	Pacific lamprey Sacramento blackfish California roach Sacramento pikeminnow Sacramento sucker rainbow trout/steelhead[1] threespine stickleback prickly sculpin riffle sculpin staghorn sculpin tule perch[2] longjaw mudsucker	

[1]Population abundances (i.e. the number of adult individuals within a population) are known to vary greatly depending on amount of total Estuary outflow and/or local stream-flow conditions.
[2]Tule perch exhibit low to moderate to high population abundances in the southern and northern Estuary, respectively.

Alameda Creek Catchment: 1999

The first TWINSPAN division clearly separated mountainous Diablo Range sites and species from those sites associated with lower elevation, densely urbanized areas including the Livermore Valley, Niles Canyon, urbanized flood channel, and rural valleys (Figure 1). The second TWINSPAN division identified four distinct groups of fishes, which we describe next.

The first group in the second division contained one native species, rainbow trout, and was associated with upper tributary/headwater stream sites within the Diablo Range (Table 6). The second group within the second division also was associated with the Diablo Mountain Range but in addition to rainbow trout, it also typically contained two other native fishes, prickly sculpin and California roach. Diablo Range stream sites are high elevation and characterized by moderate to extensive shading from riparian canopy cover or steep canyon walls, cool water temperature, low turbidity, and are dominated by gravel-cobble substrates with little silt (Table 7).

The third species group within the second division contained five native fishes, including Pacific lamprey, hitch, Sacramento blackfish, Sacramento pikeminnow, and Sacramento sucker, in addition to three non-native fishes, including channel catfish, largemouth bass, and smallmouth bass (Table 6). These species were associated with middle mainstem and lower large tributary sites characteristic of non-urbanized, alluvial valley floor and canyon stream reaches (e.g. Niles Canyon and rural valley floor sites). Compared with the first Diablo Range group, this group was typically associated with higher water temperature, conductivity, and turbidity, less shading, and sites that were dominated by smaller size-class substrates, such as silt and sand (Table 7).

The fourth group included moderate to heavily urbanized flood and valley floor stream sites and contained one native species, threespine stickleback, and eight non-native species, including common carp, goldfish, rainwater killifish, western mosquitofish, inland silverside, green sunfish, chameleon goby, and yellowfin goby (Table 6). Urbanized sites were low elevation streams with low water clarity, poorly developed riparian canopy, and high water temperature and conductivity (Table 7). The substrate was characterized by high percentages of silt and sand.

Although the TWINSPAN analysis assigned species into single groupings, several native species showed broad overlap

Table 3. Classification of native stream fishes of the San Francisco Estuary, California, by zoogeographic type[1]

Zoogeographic type	Taxon: No. Families (%)	No. Species (%)
(a) Euryhaline marine	4 (33)	6 (19)
(b) Obligatory freshwater	11 (92)	27 (81)
(c) Freshwater dispersants	3 (25)	12 (38)
(d) Saltwater dispersants	8 (67)	15 (50)
Total families (a+b)	12 (100)	
(e) Total saltwater dispersant species (a+d)		21 (63)
(f) Total freshwater dispersant species (c)		12 (37)
Total fish species (a+b) or (e+f)		33 (100)

[1]Zoogeographic types are defined in the text and follow Moyle (2002).

Table 4. Family, common name, origin (N = native; I = introduced), TWINSPAN group, and the percentage of sites where the focal species was found (number of sites; $n=154$) in streams of the San Francisco Estuary, California, 1993–1999

Family	Common name	Origin	TWINSPAN group	Percentage of sites (number of sites)
Cyprinidae	hitch	N	4	11 (7)
	hardhead	N	2	3 (4)
	California roach	N	2	58 (89)
	Sacramento pikeminnow	N	2	16 (24)
	common carp	I	4	5 (8)
Catostomidae	Sacramento sucker	N	2	45 (70)
Salmonidae	rainbow trout	N	1	53 (82)
Gasterosteidae	threespine stickleback	N	3	44 (68)
Cottidae	prickly sculpin	N	3	29 (44)
	riffle sculpin	N	1	19 (30)
Embiotocidae	tule perch	N	2	5 (7)
Fundulidae	rainwater killifish	I	4	4 (6)
Poeciliidae	western mosquitofish	I	4	10 (15)
Atherinopsidae	inland silverside	I	4	3 (4)
Centrarchidae	green sunfish	I	4	14 (22)
Gobiidae	yellowfin goby	I	4	5 (8)
Moronidae	striped bass	I	4	5 (7)

at low abundances in their distribution across TWINSPAN habitat types. For example, Sacramento suckers and prickly sculpin were abundantly found across all habitat types throughout the Alameda Creek Catchment.

DISCUSSION

The complexity of interactions between and among various urban stressors on the biotic integrity of streams results in urban fish assemblages exhibiting highly variable and complex assemblage structures often determined by local conditions (Leidy, 2007; Brown *et al.*, 2009a,b). This study demonstrates that native fishes within SFE streams persist at varying distributions and abundances, despite multiple non-native introductions and extensively altered stream habitats. These results highlight the wide diversity of life histories, zoogeographic types, environmental tolerances, and associations with local environmental factors among the native fishes of this region.

Table 5. Environmental and fish community metric variable values (means across sites) for three TWINSPAN site groupings within the San Francisco Estuary, California. Values with a different superscript letter (^{A,B}) have significant differences between site groups and values with the same superscript letter were not significantly different (one-way ANOVA, $P<0.05$)

Variable	Group 1: Upper mainstem/ headwater tributary	Group 2: Middle mainstem/ lower large tributary	Groups 3 & 4: Estuarine/ lower small to large mainstem
Elevation (m)	193.9	156.5	20.0
Strahler stream order (1–6)	2.5	3.5^{A}	4.0^{A}
Mean wetted channel width (m)	3.4	5.2^{A}	6.5^{A}
Confinement (m)	1.3^{B}	1.8^{B}	3.1
Mean depth (cm)	25.0	32.7	37.8
Mean dominant substrate (mm)	39	29	18
Maximum depth (cm)	64.5	77.7^{A}	85.7^{A}
Water temperature (°C)	15.9	17.5^{A}	19.5^{A}
Conductivity (μS)	209.0	332.2	491.8
Water clarity (1–5)	1.2^{A}	1.6^{A}	3.0^{B}
Canopy cover (%)	59.2	41.3	20.0
Instream shelter (0–2)	1.4^{A}	1.29^{A}	0.9
Discharge (cfs)	1.3	3.4^{A}	4.9^{A}
Pool habitat (%)	77.8	76.8	80.7
Riffle habitat (%)	20.1	20.1	18.1
Channel gradient (%)	2.5	3.5	0.006

Historical and recent information on native fish distribution and abundance collected during this study confirms that more than 60% of native species are characterized by moderate to high abundances in SFE streams. Predictions of the effects of urbanization on aquatic ecosystems require an understanding of spatial landscape patterns and development intensity considered within the context of environmental stressors (Alberti *et al.*, 2007). Indeed, comparison of TWINSPAN site and species classification results from the Alameda Creek Catchment and 23 other SFE catchments show consistent patterns of occurrence of native fishes. These patterns provide evidence that native fishes often maintain populations of variable abundances in streams characterized by different environmental conditions and stressors, including undisturbed headwaters, low-to-moderately disturbed rural valleys, and highly disturbed urban flood channels.

Why do native fishes persist in Estuary streams?

Natural landscapes surround much of the Estuary

Remnant natural or minimally disturbed semi-natural landscapes surrounding the SFE function to protect native fishes. Streams at elevations greater than 125 m in the majority of SFE catchments are characterized by non-urbanized, mountainous, forest and rangeland plant communities (Leidy, 2007; Bay Area Open Space Council, 2011). For example, approximately 80% of the headwaters of the Alameda Creek Catchment are within the Diablo Range, a vast expanse of undeveloped land used primarily for ranching and passive recreation (Buchan *et al.*, 1999). This and other similar landscapes have changed little since their initial use as Spanish and Mexican rancheros for cattle grazing beginning over 200 years ago. As a result, streams are largely unfragmented, contain few non-native fishes and are characterized by natural flow regimes and fluvial processes that favour the persistence of

Table 6. Family, common name, origin (N = native; I = introduced), species group, and the percentage of sites where the focal species was found (number of sites, $n=44$) in streams of the Alameda Creek catchments, California, 2009

Family	Common name	Origin	TWINSPAN group	Percentage of sites (number of sites)
Petromyzontidae	Pacific lamprey	N	3	12 (1)
Cyprinidae	hitch	N	3	18 (8)
	California roach	N	2	52 (23)
	Sacramento blackfish	N	3	2 (1)
	Sacramento pikeminnow	N	3	36 (16)
	common carp	I	4	5 (2)
	goldfish	I	4	9 (4)
Catostomidae	Sacramento sucker	N	3	64 (28)
Salmonidae	rainbow trout	N	1	25 (11)
Gasterosteidae	threespine stickleback	N	4	9 (4)
Cottidae	prickly sculpin	N	2	48 (21)
Fundulidae	rainwater killifish	I	4	2 (1)
Poeciliidae	western mosquitofish	I	4	23 (10)
Ictaluridae	channel catfish	I	3	2 (1)
Atherinopsidae	inland silverside	I	4	11 (5)
Centrarchidae	smallmouth bass	I	3	7 (3)
	largemouth bass	I	3	11 (5)
	green sunfish	I	4	14 (6)
Gobiidae	chameleon goby	I	4	2 (1)
	yellowfin goby	I	4	2 (1)

Table 7. Environmental and fish community metric variable values (means across sites) for three TWINSPAN site groupings within the Alameda Creek catchments, California. Values with a different superscript letter ($^{A\text{-}C}$) have significant differences between site groups and values with the same superscript letter were not significantly different (one-way analysis of variance, ANOVA, $P<0.05$)

Variable	Groups 1 & 2: Diablo Range-Wildlands	Group 3: Niles Canyon-Rural Valleys	Group 4: Flood Channel-Urban
Elevation (m)	296.7^{A}	67.3^{B}	57.1^{B}
Strahler stream order (1–6)	2.9^{A}	4.6^{B}	4.1^{B}
Mean wetted channel width (m)	5.1^{A}	8.9^{B}	8^{B}
Mean depth (cm)	29.8^{A}	$34.8^{A,B}$	35.7^{B}
Maximum depth (cm)	76.9^{A}	$77^{A,B}$	81.3^{B}
Water temperature (°C)	18.1^{A}	20.8^{B}	21.5^{B}
Conductivity (μS)	493.8^{A}	1004.4^{B}	1205.6^{B}
Turbidity (cm)	$>120^{A}$	74.7^{B}	69.3^{B}
Canopy cover (%)	14.5^{A}	10.1^{B}	8.1^{B}
Silt (%)	5.1^{A}	13.9^{B}	29.9^{C}
Sand (%)	6.3^{A}	15.2^{B}	11.6^{B}
Gravel (%)	63^{A}	$56.8^{A,B}$	43.6^{B}
Cobble (%)	20.3^{A}	11^{B}	10.5^{B}
Boulder (%)	5.2^{A}	3.2^{A}	4.4^{A}
D-50 (mm)	31^{A}	10^{B}	6^{B}
Pool habitat (%)	$69.8^{A,B}$	60.6^{A}	82^{B}
Riffle habitat (%)	$30.2^{A,B}$	39.4^{A}	18^{B}
Total Number Species	2.6^{A}	3.9^{B}	4.2^{B}
Native Species (%)	98.3^{A}	79.6^{B}	48^{C}

native fishes (Baltz and Moyle, 1993; Moyle *et al.*, 1998; Bunn and Arthington, 2002). In this region, undisturbed landscapes typically support fish assemblages containing two to eight native species, including Pacific lamprey, California roach, hitch, Sacramento pikeminnow, Sacramento sucker, rainbow trout, and prickly or riffle sculpin.

Undisturbed headwater streams may flow to suburban and agricultural landscapes characterized by low-density housing and setback fields, respectively, thereby permitting streams to retain some natural processes and functions, including habitat support for native fishes. For example, 13 native fish species have been documented, many in moderate to high abundances, in the lower Napa River in the northern SFE where it flows primarily through vineyards before entering the estuary (Koehler and Blank, 2010). Similarly, the study documented that native fishes dominate assemblages within the rural Niles Canyon reach of Alameda Creek even though the canyon reach lies between areas characterized by flood channels and urbanized land uses.

Streams are characterized by a prevalence of saltwater dispersant native fishes

Tidal freshwater to brackish water environments of the lower reaches of SFE streams provide suitable conditions for 21 native euryhaline marine or obligatory freshwater fish species that are saltwater dispersant. Because of their tolerances to a broad range of water salinities, these native fishes presumably maintain populations by migrating between the tidal riverine and estuarine environments of different streams through variable salinity waters. For example, in the northern SFE region, the endemic tule perch inhabits both tidal estuarine and non-tidal riverine portions of the Sonoma Creek and the Napa and Petaluma rivers, a vast interconnected maze of tidal and nontidal riverine channels (Leidy, 2007). Estuarine movement presumably allows for multiple introduction and colonization events by native fishes following localized extirpation or periods of low population abundances.

Salt water is a barrier to the movement of non-native fishes

Salt water is a chemical barrier to non-native fish invasions of, and movement between, SFE streams. Twenty (63%) of the non-native fish species in SFE streams are freshwater dispersant and therefore unable to tolerate moderate to high water salinities for prolonged periods. San Francisco Bay forms a salinity barrier to the movement between catchments for many non-native, obligatory freshwater dispersant fishes. This is especially true in the central and southern Estuary, and seasonally in portions of the northern SFE depending on how water salinity is affected by total outflow of fresh water in the

Delta. Only rarely during periods of extremely high freshwater discharge from the Central Valley can freshwater dispersant fishes migrate through the Bay between southern Estuary catchments (Snyder, 1905). Saltwater dispersal barriers presumably benefit native fish assemblages by reducing the frequency of opportunities for the invasion and establishment of non-native fishes between individual catchments.

Native stream fishes exhibit broad physiological tolerances

Many of California's non-salmonid native stream fishes have wide physiological tolerances, including tolerance to high water temperatures, high conductivity, high turbidity, and low dissolved oxygen; environmental conditions often associated with disturbed urbanized streams (Gasith and Resh, 1999; Moyle, 2002; Leidy, 2007). Native fishes may also tolerate chronic low to moderate levels of pollution, albeit at lower population abundances compared with unimpaired streams (Saiki, 1984; Brown, 2000; Leidy, 2007). Urbanized SFE streams are frequently characterized by impaired water quality often linked to reduced stream flows from the operation of dams and diversions, increased water temperatures from the removal of riparian vegetation, and nutrient enrichment and elevated levels of toxicants from non-point source runoff (Leidy, 2007). Several native fishes are particularly tolerant of stressful environmental conditions and are able to persist in streams under impaired conditions, including fishes found in middle mainstem and lower tributary reaches. At least seven native fishes from four families including hitch, Sacramento blackfish, Sacramento sucker, threespine stickleback, and prickly sculpin, are known to tolerate high water temperatures and conductivities, low dissolved oxygen, and low to moderate water pollution.

Native and non-native stream fishes may coexist in mixed assemblages

Non-native fishes often are more diverse and abundant in highly altered urbanized streams within the SFE (Leidy, 2007). However in SFE streams, native and non-native fishes are often found together in a semi-random pattern of dominance and occurrence (Leidy, 2007). Mechanisms that allow for mixed assemblages of native and non-native fishes are not well understood but they are probably determined by the interaction of human and natural disturbances operating at several spatial and temporal scales (Leidy and Fiedler, 1985). Periodic seasonal floods in late winter and early spring may provide the disturbance mechanism that allows for the persistence of native and non-native fishes together in otherwise hostile environments dominated by non-native fishes (Leidy and Fiedler, 1985; Brown and Ford, 2002). Floods disproportionately remove non-native fishes that are not adapted to natural flood flow regimes (Marchetti and Moyle, 2001). Seasonal hydrologic patterns may also allow a competitive advantage to native fishes that typically reproduce earlier in the season at lower water temperatures than do non-native fishes, which more often than not tend to spawn in warm and slow-moving water (Moyle, 2002).

Reservoirs serve as habitat for several native fishes

There are 44 reservoirs within the Estuary, ranging in size, function, and biotic diversity (California Department of Water Resources, 2011). Dams and their reservoirs are known to adversely affect native stream fishes through three primary mechanisms: (1) by their very nature, dams modify the magnitude, frequency, timing, and duration of stream discharge (Poff *et al.*, 1997); (2) dams act as barriers to fish migration (Gehrke *et al.*, 2002); and (3) dams create upstream reservoirs and thereby convert formerly lotic habitats to lacustrine environments, which are often stocked with non-native fishes to the detriment of native ones (Vondracek *et al.*, 1989). In contrast, streams with no or few reservoirs tend to exhibit a natural flow regime and are generally thought to favour native over non-native fishes (Baltz and Moyle, 1993; Moyle and Light, 1996).

Less understood are the contributions of reservoirs to the persistence of native fishes, and we suggest four possibilities. First, in streams where access from headwaters to marine environments is blocked, anadromous and non-anadromous fishes may establish resident or adfluvial populations that use tributaries to the reservoir for spawning and juvenile (Thrower *et al.*, 2008). This behaviour has been noted in land-locked lake fish populations elsewhere (Swanberg, 1997) and is found among 10 native fish species of the SFE including Pacific lamprey, hitch, Sacramento blackfish, Sacramento pikeminnow, Sacramento sucker, rainbow trout, threespine stickleback, prickly sculpin, Sacramento perch, and tule perch.

Second, reservoirs may provide refuges during prolonged periods of drought when tributary streams become partially or completely dry (Leidy, 2007). Small headwater streams in Mediterranean climates often are intermittent during the summer season, restricting fish to groundwater-fed pools (Gasith and Resh, 1999; Pires *et al.*, 1999). During years when pools completely dry or contain lethal abiotic conditions for fish, downstream reservoirs with relatively constant conditions may provide refugia and serve as a source of colonists to maintain adfluvial and stream populations under more suitable flows.

Third, some reservoirs are managed to increase downstream flows in summer for the delivery of irrigation water or for the recharge of groundwater basins. Increased summer flows allow native fishes to persist in otherwise summer-dry stream reaches. For example, rainbow trout are known to persist below reservoirs in some SFE stream reaches where they would normally be absent during dry summer periods under natural flow regimes (Smith, 1999).

Fourth, many of the large reservoirs in this region are owned and operated by public water agencies. Stringent land-use management practices are enforced on catchment lands surrounding reservoirs to protect public drinking water quality. Protective catchment management practices also protect native fish habitat in tributary and outlet streams to these reservoirs by restricting public access, urban development, poor livestock grazing practices, and the consequent input of pollutants.

Conservation recommendations

Urban SFE land-use patterns and their effects on native fishes are often complex and reach specific. Nevertheless, remarkable patterns of persistence in native fishes were observed in this heavily urbanized region suggesting that strategies for protecting native fishes will be most effective when multiple, reach-specific approaches are applied within a catchment. First priority should be given to a *protect the best* conservation approach focused on safeguarding and managing remaining natural riverine landscapes within urbanized, rapidly urbanizing, and adjacent rural lands that support assemblages of native fishes (Bay Area Open Space Council, 2011). Such a strategy focuses on protecting streams characterized by a natural flow regime, dynamic channel geomorphic processes, and maximum longitudinal connectivity between stream reaches (i.e. minimum fragmentation). This approach does not mean protecting only pristine streams. Rather, and as demonstrated in this study, streams in urbanized settings that suffer from some form of environmental impairment may nevertheless support important remnants of native fish assemblages. This study of native fishes in streams in urbanized settings supports taking a conservation approach that identifies and protects mixed assemblages of native and non-native fishes, as protecting mixed assemblages may afford the greatest conservation value to native fishes.

Priority streams may range from the headwaters to tidal-riverine marshes. Protection should include a focus on small headwater streams, which in this region is analogous to protecting the most natural or non-urbanized landscapes (Lowe and Likens, 2005); perennial stream reaches that function as critical long-term refugia for fishes during periods of drought; streamscapes characterized by steep geographic and environmental gradients in climate, topography, and geology that will maximize the diversity of available habitats for native fish species (Leidy, 2007); streams with upland buffers that extend beyond traditional wetland and riparian zones, especially steep slopes along narrow canyons (Shandas and Alberti, 2008); streams flowing through agricultural areas exhibiting the potential for enhancement or restoration of functions important to native fishes; disturbed streams with opportunities for recovering missing elements (e.g. adjacent wetlands, side channels) of the historical stream ecosystem, thereby increasing ecological complexity (Sedell *et al*., 1990; Grossinger *et al*., 2007); and tidal marshes, especially brackish and freshwater tidal marshes which support native euryhaline fishes (Saiki and Mejia, 2009).

Reservoirs and their contributing catchments should be assessed and where appropriate, managed to benefit native fishes through the establishment of natural flow regimes and the protection of tributary and outlet streams (Moyle *et al*., 1998). Because the removal of large reservoirs is often not a viable option, flow releases below reservoirs that mimic the natural flow regime will contribute to the maintenance of a quasi-equilibrium between native and non-native species (Marchetti and Moyle, 2001; Moyle and Mount, 2007). Furthermore, protecting reservoir tributaries and limiting non-native introductions into reservoirs will presumably benefit native adfluvial fish populations (Thrower *et al*., 2008).

Strategies for the reintroduction of native fishes into streams of historical occurrence may prove a useful conservation approach in urban landscapes (Charbonneau and Resh, 1992). An approach that incorporates current habitat suitability and historical ecology to inform the likelihood of successful reintroduction and restoration targets could help to restore extirpated species, enhance genetic diversity within small populations, and increase overall regional biodiversity.

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