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Expansion of the Non-native Mississippi Silverside, *Menidia audens* (Pisces, Atherinopsidae), into Fresh and Marine Waters of Coastal Southern California

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Abstract.—Mississippi Silversides, *Menidia audens*, were first recorded in southern California reservoirs and nearby outflows in the late 1980s and early 1990s. In 1997–2000 they were taken in King Harbor, Redondo Beach, and in 2000 in the Santa Ana River. By 2005–2006 they were found in several other coastal drainages from the San Gabriel River in Orange and Los Angeles counties northward to Arroyo Burro, Santa Barbara County. Initial invasion was via the California Aqueduct in the late 1980s and early 1990s and more recently dispersal has taken place along the southern California coast. The records from King Harbor occurred for a relatively short period, mid-1997–mid-2000 (mostly 1997 and 1998) before they were established in coastal drainages. Their impact on native species is not known but on some occasions Mississippi Silversides have outnumbered native Topsmelt, *Atherinops affinis*, in small coastal lagoons estuaries. Mississippi Silversides are known to prey on eggs and larvae of other fishes and could be increasing predation on small native animals as well as serving as prey for larger piscivores like steelhead and terns.

In the fall of 1967 the Mississippi Silverside, *Menidia audens* (Hay 1882), (Atherinopsidae), was introduced into Blue and Clear lakes, Lake County, northern California to control larvae of a non-biting midge, a cosmetic nuisance in the region (Dill and Cordone 1997). Fish dispersed downstream into the Sacramento and San Joaquin rivers and became widespread in the greater San Francisco Bay Delta (Bennett and Moyle 1996; DeLeon 1999; Fuller et al. 1999). By the late 1980s and early 1990s they were taken in some southern California reservoirs at the southern terminus of the California Aqueduct (Aqueduct). The Aqueduct has conveyed Delta water to southern California since the early 1970s (Swift et al. 1993; Dill and 1997; Moyle 2002). A few were taken farther downstream in the Santa Clara River near the mouth of Piru Creek below both Pyramid Reservoir and Lake Piru on the creek. These fish were thought to have come down Piru Creek through these intervening reservoirs. Otherwise they were not detected until 1997 when larvae were taken in the marine habitat at King Harbor, Redondo Beach,

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Los Angeles County and in 2000 when they began to be recorded at several freshwater and estuarine localities. Swift et al. (1993) and Schroeter and Moyle (2006) predicted this expansion and its progress is presented here.

The mostly freshwater Mississippi Silverside is native to the lower Mississippi River and Gulf of Mexico drainages east to the Pearl River, Mississippi and west to the Sabine River, Louisiana and Texas (Suttkus and Thompson 2002; Suttkus et al. 2005). It was synonymized with the coastal brackish-water Inland Silverside, *M. beryllina*, by Chernoff et al. (1981) and was again elevated as a distinct species by Suttkus and Thompson (2002), Suttkus et al. (2005), and Page et al. (2013). A third similar species, the Tidewater Silverside, *M. peninsulae*, also occurs in more marine coastal areas of the Gulf of Mexico (Suttkus and Mettee 1998). Suttkus and coauthors provided convincing evidence of the morphological distinctions between these three taxa. However, Johnson (1975) and Fuker, et al. (2011) found fewer genetic distinctions in allozymes and mtDNA, respectively, between the Mississippi and Inland Silversides than between the Inland Silverside and the Tidewater Silverside.

Methods and Materials

Live specimens were collected with small seines or dip nets and occasional dead specimens were taken by hand. King Harbor material was taken in monthly surface hauls of a one-meter conical plankton net of 333 μm mesh from 1974 through the present (Stephens et al. 1994, Stephens and Pondella 2002, Pondella et al. 2012). Voucher specimens deposited in the Fish Collection of the Natural History Museum of Los Angeles County (LACM) and some were originally preserved in ethyl alcohol for potential DNA study. The King Harbor larval collections are Moore Laboratory of Zoology, Occidental College. Below LACM catalogue numbers are followed by the number of specimens and range in standard length (SL) in brackets. To distinguish the Mississippi silversides from the local native atherinopsids and to confirm their specific identity in the genus *Menidia*, scale and gill raker counts were taken according to Hubbs and Lagler (2004) with the following clarification for lateral line scale counts. Suttkus and Mettee (1998) followed Hubbs and Lagler (1958) in presenting predorsal scale counts for species of *Mendia*. Suttkus and Thompson (2002) and Suttkus et al. (2005) provided lateral scale counts also. The posterior two-thirds or so of the pored or grooved scales of the lateral line in *Menidia* lies below the lateral midline. The anterior one-quarter to one-third lies above with a vertical gap of two to three unpored scale rows. Hubbs and Lagler (1958, 2004) define the lateral scale count as from the base of the caudal fin to the first scale touching the shoulder girdle and if some scales are not pored, "...the number of scales along the line in the position that would normally be occupied by a typical lateral line scale." A count from the caudal base along the lower pored lateral line segment, continuing forward on unpored scales ends at a narrow fleshy unscaled area just behind the pectoral base, not reaching the pectoral girdle itself; counting posteriorly from the shoulder girdle above the pectoral fin base on the upper, shorter anterior pored segment results in a complete count to the caudal base as defined, but bypasses the majority of the pored scales in the lower lateral line. The lower count is 2–4 scales less than the upper count. We present the upper counts here as Chernoff et al. (1981) described as "The lateral scale series was that row immediately above the lateral stripe, originating at the junction of the head and the dorsal margin of the pectoral girdle and terminating at the caudal base." Presumably this was methodology of Suttkus et al. (2005). Counts were taken on 50 fish as follows: Santa Clara River (58125-



Fig. 1. Specimen of *Menidia audens*, 47.8 mm SL, Los Angeles County, Malibu Lagoon, 17 November 2006, from LACM 58123-1, pectoral fin removed to show lateral pigmentation. Photo by Camm Swift

2, 10[53–85]), Malibu Lagoon (58123-1, 20[47–58]), and the Santa Ana River (58117-1, 20[55–72]). Three Malibu fish had anomalous gaps in the gill raker spacing near the lower end of the row and were excluded from those counts. Three other Malibu specimens had one or a few distinctly foreshortened gill rakers otherwise in normal position and were included in the counts.

Identification

The Mississippi Silverside's slender shape and pale, semi-translucent and yellowish or light greenish color differs from all other freshwater fishes currently in coastal southern California (Fig. 1). In the estuarine areas it can be confused with small Topsmelt, Jacksmelt, *Atherinopsis californiensis*, and California Grunion, *Leuresthes tenuis*. In southern California estuaries Topsmelt are often common. Jacksmelt and California Grunion, typically more marine, are usually uncommon in lower salinity zones of coastal lagoons but occur in larger tidal bays and estuaries. The dorsal, anal, and pectoral fins are larger and longer in Mississippi Silversides, the depressed pectoral fin extends back 90% or more of the distance to the vent whereas it extends 50% or less of this distance in the three native atherinopsids. The first unbranched pectoral ray in the Mississippi Silverside is 90% or more the length of the second, or first branched ray vs. 60–70% of that ray in the native atherinopsids. The pectoral fin base is almost vertical, sloping slightly posteroventrally on the Mississippi Silverside and is strongly sloped backward and downward about 45° in the native species. Mississippi Silversides also have a much finer and reticulated melanophore pattern on dorsolateral scales consisting of a single row of finely divided melanophores bordering each scale in contrast to several rows of darker concentrated cells in the native species. The background color in Mississippi Silversides is pale yellowish, greenish, or tan in life rather than bluish or grayish as in the three native species. The Mississippi Silverside reaches about 100 mm SL compared to ≥ 150 mm for Topsmelt, Jacksmelt, and California Grunion. Finally meristic counts are all fewer than in the native atherinopsids with little or no overlap: dorsal spines, Mississippi silversides, IV–VI vs. V–IX; dorsal rays $i + 8-9$ vs. $i + 8-14$; anal rays, $i + 15-19$ vs. $i + 19-26$; total gill rakers on first arch 23 or fewer vs. more than 30; lateral scales, 34–45 vs 60–80; predorsal scales 18–22 vs. more than 25; and scales between the dorsal fin 4–6 vs. 7–12 in the three native atherinopsid species.

Key to California Species of Atherinopsidae

- 1a. Depressed pectoral fin extends posteriorly 80–90% of distance to vent or cloaca; pectoral fin base almost vertical or only slightly sloped backward; scales large and outlined with one row of very finely divided pigment cells; lateral scales 35–45; gill rakers on first left arch 23 or fewer, size ≤ 100 mm SL (4 inches)Mississippi Silverside, *Menidia audens*
- 1b. Depressed pectoral fin extends only 50–60% of distance to vent; pectoral fin base slopes backward at about a 45° angle; lateral scales more than 50; gill rakers more than 30; size often greater than 100 mm SL and up to about 380 mm SL (17.5 inches TL)2
- 2a. Ten to 12 scales between the dorsal fin bases; anal fin origin posterior to a vertical through posterior end (insertion) of the first (spinous) dorsal fin base; teeth in multiple rows with single points (unicuspid) at all sizes.Jacksmelt, *Atherinopsis californiensis*
- 2b. Five to nine scales between the dorsal fin bases; anal origin below a vertical through some portion of the first (spinous) dorsal fin base; teeth absent or in one row (uniserial) and bifid (forked) in fish over about 50 mm SL, with single points on teeth in smaller fish3
- 3a. Teeth distinctly developed, in a single row and forked in fish over about 50 mm SL; Five to eight scales between the dorsal fins; protruded upper jaw (premaxillary bones) extends forward rather than downward; body deeper, depth 4 to 6 times in SLTopsmelt, *Atherinops affinis*
- 3b. Teeth lacking or minute, difficult to detect even in adults; seven to nine scales between dorsal fin bases; mouth protrudes forward and downward; body slender, greatest depth 6 to 8 times in SLGrunion, *Leuresthes tenuis*

Other Potential *Menidia* Invasions

Consideration of two additional similar species of *Menidia* is important because of the potential for them to be introduced into California waters. Toxicity testing of various natural and waste waters utilizes live two to seven or eight day old fish called Inland Silversides. These are laboratory cultured and widely distributed to testing laboratories and stocks originate in the coastal Gulf of Mexico and Atlantic coast of Florida or from domesticated stocks cultured specifically for water testing. Thus, depending on where they were taken either Inland (*M. beryllina*) or Tidewater (*M. peninsulae*) Silversides could be captured and utilized. Laboratory populations from widely separated areas might have unique genetic or morphological features from wild populations and could add to the non-native silverside mix in California.

The three similar, widespread species of *Menidia* (*peninsulae*, *beryllina*, and *audens*) are difficult to distinguish. Suttkus and Mettee (1998) found the ratio of pre-anal length to standard length is less than 0.7 *M. beryllina* and usually more in *M. peninsulae*. Otherwise these two species to be almost identical in meristics and morphometrics except for total gill rakers on the first left gill arch; *M. beryllina* usually 22–23, *M. peninsulae* usually 25–26, and *Menidia audens* usually has 21 or fewer. The largely brackish *M. beryllina* is separated from the largely freshwater *M. audens* since the latter is slimmer with lower head, body, and caudal peduncle depth compared to *M. beryllina*. In addition an index adding the predorsal and lateral line scale counts together separates these two species 98.4% of the time with *audens* having 58 or more and *beryllina* 57 or less (Suttkus et al. 2005). The counts for 50 southern California fish noted above (47 for gill rakers) follow: lateral line scales (see

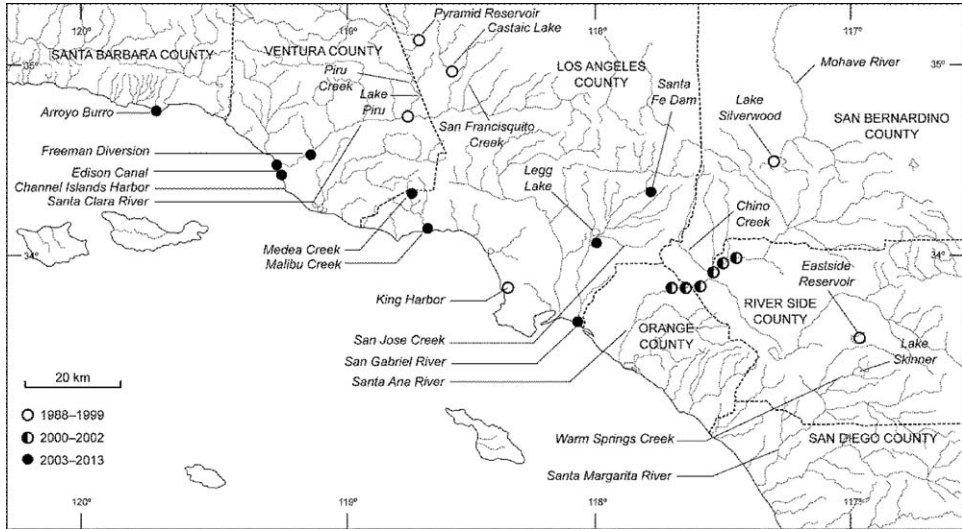


Fig. 2. Coastal southern California with locality records of Mississippi silversides. All except King Harbor and Arroyo Burro are considered established populations either because they are known to directly or indirectly receive unfiltered California Aqueduct water or have been observed continuously over several years. Lake Cachuma is the lake north of Arroyo Burro on the Santa Ynez River.

methods) $X = 41.56$, ($SD = 1.1457$); predorsal scales, $X = 22.2549$, $SD = 2.0961$; total of lateral line and predorsal scales, $X = 63.76$, $SD = 2.5117$; and gill rakers, $X = 19.1667$, $SD = 1.118$. These three counts are diagnostic for *Menidia audens* as shown by Suttkus et al. (2005) with gill rakers lower and scale counts higher than in *M. beryllina* and *M. peninsulæ*.

Records (North to South, Fig. 2)

Arroyo Burro Lagoon, Santa Barbara City and County: On June 2, 2004, two individuals were taken by ECORP biologists (58119-1, 2[69–92]). No more have been taken in repeated sampling in the next 10 years at this site or at the larger Mission Creek lagoon about 5.5 km to the east.

Santa Clara River drainage, Ventura and Los Angeles counties: Records of California Department of Fish and Wildlife biologists in 1988 and 1992 were documented by Swift et al. (1993) from Pyramid (45701-4, 6[60–105]) and Castaic reservoirs. In 1993 about 10 small individuals were observed in the River within a kilometer of the mouth of Piru Creek (45698-1; 45792-1; 58110-1; 58111-1), and two small specimens were taken in this same vicinity in 1999 (45715-1, 2[50–53]). On 24 August and the first week of September 2006 a few specimens were photographed from the Freeman Diversion on the river 16.8 km upstream of the ocean. On October 24, 2006 three specimens were kept (58120-1, 3[49–55]) and on November 17, 2007 another 15 were taken (58144-1). They were also seen in or near diversion impoundments near Santa Paula about 20 km upstream of the Freeman Diversion. Mississippi Silversides entered the diversion canal at the Freeman Diversion through a 3/16 mesh wedge wire intake screen designed to exclude steelhead. The silversides have established a population within the canal and pond system. Hundreds were observed in the canals in 2007 through 2009 and remain present but rare since.

The lagoon at the mouth of the river was sampled two to three times a year from 1999 onward, and the first Mississippi Silversides were taken on 23 October 2007 (58125-1).

About sixty juveniles to adults were taken on 14 October 2008 and about 20 were observed on September 17, 2010. They have been repeatedly taken through 2012. On January 9, 2008 two individuals (58126-1, 2[37–51]) were taken in a small separate beach pond along the open coast just south of the southern extent of the lagoon and near the cooling water outfall of the Southern California Edison (now Reliant Energy) Mandalay Power Generating Station.

Channel Islands Harbor, Edison Canal, Ventura County: Also on January 9, 2008, one (58126-1, 1 [38]) was taken in the Edison Canal within 100 m of the Mandalay Station intake. This canal carries marine water for 3 km northwest from upper end of Channel Islands Harbor to the Power Plant.

Malibu Creek Lagoon and Creek, Los Angeles County: Malibu Lagoon was sampled a few times per year from the 1970s onward with high school student classes and from 1991 onward to monitor the introduced population of the federally endangered Tidewater Goby, *Eucyclogobius newberryi*. The first Mississippi Silversides (56403-1, 18[33–68]) were taken on November 2, 2005. They were taken subsequently on 17 November 2006 and greatly outnumbered Topsmelt, *Atherinops affinis*. They continue to be taken in the lagoon, most recently on January 8, 2012 and August 5, 2013 (Rosi Dagit, Topanga-Las Virgenes Resource Conservation District, personal communication, including photographs). On June 13, 2007 Manna Warburton and Brian Zitt (ECORP Consulting, Inc., personal communications) took about 20 Mississippi Silversides in Medea Creek (tributary of Malibu Creek) near the crossing of the 101 Freeway. This site is upstream of both Rindge Dam and Malibu Lake reservoirs on Malibu Creek.

King Harbor, Redondo Beach, Los Angeles County: Early larvae with large yolk sacs still evident were taken in sixteen monthly plankton hauls from mid-1997 to mid-2001. Fourteen were taken as one or two individuals almost monthly from June, 1997 to July 1998 with one in June, 2000 and another in June, 2001. These are the only records during this continuous monthly sampling from 1974 to present (Vantuna Research Group collections, Occidental College). King Harbor is a coastal marine harbor site with marine salinities and warming influence of the adjacent AES Redondo Beach generating station.

San Gabriel River, Los Angeles and Orange counties: On October 12, 2006 two individuals (58121-1, 2[78–80]) were taken with Topsmelt in the tidal and channelized San Gabriel River at the lower end of the concrete-lined channel just downstream of the mouth of Coyote Creek. They were among at least 150 similar sized atherinopsids moving in with the rising tide. Upstream at the mouth of San Jose Creek they were common on 17 August 2007, with about 100 observed (58124-1, 31 [20–48]). Earlier on 11 October 2006 and later on 20 August 2008 none were taken at this site. The river had been very low and possibly dried out within a few weeks before the 2008 visit. On October 13, 2006 one specimen (58122-1, 1[38]) was taken in the Santa Fe Dam Recreation fishing lake, part of the flood control basin for the San Gabriel River.

Santa Ana River, Riverside and Orange counties: On March 26 and 27, 2000, several small, silvery fish were observed escaping fyke traps in a diversion channel about 200 m downstream of the River Road bridge in Norco. These were likely Mississippi silversides since ten days later, April 6th one (58113-1, 1[44]) was taken about 8 km upstream near the south end of California Avenue and the outlet of a channel draining Hidden Valley Regional Park. In the next few months individuals were taken from the mouth of Evans Lake Drain at Mission Road, City of Riverside, to about 50 km downstream at the Imperial Highway crossing (58114-1, 58116-1, 58118, and others). They became common in the lower gradient parts of the Santa Ana River from about the Interstate 15 crossing

downstream to Imperial Hwy until the heavy winter of 2004–2005 when they became uncommon. They continue to be recorded through 2012 and have clearly become established (Kerwin Russell, Riverside-Corona Resource Conservation District, Bonnie Johnson, Orange County Water District, personal communications, 12–14 January 2013).

Santa Margarita River, San Diego and Riverside counties: Mississippi silversides entered the East Side Reservoir, just south of Hemet in Riverside County, in late 1999 or 2000 as the reservoir filled with water from the California Aqueduct and Colorado River (Michael Guisti, personal communication). This reservoir lies in the Santa Margarita River drainage but does not directly release water. Water is transferred from this reservoir to Lake Skinner and then occasionally released into Warm Springs Creek, a northern tributary to the Santa Margarita River (Michael Guisti, personal communication). This creek is usually intermittent or dry but provides a potential avenue of invasion into the Santa Margarita River drainage.

Mojave River Drainage, San Bernardino County: On 2 October 1993 about 300 Mississippi Silversides were seen at the boat launch ramp area on the southern edge of Lake Silverwood and 24 were kept (58112-1, [33–46]). No other collections are known but they likely still inhabit the lake since it receives Aqueduct water, which can be released down the Mojave River.

Discussion

The introduction of second non-native species very similar to one in the same genus already established has precedents in California. The initial putative spread of Chameleon Goby, *Tridentiger trigonocephalus*, into the low salinity Delta region of San Francisco Bay was due to the arrival and spread of a second, very similar brackish water species, the Shimofuri Goby, *Tridentiger bifasicatus* (Matern and Fleming 1995), described in Japan by Akihito and Sakamoto (1989). Markle and Simon (1997) found that Fathead Minnows in Klamath Lakes (Oregon-California border) were morphologically the northern subspecies, *Pimephales promelas promelas*, a form utilized for water testing, rather than the commonly cultured bait fish, *P. p. confertus*, the southern subspecies, introduced into the southwestern United States from Texas (Dill and Cordone 1997). These species pairs are in addition to the known introductions of more than one geographically distinct population of game fishes like Largemouth Bass, *Micropterus salmoides*, Spotted Bass, *M. punctulatus*, Bluegill, *Lepomis macrochirus*, and Black Crappie, *Pomoxis nigromaculatus*, now recognized as separate species or subspecies in their native regions (Warren 2009).

Clearly the distribution of water via the California Aqueduct has led to the establishment of Mississippi Silversides in several coastal southern California localities and the species will likely spread farther to the north and south with dispersal along the coast. Coastal streams and brackish estuaries provide adequate habitat for this fish and it can tolerate higher salinities (Hubbs et al. 1971). It feeds on larval fishes and could impact the native fishes in freshwater streams and coastal lagoons (Luttrell et al. 1999; Baerwald, et al 2012). While initial entry into southern California was via the California Aqueduct, the coastal sites like Malibu Lagoon and Arroyo Burro do not directly receive unfiltered Aqueduct water and the populations at these sites may require different explanations. Dispersal may take place during the wet season when runoff makes coastal waters fresher for short periods, but *Menidia audens* from Lake Texoma, OK were found to be tolerant of marine or near marine salinities for at least two days (Hubbs et al. 1971). The presence of Mississippi Silversides in Medea Creek, tributary to

Malibu Creek, suggests anglers or others may have introduced them and then dispersed downstream. Medea Creek receives Aqueduct water but it has been subjected to chloramination and filtration before entering the drainage so silversides could not have arrived via this route (Randal Orton, Jan Dougall, Las Virgenes Water Conservation District, personal communications). Arroyo Burro can indirectly receive Aqueduct water via flush valves in a pipeline of unfiltered water from Lake Cachuma. However, the Aqueduct water is also chloraminated and filtered before entering Lake Cachuma (Rosemary Thompson, Cardno ENTRIX, Santa Barbara, personal communication). Thus Mississippi Silversides would have to have been independently introduced into Lake Cachuma to be transferred to Arroyo Burro. Possibly they occur in Lake Cachuma and have been undetected to date. Both freshwater and coastal marine dispersal have been factors in the Mississippi silverside dispersal in southern California and it is likely they will become more widespread.

Swift et al. (1993) noted four other fish established outside the receiving reservoirs after likely arrival in Aqueduct water. In the late 1980s a population of Blackfish, *Orthodon microlepidotus*, was present in the Santa Ana River below Prado Dam but disappeared in the late 1990s. The inland form of Prickly Sculpin, *Cottus asper*, became established in the Santa Clara and Mohave rivers in the early 1990s and persists. Specimens of Prickly Sculpin have been observed in a diversion and associated groundwater infiltration basins of the Santa Margarita River near Lake O'Neill on Marine Corps Base Camp Pendleton every year from 2008 to 2012 (Michael Rouse, Manna Warburton, personal communication). They may be more widespread in the drainage, which occasionally receives water from Lake Skinner as noted above. This indicates the Mississippi Silverside is to be expected in the Santa Margarita River. Finescale Logperch, *Percina microlepada*, were present in Irvine Lake in the Santa Ana River drainage the early 1990s. Then one was taken downstream in the Santa Ana River in Burris Basin, adjacent to the river in Anaheim on June 30, 2012 (Bonnie Johnson, Orange County Water District, personal communication with photo). A population of Hitch, *Lavinia exilicauda*, (Cyprinidae) has been recently documented in the Mohave River downstream of Lake Silverwood where they have hybridized with Arroyo Chub, *Gila orcutti*, (Jeffrey Seigel, LACM, personal communication, LACM specimens; Chen et al. 2013). The Arroyo Chub were introduced long ago (Swift et al. 1993) in upper tributaries of the Mohave River. Other reservoir species from the Central Valley of California like the native Tule Perch, *Hysterothorax traski*, and non-native species like Striped Bass, *Morone saxatilis*, and Shimofuri Goby, *Tridentiger bifasciatus*, had not become established downstream of Aqueduct reservoirs like Pyramid, Castaic, Silverwood, and East Side. However, a few shimofuri gobies have recently been discovered in Piru Creek below San Felicia Dam and in the Freeman Diversion (Ventura County) in late 2013 and early 2014 (Howard, personal observations). In some cases these occurrences may be repeated invasions via the same routes rather than established populations but the prickly sculpin, finescale logperch, and Mississippi silversides have been established for ten or more years. In the case of the logperch and sculpin, more than twenty years in the Santa Ana and Santa Clara rivers, respectively. Stephen et al. (2007) and Foss et al. (2007) note several mechanisms of coastal movement/transport of non-indigenous aquatic organisms in California without considering the inland movement with water deliveries, clearly an important avenue with subsequent local coastal movement.

The Santa Clara River was extensively sampled from Santa Clarita to the ocean by a variety of biologists after the few Mississippi silversides were taken in 1993 near the

mouth of Piru Creek and before the two that were taken in 1999. This included annual monitoring for steelhead at the Freeman Diversion. Apparently they were absent or rare and relatively unsuccessful from 1993 until they appeared in 2006 and became established. They arrived either 1) via Piru Creek from Pyramid Reservoir to Lake Piru and over San Felicia Dam, 2) from releases of California Aqueduct Water from Castaic Reservoir down Castaic Creek into the Santa Clara, or 3) via San Francisquito Creek from Metropolitan Water District pipeline maintenance releases. These latter releases occur about every five years and Castaic releases occur occasionally related to demand by water users downstream. Apparently conditions were not satisfactory for establishment for the species in the Santa Clara River as they were in the Santa Ana River. However in 2006 increasing numbers of Mississippi silversides became apparent and at least thousands were found in the estuarine mouth of the Santa Clara River in October of 2007 and in the settling ponds below the Freeman Diversion. Based on collections at the Freeman Diversion after the 2005 floods these fish became widely distributed after spills from reservoirs. They continue to be present in the system through 2012 but in smaller numbers at the Freeman Diversion and no spills over the Santa Clara River reservoirs have occurred since 2005.

The Santa Ana River was also extensively sampled beginning in 1997 leading up to the appearance of the silversides in early 2000. The river receives water from Aqueduct sources via its tributary, Chino Creek. Presumably this was the source of the silversides. The San Gabriel River was not extensively collected before or since the sampling in 2006, 2007, and 2008 and it is not known if the populations are persisting. At least two lakes in the system, Santa Fe Dam and Legg Lake, receive Aqueduct water. Small numbers of these fish probably leak through the system occasionally, sometimes find conditions favorable to expand their populations, and if conditions change, disappear as described for other introduced fish species in the lower Colorado River (Minckley 1982; Minckley and Marsh 2009).

As noted above Malibu Creek does not directly receive aqueduct water and the presence of fish in Medea Creek upstream of two dams in the system requires artificial introduction. The sources of these introductions are not known and were possibly to provide forage for game fish in Malibu Lake downstream. It would be impossible for fish from the lagoon to move upstream over these two dams on Malibu Creek. Thus fish may have invaded Malibu Lagoon from upstream rather than having moved along the coast in the ocean from the Santa Clara River or elsewhere.

The relatively brief period of larval records at King Harbor (1997–2000) from an almost 40 year monthly times series is exceptional, requiring local spawning or long distance dispersal of late stage larvae from unknown sites. Our records indicate no southern California source populations were present north of King Harbor in those years. Transport south from as far north as San Francisco Bay seems very unlikely, even in the strong freshwater runoff and warm conditions of the 1997–1998 El Niño event, particularly for late stage larvae which presumably resulted from spawning within the local area. Otherwise they would have to have come from the southern sites like the San Gabriel or Santa Ana rivers where they were not recorded until at least 2000. Coastal longshore movement of water is largely from north to south and the source presumably was to the north where other records in the lower Santa Clara River and Malibu Creek lagoons did not occur until 2005 or 2006. Otherwise only occasional rare individuals were taken in the early 1990s and 1999 as noted above for the Santa Clara River, and well upstream.

Mississippi silversides spawn from April to September in San Francisco Bay (Moyle 2002) and the presence of late larvae at King Harbor in several winter months is surprising also. In 1997–1998 the warmer El Niño ocean temperatures combined with the artificial warming by power plant outflows may have supported a population of *Menidia* but possibly not *M. audens* since low salinity environment is lacking. The source of this brief pulse of *Mendia* at King Harbor remains speculative and may have involved some kind of locally introduced fish. The nearby Hyperion Wastewater Plant utilized 7–11 day old *Menidia* larvae for testing from December 1994 to July 2005 when they were discontinued in favor of larval Topsmelt. At this age the fish are much larger than yolk sac larvae and the testing protocols requires disposal of all test organisms and none were released (Gerald McGowan, retired, City of Los Angeles, personal communication).

Mississippi Silversides may compete with Topsmelt, a species it overlaps with ecologically in southern California bays and estuaries. Particularly in Malibu Lagoon and the Santa Clara River lagoon the Mississippi Silversides were more common than Topsmelt in some collections. Most of the other sites were not sampled on a regular basis to determine relative abundance and it is not known if the Mississippi Silversides have spread to the lower estuarine areas of the Santa Ana River. It is less likely competition will occur with the more marine California Grunion and Jacksmelt but juveniles of these species utilize larger tidal bays and estuaries and could be impacted. Potentially serious is the known propensity for Mississippi Silversides to feed on the larvae of other fishes and such predation might impact several other species like the federally endangered tidewater goby, *Eucyclogobius newberryi* (U. S. Fish and Wildlife Service 2005), other estuarine gobies, killifish, sculpin, and others (Luttrell et al 1999; Baerwald et al. 2012). Reduction or management of these populations may be necessary in face of their possible adverse impacts. In addition, Foss et al. (2007) considered coastal non-indigenous aquatic species entirely in terms of coastal dispersal. The inland movement of estuarine fresh water from San Francisco Bay into southern California is also transporting freshwater and estuarine aquatic organisms. Small fishes leak through this system and many other smaller organisms must be carried along also. More study is needed to assess the impact of these invasive species in southern California and elsewhere in the southwestern United States (Minckley and Marsh 2009).

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