California Fish and Wildlife 106(3):226-257; 2020

Striped Bass on the coast of California: a review

DAVID A. BOUGHTON[1*]

[1] *National Marine Fisheries Service, Southwest Fisheries Science Center, 110 McAllister Way, Santa Cruz, CA 95060, USA*

**Corresponding Author: David.Boughton@noaa.gov*

Striped Bass (*Morone saxatilis*), a non-native, anadromous fish introduced to California in 1879, is a popular sport fish and piscivorous predator in the San Francisco Bay/Delta ecosystem, but comparatively little is known about its distribution and ecology in estuaries and rivers of the California coast. Here we review recent scientific papers, consultant reports, and correspondence to evaluate its distribution in coastal estuaries and rivers, evidence for local reproduction, and scope for impacts on native fishes, especially salmonids. Striped Bass is extremely rare in the ocean along the north coast, and has not turned up in extensive surveys of Humboldt Bay, the Eel River estuary, or the Russian River estuary. It is, however, a perennial feature of seining surveys in estuaries south of the Golden Gate and along Monterey Bay, usually sporadically and as a very small proportion of total catch. It has become quite common in the Carmel River estuary, and is occasionally caught in the ocean further south. Small upstream migrations, possibly for spawning, have been observed in the Salinas River and Carmel River, but no evidence of eggs or larvae has been found—perhaps due to a lack of ichthyplankton surveys anywhere except in Elkhorn Slough. However, the species' reproductive ecology is not a good match to the hydrologic structure of most coastal stream systems, requiring a large long river where adults can spawn, in combination with an extensive, ramifying estuarine system where larvae can accumulate. One potential good match is the Salinas River system, especially in its historic form as the Salinas River/Old Salinas River Channel/Elkhorn Slough complex of the 19th century. Despite the modest presence of the species on the coast between the Golden Gate and Carmel, it still has scope for large impacts on emigrating salmonids, due to its extreme piscivory at larger size-classes and its ability to exploit migration bottlenecks as feeding grounds. Most likely the individuals observed in coastal estuaries originated in the San Francisco Bay/Delta system and use local systems opportunistically for foraging, but the hypothesis of local reproduction cannot be ruled out without further study.

Key words: estuary, impacts, naturalized species, salmonids, Striped Bass

---

Striped Bass (*Morone saxatilis*) is a native fish of the Atlantic and Gulf Coast that was transplanted into California's San Francisco Estuary in 1879 and has since become naturalized (Scofield 1930). The species was actively stocked and initially very successful, supporting a commercial fishery by 1888 and an annual catch of more than 1.2 million pounds by 1899. Being facultatively anadromous, Striped Bass soon expanded into the ocean and could be caught up and down the Pacific coast, with two individuals each weighing six pounds caught by seine off of Redondo Beach near Los Angeles in September 1894 (Smith and Kendall 1898; Dill and Cordone 1997), and half a dozen individuals trapped by the U.S. Bureau of Fisheries off the mouth of the Columbia River in the Pacific Northwest in 1906 (Scofield and Bryant 1926). The species appears to have self-established a commercially fishable population in Coos Bay, Oregon by 1922 (Morgan and Gerlach 1950) and was eventually caught off the west coast of Vancouver Island, British Columbia in 1971 (Forrester et al. 1972).

The success, abundance, and broad distribution of Striped Bass have generated concerns about its impacts on native fish species in California, especially since subadults and adults are highly piscivorous (Thomas 1967; Loboschefsky et al. 2012). That said, the conditions necessary to support viable populations of the species appear to be rather restrictive on the Pacific coast. Two self-sustaining populations still occur in the San Francisco Estuary, one breeding in the Sacramento River and the other in the San Joaquin Delta (Moyle 2002), but the only other documented reports of wild-established, self-sustaining populations appear to be in Coos Bay, Oregon, and smaller populations in the nearby Coquille, Siuslaw, and Umpqua systems (Morgan and Gerlach 1950; Parks 1978; Karas 2016). The species has formed self-sustaining populations in several reservoirs where it was planted, notably Millerton Reservoir on the San Joaquin River, the system of reservoirs in the lower Colorado River (Dill and Cordone 1997), and San Antonio Reservoir in Monterey County (MCWRA and USACE 2001). Many other attempted introductions to reservoirs or coastal estuarine systems have failed (Dill and Cordone 1997).

Here I review scientific literature and consultant reports on the occurrence and potential impacts of *M. saxatilis* in the estuaries of the larger river systems along the coast of California. Since the listing under the Federal Endangered Species Act of coastal Steelhead (*Oncorhynchus mykiss*), Coho Salmon (*Oncorhynchus kisutch*), and Chinook Salmon (*Oncorhynchus tshawytscha*) stocks in the late 1990s, and recognition of the importance of coastal estuaries to the rearing of juveniles of these species (Smith 1990; Bond et al. 2008; Koski 2009), there is great value in better understanding the occurrence and potential impacts of Striped Bass in estuaries and rivers of the California coast. Here I consider three general questions: (1) Where do Striped Bass occur on the California coast? (2) Do they comprise locally reproducing populations, strays from the Golden Gate, or both? and (3) What is the general scale or scope of their potential impact on coastal salmonid populations?

DISTRIBUTION IN COASTAL RIVERS AND ESTUARIES

The questions raised above are not new. Scofield (1930), in his treatise on California Striped Bass, observed that:

> At the present time the bulk of the striped bass is confined to the San Francisco Bay region and along the coast to a distance of 75 miles to the north and to the south of the Golden Gate. To the south, excellent hook-and-line fishing is enjoyed most of the year at Marina

> Beach, Salinas River, Elkhorn Slough (all in Monterey Bay), Waddell Creek and many unnamed beaches. To the north, Bolinas Bay, Bodega Bay and Russian River all afford fine bass fishing.
>
> Many interested individuals contend that the striped bass which occur in the coastal waters south of the Golden Gate are of a separate race from those of the San Francisco Bay region. The bass, for instance, that inhabit Monterey Bay and its flanking sloughs and rivers, are believed to spawn there year after year. These rather serious contentions on the part of several interested sportsmen led to a study of the population of these fish occurring in this region several miles south of the Golden Gate. The results of this study seemingly disproves the theory that they are a separate population. For instance, no evidence of bass fry was obtained during the spring or summer when they should have been found in great quantities if the mature fish spawned in these southern regions. The smallest bass observed were in their second year or three inches in length and larger. The large bass examined during May, or about the time spawning was in progress in the San Francisco Bay region, contained ovaries in mature condition, but they were far from ripe. Over 95 per cent of the fish examined were females. None of the males were in ripe condition. Another fact noted as a result of seine hauls in Salinas River and Waddell Creek during May, 1927, was the complete absence of the third and fourth year classes. The second, sixth, seventh and eighth year groups were quite evident while the fifth year class was represented by only a few individuals. Samples of specimens received from anglers in this region were well over twenty inches in length, which classed them at five years of age or older. An interesting point was made when sportsmen reported that good catches of large mature bass are made in the spring until May, after which time they apparently disappear and as a consequence very few are taken. Late in July and early August these large bass again appear in Monterey Bay and are caught in considerable numbers. It is not probable that these fish refuse to take the hook during May and June, for in San Francisco Bay anglers have no difficulty in making substantial catches during this period. […]
>
> All of these points seemingly indicate that the movement of the striped bass along the southern coast of California is entirely seasonal, and the spring months reveal a migration of mature bass back to San Francisco Bay for the purpose of spawning. (Scofield 1930, pp. 53-55)

Although the above account documents the regular occurrence of the species along the coastal flanks of the Golden Gate by an early date, Scofield concluded they were wholly migrants from the San Francisco Estuary. In contrast, thirty years later Skinner (1962) noted that "In California a few striped bass spawn in the larger coastal rivers, the Russian River particularly, and formerly the Salinas River. A few apparently persist in Elkhorn Slough, which enters Monterey Bay, and spawn there also. The major tributaries to San Francisco Bay are the principal spawning grounds, however…" Unlike Scofield, he did not describe any specific observations to back up the claim. Both views are consistent with the species' behavior in its native range on the Atlantic coast, where fish move broadly between natal and non-natal estuaries (Grothues et al. 2009).

In the years since these reports, the abundance of *M. saxatilis* in the San Francisco Estuary drainage system has declined significantly (Stevens et al. 1985; Dill and Cordone 1997; Feyrer et al. 2007), but what is the status of the species on other drainages along the coast? Recent estimates of recreational catch from the California Recreational Fisheries Survey show, not surprisingly, that the greatest catch is from the inland portion of the San Francisco Bay Area, nearly 800,000 individuals during the period 2004 – 2019 (Figure 1, top left). However, over 100,000 have also been recovered in the coastal ocean (<3 miles from shore) in each of the Bay Area and Central Coast districts (Figure 1, top middle), and on the order of 1000s of Striped Bass were captured during this period from the Channel Islands district and from the Bay Area district >3 miles from shore. Smaller numbers (100s) were estimated for capture in inland waters of the Central Coast, and smaller numbers still (<100) in the inland waters of the South Coast and further offshore (>3 miles) in the Channel Islands district and the South Coast.

Notably, estimated catch is zero for all inland and marine waters north of the Bay Area (Figure 1, top, Wine and Redwood districts). This reflects a lack of records in the

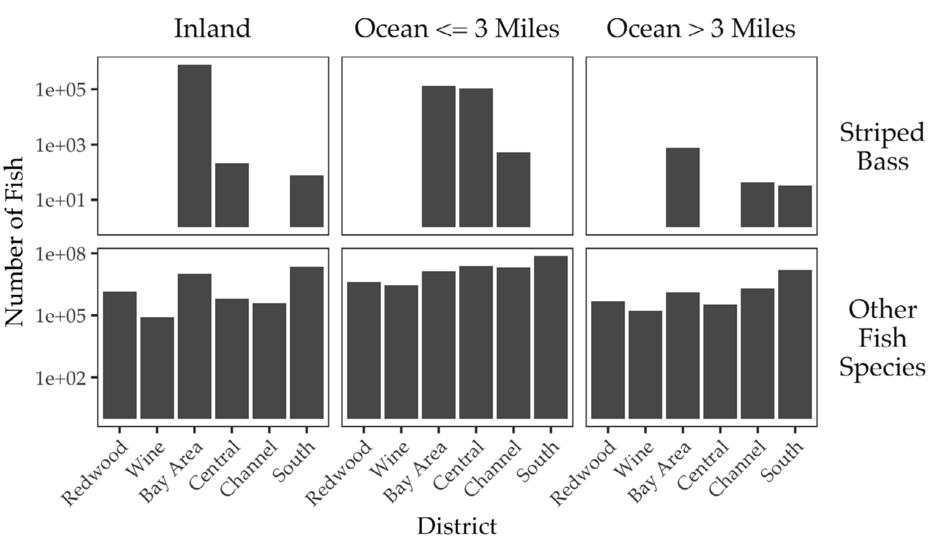

Figure 1. Estimates of total numbers of Striped Bass in the recreational catch for 2004 – 2019, in coastal regions from north to south (top). For reference, numbers of fish from all other species are also shown (bottom). Regions from north to south are Redwood (Humboldt, Del Norte Counties, except Shelter Cove area after 2007), Wine (Mendocino County, Shelter Cove Area after 2007, Sonoma County before 2008), Bay Area (Marin, Solano, Napa, Contra Costa, Alameda, Santa Clara, San Mateo, San Francisco Counties; Sonoma County after 2007), Central (San Luis Obispo, Monterey, Santa Cruz Counties), Channel (Ventura, Santa Barbara Counties), and South (San Diego, Orange, Los Angeles Counties). Estimates are from the California Recreational Fisheries Survey (CRFS); see https://wildlife.ca.gov/Conservation/Marine/CRFS for methods and https://www.recfin.org for data.

RECFIN database for interviews with recreational fishers from the North Coast who have captured Striped Bass. However, Ed Roberts (California Recreational Fisheries Survey, California Department of Fish and Wildlife, personal communication), who has monitored recreational fisheries in the Redwood district since 2007, has heard of Striped Bass being taken occasionally from the beaches between Enderts Beach south of Crescent City all the way down to Shelter Cove in Humboldt County, but not from Mendocino County. His staff have encountered them twice: once in 2009, caught by an angler from the surf near Humboldt Bay (Samoa), and once in 2018 from the surf at Gold Bluffs beach north of Mad River. Both records were verified by staff but did not end up in the RECFIN database, due to a language barrier preventing an interview in the 2009 case, and the interview being made in a pilot study for a new sampling procedure in the 2018 case.

Overall this suggests the species ranges broadly in the ocean, but declines in abundance with distance from the Golden Gate, and would most likely use coastal estuaries and rivers in the zone directly flanking the Golden Gate, encompassed by the Russian River on the north and Morro Bay on the south (Figure 2). Below I summarize evidence of Striped Bass occurrence in the major stream systems from Mad River in the north to San Diego Bay in the south, giving more focused attention to the region flanking the Golden Gate. For the most part these data come from generalized seining surveys with no correction for capture effort or efficiency; I therefore summarize not just the number of Striped Bass captured during a survey, but also the total number of fish species captured to give a sense of the scale or effectiveness of the sampling. Most samplers did not include age or length data but when reported it is included in the narrative.

Mad River.—Osborn (2017) sampled fish from four sites in the estuary, using two to three beach seines per site in June and January from mid-2014 to mid-2016. She found 33 fish species but did not find Striped Bass. Ed Roberts (California Recreational Fisheries Survey, California Department of Fish and Wildlife, personal communication) reports observing Striped Bass in the Mad River while conducting snorkel surveys in the late 1990s.

Humboldt Bay.—Gottshall et al. (1980) reviewed twenty years of published surveys, unpublished trawl data, and various other records of fish occurrence in Humboldt Bay. They found accounts of 110 fish species captured from the bay, including 45 species taken by recreational fishers. For Striped Bass they found "One questionable record from Bay; a fish reported caught over 90 years ago" (Gottshall et al. 1980:229).

More recently, Cole (2004) sampled fish from 321 sites around the periphery of the bay from September 2000 to November 2001 using a variety of nets and sampling techniques, and also conducted a total of 41 trawls using three different types of trawl within the bay. She identified 67 species of fish but Striped Bass was not among them. Shaughnessy et al. (2017) sampled fish from four sites using two to three beach seines per site in June and January from mid-2014 to mid-2016. They found 23 fish species but did not find Striped Bass.

Eel River.—Gleason et al. (2010) reviewed a half-century of fish surveys in the Eel River estuary (Murphy and De Witt 1951; Monroe et al. 1974; Puckett 1977; Cannata and Hassler 1995; Gilroy 2002). These surveys collectively documented 47 fish species using the Eel River estuary, including five introduced species and 14 anadromous species, but Striped Bass was not among them. The surveys by Puckett (1977) and Cannata and Hassler (1995) were especially thorough (see Table 9 in Gleason et al. 2010), sampling in winter, spring, summer, and fall of 1973-74 and 1994-95 respectively. They sampled in each of the McNulty and Hawk Sloughs, the lower channel including North Bay, Salt River, middle channel, and the upper channel as far as Fernbridge, and together documented 33 species total, but no Striped Bass.

More recently, Scheiff et al. (2013) sampled fish using seines at seven sites in McNulty Slough and two in Hawk Slough during each of fourteen months from January 2008 to June 2009. They identified 23 species of fish but did not report Striped Bass.

Mendocino Coast.—In the estuaries of Ten Mile River and Big River, Osborn (2017) sampled fish from four sites each, using two to three beach seines per site in June and January from mid-2014 to mid-2016. She found 17 fish species in Ten Mile River and 32 in Big River, but did not find Striped Bass in either system. Higgins (1995) sampled fish from

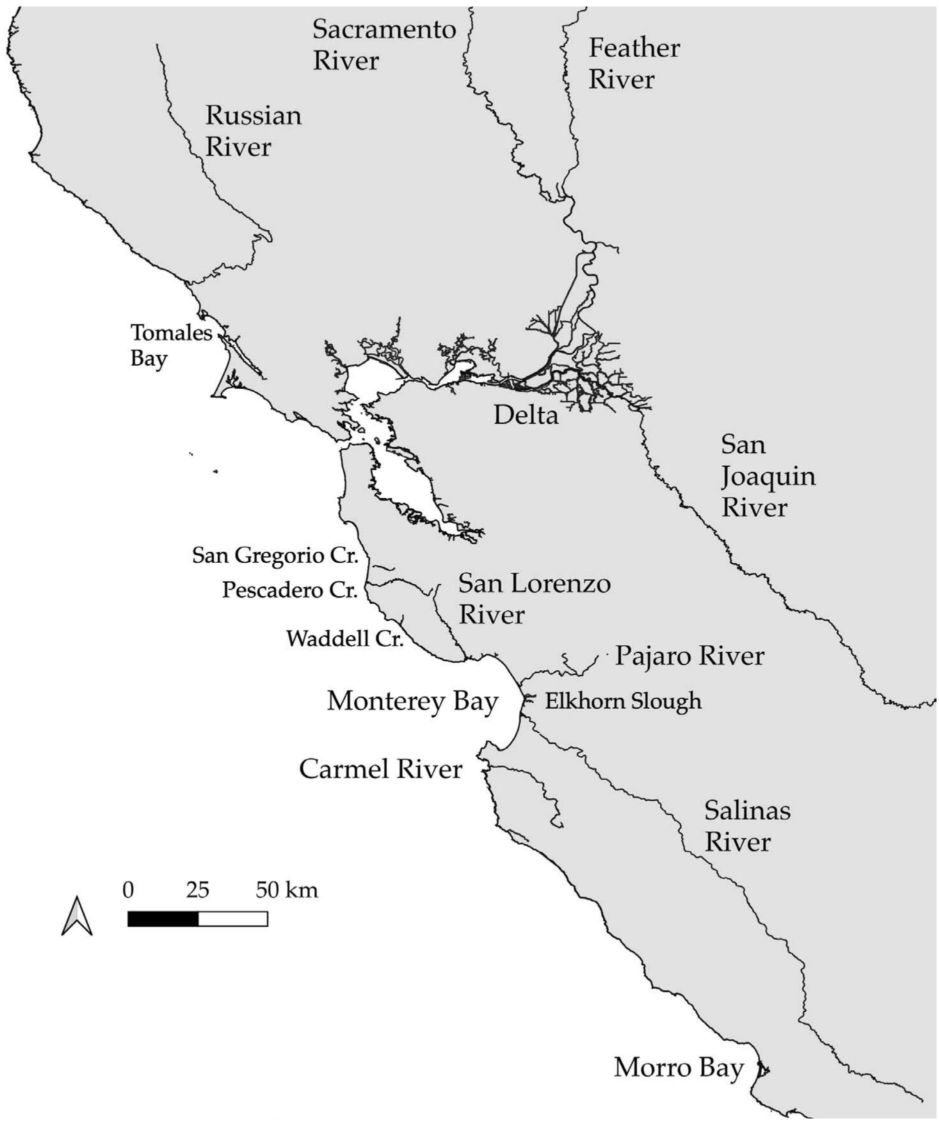

Figure 2. The San Francisco Bay-Delta region and coastal flanks of the Golden Gate.

seven sites in the Garcia River estuary monthly from June to August 1995, and captured 11 species total but no Striped Bass. In the Gualala River estuary, ECORP and KHE (2005) characterized fish diversity by sampling an average of ~20 seine hauls in each of 13 months between June 2002 and October 2003 (Table 1). They captured 12 species of fish but Striped Bass was not among them.

Table 1. Occurrence of Striped Bass in seining surveys of the estuary of Gualala River (ECORP and KHE 2005).

Month	Lagoon Status[a]	Number of Fish Species Reported	Striped Bass Reported?
Jun 2002	Closed	8	No
Jul 2002	Closed	6	No
Aug 2002	Closed	6	No
Sep 2002	Closed	6	No
Oct 2002	Closed	5	No
Nov 2002	Open	4	No
Feb 2003	Open	6	No
May 2003	Unknown	7	No
Jun 2003	Open	9	No
Jul 2003	Closed	6	No
Aug 2003	Closed	7	No
Sep 2003	Closed	7	No
Oct 2003	Closed	7	No

[a] Inferred from Table 2.1 in ECORP and KHE (2005).

Russian River.—Nearly a century ago, Scofield and Bryant (1926) reported a 57-pound bass caught in the Forest Pool on October 1924, a 32- and a 54-pound bass caught near Monte Rio on 27 February 1925, and several 40- and 45-pound bass taken elsewhere in the Russian River in 1925. As noted earlier, Skinner (1962) asserted a spawning population once existed in the Russian River, but Shapovalov (1944) asserted that Striped Bass enter the Russian River irregularly; neither author provided supporting evidence.

In more recent years, the estuary of the Russian River was sampled for fish diversity in 1992–93 and 1996–2000; sampling occurred in 33 months over this period, mostly in the summer and fall (Table 2). Forty-seven species of fish were identified, but *M. saxatilis* was not among them. The estuary was sampled for fish again during 2003–2005 (Table 2), identifying 38 species, but again *M. saxatilis* was not among them.

Upstream from the estuary, Chase et al. (2005) used an electrofishing boat to sample fish from Wohler Pool, a 5-km impoundment on the river backed up by a rubber dam at river kilometer 40. Over the five years of annual sampling available (Chase et al. 2000, 2001, 2002, 2004, 2005), between 13 and 21 species were caught annually, but only one Striped Bass, an adult, was caught over the period (Table 3). This low abundance was in great contrast to three other introduced predators, Sacramento Pikeminnow (*Ptychocheilus grandis*), Smallmouth Bass (*Micropterus dolomieu*) and Largemouth Bass (*Micropterus salmoides*),

Table 2. Occurrence of Striped Bass in seining surveys/otter trawls of the Russian River estuary (Goodwin and Cuffe 1993; Roth et al. 1997, 1998, 1999, 2000; Martini-Lamb 2001; Cook 2004, 2005, 2006).

Month	Lagoon Status	Number of Fish Species Observed		Striped Bass Observed?
		Seining	Otter Trawls	
Jun 1992	Closed/Open	6	-	No
Jul 1992	Open	5	-	No
Aug 1992	Closed/Open	5	14	No
Oct 1992[a]	Closed/Open	5	-	No
Nov 1992	Closed/Open	5	8	No
Mar 1993[a]	Open	7	-	No
Apr 1993	Open	7	5	No
May 1993	Open	7	-	No
Jul 1996	Closed/Open	6	10	No
Aug 1996	Closed/Open	10	9	No
Sep 1996	Closed/Open	6	14	No
Oct 1996	Closed/Open	10	10	No
Nov 1996	Open	5	-	No
May 1997	Closed/Open	12	14	No
Jun 1997	Closed/Open	12	17	No
Jul 1997	Open	8	9	No
Aug 1997	Closed/Open	6	9	No
Sep 1997	Closed/Open	8	11	No
Oct 1997	Closed/Open	9	11	No
Nov 1997	Open	4	12	No
Aug 1998	Open/Closed	8	9	No
Sep 1998	Open/Closed	11	13	No
Oct 1998	Open/Closed	8	12	No
Nov 1998	Open	4	5	No
Jun 1999	Closed	2	5	No
Jul 1999	Open	7	11	No
Aug 1999	Open	5	3	No
Sep 1999	Closed/Open	8	5	No
Oct 1999	Closed/Open	7	14	No
Nov 1999	Closed/Open	5	7	No
Sep 2000	Closed/Open	8	11	No
Oct 2000	Closed/Open	8	10	No
Nov 2000	Closed/Open	5	7	No
Aug–Oct 2003	Closed/Open	22	-	No
May–Aug 2004	Closed/Open	31	-	No
May–Oct 2005	Closed/Open	23	-	No

[a] Some electrofisher sampling as well.

Table 3. Occurrence of Striped Bass in boat-electrofishing surveys of Wohler Pool, a rubber-dam impoundment on the Russian River at river kilometer 40 (Chase et al. 2000, 2001, 2002, 2004, 2005).

Month	Number of Fish Species Observed	Striped Bass Observed?
Aug 1999	13	Yes (1 fish)
Aug 2000	20	No
Aug 2001	21	No
Aug 2003	18	No
Aug 2004	19	No

which regularly showed up in surveys. Chase et al. (2005) also reported that in 2002, one subadult Striped Bass was observed moving downstream through the fish passage structure on the dam, which has a video monitoring system. Upstream further still, Striped Bass were planted in 1967 in Lake Mendocino (Dill and Cordone 1997), a reservoir on the East Fork about 153 km upstream of the ocean. The species is still stocked there (USACE 2019) and was perhaps the source of the few individuals observed at Wohler Pool.

Bodega Bay to Golden Gate.—A few records were found of Striped Bass in the various embayments and coastal streams north of the Golden Gate. Fong (1996) observed an unspecified number of Striped Bass in Big Lagoon, an intermittent tidal lagoon in southern Marin County, and Ettlinger (2017) captured four individuals in Lagunitas Creek, a tributary of Tomales Bay, during the 2017 operation of a rotary-screw trap from mid-March to late May. The RECFIN dataset (Table 4) has 14 accounts of recreational fishers catching Striped Bass in Tomales Bay in 2018 and 2019, and one account for Bodega Bay in 2014.

San Gregorio Lagoon.—In order to document Steelhead survival and growth in the lagoon of San Gregorio Creek, south of Half Moon Bay, Atkinson (2010) conducted seining surveys five times from the beginning of July 2005 through the end of October, and seven times from mid-February 2006 to the beginning of November. In the process she captured 11 species of fish, including Striped Bass, the only non-native species in the sample. Of the 11 species, Steelhead had the highest capture rate, while Striped Bass ranked ninth, and Coho Salmon tenth. Striped Bass were only captured during three consecutive sampling events in May, June, and July of 2006, when the estuary was intermittently open and closed due to breaching. Twenty-five individuals were captured, ranging in size from 75 mm to 174 mm Standard Length, which are consistent with age 1 fish (Scofield 1930, p. 40).

Pescadero Lagoon.—Huber (2018) made 410 seine hauls in the lagoon of Pescadero Creek between July 2011 and September 2013, catching a total 15 species. Of the 18,142 fish he caught, three were Striped Bass. Jankovitz (2015, 2017, 2018; Jankovitz and Diller 2019) sampled the lagoon in 15 months during the period June 2014 to October 2018, mostly as two-day seining events to make mark-recapture estimates of steelhead abundance (Table 5). He generally reported capture of three to seven fish species per occasion, but Striped Bass was not reported from any of them.

Waddell Creek.—During their decade-long study of Steelhead and Coho Salmon in Waddell Creek, Shapovalov and Taft (1954) observed that "The Striped Bass enters the lagoon only occasionally, but at such times may remain for over a month. In former years this species was reported by local residents on occasion to have ascended about a mile into the flowing water of the stream, but since the start of the experiments, in 1933, no individuals of this species have been seen above the limits of tidewater. No evidence has been gathered

Table 4. Accounts of recreational catch of Striped Bass taken from "inland" coastal habitats during the period 2004 – 2019, from interviews in the RECFIN database.

Water Body[a]	Interview Site[b]	Trip Date	Total Catch	Primary Target Species
Bodega Bay	Westside launch ramp	11 Jul 2014	1	California halibut
Tomales Bay	Lawson's Landing	15 Jul 2018	1	California halibut
		8 Jun 2019	1	Bivalve class
		3 Jul 2019	1	California halibut
		3 Aug 2019	1	California halibut
		4 Aug 2019	7	California halibut
	Miller Park launch ramp	8 Aug 2018	1	California halibut
		9 Sep 2018	1	California halibut
		31 May 2019	1	California halibut
		26 Jun 2019	1	California halibut
		21 Jul 2019	1	California halibut
		31 Jul 2019	1	California halibut
		5 Aug 2019	14	California halibut
		9 Aug 2019	1	California halibut
		28 Aug 2019	1	California halibut
Elkhorn Slough	South jetty	11 Apr 2016	1	Surfperch family
		22 Jul 2018	2	Striped bass
Alamitos Bay	Davies launch ramp	27 Oct 2012	1	Kelp bass
Newport Bay	Davey's Locker	22 May 2005	1	Unidentified fish
Mission Bay	Dana Basin launch ramp	30 Apr 2011	1	California halibut
San Diego Bay	Chula Vista launch ramp	21 May 2017	1	Unidentified fish

[a] Inferred from interview sites where Striped Bass was recorded in catch.
[b] Omits interviews on San Francisco Bay or San Pablo Bay (n = 2802), two coastal interviews marked as inland but judged to be marine (Santa Cruz Marina side jetty, Oceanside launch ramp), and all trips not marked as inland (Ocean, ocean <= 3 miles, ocean > 3 miles, bay, not known; n = 2569).

to show that the species spawns in Waddell Creek." They reported records of occurrence of the species in the creek or estuary in May 1927 (unknown number), November 1931 ("two dozen"), April 1932 (two fish), March 1934 (one fish), April 1935 (47 fish), and June 1939 ("several"). In recent times, a single large individual (79 cm Fork Length) was captured in Waddell Creek estuary on 13 August 2008, during a routine seining survey for juvenile salmonids (A. Osterback and J. Kiernan, University of California Santa Cruz and NMFS SW Fisheries Science Center, personal communication). This was the only individual caught during 2008–2009, when the estuary was surveyed approximately monthly from August to November of each year.

Table 5. Occurrence of Striped Bass in seining surveys of the estuary of Pescadero Creek (Jankovitz 2015, 2017, 2018; Jankovitz and Diller 2019).

Month	Lagoon Status	Number of Fish Species Reported[a]	Striped Bass Reported?
Jun 2014	Closed	6	No
Jul 2014	Closed	5	No
Oct 2014	Closed	7	No
Jul 2016	Open	3	No
Oct 2016	Closed	6	No
Nov 2016	Closed[b]	4	No
July 2017	Open	5	No
Aug 2017	Open	5	No
Sep 2017	Open	4	No
Oct 2017	Closed	5	No
Nov 2017	Open	5	No
Jul 2018	Open	6	No
Aug 2018	Open	6	No
Sep 2018	Open	5	No
Oct 2018	Closed	4	No

[a] Sampling focused on Steelhead, and species lists were reported as "Other fish species captured during this sampling included <list of species>" suggesting that reporting may be incomplete.
[b] Eight days after major fish kill event.

San Lorenzo River.—The estuary of the San Lorenzo River was regularly sampled for fish in summer and fall during 2008–2016 (HES 2017 and earlier annual reports). Of 26 seining surveys, *M. saxatilis* was observed in six of them: once in 2010 and five of the eight surveys during 2015–2016 (Table 6). In each of these latter years, one survey caught dozens of fish while the remaining surveys caught bass in the single digits.

Pajaro River.— The estuary of the Pajaro River has been annually sampled for fish diversity via seining during 2012–2018 (Alley and Steiner 2016; Alley 2017; Alley 2018; earlier annual reports by same authors). Four Striped Bass were caught in 2012 when the lagoon entrance was closed, but the species has not been observed since (Table 7). Overall fish diversity was also highest in 2012 at 15 species captured, declining to 7–9 species in subsequent years. Ken Oda (Marine Region, California Department of Fish and Wildlife, personal communication) reports that "during the course of conducting fisheries-independent surveys, I observed anglers targeting and catching Striped Bass from shore as well as small boats in the Pajaro estuary."

Well upstream at the source of Pajaro River, Casagrande (2010) sampled San Felipe Lake with gill nets in 32 hours of sets during seven sampling periods from December 2004 through November 2006. She captured 647 individuals and 12 species of fish, including two Striped Bass with lengths 290 mm and 360 mm Standard Length. Five additional species

Table 6. Occurrence of Striped Bass in seining surveys of the estuary of the San Lorenzo River in Santa Cruz (HES 2017 and earlier annual reports).

Month	Lagoon Status	Number of Fish Species Observed	Striped Bass Observed?
Jun 2008	Open	11	No
Oct 2008	Closed/Open	10	No
Jun 2009	Open	10	No
Sep 2009	Closed	8	No
Oct 2009	Open	3	No
Jun 2010	Open	11	Yes (1 fish)
Jul 2010	Open	5	No
Oct 2010	Closed	3	No
Jun 2011	Open	11	No
Oct 2011	Open	15	No
Jun 2012	Open	11	No
Sep 2012	Closed/Open	7	No
Jun 2013	Open/Closed	9	No
Jul 2013	Closed	8	No
Sep 2013	Open	6	No
Jun 2014	Newly Closed	12	No
Jul 2014	Newly Closed	7	No
Sep 2014	Closed	7	No
Jun 2015	Closed	8	Yes (37 fish)
Jul 2015	Closed	4	No
Aug 2015	Open	6	Yes (3 fish)
Oct 2015	Closed	6	Yes (1 fish)
Jun 2016	Open/Closed	11	No
Jul 2016	Newly Closed	11	Yes (2 fish)
Aug 2016	Newly Closed	11	Yes (28 fish)
Sep 2016	Open	9	No

were documented from seining surveys, but Striped Bass was not among them, confirming that gill nets are a more effective form of capture. The bass were caught in 2006, and two adult Chinook Salmon (*Oncorhynchus tshawytscha*) were captured in 2005 as part of the same study, indicating migratory access (and attraction) from the ocean sometimes occurs. Casagrande (2011) sampled 10 sites in five different water bodies of the upper Pajaro River basin, between 26 June and 7 August 2011. Using a combination of electrofishing, seining, and gillnetting, he captured a total of 19 species, including 19 Striped Bass ranging from 310 mm to 550 mm Standard Length. Striped Bass were captured at two sites on the Pajaro River using gillnets, one at the confluence with Miller Canal and the other immediately upstream of Carnadero Creek confluence, both downstream of Felipe Lake via Miller Canal. The species was not observed at the other eight sites, which were in tributaries.

Elkhorn Slough.—Yoklavich et al. (2002) summarized data on the fish fauna of Elkhorn Slough in the 1970s through 1990s. Creel surveys in the 1970s (Cailliet et al. 1977) reported catches of *M. saxatilis* in both the western and eastern parts of the slough (west of Highway 1, near Kirby Landing, respectively), though at much lower rates than many native species such as surfperches, rockfishes, sculpins and flatfish. In contrast, later in the 1980s and 1990s the species was not reported in creel censuses (Marine Recreational Fishing Statistics Survey, cited in Yoklavich et al. 2002), though the data were not strictly comparable due to differences in reporting techniques. Juvenile and adult *M. saxatilis* were caught in otter trawls conducted during the 1970s, but like the creel surveys, were not observed in subsequent trawls conducted in the 1980s and 1990s (Yoklavich et al. 2002). More recently, the RECFIN dataset (Table 4) has two accounts of recreational fishers catching Striped Bass from the south jetty.

Salinas River.—Scofield and Bryant (1926) report that Striped Bass were "fairly abundant" in the mouth of the Salinas River by 1896; at this time the lower river would have had its old configuration of running north parallel to the coast, connecting with Elkhorn Slough and discharging to the ocean just north of the present engineered harbor entrance at Moss Landing (Gordon 1996). Five fish weighing 15 pounds or greater were captured at an unspecified location on Salinas River on 9 June 1921 (Scofield and Bryant 1926, Fig. 14), about a decade after the river changed configuration to its present mouth in 1909-1910.

MCWRA and USACE (2001) report that experimental stocking of Striped Bass was initiated in 1971 in San Antonio Reservoir, on a major tributary of the Salinas River approximately 180 km upstream of the mouth of the estuary. Regular annual plants were conducted from 1976 into the 1980s but were later discontinued. A small self-sustaining population appears to have persisted until at least November 2014, when M. Michie posted a video on YouTube of a large Striped Bass being caught in the reservoir. However, it has not been documented in the reservoir since the recent drought.

In recent times, the lagoon of the Salinas River was sampled for fish four times during 1990–1991 and one to three times annually during 2002–2014 (Table 8). *M. saxatilis* was captured in 12 of the 23 months sampled during these periods. From fall 2009 to fall 2013 it was captured in nine out of 11 months surveyed, including May 2011, April 2012, and April 2013, which coincides with the early spawning season of the species for three consecutive years. The species was not found in April 2014, at the height of the drought when the lagoon had been closed continuously for 15 months (HES 2015). Only three species of fish were observed during sampling: Threespine Stickleback (*Gasterosteus aculeatus*), Tidewater Goby (*Eucyclogobius newberryi*), and Prickly Sculpin (*Cottus asper*). J. Casagrande (National Marine Fisheries Service, personal communication) reports that anglers still commonly capture Striped Bass in Old Salinas River Channel, and that in March 2012, a large number of Striped Bass carcasses was were found in the channel of the Salinas River near Chualar after reservoir releases were cut back for emergency repairs.

Carmel River.—Striped Bass was one of six fish species observed by Dettman (1984) during biological surveys of the Carmel Lagoon in 1982. Casagrande (2006) seined the Carmel Lagoon on 27 July 2006 for Steelhead and reported capturing one Striped Bass (37 cm Fork Length). From 2010 to 2017, a hook-and-line removal project conducted by California Department of Fish and Wildlife removed a total of 551 Striped Bass from Carmel Lagoon in the summers and falls (Table 9). During visual-encounter surveys on 10 June

Table 7. Occurrence of Striped Bass in seining surveys of Pajaro River estuary (Alley and Steiner 2016; Alley 2017; Alley 2018; earlier annual reports by same authors).

Month	Lagoon Status	Number of Fish Species Observed	Striped Bass Observed?
Oct 2012	Closed	15	Yes (4 fish)
Oct 2013	Slightly Open	9	No
Oct 2014	Closed	7	No
Sep–Oct 2015	Closed	7	No
Sep–Oct 2017	Open	9	No
Oct 2018	Open	10	No

Table 8. Occurrence of Striped Bass in seining surveys of Salinas River estuary (Gilchrist et al. 1992; Krafft et al. 2012, 2013; Leal et al. 2014; HES 2015).

Month	Number of Fish Species Observed	Striped Bass Observed?
Aug 1990[a]	9	No
Apr 1991[b]	3	No
Jun 1991[b]	9	No
Aug 1991[a]	18	Yes (3 fish, 27-30 cm SL)
Sep 1991[a]	16	Yes (17 fish, 24-44 cm SL)
Fall 2002	10	No
Fall 2003	10	No
Fall 2004	11	No
Fall 2005	11	Yes (6 fish)
Fall 2006	4	No
Fall 2008	11	No
Fall 2009	13	Yes (1 fish)
Fall 2010	11	No
May 2011	10	Yes (4 fish)
Aug 2011	7	No
Oct 2011	12	Yes (11 fish)
Apr 2012	14	Yes (41 fish)
Jul 2012	9	Yes (31 fish)
Oct 2012	5	Yes (3 fish)
Apr 2013	7	Yes (8 fish)
Jul 2013	14	Yes (47 fish)
Oct 2013	14	Yes (8 fish)
Apr 2014	3	No

[a] Gillnets used at some stations, seines at others.

[b] Gillnets only.

Table 9. Removals of Striped Bass from Carmel Lagoon, summer and fall 2010–2017 by hook-and-line capture (Anderson 2010, 2011, J. Casagrande, National Marine Fisheries Service, personal communication).

Year	CPUE (fish/hr)	Number of Striped Bass Removed	Size Range (TL in cm)
2010	0.79	143	31 - 92
2011	0.87	69	36 - 96
2012	0.725	88	–
2013	0.605	82	–
2014	1.33	62	–
2015	0.33	13	–
2016	0.02	32	–
2017	1 Seine	62	–

2016, Stoddard (2016) observed schools of approximately 9–11 fish and 15–20 fish at two locations, well upstream of the estuary (near Schulte Bridge and Quail Lodge); but not at two other sites where the species had been reported by local residents. Local anglers and Steelhead enthusiasts first observed Striped Bass upstream of the estuary in 2013 and have since observed the species as far upstream as river kilometer 30 (Boughton and Ohms 2018). Some of these fish were visually estimated to be as small as ~12 cm, consistent with age 1 fish (Scofield 1930). However, Ken Oda (Marine Region, California Department of Fish and Wildlife, personal communication) reports that "my co-workers and I never hooked or observed 1+ sized Striped Bass during the Carmel River surveys or caught fish in that size range in the Carmel, Pajaro, or Salinas [Rivers] during the open fishing season," a sample he estimates to be well in excess of 1000 fish. His father used to catch Sacramento Pikeminnow (*Ptychocheilus grandis*) in the former San Clemente Reservoir on the Carmel River, back in the 1960s, and he cannot help but wonder if that is what was actually observed by local anglers and steelhead enthusiasts. Pikeminnows are native to the Sacramento and San Joaquin River systems and, due to a Pleistocene freshwater connection, also to the Pajaro and Salinas Rivers, but according to Moyle (2002) they are not found in the Carmel River.

Morro Bay.—Scofield and Bryant (1926) reported *M. saxatilis* was planted in Morro Bay in 1916 and again in 1919, but no follow-up information was found. During 1968–1970, the bay was sampled every month for fish using a variety of techniques, with sampling effort distributed throughout the bay and entrance (Fierstine et al. 1973); 66 species were captured but *M. saxatilis* was not among them. Horn (1980) sampled Morro Bay via four nighttime and four daytime beach seines on each of four occasions throughout 1974–1976 (Table 10). He captured 21 species overall, but Striped Bass was not among them. Williams et al. (2013) sampled fish from Morro Bay using a variety of seining and trawling methods in April, August and November of 2005–2007 and in May of 2008. They reported 22 species but no Striped Bass.

Southern California.—Along the coast further south, Striped Bass are sometimes captured in the ocean but do not commonly occur in estuaries or inland (Allen et al. 2006). The Santa Ynez River estuary in Santa Barbara County was sampled for fish in 1997 and 1999 (Robinson et al. 2009). Sixteen species were identified, none of which were *M. saxatilis*. Williams et al. (2013) sampled San Diego Bay in April and July of 2005, 2008 and 2012,

Table 10. Occurrence of Striped Bass in seining surveys of Morro Bay (Horn 1980).

Month	Number of Fish Species Observed	Striped Bass Observed?
Feb 1976	13	No
May 1975	16	No
Aug 1975	11	No
Nov 1974	16	No

using methods similar to their Morro Bay survey, and found 48 species but no *M. saxatilis*. For the period 2004-2019, the RECFIN dataset (Table 4) has accounts of recreational fishers catching one Striped Bass each in Alamitos Bay, Newport Bay, Mission Bay, and San Diego Bay.

In the early 20th Century, the California Department of Fish and Game introduced Striped Bass to Newport Bay, Anaheim Bay, Bolsa Chica River, Sunset Beach in Orange County, and Mission Bay at San Diego, but none of these plants appear to have persisted (Dill and Cordone 1997). The Department again introduced the species to Newport Bay in the 1970s, but the population eventually failed (Allen et al. 2006). Although adult Striped Bass may occur irregularly in southern California estuaries (Monaco et al. 1990), the only location that appears to have a self-sustaining population of *M. saxatilis* is the Colorado River.

Overall the species appears to be widespread: rarest north of the Golden Gate, sporadically seen in estuaries on the coast south of the Golden Gate and in Monterey Bay, and quite common in the Carmel River estuary but then rarely seen further south. Occurrence is intermittent, often coinciding with periods when the estuaries are opening and closing in the late spring and summer. Occurrence may be underestimated due to the prevalence of seining, which appears to be less effective than gill nets at sampling the species. Striped Bass have also occasionally been observed significant distances upstream in the larger river systems, suggesting attempts to spawn.

Local Reproduction?

The various sampling techniques described above, mostly seining, were only suitable for detecting subadults and adults, which may have migrated from elsewhere and thus do not demonstrate local reproduction. Although sizes were generally not reported, sizes that were reported were typically >15 cm and always >10 cm, indicating fish at least a year old and usually much older. Yoklavich et al. (1992) described one of the few studies capable of detecting whether *M. saxatilis* has actively reproduced in a coastal system. Ichthyoplankton in Elkhorn Slough were collected monthly via trawls from September 1974 through September 1976 at five different stations distributed from the harbor entrance to inland near Kirby Landing. *M. saxatilis* was not reported among the 29 taxa of larvae and eggs that were observed, despite the presence of adults in Elkhorn Slough during this same general time period (Yoklavich et al. 2002). TES (2000) also conducted an extensive survey of Elkhorn Slough ichthyoplankton, sampling for 24 hours at biweekly or shorter intervals from March 1999 through February 2000, at two locations in front of water intakes at Moss Landing Harbor, for a total of 42 samples of 40 m^3 of water each. They also made six monthly samples using oblique tows or push nets at four stations distributed throughout Elkhorn Slough, filtering ~40 m^3 of water for each sample. At the two harbor locations 66 taxa of fish were identified, while in the slough 53 taxa were identified (not all identified to species), but *M. saxatilis* larvae were not reported.

Short plankton tows were conducted in the Russian River estuary from 1996–1998 in the summer and fall months (Table 11), a period bracketed by high rainfall and streamflows in 1995 and 1998. Only four species of fish (juveniles and larvae) were detected, and *M. saxatilis* was not among them. The tows were aimed at characterizing the invertebrate community before and after lagoon breaching events and took place in shallow water (1 m) just above the river bottom at one location (Willow Creek). The four species of fish observed—Sacramento Sucker (*Catostomus occidentalis*), Threespine Stickleback (*Gasterosteus aculeatus*), Prickly Sculpin (*Cottus asper*), and Bay Pipefish (*Syngnathus leptorhynchus*) all tend to be bottom-dwellers, indicating the tows were probably not particularly effective at detecting *M. saxatilis* larvae if they were present.

Puckett (1976) surveyed the downstream migrations of juvenile anadromous fishes in the Eel River periodically from 1959 through 1970 on the mainstem Eel River, its middle and south forks and on the Van Duzen River. He generally used funnel nets with mesh sizes scaling from 3.8 cm down to 1.3 cm within the funnel, and captured fourteen species of anadromous fish, but no larval Striped Bass were reported. However, it is not clear that the funnel nets had sufficiently fine mesh to capture Striped Bass larvae if they were present.

Eldridge and Bryan (1972) extensively sampled larval fish in Humboldt Bay in 1969. They made biweekly oblique and bottom trawls at 5 stations throughout the bay for a total of 118 tows during January to December 1969. Thirty-seven species of larval or juvenile fish were collected, but Striped Bass larvae were not reported.

To understand the potential for local reproduction, it is helpful to consider the particular life-history requirements of Striped Bass. Although subadults and adults tend to be specialized on piscivory (Shapovalov and Taft 1954; Thomas 1967; Loboschefsky et al. 2012), they have wide tolerance for temperature, salinity, and habitat structure, and move readily between fresh, brackish, and marine systems to follow foraging opportunities (Calhoun 1952; Sabal et al. 2019). In contrast, the requirements for spawning, eggs and fry are rather constrained. In the Sacramento River system, spawning begins in April after water temperatures exceed 14°C; it peaks in May and extends through June (Moyle 2002); in the San Joaquin River it peaks about 15 days earlier (Stevens et al. 1987), while in Coos Bay Oregon it begins and peaks a month later (Morgan and Gerlach 1950), perhaps due to cooler climate. A key constraint is that the species requires flowing freshwater to spawn. Adults not already in freshwater move upstream and form large spawning aggregations on the surface in the main current. In Coos Bay and the San Joaquin River, they spawn in tidally influenced freshwater reaches just outside the estuary, but in the Sacramento system adults may move some distance upstream to spawn (Moyle 2002).

Striped Bass are broadcast spawners that release vast numbers of small eggs (hundreds of thousands to more than 2 million eggs/female) into the water column (Scofield 1930). A key requirement is that eggs and larvae remain suspended in the current until reaching habitat suitable for larval feeding. Adults are never observed to spawn in still or stagnant water (Skinner 1962). Eggs are slightly negatively buoyant and without a current on the order 0.3 m/s (Reinert et al. 2004), will sink to the bottom where they perish from anoxia. River currents can be sufficient but the back-and-forth movement of tidally influenced rivers

Table 11. Occurrence of Striped Bass larvae in plankton tows conducted in the Russian River estuary (Roth et al. 1997, 1998, 1999).

Month	Number of Sampling Events	Number of Fish Species Observed	Striped Bass Larvae?
Aug 1996	1	0	No
Sep 1996	2	1	No
Oct 1996	2	0	No
May 1997	2	3	No
Jun 1997	4	0	No
Aug 1997	2	0	No
Sep 1997	2	0	No
Oct 1997	3	0	No
Nov 1997	1	0	No
Aug 1998	1	0	No
Sep 1998	4	3	No
Oct 1998	4	0	No

and estuaries is also highly suitable (Skinner 1962). Hatching normally occurs after 48 to 60 hours depending on temperature, and the resulting larvae subsist on yolk and drift with the current for another 200 hours, after which they must soon feed or die. So ideally 10–11 days after spawning a larval *M. saxatilis* finds itself in suitable feeding habitat—generally recognized to be estuarine waters with abundant microinvertebrates, or certain reservoirs. Thus, Moyle (2002) described Striped Bass as having three fundamental requirements to complete their lifecycle: (1) a large cool river for spawning, with water velocities swift enough to suspend eggs and larvae in the water column until they become free-swimming, (2) a productive estuary where larvae and juveniles accumulate and can prey on abundant invertebrates, and (3) a relatively large body of water with abundant small fishes for subadults and adults to prey on. The latter may be an estuary such as San Francisco Bay, a reservoir, or the Pacific Ocean.

The combination of (1) and (2) above is rare in the coastal area flanking the Golden Gate: The only large rivers are the Russian, Salinas, and perhaps Pajaro rivers (Figure 2), whereas the only large, productive estuaries with the type of tidal influence benefiting Striped Bass would be Elkhorn Slough, Morro Bay and perhaps some of the embayments north of the Golden Gate such as Bolinas Bay or Bodega Bay. None of these bays and estuaries have freshwater tributaries expected to be large and swift enough for spawning. On the other hand, the rivers that *are* potentially large enough for spawning probably have unsuitable estuaries—typically long, narrow bar-built estuaries that maintain swift river currents during the rainy season and develop sand-bar barriers closing them off from tidal influence in the dry season (Rich and Keller 2013; Behrens et al. 2015). An egg/larva drifting for 10 days at 0.3m/s covers about 250 km; in these bar-built estuaries most such propagules would likely drift out to sea during the open estuary phase or accumulate in the perched pool of still, stratified water that builds up during the closed phase. Some rivers such as the Russian River undergo a multi-week cycle of closing, perching, opening and draining, but such dynamics seem likely to sluice midwater larvae out to sea rather than circulating them between fresh and brackish waters.

The one exception that might just prove the rule is the Salinas River in its original configuration, when the permanent sand-bar that used to be at the location of the current mouth would sluice water and larvae northward along the Old Salinas River Channel into Tembladero, Moro Cojo, and Elkhorn sloughs (Figure 3). This extensive, branching embayment would have had complex tidal circulation patterns mixing with the freshwater inflow (e.g., see Figure 19 in Beller et al. 2009), and is the only such embayment that received flow from a large coastal river system, other than the San Francisco Bay/Delta itself. In its current configuration the interaction between the river and complex of sloughs occurs along a vestigial channel controlled by an outlet gate and a tide gate (Figure 3), and the bulk of the river flow typically breaches the sandbar directly into the ocean upstream of these gates, bypassing the sloughs. We can get a sense of whether reproduction is being attempted in this current configuration from data collected upstream of the estuary during 2010–2014 (Table 12). Upstream migration of adult Striped Bass has been detected at a weir 4 km from the ocean in every year that fish movement was monitored, although the annual totals were small ($\leq$ 11 fish). No *M. saxatilis* have been captured moving downstream at three rotary-screw trapping sites considerably further upstream (103–175 km from the ocean; Table 12), although in one of these years (2014) lack of downstream surface flow would have prevented access by migratory Striped Bass. These traps are operated more within the expected season of reproduction than the weir (March to May versus January to March for the weir), and have commonly captured other bass present in the Salinas system (*Micropterus* spp.), suggesting that if Striped Bass were moving this far upstream they would have been observed, at least occasionally (though in the drought year 2014, lack of surface flow would have prevented such movement). Reproduction further downstream would likely result in eggs floating out to sea or settling to the bottom of the estuary depending on whether the estuary is closed or open. To sum up, though Striped Bass are caught in the Old Salinas River Channel and a small number of appear to attempt immigration annually, perhaps to spawn, I find no substantial evidence for successful reproduction in the Salinas River or the complex of sloughs in their current configuration.

Potential Impacts on Salmonids

The most likely impact of *M. saxatilis* on local salmonids is piscivory of juveniles rearing in the estuaries or emigrating through them (Shapovalov 1936), but clearly subadult and adult *M. saxatilis* are likely to move up into freshwater sections of the river to forage as well. Piscivory is age-dependent. The younger, smaller Striped Bass ($\leq$ 40 cm Total Length) seined from Waddell lagoon by Shapovalov (1936) had fed mostly on small crustaceans (63% of stomach contents); and on smaller fish, especially gobies (26%). The larger fish (40–49 cm) were much more piscivorous, with 85% of stomach contents consisting of salmonids, sculpins, or unidentified fish remains. Scofield (1928) observed that in the ocean, "Bass will follow a school of fish for miles if the water is clear. Where there are sea gulls and pelicans flying over the water one is sure to find a school of small fish, and there also will always be a school of feeding bass." More recently, Loboschefsky et al. (2012) compiled extensive records from diet studies of Striped Bass in the San Francisco Estuary system, and found that while age-1 fish consumed mostly invertebrates, by age 2 their diet was mostly fish, and from age 3 onward their diet was almost entirely fish (Table 13). However, they do exhibit some flexibility in feeding: Ken Oda (Marine Region, California Department of Fish and Wildlife, personal communication) reports stomach contents for 43 Striped Bass subsampled from fisheries-independent surveys conducted from 2010 to 2020 along Monterey Bay sandy

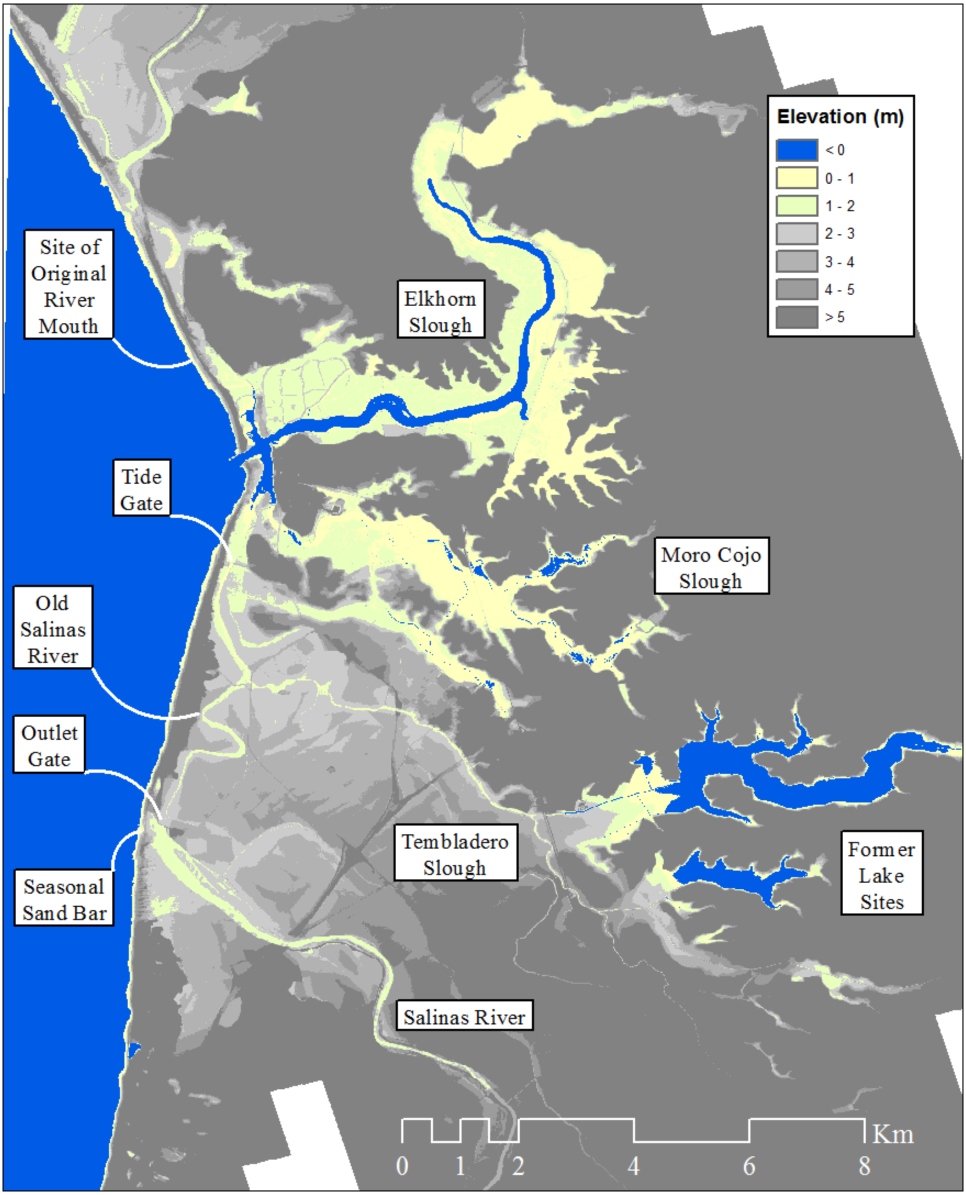

Figure 3. High-resolution topography/bathymetry of the Salinas Estuary/Elkhorn Slough complex (Data from OCMP 2019). In the 19th century, the seasonal sand bar at the current mouth was permanent, and the river ran northward behind the sand dunes to connect with Tembladero Slough, Moro Cojo Slough and Elkhorn Slough before discharging to the ocean north of the current harbor entrance. Currently, flow along this pathway is regulated by an outlet gate at the current estuary and a tide gate at Moss Landing.

Table 12. Movements upstream of the estuary by Striped Bass in the Salinas River system, 2010–2014 (Cuthbert et al. 2010; Krafft et al. 2012, 2013; Cuthbert et al. 2014a, 2014b; Leal et al. 2014).

Year	Location[a]	Dates of Operation[b]	# Species Captured	Striped Bass Observed?	TL (cm) mean (range)
2010	Salinas R.	Mar 12–May 28	14	No	
	Nacimiento R.	Mar 12–Jun 1	15	No	
	Arroyo Seco R.	Mar 18– Jun 1	10	No	
2011	Upstream Passage	Jan 19–Feb 17	6	Yes (1 fish)	41
	Salinas R.	Mar 12– May 20	9	No	
	Nacimiento R.	Mar 12– Jun 1	16	No	
	Arroyo Seco R.	Mar 12– May 31	9	No	
2012	Upstream Passage	Nov 30– Apr 2	6	Yes (6 fish)	47 (43–50)
	Salinas R.	Mar 23– May 5	11	No	
	Nacimiento R.	Mar 23– May 31	16	No	
	Arroyo Seco R.	Mar 13– May 14	10	No	
2013	Upstream Passage	Dec 1–Apr 1	7	Yes (4 fish)	43 (25–59)
	Salinas R.	Flows too low			
	Nacimiento R.	Mar 14– May 31	15	No	
	Arroyo Seco R.	Flows too low			
2014	Upstream Passage	Nov 26–Apr 1	6	Yes (11 fish)	51 (35–70)
	Salinas R.	Flows too low			
	Nacimiento R	Mar 15– May 31	11	No	
	Arroyo Seco R.	Flows too low			

[a] Rotary screw trap operations 175 km upstream of the ocean (Salinas R., Nacimiento R.) or 103 km upstream of the ocean (Arroyo Seco R.). Upstream passage monitored at weir/Vaki system 4 km upstream from the ocean.
[b] Dates with Nov or Dec refer to previous calendar year.

beaches throughout the year. The entire sample of stomachs (100%) "contained [Pacific mole crab] *Emerita analoga* in various stages of digestion. One of the stomachs contained a Barred Surfperch [*Amphistichus argenteus*], and two contained Northern Anchovies [*Engraulis mordax*]." This suggests an ability for the species to consistently exploit locally abundant prey species that happen to not be fish.

The only other recent information for stomach contents of Striped Bass caught on the coast flanking the Golden Gate is from the Carmel lagoon and river. Of 243 adults (31–96 cm Total Length) sampled from the lagoon in the years 2010–2014 (Anderson 2010, 2011, 2014), 66% had empty stomachs; only 9% had discernable fish in them; and only 1% had fish identifiable as salmonids (Table 14). As with a similar finding of 74% empty stomachs for Striped Bass caught in 1935 in San Francisco Bay, "the fact that the fish were taken by hook and line may be a factor, in that the fish caught may have been the particular individuals that were hungry and therefore taking bait, out of a large number of fish present" (Shapovalov 1936, p. 266). However, another 22 Striped Bass were sampled via spear gun from Carmel River in 2017, and these too had mostly empty stomachs (59%), though 32% had discernable fish (CRSA 2017). In this case the stomachs were also screened for presence of DNA markers for Steelhead (Table 15). Five of the 7 stomachs with fish inside them tested positive for Steelhead DNA. Interestingly, half of all the other stomachs (empty + invertebrates) also tested positive for Steelhead DNA, suggesting that those Striped Bass had recently eaten and digested Steelhead (Brandl et al. 2016). If so, then 60% of the 22 Striped Bass had recently consumed one or more Steelhead. This high percentage should be interpreted cautiously, however, as it stems from a single sampling occasion that may simply represent an opportunistic encounter between a school of Steelhead and of Striped Bass, rather than an overall mean rate of predation. In addition, CRSA (2017) noted that

Table 13. Estimated per–capita consumption of fish by Striped Bass in the San Francisco Estuary (Loboschefsky et al. 2012).

Stage	Age	Sex	Proportion of Fish in Diet[a]	Per-Capita Annual Consumption of Fish (kg)[b]	Steelhead daily YOY equivalents[c]
Subadult	1	–	2.5%–12.2%	0.03–0.22	n/a
	2	–	78.5%–82.1%	3.22–4.99	1.5–2.3
Adult	3	F	All adults: 98.7%–99.9%	8.4–11.8	3.8–5.4
		M		6.9–9.3	3.2–4.2
	4	F		12.6–16.8	5.8–7.7
		M		10.3–13.9	4.7–6.3
	5	F		17.5–22.1	8.0–10.1
		M		13.7–18.6	6.3–8.5
	6	F		22.2–27.7	10.1–12.6
		M		16.2–23.0	7.4–10.5

[a] Loboschefsky et al. (2012) and references therein.
[b] Estimated using Wisconsin-style bioenergetics model from growth and temperature data by Loboschefsky et al. (2012). Ranges for annual total consumption in years 1981–2003 (ages 1–2) or 1969–2004 (ages 3–6).
[c] Estimated here as average daily consumption if all prey fish were young-of-the-year (YOY) Steelhead with FL = 80 mm and weight = 6 g.

Table 14. Number of Striped Bass with different stomach contents, from fish removed from Carmel Lagoon (Anderson 2010, 2011, 2014). Most fish recovered from stomachs were unidentifiable, but numbers of recognizable steelhead are reported in parentheses.

Year	Empty	Crustaceans	Fish (SH)[a]	Other
2010	51	19	13 (1)	29
2011	50	7	10 (2)	2
2014	59	3	0	0
Total	160	29	23 (3)	31

[a] Includes bass with both fish and crustaceans in stomachs.

Table 15. Stomach contents of 22 Striped Bass captured in the Carmel River in summer 2017a (CRSA 2017).

Stomach Contents	Steelhead DNA Detected?	Number of Fish
Empty	Yes	7
	No	6
Fish or Fish + Invertebrates	Yes	5
	No	2
Invertebrates Only	Yes	1
	No	1

[a] Locations: Quail Lodge, Robinson Canyon Bridge, Garland Park, Rio Road. Lengths: 41–78 cm.

Steelhead were the most abundant fish in the reach where the Striped Bass were speared, and it is possible that environmental DNA in the water may be finding its way into their stomachs to generate the positive result from empty stomachs.

Very few diet studies from elsewhere in California have identified prey fish to species. Two exceptions are Michel et al. (2018) and Stompe (2018), who isolated DNA from Striped Bass stomachs and used it to determine presence/absence of common prey species. Michel et al. (2018) sampled Striped Bass over two years from three locations on the lower San Joaquin River, in late April/early May during the peak of smolt emigration season. They analyzed DNA from 186 stomachs of Striped Bass ranging from 15 to 65 cm Fork Length, and found that 4.8% of stomachs tested positive for Chinook Salmon and 2.2% tested positive for Steelhead; the proportions did not differ significantly between the two years of the study. The distribution of Striped Bass among the three sites was patchier than other introduced predators such as Largemouth Bass (*Micropterus salmoides*). For example, in 2015 the density at one site, where Old San Joaquin River branched from current San Joaquin River, averaged 1200 Striped Bass per km compared to 20–35 per km at the other two sites, leading to estimates of substantially higher predation at this site versus the others (~0 versus 24 salmon consumed per day per kilometer of river channel; Michel et al. 2018).

Stompe (2018) used genetic techniques to estimate relative abundance of different fish species in the diet of Striped Bass obtained from sites on the Sacramento River near Chico and near Sacramento. For fish from these two locations the percent index of relative abundance (%IRI; Pinkas et al. 1971) of stomach contents was 17% and 4.6% for Chinook Salmon, and 0% and 0.2% for steelhead, respectively. The main diet items for the slightly smaller fish caught at Chico (mean Fork Length = 32 cm) were non-crayfish macroinvertebrates (%IRI = 78%), while the main diet items for the larger fish caught near Sacramento (mean Fork Length = 48 cm) were Threadfin Shad (*Dorosoma petenense*) (%IRI = 55%) and crayfish (%IRI = 26%).

For the Striped Bass caught near Chico, the diet had much more overlap with Sacramento Pikeminnows (*Ptychocheilus grandis*) caught at the same location than to Striped Bass caught near Sacramento (Pianka's (1974) dietary niche breadth overlap = 0.998 vs 0.023, respectively), confirming the view of Moyle (2002) and many others that the species is highly opportunistic in the species of fish it preys on. This can lead to "hot spots" of predation in areas where salmonids become concentrated. For example, Sabal et al. (2016) found that relative to other areas, Striped Bass had higher per-capita consumption rates of emigrating Chinook Salmon at a point on the Mokelumne River where both species were aggregated by a diversion dam with a fish ladder. They estimated that the Striped Bass consumed between 8% and 29% of the emigrating salmon population at that point.

Similarly, the estuaries and lower mainstems of coastal rivers could be potential hotspots for predation on emigrating and rearing salmonids, depending on prey vulnerability and abundance relative to other fish species. To get a sense of the scope for impact, I converted the annual consumption of fish per Striped Bass, estimated by Loboschefsky et al. (2012) for each age class, into daily "*O. mykiss YOY* equivalents," assuming a standard YOY weight and size of 6 g and 80 mm Fork Length. This scope for impact ranges from 1.5 fish to over 12 fish consumed per predator per day depending on age class, if steelhead YOY made up the entire fish component of Striped Bass diet (Table 13). Of course, these estimates were made for the San Francisco Estuary system and would differ for the coast due to differences in temperature and ability of Striped Bass to feed to capacity (Loboschefsky et al. 2012), as well as availability of other fish species.

Pertinent Questions and Future Directions

Although the species did not show up in recent fish surveys of the Russian River Estuary or Morro Bay, it turned up frequently in all the major tributaries of Monterey Bay as well as the Carmel River. It is occasionally seined in large numbers and in the Carmel Lagoon, 551 individuals were removed from the river over 8 years, indicating the potential for large impacts on juvenile salmonids. Interestingly, though the species was observed in Elkhorn Slough in the 1970s, since then the only observations are by anglers despite several intensive fish surveys.

I found no evidence for local reproduction either historically or recently, but very few studies capable of detecting it have been conducted. Based on habitat, the likeliest spot for local reproduction is probably the Salinas River, especially in years when the timing of sandbar formation and the operation of the outlet gate from the estuary to Old Salinas River Channel would tend to shunt eggs and larvae into the Old River / Elkhorn Slough system (Figure 3). However, neither eggs nor larvae of *M. saxatilis* have ever been detected in Elkhorn Slough or Moss Landing Harbor (part of the Old Salinas River Channel) despite extensive sampling of ichthyoplankton.

There are two types of studies that could be pursued to definitively settle the question of local reproduction. The first, like that of Yoklavich et al. (1992), would consist of a sustained effort to sample the ichthyoplankton of lower rivers or estuaries over a number of years. The sporadic occurrence of larger size classes of *M. saxatilis* in the seining surveys described above suggest that spawning, if it does occur, may be very irregular; thus sampling would need to continue for 5 years to a decade to establish if successful recruitment is occurring. The second and perhaps simpler and more powerful type of study would examine the otolith microchemistry of adults or subadults captured in the river of interest. The elemental isotopes in the inner parts of the otolith should provide information on the geology of the natal stream, which could be used to determine if fish originated in the Sacramento Basin, San Joaquin Basin, or the local coastal basin where it was caught.

Piscivory of juvenile salmonids, especially ESA-listed Steelhead and Coho Salmon, seems likely and the scope for it quite large, but the true level of impact is not known. The diet data from the Carmel system suggests that fish often have empty stomachs (66% and 59% in Table 13 and Table 14 respectively) and may therefore have trouble catching food. These proportions of empty stomachs are comparable to historic studies in Coos Bay Oregon (49.6% of 1018 stomachs empty in 1948-50; Morgan and Gerlach 1950) and San

Francisco Bay (50.4% of 4551 stomachs in 1957-61; Thomas et al. 1967). However, the 47 Striped Bass seined from Waddell Creek by Shapovalov (1936) in 1935 had a much lower proportion of empty stomachs, only 15% (lumping empty stomachs with those only containing sand or debris).

The data also indicate a potential for non-negligible consumption of *O. mykiss* and a willingness to move upstream out of the estuary, perhaps to forage. Striped Bass are clearly opportunistic foragers, and in many estuaries *O. mykiss* are the prey species with the most biomass, especially during smolt migration season or when the estuary is in its closed phase. Future diet studies would help clarify this impact, especially if they were spread across the various river systems and seasons, and used unambiguous genetic techniques like those of Stompe (2018) to identify fish prey items down to species. Since hook-and-line sampling may bias the sample toward fish with empty stomachs, it would be preferable to sample fish via gill netting, spear fishing, or some other method that does not depend so strongly on a hungry fish. Gill netting appears effective (Casagrande 2010, 2011) but may pose unacceptable bycatch mortality on Steelhead.

Even if salmonids avoid predation, however, Striped Bass may prevent them from effectively exploiting estuarine habitat. Presence of Striped Bass may inhibit feeding behavior by salmonids in the estuary, or simply lead them to flee upstream. This sublethal effect may have outsized impacts, by preventing the population as a whole from exploiting the high-growth opportunities in the estuary. This in turn could depress size-at-ocean-entry and subsequent marine survival (Bond et al. 2008), or undermine the resilience provided by alternative life-history pathways (Koski 2009).

Although the recent data do not rule out local reproduction, they are largely consistent with the idea of anadromous migrants from the San Francisco Bay, foraging in the ocean between the Golden Gate and Carmel and occasionally entering estuaries to feed. This hypothesis could be definitively tested with a suitably designed acoustic-telemetry study. On the Atlantic Coast, Grothues et al. (2009) used acoustic tags to track the movements of Striped Bass captured and released in two small estuaries in New Jersey and Maine, each lacking access to suitable upstream spawning habitat. They found their tagged fish exhibiting a broad diversity of behaviors, including taking up residency in non-natal estuaries, moving upstream during spawning season and then abruptly exiting to the ocean, moving upstream during spawning season and then taking up residency in the estuary, and moving back to a known self-sustaining population in Delaware Bay. They even found fish moving between the two estuaries of the study—in New Jersey and Maine—which are separated by 700 km of coastline, two major coastal cities, a large self-sustaining population in the Hudson River, and innumerable smaller estuaries similar to the ones used in the study. Perhaps California Striped Bass are similarly opportunistic, roving, and crafty.

If so, then the primary management implication is that as long as Striped Bass inhabit the San Francisco Bay/Delta ecosystem, they are likely to show up in coastal rivers and estuaries, especially in the area flanking the Golden Gate, and impact native fish populations to some lesser or greater degree. Efforts to recover salmonids by restoring cool spring flows to managed rivers may also tend to attract mature Striped Bass for spawning, but there is little evidence that such spawning will lead to self-sustaining populations. It is likely, however, to increase the predation pressure on local salmonid populations, as well as other vulnerable fish species such as Tidewater Goby. Efforts to remove Striped Bass via hook-and-line removal, spearfishing, seining, or other methods seem likely to reduce this impact, but would be required in perpetuity. Such removal activities may also have direct impacts on native fish themselves via capture or habitat disturbance, and so the real question is whether such impacts are greater or smaller than the benefits to local species of ongoing Striped Bass removal or harvest.

ACKNOWLEDGMENTS

Thanks to T. Frahm, M. Paul, T. Williams, J. Pearson-Meyer, J. Casagrande, R. Stoddard, H. Ohms, and C. Michel for interesting discussions about Striped Bass ecology in California. C. Michel, B. Spence, J. Nelson, D. Michniuk, M. Sabal, and one unidentified reviewer provided excellent and informative reviews of the manuscript.

LITERATURE CITED

Allen, L. G., M. Yoklavich, G. Cailliet, and M. H. Horn. 2006. Chapter 5: Bays and estuaries. Pages 119–148 in L. G. Allen, D. J. Pondella II, and M. H. Horn, editors. The ecology of marine fishes, California and adjacent waters. University of California Press, Berkeley, CA, USA.

Alley, D. W. 2017. Fishery and water quality monitoring of Pajaro River Lagoon in 2017. Santa Cruz County Environmental Health Department, Santa Cruz, CA, USA.

Alley, D. W. 2018. Fishery and water quality monitoring of Pajaro River Lagoon in 2018. Santa Cruz County Environmental Health Department, Santa Cruz, CA, USA.

Alley, D. W., and C. Steiner. 2016. 2015 Draft summary report - juvenile steelhead densities in the San Lorenzo, Soquel, Aptos and Corralitos watersheds, Santa Cruz County, CA. Appendix B. Santa Cruz County Environmental Health Department, Santa Cruz, CA, USA.

Anderson, P. 2010. Carmel lagoon striped bass removal project report 2010. California Department of Fish and Wildlife, Monterey, CA, USA.

Anderson, P. 2011. Lower Carmel River striped bass removal pilot project report 2011, NOAA, 4d application #15829 from California Department of Fish and Wildlife. California Department of Fish and Wildlife, Monterey, CA, USA.

Anderson, P. 2014. Lower Carmel River striped bass removal project, annual 4d report to NOAA Fisheries. California Department of Fish and Wildlife, Monterey, CA, USA

Atkinson, K. A. 2010. Habitat conditions and steelhead abundance and growth in a California lagoon. Master's thesis, California State University, San Jose, CA, USA.

Behrens, D., M. Brennan, and B. Battalio. 2015. A quantified coneptual model of inlet morphology and associated lagoon hydrology. Shore & Beach 83(3):33–42.

Beller, E., R. Grossinger, and A. Whipple. 2009. Historical ecology reconnaissance for the lower Salinas River. San Francisco Estuary Institute, Oakland, CA, USA.

Bond, M. H., S. A. Hayes, C. V. Hanson, and R. B. MacFarlane. 2008. Marine survival of steelhead (*Oncorhynchus mykiss*) enhanced by a seasonally closed estuary. Canadian Journal of Fisheries and Aquatic Sciences 65:2242–2252.

Boughton, D. A., and H. A. Ohms. 2018. Fisheries River Steelhead Fishery Report 2018. Report to California American Water under Memorandum of Understanding between Cal Am Water and NMFS SWFSC, SWFSC Agreement No. SWC–156. NOAA Fisheries, SW Fisheries Science Center, Santa Cruz, CA, USA.

Brandl, S. C., B. M. Schreier, J. L. Conrad, B. May, and M. R. Baerwald. 2016. Generation of quantitative polymerase chain reaction detectability half-lives and comparison of sampling protocols for genetic diet studies of San Francisco Estuary Fishes. Transactions of the American Fisheries Society 145:441–449.

Cailliet, G. M., B. Antrim, D. Ambrose, S. Pace, and M. Stevenson. 1977. Species composition, abundance, and ecological studies of fishes, larval fishes, and zooplankton in Elkhorn Slough. Pages 218–386 in J. Nybakken, G. Cailliet, and W. Broenkow, editors. Ecologic and hydrographic studies of Elkhorn Slough Moss Landing Harbor and nearshore coastal waters, July 1974–June 1976. Moss Landing Marine Laboratories Technical Publication, Moss Landing, CA, USA.

Calhoun, A. J. 1952. Annual migrations of California striped bass. California Fish and Game 38:391–403.

Cannata, S., and T. Hassler. 1995. Juvenile salmoonid utilizaton of the Eel River estuary. California Cooperative Fishery Research Unit, Humboldt State University, Arcata, CA, USA.

Casagrande, J. 2006. Carmel Lagoon seine results July 27, 2006. Watershed Institute, California State University Monterey Bay, Seaside, CA, USA.

Casagrande, J. 2011. Aquatic species and habitat assessment of the Upper Pajaro River basin, Santa Clara and San Benito Counties, California: summer 2011. The Nature Conservancy, San Francisco, CA, USA.

Casagrande, J. R. 2010. Aquatic ecology of San Felipe Lake, San Benito County, California. Master's thesis, California State University, San Jose, CA, USA.

Chase, S., R. Benkert, D. Manning, and S. White. 2001. Sonoma County Water Agency's Mirabel rubber dam/Wohler Pool reconnaissance fish sampling program: year 1 results 2000. Sonoma County Water Agency, Santa Rosa, CA, USA.

Chase, S., R. Benkert, D. Manning, and S. White. 2002. Sonoma County Water Agency's Mirabel rubber dam/Wohler Pool reconnaissance fish sampling program: year 2 results 2001. Sonoma County Water Agency, Santa Rosa, CA, USA.

Chase, S., R. Benkert, D. Manning, and S. White. 2004. Sonoma County Water Agency's Mirabel rubber dam/Wohler Pool reconnaissance fish sampling program: year 4 results 2003. Sonoma County Water Agency, Santa Rosa, CA, USA.

Chase, S., R. Benkert, D. Manning, and S. White. 2005. Sonoma County Water Agency's Mirabel rubber dam/Wohler Pool reconnaissance fish sampling program: year 5 results 2004. Sonoma County Water Agency, Santa Rosa, CA, USA.

Chase, S., R. Benkert, D. Manning, S. White, and S. Brady. 2000. Results of the Sonoma County Water Agency's Mirabel rubber dam/Wohler Pool reconnaissance fish sampling program. Sonoma County Water Agency, Santa Rosa, CA, USA.

Cole, M. E. 2004. Distribution of fish species in Humboldt Bay, Humboldt County, California, USA: a GIS perspective. Master's thesis, Humboldt State University, Arcata, CA, USA.

Cook, D. 2004. Russian River estuary flow-related habitat project, survey methods report 2003. Sonoma County Water Agency, Santa Rosa, CA, USA.

Cook, D. 2005. Russian River estuary fish and macro-invertebrate studies, 2004. Sonoma County Water Agency, Santa Rosa, CA, USA.

Cook, D. 2006. Russian River estuary fish and macro-invertebrate studies, 2005. Sonoma County Water Agency, Santa Rosa, CA, USA.

CRSA (Carmel River Steelhead Assocation). 2017. Striped Bass predation study report for the Carmel River, September 2017. Carmel River Steelhead Association, Carmel, CA, USA.

Cuthbert, R., P. Cuthbert, A. Fuller, and M. Hellmair. 2014a. Salinas basin juvenile *O. mykiss* downstream migration monitoring, 2014 annual report. Monterey County Water Resources Agency, Salinas, CA, USA.

Cuthbert, R., P. Cuthbert, A. Fuller, and M. Hellmair. 2014b. Salinas River basin adult steelhead escapement monitoring, 2014 annual report. Monterey County Water Resources Agency, Salinas, CA, USA.

Cuthbert, R., M. Palmer, D. Demko, and S. Ainsley. 2010. Salinas basin rotary screw trap monitoring, 2010 final report. Monterey County Water Resources Agency, Salinas, CA, USA.

Dettman, D. H. 1984. The Carmel Lagoon and its use by steelhead, Appendix A. D.W. Kelley and Associates, Newcastle, CA, USA.

Dill, W. A., and A. J. Cordone. 1997. History and status of introduced fishes in California, 1871 - 1996. California Fish and Game Fish Bulletin 178:1–414.

ECORP (ECORP Consulting, Incorporated), and KHE (Kamman Hydrology and Engineering, Incorporated). 2005. Gualala estuary and lower river enhancement plan: results of 2002 and 2003 physical and biological surveys. Sotoyome Resource Conservaton District and California Coastal Conservancy, Santa Rosa, CA, USA.

Ettlinger, E. 2017. Smolt monitoring in the Lagunitas Creek watershed - 2017. Marin Municipal Water District, Corte Madera, CA, USA.

Feyrer, F., M. L. Nobriga, and T. R. Sommer. 2007. Multidecadal trends for three declining fish species habitat patterns and mechanisms in the San Francisco Estuary, California, USA. Canadian Journal of Fisheries and Aquatic Sciences 64:723–734.

Fierstine, H. L., K. F. Kline, and G. R. Garman. 1973. Fishes collected in Morro Bay, California between January, 1968 and December, 1970. California Fish and Game 59:73–88.

Fong, D. 1996. Usage of lower Redwood Creek and Big Lagoon by juvenile coho salmon and steelhead. Aquatic Ecology Program 1995 Annual Report. United States National Park Service, Golden Gate National Recreation Area, San Francisco, CA, USA.

Forrester, C. R., A. E. Peden, and R. M. Wilson. 1972. First records of the striped bass, *Morone saxatilis*, in British Columbia waters. Journal of the Fisheries Research Board of Canada 29:337–339.

Gilchrist, J., D. Suddjian, B. Mori, K. Reeves, K. Lyons, J. Smith, L. Herter, S. Nielson, J. Haltiner, L. Sklar, J. Buchholz, and D. Spicher. 1992. Salinas River lagoon management and enhancement plan, volume 2: techical appendices. Monterey County Water Resources Agency, Salinas, CA, USA.

Gilroy, M. M. 2002. The essential Eel River estuary. California Department of Fish and Game, Eureka, CA, USA.

Gleason, E., B. deWaard, A. Shows, S. Cannata, D. Kajtaniak, M. Wheetley, K. Pettit, V. Avara-Snider, K. Wilson, D. Heaton, and S. Downie. 2010. Lower Eel River watershed assessment. Coastal Watershed Planning and Assessment Program, California Department of Fish and Game, Sacramento, CA, USA.

Goodwin, P., and C. K. Cuffe. 1993. Russian River estuary study 1992-1993. Philip Williams and Associates, Limited, San Francisco, CA, USA.

Gordon, B. L. 1996. Monterey Bay area: Natural history and cultural imprints, third edition. Boxwood Press, Pacific Grove, CA, USA.

Gotshall, D. W., G. H. Allen, and R. A. Barnhart. 1980. An annotated checklist of fishes from Humboldt Bay, California. California Fish and Game 66:220–232.

Grothues, T. M., K. W. Able, J. Carter, and T. W. Arienti. 2009. Migration patterns of striped bass through nonnatal estuaries of the U.S. Atlantic coast. American Fisheries Society Symposium 69:135–150.

HES (Hagar Environmental Science). 2015. Salinas River lagoon monitoring report, 2014. Monterey County Water Resources Agency, Salinas, CA, USA.

HES (Hagar Environmental Science). 2017. Technical memorandum, City of Santa Cruz habitat conservation plan, lagoon fish population sampling 2016. City of Santa Cruz, Santa Cruz, CA, USA.

Higgins, P. 1995. Fisheries elements of a Garcia River estuary enhancement feasibility study. Mendocino County Resource Conservation District, Ukiah, CA, USA.

Horn, M. H. 1980. Diel and seasonal variation in abundance and diversity of shallow-water fish populations in Morro Bay, California. Fishery Bulletin 78:759–770.

Huber, E. 2018. The management and ecology of *Oncorhynchus* spp. and other estuarine-dependent native California fishes in artificially and naturally disconnected landscapes. Dissertation, University of California, Berkeley, CA, USA.

Jankovitz, J. 2015. Summary of water quality monitoring and fish sampling Pescadero Creek Lagoon 2014. California Department of Fish and Wildlife, Fairfield, CA, USA.

Jankovitz, J. 2017. Annual water quality monitoring, fish sampling, and fish kills Pescadero Creek Lagoon 2016. California Department of Fish and Wildlife, Fairfield, CA, USA.

Jankovitz, J. 2018. Summary of annual water quality monitoring, fish sampling, and active management Pescadero Creek Lagoon 2017. California Department of Fish and Wildlife, Fairfield, CA, USA.

Jankovitz, J., and R. Diller. 2019. Summary of annual fish sampling, water quality monitoring, and active management Pescadero Creek Lagoon complex 2018. California Department of Fish and Wildlife, Fairfield, CA, USA.

Karas, N. 2016. The complete book of striped bass fishing. Skyhorse Publishing, New York, NY, USA.

Koski, K. V. 2009. The fate of coho salmon nomads: The story of an estuarine-rearing strategy promoting resilience. Ecology and Society 14(1):Article 4.

Krafft, E., C. Leal, and T. Voss. 2013. Salinas Valley water project, annual fisheries report for 2012. Monterey County Water Resources Agency, Salinas, CA, USA.

Krafft, E., T. Skiles, and T. Voss. 2012. Salinas Valley water project, annual fisheries report for 2011. Monterey County Water Resources Agency, Salinas, CA, USA.

Leal, C., E. Krafft, and T. Voss. 2014. Salinas Valley water project, annual fisheries report for 2013. Monterey County Water Resources Agency, Salinas, CA, USA.

Loboschefsky, E., G. Benigno, T. Somer, K. A. Rose, T. Ginn, A. Massoudieh, and F. Loge. 2012. Individual-level and population-level historical prey demand of San Francisco estuary striped bass using a bioenergetics model. San Francisco Estuary and Watershed Science 10(1):Article 3.

Martini-Lamb, J. 2001. Biological and water quality monitoring in the Russian River estuary, 2000. Fifth Annual Report. Sonoma County Water Agency, Santa Rosa, CA, USA.

MCWRA (Monterey County Water Resources Agency), and USACE (United States Army Corps of Engineers). 2001. Draft Environmental Impact Report / Environmental Impact Statement for the Salinas Valley Water Project. Monterey County Water Resources Agency, Salinas, CA, USA.

Michel, C. J., J. M. Smith, N. J. Demetras, D. D. Huff, and S. A. Hayes. 2018. Non-native fish predator density and molecular-based diet estimates suggest differing effects of predator species on juvenile salmon in San Joaquin River, California. San Francisco Estuary and Watershed Science 16(4):Article 3.

Monaco, M. E., R. L. Emmett, D. M. Nelson, and S. A. Hinton. 1990. Distribution and abundance of fishes and invertebrates in West Coast estuaries. Volume 1: Data summaries. NOAA Estuarine Living Marine Resources Report Number 4:1–232.

Monroe, G. W., F. Reynolds, B. M. Browning, and J. W. Speth. 1974. Natural resources of the Eel River delta. Coastal Wetlands Series #9, California Department of Fish and Game, Eureka, CA, USA.

Morgan, A. R., and A. R. Gerlach. 1950. Striped bass studies on Coos Bay, Oregon in 1949 and 1950. Oregon Fish Commission Contribution Number 14:1–31.

Moyle, P. B. 2002. Inland fishes of California. University of California Press, Berkeley, CA, USA.

Murphy, G. I., and J. W. De Witt, Jr. 1951. Notes on the fishes and fishery of the lower Eel River, Humboldt County, California. California Department of Fish and Game, Sacramento, CA, USA.

OCMP (Office for Coastal Management Partners). 2019. 2017 United States Geological Survey CoNED topobathymetric model (1929 - 2017): central coast of California. Available from: https://inport.nmfs.noaa.gov/inport/item/55319 (October 2019).

Osborn, K. 2017. Seasonal fish and invertebrate communities in three northern California estuaries. Master's thesis, Humboldt State University, Arcata, CA, USA

Parks, N. B. 1978. The Pacific Northwest commercial fishery for striped bass, 1922-74. Marine Fisheries Review 40(1):18–20.

Pianka, E. R. 1974. Niche overlap and diffuse competition. Proceedings of the National Academy of Sciences of the United States of America 71:2141–2145.

Pinkas, L., M. S. Oliphant, and I. L. Iverson. 1971. Food habits of albacore, bluefin tuna, and bonita in California waters. California Fish and Game Fish Bulletin 152:1–105.

Pucket, L. 1976. Observations on the downstream migrations of anadromous fishes within the Eel River system. Memorandum Report. California Department of Fish and Game, Sacramento, CA, USA.

Puckett, L. 1977. The Eel River – observations on the morphometry, fishes, water quality and invertebrates. Memorandum Report. California Department of Fish and Game, Sacramento, CA, USA.

Reinert, T. R., T. A. Will, C. A. Jennings, and W. T. Davin. 2004. Use of egg surrogates to estimate sampling efficiency of striped bass eggs in the Savannah River. North American Journal of Fisheries Management 24:704–710.

Rich, A., and E. A. Keller. 2013. A hydrologic and geomorphic model of estuary breaching and closure. Geomorphology 191:64–74.

Robinson, T., C. Hanson, S. Engblom, S. Volan, J. Baldrige, L. Riege, B. Wales, A. Shahroody, and C. Lawler. 2009. Summary and analysis of annual fishery monitoring in the lower Santa Ynez River, 1993-2004. Cachuma Conservation Release Board, Santa Barbara, CA, USA.

Roth, J. C., M. H. Fawcett, and D. W. Smith. 1997. Biological and water quality monitoring in the Russian River estuary, 1996. Merritt Smith Consulting, Lafayette, CA, USA.

Roth, J. C., M. H. Fawcett, and D. W. Smith. 1998. Biological and water quality monitoring in the Russian River estuary, 1997. Second annual report. Merritt Smith Consulting, Lafayette, CA, USA.

Roth, J. C., M. H. Fawcett, D. W. Smith, J. Martini, J. Mortenson, and J. Hall. 2000. Biological and water quality monitoring in the Russian River estuary, 1999. Fourth annual report. Merritt Smith Consulting, Lafayette, CA, USA.

Roth, J. C., M. H. Fawcett, D. W. Smith, J. Mortenson, and J. Hall. 1999. Biological and water quality monitoring in the Russian River estuary, 1998. Third annual report. Merritt Smith Consulting, Lafayette, CA, USA.

Sabal, M., S. Hayes, J. Merz, and J. Setka. 2016. Habitat alterations and a nonnative predator, the striped bass, increase native Chinook salmon mortality in the Central Valley, California. North American Journal of Fisheries Management 36:309–320.

Sabal, M. C., C. J. Michel, J. M. Smith, A. Hampton, and S. A. Hayes. 2019. Seasonal movement patterns of striped bass (*Morone saxatilis*) in their nonnative range. Estuaries and Coasts 42:567–579.

Scheiff, A., M. Wallace, and M. Gilroy. 2013. McNulty Slough, thence Eel River estuary fish and water quality sampling Jauary 2008 through June 2009. California Department of Fish and Game, Sacramento, CA, USA.

Scofield, E. C. 1928. Striped bass studies. California Fish and Game 14:29–37.

Scofield, E. C. 1930. The striped bass of California (*Roccus lineatus*). California Fish and Game Fish Bulletin 29:1–82.

Scofield, N. B., and H. C. Bryant. 1926. The striped bass in California. California Fish and Game 12:55–74.

Shapovalov, L. 1936. Food of the striped bass. California Fish and Game 22:261–271.

Shapovalov, L. 1944. Preliminary report on the fisheries of the Russian River system, California. California Division of Fish and Game, Bureau of Fish Conservation, Sacramento, CA, USA.

Shapovalov, L., and A. C. Taft. 1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and silver salmon (*Oncorhynchus kisutch*). California Fish and Game Fish Bulletin 98:1–376.

Shaughnessy, F., T. Mulligan, S. Kramer, S. Kullmann, and J. Largier. 2017. Baseline characterization of biodiversity and target species in estuaries along the north coast of California, final report. Humboldt State University, Arcata, CA, USA.

Skinner, J. E. 1962. An historical review of the fish and wildlife resources of the San Francisco Bay area. California Department of Fish and Game, Water Projects Branch Report Number 1:1–225.

Smith, H. M., and W. C. Kendall. 1898. Notes on the extension of the recorded range of certain fishes of the United States coast. U.S. Commission on Fish and Fisheries, Part XXII, Rep. Comm. 1896 Part XXII:169–176.

Smith, J. J. 1990. The effects of sandbar formation and inflows on aquatic habitat and fish utilizaton in Pescadero, San Gregorio, Waddell and Pomponio Creek Estuary/ Lagoon systems, 1985 - 1989. California State University, San Jose, CA, USA.

Stevens, D. E., H. K. Chadwick, and R. E. Painter. 1987. American shad and striped bass in California's Sacramento-San Joaquin River system. American Fisheries Society Symposium 1:66–78.

Stevens, D. E., D. W. Kohlhorst, L. W. Miller, and D. W. Kelley. 1985. The decline of striped bass in the Sacramento-San Joaquin Estuary, California. Transactions of the American Fisheries Society 114:12–30.

Stoddard, R. 2016. June 10, 2016 striped bass surveys. Memorandum to Brian Leneve, Carmel River Steelhead Association, dated 2 August 2016. Cardno Incorporated, Concord, CA, USA.

Stompe, D. K. 2018. Habitat-specific diet analysis of Sacramento pikeminnow (*Ptychocheilus grandis*) and striped bass (*Morone saxatilis*) in the Sacramento River. Thesis, California State University Chico, Chico, CA, USA.

TES (Tenera Environmental Services). 2000. Moss Landing power plant modernization project 316(b) resource assessment. Prepared for Duke Energy Moss Landing, LLC, San Francisco, CA, USA.

Thomas, J. L. 1967. Diet of juvenile and adult striped bass *Roccus saxatilis* in Sacramento-San Joaquin River system. California Fish and Game 53:49–62.

USACE (United States Army Corps of Engineers). 2019. Draft Lake Mendocino master plan. San Francisco District, San Francisco, CA, USA.

Williams, C. M., J. P. Williams, J. T. Claisse, D. J. Pondella II., M. L. Domeier, and L. A. Zahn. 2013. Morphometric relationships of marine fishes common to central California and the southern California bight. Bulletin of the Southern California Academy of Sciences 112:217–227.

Yoklavich, M., G. M. Cailliet, D. Oxman, J. Barry, and D. Lindquist. 2002. Chapter 10. Fishes. Pages 163–186 in J. Caffrey, M. Brown, W. B. Tyler, and M. Silberstein, editors. Changes in a California estuary: A profile of Elkhorn Slough. Elkhorn Slough Foundation, Moss Landing, CA, USA.

Yoklavich, M. M., M. Stevenson, and G. M. Cailliet. 1992. Seasonal and spatial patterns of ichthyoplankton abundance in Elkhorn Slough, California. Estuarine Coastal and Shelf Science 34:109–126.

Submitted 14 April 2020
Accepted 19 May 2020
Associate Editor was P. Reilly