# A Southern California Icon Surfs North: Local Ecotype of California Grunion, *Leuresthes tenuis* (Atherinopsidae), Revealed by Multiple Approaches during Temporary Habitat Expansion into San Francisco Bay

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**California Grunion *Leuresthes tenuis,* a beach spawning marine teleost, was described from a specimen purchased at a San Francisco market in 1859, but not subsequently seen there for 140 years. From 2001–2007, *L. tenuis* spawned on beaches in San Francisco Bay (SFB, 37°45′N, 122°15′W) at multiple locations, but disappeared after 2008. In 2005, *L. tenuis* started spawning for the first time on a beach in Tomales Bay (TB, 38°14′N, 122°58′W), 64 km north of SFB, but this population disappeared after 2009. Adult size, clutch volumes, and egg diameters of *L. tenuis* in SFB were consistently smaller than *L. tenuis* from southern California, though the population was not genetically distinct. Population size structure suggests few *L. tenuis* survived more than one year in these northern bays, rather than the two or three years expected in the typical southern California habitat. Climate change models predict conditions supporting poleward expansion of ranges of marine organisms, but colonization of northern habitats by this beach spawning species resulted in significant phenotypic changes including smaller size, shorter life span, and reduced reproductive output. The multiple environmental challenges and rapid extirpation of two disjunct colonization events indicate this species will require repeated events for habitat expansion to succeed.**

THE response of marine organisms to climate change is complex and challenging to predict. As ocean surface temperatures warm, some marine pelagic fishes are shifting habitat ranges (Perry et al., 2005), particularly those that are small and short-lived.

In California, USA, an endemic marine fish that is a southern California icon expanded its habitat range dramatically but temporarily during the past decade, colonizing and reproducing successfully in areas hundreds of kilometers north of its previous range. In 2001, *L. tenuis* was reported in San Francisco Bay (SFB) for the first time since its original description in 1860, over 140 years earlier (Johnson et al., 2009). The single type specimen was dead when purchased in a San Francisco fish market (Ayres, 1860). Although San Francisco (37°45′N, 122°15′W) is considered the type locality for this species (e.g., Miller and Lea, 1972; Eschmeyer et al., 1983), there was no evidence of *L. tenuis* spawning within SFB until its larvae were found in an Oakland Middle Harbor pool in 2002 (Jahn and Jolliffe, 2004). In 2005, *L. tenuis* was observed spawning also in Tomales Bay (TB), a true range extension (38°14′N, 122°58′W) over 60 km north of San Francisco Bay (Roberts et al., 2007).

The primary habitat range for California Grunion *Leuresthes tenuis* is from mid- Baja California, Mexico, to central California, USA (Walker, 1952; Gregory, 2001). Rarely, this species has been observed farther south, and occasionally it has been observed north of Pt. Conception, California, for example in Morro Bay (Walker, 1952), Estero Bay (Straughan, 1982), Monterey Bay (Phillips, 1943; Spratt, 1981; Gobalet and Jones, 1995), and Elkhorn Slough (Yoklavich et al., 2002). During the past decade, spawning runs of *L. tenuis* occurred regularly within Monterey Bay (Byrne et al., 2013; pers. obs.), an area 190 km south of the mouth of SFB, and more than 400 km north of Pt. Conception.

*Leuresthes tenuis* (Atherinopsidae) is an indigenous beach spawning fish, well known for its spectacular midnight spawning runs during spring and summer months (Walker, 1952). Females surf onshore onto sandy beaches following full and new moon high tides and emerge from waves to dig tail-first into the sand to deposit up to 3000 eggs in a clutch. At the same time, one or more males wrap around her while out of water on the sand surface and provide milt. The adults return to the ocean on a subsequent wave. As the tides fall, embryos within the eggs remain to develop above the mean high tide line, buried in damp sand (Martin et al., 2009; Moravek and Martin, 2011). A little over a week later, rising waters leading to the next syzygy tides free them, trigger hatching (Griem and Martin, 2000; Speer-Blank and Martin, 2004; Martin et al., 2011), and send the larvae out to the sea.

Because of its unusual life history, with spawning and incubation of eggs in beach sand, *L. tenuis* is vulnerable to many human activities on shore. Its susceptibility to overharvest while emerged on land led to recreational gear and season restrictions beginning in 1927 by California Department of Fish and Game (now Fish and Wildlife; Clark, 1926; Spratt, 1986). Incubating eggs can be destroyed by construction activities on shore, vehicles driving over them, beach grooming, sand replenishment, and other actions (Ehrlich, 1977; Lawrenz-Miller, 1991; Martin et al., 2006; Matsumoto and Martin, 2008).

Difficult to monitor, *L. tenuis* may be confused with other atherinopsids and is regularly observed only during spawning runs. *Leuresthes tenuis* is rarely collected by typical fisheries stock assessment methods in southern California, and this endemic species has never been abundant in the Southern California Bight (Clark, 1926; Allen et al., 1983, 2002; Gregory, 2001); adults are only reliably observed during spawning aggregations. The life history of this species complicates its response to changing air and ocean

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temperatures. Unlike pelagic species with all life stages existing submerged in the marine environment, this species requires sandy beaches as critical habitat for spawning and incubation of the embryos until hatching (Thompson, 1919; Jordan, 1926; Walker, 1952). Oviposition on beaches places the eggs and embryos at risk of overheating if air temperatures are above the zone of physiological tolerance (Hubbs, 1965; Middaugh et al., 1983; Smyder and Martin, 2002), and this limitation probably defines the current southern boundary of the habitat range for this species, which is about halfway down the peninsula of Baja California, Mexico. With increasing air and water temperatures, over time the habitat range of species must shift poleward. This rapidly growing, iteroparous species requires warm temperatures for the eggs and larvae (Ehrlich and Farris, 1970, 1972; Reynolds et al., 1976), and given the typical habitat range, probably throughout the year, not just seasonally.

Adult *L. tenuis* are seen only around the time of spawning runs but it is presumed that they remain in the nearshore environment (Walker, 1952; Eschmeyer et al., 1983; Gregory, 2001). Planktivorous, they are almost never captured on a hook and line and they avoid trawl nets in the open ocean. It is impossible to census the population of this managed species using traditional fisheries methods throughout most of its habitat range. In 2002, a citizen scientist data acquisition method, the Grunion Greeters, was developed in southern California to assess spawning run strength, duration, and location in order to inform beach management and natural resource agencies (Martin et al., 2006). This assessment method involved a series of training workshops for volunteers, with outreach and publicity materials, and as a result this organization has become a repository for reports and sightings of grunion runs.

In southern California, most *L. tenuis* spawn on the open outer coast on sandy beaches with energetic surf waves. The family Atherinopsidae is estuarine in origin (Bamber and Henderson, 1988), and juvenile *L. tenuis* in the southern parts of the range access bays and estuaries for feeding and protection from large predators. *Leuresthes tenuis* has been observed in southern California within San Diego Bay (Allen et al., 2002), Mission Bay, Newport Bay, Topanga Creek Lagoon, and Malibu Lagoon (KLM and Grunion Greeters, obs.). However, it is very rare to observe adult *L. tenuis* within bays or lagoons in the southern portion of the habitat range, except on the days and nights of spawning runs. Spawning runs of *L. tenuis* have been observed within southern California bays including San Diego Bay (Olson, 1950), Batiquitos Lagoon (C. Swift, pers. comm.), Newport Bay (Grunion Greeters, pers. comm.), Mission Bay, San Diego (KLM and Grunion Greeters, obs.), and both Avalon Harbor and Cat Harbor on Catalina Island (KLM, obs.). Within bays with low wave action, *L. tenuis* spawn in shallow water at appropriate tidal heights and may not fully emerge from water. Similar beach spawning behavior is seen in the congener *L. sardina*, the Gulf Grunion, in the low waves at the apex of the Gulf of California (Moffatt and Thomson, 1978). It is likely that some *L. tenuis* from the coastal population occasionally move into these southern bays just for spawning, then return to the open ocean afterwards.

San Francisco Bay is a large, relatively shallow complex enclosure of water, strongly influenced by freshwater inputs, with very low wave energy. Tidal heights and excursion are similar in SFB to the open coast, but water temperatures within SFB are warmer than coastal waters outside the Golden Gate, more similar to coastal waters of southern California (Johnson et al., 2009). San Francisco Bay has undergone many anthropogenic modifications including urbanization and armoring of much of its shoreline (Cloern et al., 2007). Sandy beaches within it are typically artificially constructed narrow recreational parks built from imported sand.

The unexpected appearance of *L. tenuis* in SFB, and a few years later in TB, created public enthusiasm for monitoring and learning more about these previously unknown populations. Initial observations were that these fish were somewhat smaller, and different in spawning behavior from the southern California fish (Johnson et al., 2009). Because SFB is relatively enclosed and shallow, it is one of the few locations where trawling may be effective in assessing the population of *L. tenuis*, providing a rare opportunity for the use of multiple population assessment methods to track this elusive species. This study characterizes the growth, size structure, reproductive efforts, spawning locations, and rapid decline of these populations of *L. tenuis* during colonization and local extirpation in the very northern boundary of their habitat range.

## MATERIALS AND METHODS

Multiple approaches were used to obtain data for *L. tenuis* in San Francisco Bay. California Department of Fish and Wildlife (CDFW, formerly Fish and Game) has conducted monthly trawls within SFB at pre-determined stations from 1980 to the present with an otter trawl, cod end of 6 mm mesh, and a midwater trawl, cod end mesh of 13 mm, towed obliquely no deeper than 10 m. Trawls were conducted identically at all stations monthly except on rare occasions when equipment was unavailable due to mechanical breakdown. It is likely that atherinopsids less than 40 mm fork length (FL) pass through the net. Measurements were converted to standard length (SL) for statistical comparisons using a conversion calculated from this population. Numbers, lengths, and species identification of all fish including *L. tenuis* were recorded, as well as salinity and temperature for each location and date.

California Least Terns *Sterna antillarum browni* are present at the Alameda Least Tern Colony only during the breeding season, mid-May through mid-August. Dropped fish were monitored by PRBO Conservation Science during the breeding season with Type I nest surveys, when people walked through the colony one or two days per week (Elliott et al., 2007). Monthly numbers, standard lengths (SL), and taxonomic identification of whole fish have been obtained from 1976 through the present.

Citizen scientist Grunion Greeters were trained in Oakland to observe spawning runs at sites in SFB and TB. They made reports from 2005 through 2008 using standardized methods (Martin et al., 2006, 2007; www.Grunion.org). Observations were focused on Crown Memorial State Beach on east SFB in Alameda, Crissy Field in Golden Gate National Recreation Area, just inside the Golden Gate, and on Dillon Beach, Lawson's Landing, at the mouth of Tomales Bay. Additional beaches were monitored opportunistically. Observations were scheduled for two hours starting at the time of the high tides, on the second and third nights following each new or full moon in May, June, and July. Runs that were reported were confirmed subse-

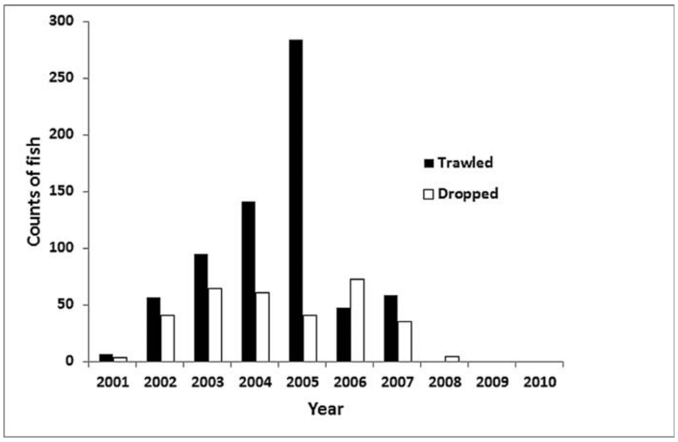


**Fig. 1.** Numbers of *L. tenuis* among the dropped fishes at Alameda Least Tern Colony, and as caught in monthly trawl surveys by California Department of Fish and Wildlife in San Francisco Bay from 2001 through 2008. Trawls were done year-round. Dropped fishes were counted only when birds were present, from May to August.

quently by locating eggs buried in sand on those beaches the next day. Run strength was reported according to the Walker Scale, from W0, no fish, to W5, an enormous, long-lasting run (Martin et al., 2006, 2007). Beaches on the outer coast of California near SFB were monitored sporadically by Grunion Greeters during the times of potential spawning runs, and on multiple occasions by searching for eggs of *L. tenuis* on days after runs were predicted.

Spawning adults were caught by hand during runs and measured for SL and total length (TL) with calibrated digital calipers (Fisher Scientific, Model 06-664-16). Measurements were converted to SL for statistical calculations with a conversion factor for the population. Voucher specimens were deposited in the Marine Vertebrate Collection at Scripps Institution of Oceanography, La Jolla, CA.

Eggs were collected from beaches where spawning runs had occurred as complete clutches to determine clutch volumes, egg diameters, and total numbers of eggs per clutch. For egg diameters, from each clutch, 10 to 30 eggs were measured to calculate a grand mean to use in statistical comparisons from SFB ($n = 23$) and southern California ($n = 40$). As the runs were so small, only one clutch from TB was collected, with 30 eggs measured for diameters. Egg diameters were measured at the widest point with an ocular micrometer on a dissecting microscope.

Statistical comparisons were made with Statview v. 5.01 (SAS Institute, Inc., Cary, NC) using Student's t-tests or analysis of variance (ANOVA) followed by Fisher's *post-hoc* PLSD and linear regression. For comparisons, mean±SD are given. An alpha of $<0.05$ was considered a significant difference.

## RESULTS

Over 13,000 monthly trawls have been performed in SFB by CDFW since the program began in 1980. *Leuresthes tenuis* were first collected in 2001 (Fig. 1). In that first year, only six individuals were caught over all the stations, but by 2005 the trawls netted 284 *L. tenuis*. Numbers declined in 2006 and 2007, to zero in subsequent years. A total $n = 686$ were taken by trawl from 22 of the 52 stations sampled within San Francisco Bay, including all those within central and south San Francisco Bay (Fig. 2). None were found upstream of western San Pablo Bay, stations 345 and 317. From December 2007 through June 2013, only one additional individual was caught in SFB, 118 mm SL, in July 2010. For all trawls in San Francisco Bay with *L. tenuis*, salinity was 27.5±4.1 PSU, ranging from 13.5 to 30.9, and the temperature was 16.9±2.7°C, ranging from 10.7 to 22.4°C.

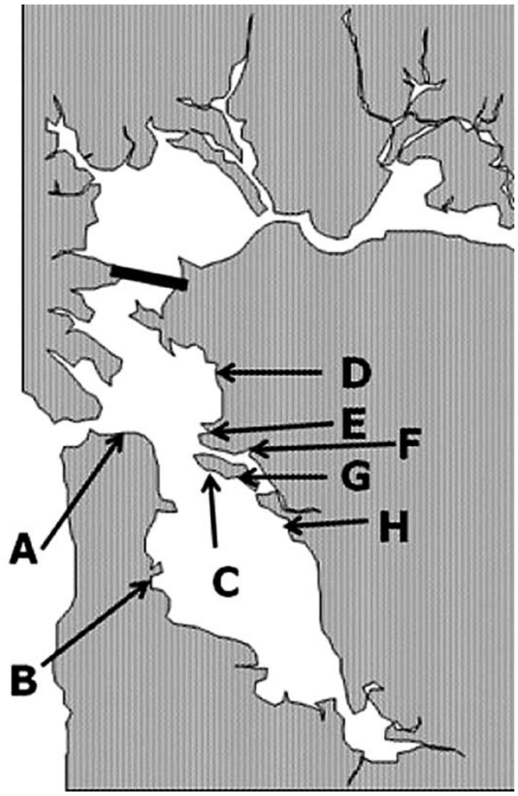


**Fig. 2.** Map of SFB showing confirmed locations of spawning runs of *L. tenuis*. A = Crissy Field; B = Foster City; C = Seaplane Lagoon, and also Alameda Least Tern Colony; D = Albany Bulb; E = Emeryville; F = Middle Harbor, Shoreline Park, Oakland; G = Crown Memorial State Beach; H = San Leandro. *Leuresthes tenuis* were collected at least once at all trawl stations within south and central SFB, and the two most western stations in San Pablo Bay, all areas below the heavy bar.

In 2001, at the Alameda Least Tern Colony, dropped fishes included a few *L. tenuis* (Fig. 1) for the first time. Over the ensuing years, the numbers increased and then decreased. With an average of 1800 total fishes dropped annually that were complete enough to identify, relatively few, about 2%, were *L. tenuis* (total $n = 308$ over eight years). No *L. tenuis* were dropped before 2001 or from 2008 to the present (June 2013). Atherinopsids including Topsmelt *Atherinops affinis* and Jacksmelt *Atherinopsis californiensis* are the most common dropped fish, followed by Northern Anchovy *Engraulis mordax*.

Observations by Grunion Greeter volunteers began in 2005 and continued for four years, through the summer of 2008. Spawning runs were observed or confirmed by locating nests on multiple sandy beaches in SFB (Fig. 2), including Crissy Field in Golden Gate National Recreation Area; the beach at Foster City; Robert's Landing in San Leandro; Crown Memorial State Beach in Alameda; Seaplane Lagoon on the Alameda Naval Base; Middle Harbor Beach in Shoreline Park, Oakland; Albany Bulb, and a pocket beach at Emeryville. The Alameda Least Tern Colony is near Seaplane Lagoon, on the Alameda Naval Base.

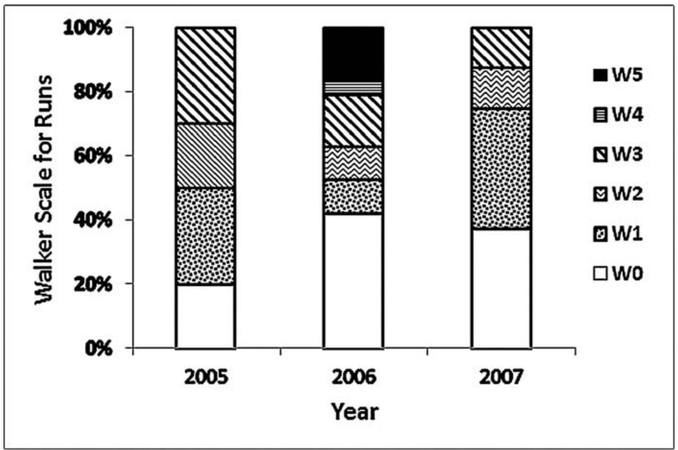


**Fig. 3.** Walker Scale ratings (see text) for 82 observations for spawning runs of *L. tenuis* on beaches in San Francisco Bay (SFB) and Tomales Bay (TB) from 2005 to 2008. If multiple nights were observed during a spawning period, the largest sighting is reported. No runs were seen in 2008 or subsequently, despite repeated attempts, although two *L. tenuis* were observed at TB in 2009.

Largest runs observed for each monitored tide series in SFB and TB are reported (Fig. 3). In Tomales Bay, runs of *L. tenuis* were observed opportunistically from 2005 to 2009 at Dillon Beach at Lawson's Landing, but no evidence was found of runs at any other beaches within Tomales Bay. Run strength declined in 2007 and no runs were seen in 2008 or subsequently, either in SFB or TB, although two *L. tenuis* were seen briefly on the beach in TB in August of 2009.

Outer coast beaches examined for spawning runs for *L. tenuis* included Stinson Beach, Baker Beach, Ocean Beach, and Half Moon Bay. These beaches were checked repeatedly during times of predicted runs and by looking for nests in the sand on appropriate days. No evidence of runs or eggs at any of these beaches was ever found. However, once, in October of 2001, four *L. tenuis* were caught in a trawl survey off Stinson Beach in Bolinas Bay (Jeff Harding, NOAA, pers. comm.).

Dropped *L. tenuis* from the Alameda Least Tern Colony ($n$ = 308), collected from May through August and aggregated over all years, ranged from 40 to 124 mm SL, with the majority between 90 and 110 mm (Fig. 4). *Leuresthes tenuis* collected in the monthly trawls ($n$ = 686) ranged from 39 to 150 mm SL, with the majority between 85 and 105 mm. Fish were caught in trawls every month of the year, but not in every month sampled (Table 1). Conspecifics were collected during spawning runs in southern California ($n$ = 277) at Malibu State ''Surfrider'' Beach, Los Angeles County in 2005 and 2006, and at Doheny State Beach, Orange County, in 2005 and 2006.

Sexually mature fish ($n$ = 71) were caught by hand during spawning runs on Crown Memorial State Beach in Alameda, SFB in 2005 ($n$ = 16), 2006 ($n$ = 35), and 2007 ($n$ = 20), and at Lawson's Landing in TB in the same years ($n$ = 20 in 2005, $n$ = 10 in 2006, $n$ = 1 in 2007). Lengths were compared with conspecifics from spawning runs in southern California (Fig. 5). The spawning *L. tenuis* from SFB in all three years, and TB in 2006 and 2007, were significantly smaller than fish from southern California ($F_{3,243} = 175.84$, $P < 0.001$, Fisher's PLSD).

In southern California, fewer than 1% of the spawning adults of *L. tenuis* were under 110 mm SL. In SFB, only 10.7% of all the *L. tenuis* collected were more than 110 mm SL (83 of 686 trawled specimens, 0 of 308 dropped specimens, and 31 of 71 collected during spawning runs, a total of 114 out of 1065 specimens). Notably, the mean SL for spawning *L. tenuis* in SFB, 95.6 mm, was shorter than the smallest spawning *L. tenuis* seen from southern California at 105 mm SL.

Looking more closely, in 2001, the first year that *L. tenuis* appeared in SFB trawls, 4 of 6 specimens, 67%, were above 110 mm SL. In TB in 2005, the first year that *L. tenuis* appeared there, 95% of the specimens were above 110 mm SL, and this group was not significantly different in mean length from *L. tenuis* from southern California. *Leuresthes tenuis* collected during spawning runs in SFB from 2005 to 2007 were significantly shorter than those from southern California (Fig. 5). Similarly, in subsequent years 2006 and 2007, the TB specimens were significantly smaller and not different in length from *L. tenuis* in SFB.

The largest individuals taken by trawl in SFB were seen during the summer spawning season, April through July (Fig. 6) Mean size in July includes new age-0 fish that may mask the age-1 fish. *Leuresthes tenuis* collected by trawl at other times of year were significantly smaller ($F_{2,441}$ = 200.03, $P < 0.0001$). Dropped fish were counted between the months of May and August at the Alameda Least Tern Colony, when these birds are nesting and feeding their chicks (Elliott et al., 2007). This coincides with the time that *L. tenuis* are also reproducing, spawning, and hatching. Sizes of SFB *L. tenuis* collected during the spawning season between April and August by all these different methods, for trawl data, for dropped fish, and for adults collected during spawning runs, were similar, indicating that these different methods sampled the same population.

The *L. tenuis* from SFB had significantly smaller clutch volumes (t = −7.377, df = 45, $P < 0.0001$) and number of eggs per clutch (t = −7.227, df = 45, $P < 0.0001$) than the southern populations (Fig. 7). Egg diameters in SFB were $1.45 \pm 0.05$ mm ($n$ = 23 clutches), significantly smaller than eggs from *L. tenuis* in southern California at $1.74 \pm 0.10$ mm ($n$ = 40 clutches; t = −12.92, df = 51, $P < 0.0001$). Eggs from a single clutch collected in 2007 from TB were not used in statistical analysis, but mean diameter ($n$ = 30 eggs) was $1.50 \pm 0.07$ mm.

Conversions between total length (TL), fork length (FL), and standard length (SL) from different measurements were calculated from specimens measured for two of the three. Conversion factors for this species are as follows: SL = 0.83 TL; FL = 0.87 TL; SL = 0.95 FL.

## DISCUSSION

Recent warming of oceans on a global scale has caused great concern for the impacts on marine fishes, in particular, in habitat range shifts to maintain thermal equilibrium (Perry et al., 2005; Booth et al., 2011; Hazen et al., 2013). This study suggests that coastal species with complex life histories, requiring specific intertidal substrates as critical reproductive habitat (Middaugh et al., 1983; Rice, 2006), may find these range shifts even more problematic than pelagic species with broadcast spawning and planktonic eggs.

Pt. Conception is a well-known ''break point'' between two different oceanic biogeographic provinces, with differences not only in temperature but also in wave regime, circulation patterns of surface waters, productivity, and

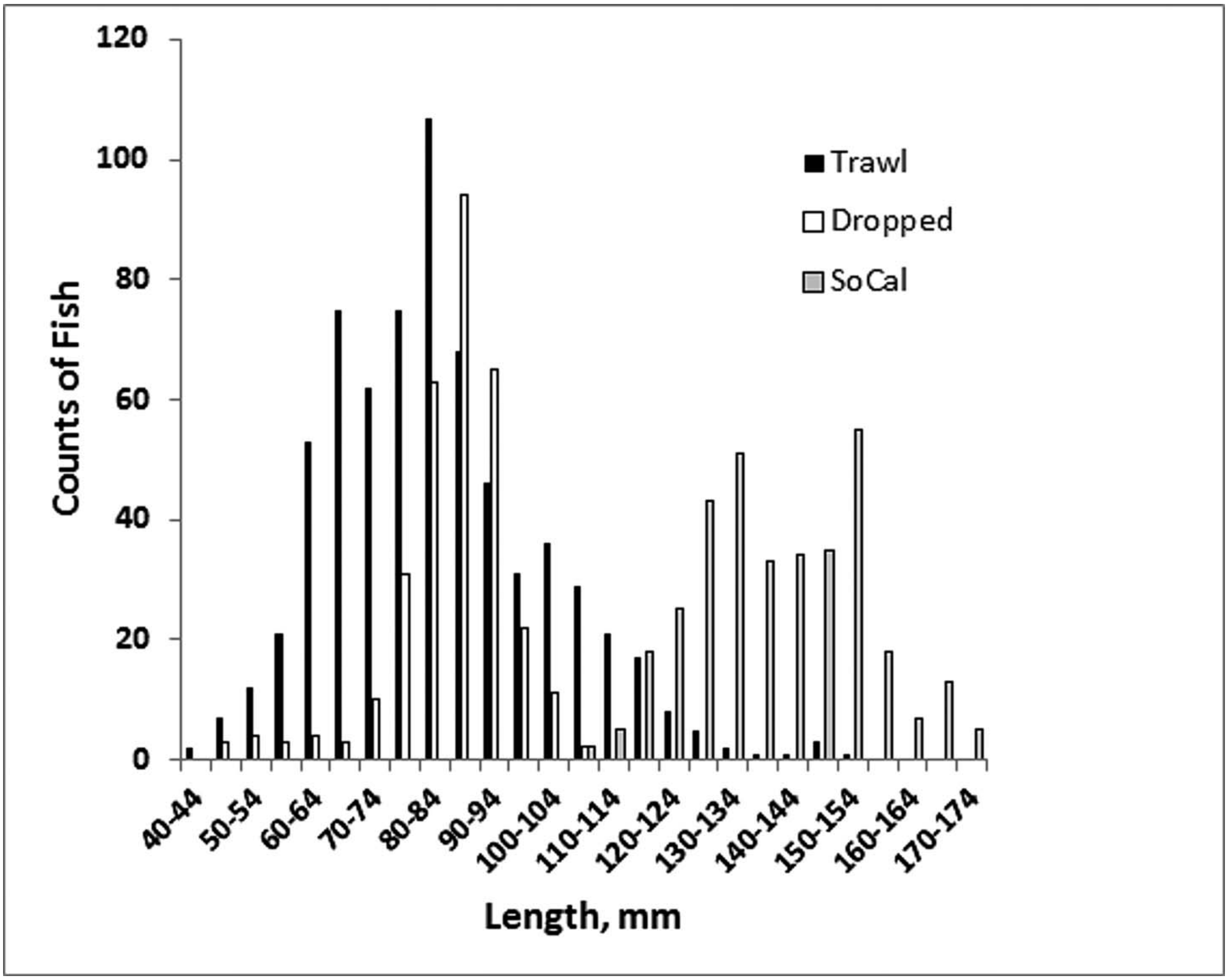


**Fig. 4.** Frequency distribution of sizes (SL) of dropped *L. tenuis* ($n = 308$) from the Alameda Least Tern Colony and trawled *L. tenuis* ($n = 686$) from CDFW surveys. Fish smaller than 40 mm would have passed through the trawls without being caught. For comparison, the size of mature *L. tenuis* ($n = 277$) caught during spawning runs in 2005 and 2006 in southern California are shown.

**Table 1.** Trawl Catches from Monthly Surveys in San Francisco Bay (SFB) Showing Numbers of *L. tenuis* by Month Each Year from 2001 to 2007. No *L. tenuis* was caught before or after these years in SFB.

| Month | 2001 | 2001 | 2003 | 2004 | 2005 | 2006 | 2007 | Total |
|---|---|---|---|---|---|---|---|---|
| January | | | | 10 | | | | 10 |
| February | | | | 6 | 1 | | 1 | 8 |
| March | | | | | 1 | | 2 | 3 |
| April | 5 | | | 43 | 19 | 3 | 14 | 84 |
| May | | 4 | | 5 | 13 | 4 | 13 | 39 |
| June | 1 | | 1 | 4 | 1 | 20 | 6 | 33 |
| July | | | 2 | 12 | | 2 | 6 | 22 |
| August | | 50 | 12 | 15 | 9 | 2 | | 88 |
| September | | | 17 | 30 | 19 | 2 | 4 | 72 |
| October | | | 50 | 16 | 20 | 4 | 11 | 101 |
| November | | | 10 | | 1 | 2 | | 13 |
| December | | 2 | 2 | | 200 | 8 | 1 | 213 |
| Total | 6 | 56 | 94 | 141 | 284 | 47 | 58 | 686 |

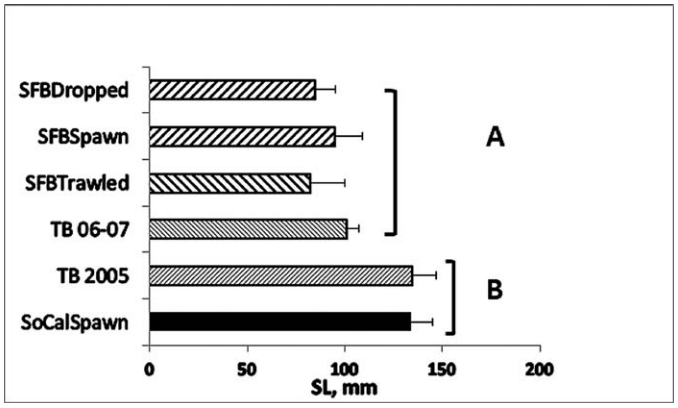


**Fig. 5.** *Leuresthes tenuis* that first appeared in TB in 2005 are not different from *L. tenuis* from southern California (SoCal) in length (mean±SD). The SL of *L. tenuis* from SFB and TB in later years were not significantly different from each other whether collected by trawl, dropped fish, or during spawning runs, but SFB specimens were significantly smaller than *L. tenuis* from southern California. Different letters indicate significant differences.

endemic species (Horn et al., 2006). It was unusual to observe *L. tenuis* spawning north of Pt. Conception before the year 2000 (Phillips, 1943; Spratt, 1981; Straughan, 1982). After that year, *L. tenuis* began spawning in Monterey Bay on an annual basis (Byrne et al., 2013; KLMM and Grunion Greeters, pers. obs.; G. Bernardi, pers. comm.). Although the proportion of shoreline that is sandy beach is similar on the northern coast above Pt. Conception to the shoreline below it (Regional Profiles, Marine Life Protection Act), wave energy is higher and distances between beaches with appropriate habitat conditions for *L. tenuis* may be much greater on the northern coast, possibly reducing connectivity between populations.

Oceanographic events such as the 1997–1998 ENSO event and the 2005 and 2006 late onset of upwelling are occasions when coastal currents in California flow in a poleward direction providing warmer ocean water (Schwing et al., 2000; Bjorkstedt et al., 2012) and enabling southern species to occupy northern climes (Lea and Rosenblatt, 2000). Coastal bays and estuaries may be providing safe haven for *L. tenuis* during intervening colder periods when cold equator-ward currents dominate (Johnson et al., 2009).

No evidence of runs or individuals at any outer coast beaches has ever been found north of Pt. Conception, and

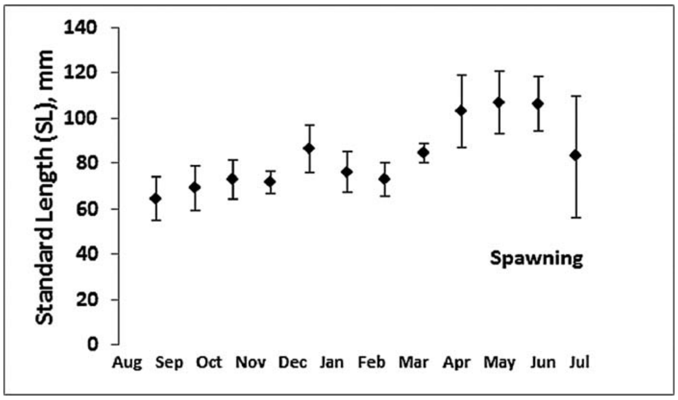


**Fig. 6.** Larger *L. tenuis* were rarely seen outside of the summer spawning season. July shows the greatest variability as young-of-the-year are large enough to appear along with spawning adults. The remainder of the year shows growth of the juveniles to maturity.

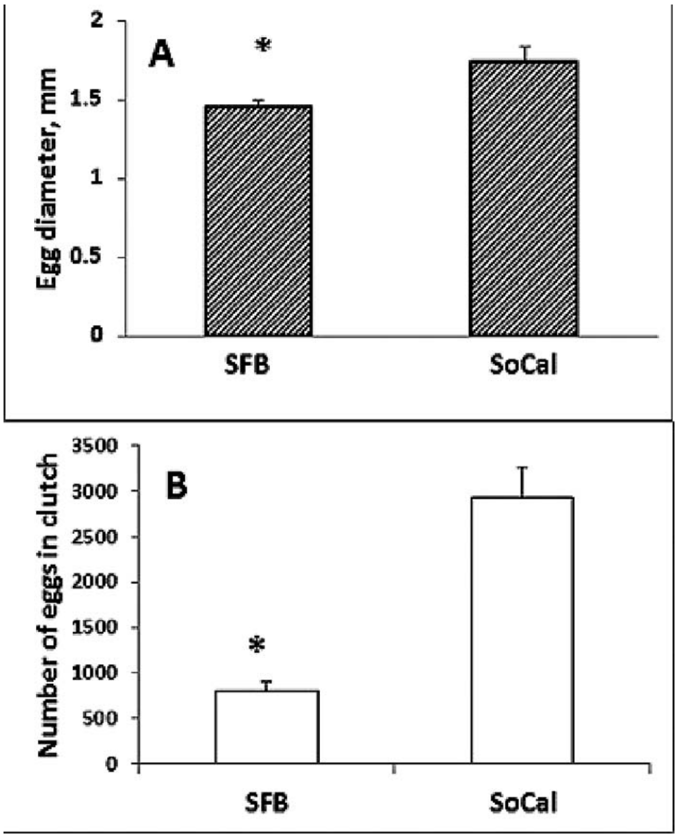


**Fig. 7.** (A) Clutch volumes for *L. tenuis* spawning on beaches in SFB were significantly smaller than clutches from southern California. (B) Egg diameters (mean±SD) of eggs of *L. tenuis* collected. SFB eggs were significantly smaller than those from southern California.

there is no evidence that *L. tenuis* ever migrated out of a northern bay after colonizing it. There are no records or specimens of *L. tenuis* in SFB before 2001 from the California Academy of Sciences collections (Skinner, 1962; CDFW Marine Recreational Fisheries Survey for San Francisco Bay 1980–present); if the type specimen was preserved, it was lost in the 1906 Great Earthquake.

Colonization of northern bays likely took place by adult fish from southern California in 2001 (Fig. 1), as evidenced by their appearance in monthly trawls and among fishes dropped by nesting Least Terns. Later generations apparently replaced the earlier group each year without additional recruits from the south, spawning on multiple beaches within SFB and collected from throughout south and central SFB (Fig. 2).

Spawning runs are highly variable in space and time for *L. tenuis* (Walker, 1949; Spratt, 1986; Gregory, 2001). In southern California, the spawning season for *L. tenuis* begins in March and continues into August or early September following both the new moon and the full moon. Grunion Greeter observations for spawning *L. tenuis* in SFB began in 2005, and ended after 2008 when no fish were seen spawning or in trawls for that entire summer. In SFB, there was no evidence of spawning *L. tenuis* before mid-May or after July each year). The largest runs usually occurred on the second night following the new or full moon.

In the northern bays of SFB and TB, it appears that growth of *L. tenuis* was limited, and adults matured at a significantly smaller size than individuals from more southern waters (Fig. 5). There is little overlap in adult size between the northern and southern populations, which are significantly different in SL. In SFB, the mean SL of spawning adults is smaller than the smallest spawning *L. tenuis* from southern California. Mass differences were also dramatic, with southern fish around 22 g and SF fish on average only 8 g (Johnson et al., 2009).

*Leuresthes tenuis* from 2005, the presumptive initial year of colonization for TB, were significantly larger than adult fish of subsequent years (Fig. 5). *Leuresthes tenuis* mature and can spawn in one year (Walker, 1952). Numbers of *L. tenuis* collected were highest in 2005 and 2006 (Table 1), and spawning runs were large in those years as well (Fig. 3). In southern California the life span is three to four years (Thompson, 1919; Walker, 1952). The small percentage of larger fish in SFB and TB suggests that they grew more slowly during the first year and that very few northern *L. tenuis* survived over winter as adults for a second spawning season (Fig. 5). Alternatively the larger individuals may have left SFB for the open ocean after spawning and not returned, or a handful of new migrants from the south may have appeared occasionally. These data indicate that *L. tenuis* was predominantly an annual fish in northern bays (Fig. 6). As a result, these isolated SFB and TB populations were vulnerable to local extirpation after one bad recruiting year.

The shortened northern California spawning season resulted in fewer seasonal runs and fewer seasonal opportunities for production of clutches. Those clutches that were produced were small in number of offspring (Fig. 7). The tidal synchronization of spawning and hatching for this species means that each pulse of reproduction is discrete, with all in the cohort the same age. Any negative impact on that group would be felt throughout the population.

Monitoring for fishes dropped by California Least Terns, trawl surveys, and nests of *L. tenuis* on the beaches is ongoing through June 2013, but no additional evidence of spawning of *L. tenuis* has been observed in SFB since 2007. Given the multiple lines of evidence, one may conclude that *L. tenuis* arrived in San Francisco Bay in 2001 and produced six generations over the next few years, but were essentially extirpated by mid-2008 (Fig. 1). In Tomales Bay, the trajectory went from arrival in 2005 to extirpation after 2009. Initially colonizing individuals were large, then subsequent generations were smaller in length.

Previous genetic studies indicate little differentiation between widely separated populations of *L. tenuis* (Gaida et al., 2003), and many clutches reveal multiple paternity (Byrne and Avise, 2009). The SFB population was not genetically distinguishable from southern California populations (Johnson et al., 2009). Similarly, the population of *L. tenius* that spawned in Monterey Bay also was not genetically different from populations farther south (Byrne et al., 2013). When reared in a common garden at three different temperatures, young *L. tenuis* from three different latitudes grew at the same rate (Brown et al., 2013). This contrasts with spatial adaptation in other estuarine silversides that compensate in northern latitudes with increased growth rates (Conover and Present, 1990; Baumann and Conover, 2011), suggesting that *L. tenuis* is not adapted to the cooler temperatures found outside of its typical southern California habitat.

The smaller size of adult fish in SFB contributed to the smaller egg diameters (Martin et al., 2009), reduced clutch volumes, and decreased number of eggs in northern *L. tenuis* as compared with southern California populations (Fig. 7). Along with the shorter spawning season and reduced life span, this decreased reproductive output made successful colonization in the northern habitat more difficult. Although egg size in *L. tenuis* is variable to some degree between females (Martin and Carter, 2013), the significantly smaller egg diameter in the northern populations provided less energy for embryo survival by extending incubation in this species with environmentally cued hatching (Moffatt and Thomson, 1978; Martin, 1999; Moravek and Martin, 2011; Martin et al., 2011).

An alternative to the hypothesis that *L. tenuis* were behaving as annual fish in SFB is that perhaps adult *L. tenuis* left the northern bays in fall after spawning and only the young-of-the-year remained within. Later the next spring, adults could re-enter the bays, causing the mean sizes of specimens to increase. This scenario seems unlikely because sea temperatures on the outer coast in winter and spring are inhospitable to survival for this warm water species, and because members of this species have been observed in the waters or on beaches of the outer coast only once before, after the spawning runs occurred within SFB during the initial colonization year of 2001 (Jeffrey Harding, NOAA Fisheries, pers. comm.). In addition, during the spawning season there was not a sudden appearance of larger fish (Fig. 5); instead, there was a monthly progression of size from smaller to larger, indicating growth of the young-of-the-year cohort (recognizing that the net mesh size prevents the smallest fish from being captured).

Between Pt. Conception and Monterey Bay, well south of SFB, adult *L. tenuis* have been observed sporadically but repeatedly (Phillips, 1943; Walker, 1952; Spratt, 1981; Straughan, 1982; Yoklavich et al., 2002). Remains from adult *L. tenuis* have been found in Native American middens on the Central California coast between Morro Bay and Estero Bay (Gobalet and Jones, 1995), indicating they were present at least occasionally during prehistoric times between 8200 BC and AD 1830. The type specimen, a lone individual probably caught schooling with other atherinids, fits the southern ecotype at 132 mm SL (calculated from Ayres, 1860). The single trawled specimen from 2010 was 118 mm. Both are more similar in size to the southern California and presumptive initial SFB and TB colonists, unlike the smaller *L. tenuis* that began life in SFB during this study. Thus it seems likely that adult *L. tenuis* are able to move north of Pt. Conception whenever oceanographic conditions are favorable, but to date, these events have resulted in sinks that have failed to establish permanent, self-supporting local populations.

The low temperatures and variable salinities in SFB may have posed increased physiological costs on developing *L. tenuis*. (Reynolds et al., 1976; Ehrlich and Muszynski, 1982). Temperature affects the number of vertebrae and myomeres in this species (Ehrlich and Farris, 1970, 1972), as in the Atlantic silverside *Menidia menidia* (Baumann et al., 2012). Higher temperatures and increased lipids in food allow Atlantic salmon to mature at a smaller size (Jonsson et al., 2012), but the *L. tenuis* in SFB grew at lower temperatures with likely a poorer diet than *L. tenuis* in southern California. Temperature and latitude also affect sex determination in *M. menidia* (Baumann et al., 2012), but this has not been examined for *L. tenuis* to date. These effects may have led to the profound plastic differences in size at maturity, resulting in a local ecotype that was not genetically distinct (Johnson et al., 2009).

Colonization of new habitats as climate shifts may be difficult for marine species, more than simply a matter of shifting the habitat range at both ends. For the endemic species *L. tenuis* in particular, critical habitat for spawning includes sandy beaches and relatively temperate conditions year round. This need for consistent temperatures and a particular spawning habitat may force this species into estuaries that are far more variable in salinity, temperature, and food availability than the open ocean (Cloern, 1991; Kimmerer, 2004; Cloern et al., 2007). Although atherinopsids evolved in estuarine habitats (Bamber and Henderson, 1988), extremely low or high salinity reduces hatching success and increases mortality in embryos of *L. tenuis* (Matsumoto and Martin, 2008), and impedes larval growth (Reynolds et al., 1976).

Enclosed, relatively shallow bays also may increase the risk of anthropogenic toxicity and decrease refuge space for avoiding natural predators. Within San Francisco Bay, anthropogenic chemicals were present at some of the beaches at times when spawning of *L. tenuis* occurred. In Alameda, Seaplane Harbor was a toxic waste dump, and a strong hydrocarbon odor was evident when beach sand was sampled for clutches. In San Leandro, aerial and shoreline spraying of the herbicide Imazapyr (BASF) that was applied for removal of *Spartina*, occurred directly over active nesting areas of *L. tenuis* during the spawning season in July of 2006, 2007, and 2008. All life stages of *L. tenuis* are sensitive to hydrocarbons, and the larvae have been used in toxicity tests for pesticides and fuel spills (Valentine and Soulé, 1973; Winkler et al., 1983; Hose and Puffer, 1984; Borthwick et al., 1985; Newton et al., 1985; Gellert et al., 1994; McCoy, 1998).

In November 2007, a fuel oil spill occurred near the San Francisco-Oakland Bay Bridge from the cargo vessel *Cosco Busan*. The oil spread over many of the areas where large spawning runs had been seen and live *L. tenuis* had previously been collected by trawls. The actions of these chemicals on the population may have interacted with other environmental factors to increase stress on this population. No *L. tenuis* was recovered by trawl or any other method in SFB following the spill. Pacific Herring *Clupea pallasii*, another small planktivorous teleost, had its reproductive efforts greatly affected by the *Cosco Busan* spill (Incardona et al., 2011), with extremely low survival of embryos in 2008 from oiled areas within SFB. Because of poor tolerance of low temperatures, any *L. tenuis* that left SFB during winter to escape local conditions and the oil spill was unlikely to survive.

Exploiting the short-term availability of favorable conditions in new northern habitats exposed *L. tenuis* to new combinations of risks that ultimately prohibited long-term colonization. The changes in habitat in these new settings apparently altered phenotypes including body size, reproductive output, and life span of these fish, making them more vulnerable to environmental threats and local events. The effects of climate change may be more acute for marine animals that reproduce in the intertidal zone or on beaches (Martin et al., 2004; Martin and Carter, 2013), as the vulnerable embryos of these species must contend with warmer temperatures of the air during tidal exposure, as well as changes in the surface waters of the ocean (Martin and Strathmann, 1999). The congener of *L. tenuis*, the Gulf Grunion *L. sardina*, will face a more extreme loss of habitat if oceans warm, as its habitat range is the northern region of the Gulf of California, and northerly expansion is not possible, while escape to the south seems unlikely even in today's conditions (Bernardi et al., 2003).

Newly colonized habitats may act as population sinks (Pulliam, 1988; Gaggioti, 1996) and require repeated colonization events from a distant source before successful, permanent establishment can occur. The rapid demise seen in both of these two disjunct populations indicates that a shift in habitat may require complex responses from each species that may have unpredictable effects on life history, growth and reproduction, and ultimately, species survival.

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