




Contribution to the Themed Section: ‘Marine recreational fisheries – current state and future opportunities’

Original Article

Population trends of beach-spawning California grunion *Leuresthes tenuis* monitored by citizen scientists

Karen L. M. Martin ^{1*}, Emily A. Pierce², Vincent V. Quach¹, and Melissa Studer³

¹Department of Biology, Pepperdine University, 24255 Pacific Coast Highway, Malibu, CA 90263-4321, USA

²Moss Landing Marine Laboratories, Moss Landing, CA 95039, USA

³Beach Ecology Coalition, Grunion Greeters, La Jolla, CA 92037, USA

*Corresponding author: tel: 310-506-4808; e-mail: Karen.Martin@pepperdine.edu.

Martin, K. L. M., Pierce, E. A., Quach, V. V., and Studer, M. Population trends of beach-spawning California grunion *Leuresthes tenuis* monitored by citizen scientists. – ICES Journal of Marine Science, 77: 2226–2233.

Received 31 January 2019; revised 7 April 2019; accepted 13 April 2019; advance access publication 23 May 2019.

California Grunion *Leuresthes tenuis* (Atherinopsidae), an indigenous endemic marine fish, makes spectacular midnight spawning runs onto sandy beaches on the Pacific coast of California and Baja California. In a unique recreational fishery, people capture the fish out of water with bare hands. Grunion hunters are not required to report their catch, and there is no bag limit. California Grunion rarely appear in trawls and do not take a hook, so population status for this species is impossible to obtain by traditional fishery methods. With citizen scientists, the “Grunion Greeters,” we monitored spawning runs along most of their habitat range. California Grunion recently underwent a northward range extension, but runs appear to be declining broadly across the core habitat. Noisy activities of recreational grunion hunters on shore disrupt spawning runs, preventing fish from reproducing before capture. *Leuresthes tenuis* has been identified as a Key Indicator Species for the South and Central regions of California Marine Protected Areas, and as an indicator species for climate change on beaches. Gear restrictions, license requirements, and a two-month closed season are rarely enforced late at night. We recommend continued monitoring for *L. tenuis* in California and increased protections for this unique charismatic fish.

Keywords: beach-spawning, citizen science, closed season, endemic species, Atherinopsidae, fishing gear, poaching, recreational fishery, reproduction, spawning run, spawning aggregations.

Introduction

California Grunion *Leuresthes tenuis* (Atherinopsidae) is an indigenous endemic marine fish on the Pacific coast of California. Famous for forming large assemblages that lead to massive runs, individual fish emerge fully out of waves onto beach sand to spawn (Martin, 2015). Runs may last for over an hour following full or new moons in spring and summer, and fish may cover the beach along the water line (see [Supplementary Material](#)). In the traditional habitat range of southern California, between Pt. Conception, California and Punto Abreojos, Mexico, spawning season starts in March and may extend into August, peaking between April and June (Clark, 1938; Walker, 1952).

Females dig into the soft wet sand to deposit 1500–3000 eggs while surrounded by males providing milt for external fertilization. Males do not dig into the sand, and may outnumber females by 10 to 1 during the run. Multiple paternity of clutches is typical (Byrne and Avise, 2009), and each male may repeatedly return to shore during a single night’s run (Walker, 1949), providing milt for multiple females with a muscular genital papilla (Aryafar et al., 2019). Thus, multiple waves may carry hundreds of the same individuals over and over again. Females spawn once during a series but can spawn multiple times across the season (Clark, 1925; Walker, 1949). The number of fish on shore cannot be easily counted during a large run, but the density, duration, and

extent of the fish are far greater during some runs than others (Walker, 1949; Martin *et al.*, 2007).

Leuresthes tenuis is targeted by a unique recreational fishery, solely during these spawning runs (Spratt, 1986; Sandrozinski, 2013). Because of their unusual life cycle, California Grunion are particularly vulnerable to overharvest. Less than 10 years after the first published scientific description of their spawning behaviour (Barnhart, 1918; Thompson, 1919), the first regulations to protect them were enacted in 1927 (Clark, 1926, 1938) by the California Department of Fish and Game (now Wildlife), CDFW. At that time, people would line the shore and capture hundreds of grunion with improvised nets made of bed sheets (Andrew Olson, pers. comm.). Early protections included a closure with no take from April to June, the peak of the spawning season, and gear restrictions that specify no gear at all. Only bare hands were (and are) allowed for capturing the fish, presumably to give them a sporting chance while on shore. Those under the age of 16 did not (and still do not) need a fishing license to catch grunion during the open season.

Walker (1949) observed grunion runs on Scripps Beach directly following World War II. On the basis of his recommendations, CDFW reduced the closed season to just April and May. Gear restrictions and license requirements remain in place. At that time California's population was substantially smaller, around 10 million, than it is today, with >35 million people living along one of the most extensively populated and urbanized coasts in the world.

During open season there is no bag limit and no requirement to report catch of this species. No commercial use of the species is permitted. Some anglers catch this species for bait, some people catch these small fish to consume whole, but most of those capturing the grunion report they are doing so for the sport, not for any particular use but because it is part of popular culture.

In reality, regulations are rarely enforced, in part because spawning runs always occur in the dark of night. Although this endemic species enjoys some unique protections, regulations have not been changed since 1949.

California Grunion runs are highlighted in public education programs of coastal public aquariums and California State Beaches, and for youth organizations such as the Boy Scouts. Because runs follow the highest spring tides of full or new moons, likely nights and times can be predicted with some success (Walker, 1952; Spratt, 1986). Especially during closed season, observation of runs can be dazzling, with thousands of fish moving out onto shore from waves for an hour or more. Runs may occur when tides are suitable, within a 2-h window following the highest nightly tide in four nights after full and new moons in spring and summer. However, often on nights when runs are forecast, no grunion are seen on shore.

Sandy beaches are critical to *L. tenuis* as essential fish habitat for spawning (Robbins, 2006). However, beaches in California and worldwide are undergoing habitat loss by coastal squeeze (Defeo *et al.*, 2009; Schoeman *et al.*, 2014; Martin, 2015), with sea level rise and erosion encroaching on the beach from the seaward side, and coastal development and shoreline armouring preventing natural retreat of the beach on the landward side (Dugan *et al.*, 2008). Exacerbated by climate change and increasing human population, California is predicted to lose 31–67% of its sandy beaches by the year 2100 under current predictions of sea level rise (Vitousek *et al.*, 2017).

Because of its beach-spawning habits, *L. tenuis* has been identified as a Key Indicator Species for the South and Central regions

of California Marine Protected Area (Marine Protected Area Monitoring Action Plan, 2018), and as an indicator species for climate change on beaches in the Ventura County Coastal Resilience Plan (<https://www.vcrma.org/vc-resilient-coastal-adaptation-project>). However, monitoring for *L. tenuis* is problematic. This species has never been abundant (Gregory, 2001). *Leuresthes tenuis* is planktivorous (Higgins and Horn, 2014); this species does not take a hook. Adults are rarely caught in trawl surveys except within enclosed bays (Allen *et al.*, 2002; Martin *et al.*, 2013; Williams *et al.*, 2016). Recreational fishers are not required to report catch of this species. Thus, traditional fishery methods cannot be used for stock assessments. The only time *L. tenuis* adults can reliably be observed is during their spawning runs.

We developed a group of volunteer citizen scientists, the Grunion Greeters, to report observations of spawning runs on suitable nights all along the California Coast. This started as a way of addressing management issues on sandy beaches, particularly the ecological effects of raking or grooming of beach sand for aesthetic purposes (Martin *et al.*, 2006; Defeo *et al.*, 2009; Dugan and Hubbard, 2010). On the basis of observations and reports across the habitat range over two decades (Martin *et al.*, 2007, 2011), we have become concerned about the status of the California Grunion population as a whole. We hypothesized that this long-term dataset from Grunion Greeter observations would enable us to discern broad trends in population size of this species along its habitat range, in order to guide conservation of this endemic species.

Methods

Metric for spawning run assessment

Strength, duration, and extent of the spawning runs are assessed by a species-specific metric, the Walker Scale, developed in 1999 by the first author with Mike Schaadt and Suzanne Lawrenz-Miller of Cabrillo Marine Aquarium in San Pedro, CA (Table 1). Initially used to compare runs in Malibu with runs in San Pedro, this method was adopted for volunteers in the Grunion Greeter program starting in 2002 (Martin *et al.*, 2007, 2011). The metric was named after Boyd Walker, in honour of his research on the timing of grunion spawning runs, mainly at Scripps Beach in La Jolla, CA. Walker also relied on volunteer observers to assess runs on two nights in 1947 from multiple different beach locations (Walker, 1949), although they used a different metric than ours.

Grunion Greeters were trained in a series of short workshops from 2002 to 2018 to understand the Walker Scale categories and assess the number of fish on shore at the peak of the run, the duration of the peak of the run, and the extent of shoreline involved in the peak of the run. Greeters make other observations about the conditions during a night when a grunion run is forecast, including weather and presence of animal predators or grunion hunters. Observers use an online web portal to input their data, usually within 24 h. The data portal is open to the public, and the questionnaire includes an assessment of the experience of the observer and whether or not they attended previous training workshops. See www.Grunion.org for additional details. Grunion Greeter data focus on closed season, April and May, but also includes reports from open season before and after. Because the Greeters are volunteers, the locations and number of reports are not constant from year to year, however some beaches are more consistently observed, and may be considered sentinel beaches.

Table 1. The Walker Scale for assessment of grunion runs.

Scale	Number of Grunion on shore at the peak of the run	Duration of peak	Descriptor
W0	No fish or only a few, little or no spawning	Up to an hour	Not a run
W1	Up to 100 fish scattered over a wide area of the beach at a time, some spawning	Up to an hour	Light run
W2	100–500 fish spawning over time, many fish ashore with many of the waves	Up to an hour	Good run
W3	Hundreds of fish spawning at once on several areas of the beach, or thousands in one area	Up to an hour or more	Strong run
W4	Thousands of fish together over a broad area, little sand visible between fish at peak of run	Peak lasts minutes up to an hour	Excellent run
W5	Fish covering the beach several individuals deep, a silver lining of the surf over an extensive area, impossible to walk through run without stepping on fish	Peak spawning continues longer than 1 h	Incredible run

Boyd Walker's pioneering research on grunion provided the scientific basis for understanding the periodicity of the spawning runs in California. The Walker Scale, developed by K. Martin, M. Schadt, and S. Lawrenz-Miller, is a way to assess the spawning run without actually counting the fish, for comparisons across space and time. Observations should start at or before the time of the highest tides on the four nights following a new or full moon, and continue for 2 h as the tide falls. The number of grunion should be assessed at the peak of the run; most runs start small but some may build up over time. At the peak of the run, how many fish are on shore at any given time? Are they on shore over a short or long period of time? Over a small area or a large extent of the beach? How long does the peak spawning aggregation last? (c) Grunion Greeters and Beach Ecology Coalition, used by permission.

Quality control for Grunion Greeter data

All data were evaluated by scientists before use in analysis. Incomplete forms or forms with no identification from the observer were discarded. Forms from dates or times that were unlikely for grunion to run, or from unclear locations were discarded. Grunion Greeters generally work in pairs to provide internal validation. If multiple observer groups on the same run gave different scores, more credence was given to a more experienced, trained observer. Multiple observers on the same run may have different scores because they observed from different locations on the shore; this was evaluated in the reports. Unusual or atypical reports for a location or time are followed up with an e-mail or phone call for additional details. Reports were verified on subsequent days by sampling for presence and density of clutches of eggs in the sand in some but not all cases.

For the purposes of this study and to avoid bias for data from certain beaches that have more frequent observations, we selected for each beach, only the highest Walker score reported from each spawning series (the four-day period following a new or full moon), from our verified data. Thus, a spawning series with few grunion on the first two nights after a full moon but a large run on the third would be represented only by the highest Walker score for that series.

Data were compared by beach location, county, and year using non-parametric statistics. Data from within the primary habitat of southern California, containing over 90% of the species population (Martin et al., 2013; Martin, 2015), were analysed separately from much sparser data for the central coast that followed a northward range extension in 2002 (Roberts et al., 2007; Johnson et al., 2009).

Results

Since 2002, over 4500 Grunion Greeters have provided over 5000 reports. This Grunion Greeter compilation is the most complete dataset for spawning runs of this species in existence, both in terms of geographic coverage and duration of observations. Reports have come from the entire range of the species, over 50 beaches in California and Baja California, Mexico. A northern range extension for spawning runs was discovered in 2002 in San Francisco Bay (Johnson et al., 2009), followed by a northward range extension to Tomales Bay in 2005 (Roberts et al., 2007). Many Grunion Greeters provided multiple observations over

several years. Verified data from professional biologists using our methods to observe California Grunion as part of their monitoring efforts for coastal construction projects are also included.

Grunion Greeters reliably report the location of a run and its strength, based on both multiple independent observations of the same run, and on sporadic post-run sampling of beaches for clutches. In 445 runs with multiple observers, there is 87.6% agreement on the ranking of the Walker Scale. Even with disagreement, scores rarely differ more than one rank between observers.

The core of the habitat range is from the border of California and Mexico in San Diego County through Orange County and Los Angeles County through Malibu. From 2002 to 2010, typically the median run strength in this core area was W2, with a small percentage of the runs at W4 or W5 level (Figure 1). Large spawning runs (W4 and W5) have been seen in every year, on occasion. On a year with a low median, the number of large runs is very low as well. Although large runs still occurred in 2018, in 6 of the past 8 years, 75% of the runs have been W2 or lower in the core habitat for this endemic species.

Examining by county, runs in Los Angeles County, Orange County, and San Diego County have decreased in Walker Score over the time of the study (Figure 2). The five years 2004–2008 compared with the five years 2014–2018 show a significant decrease in the Walker Score of runs in the core habitat over time. This decline is consistent whether testing the three core counties together (Figure 1), looking within individual counties in southern California (Figure 2), or comparing across time within individual sentinel beaches (Figure 3). For the three core counties, significant differences are seen in frequencies of large and small runs between decades ($N=1952$, $X^2=18.42$, $df=5$, $p<0.01$). By county, these differences are also significant. For San Diego County, $N=742$, $X^2=11.81$, $df=5$, $p<0.037$; for Orange County, $N=500$, $X^2=78.12$, $df=5$, $p<0.0001$; and for Los Angeles County $N=465$, $X^2=18.5$, $df=5$, $p<0.01$).

Runs are highly variable in space and time. Although on a given night one beach may hold a large run, other beaches on the same night or run series may show little activity (Figure 4). The proportion of runs that are small (W0 or W1) has significantly increased over the past 15 years (Spearman Rank Correlation Coefficient $r_s=0.57$, $df=13$, $p=0.025$). For the three counties of San Diego, Orange, and Los Angeles, small runs were 48.9% of reports from five years between 2004 and 2008, and increased to

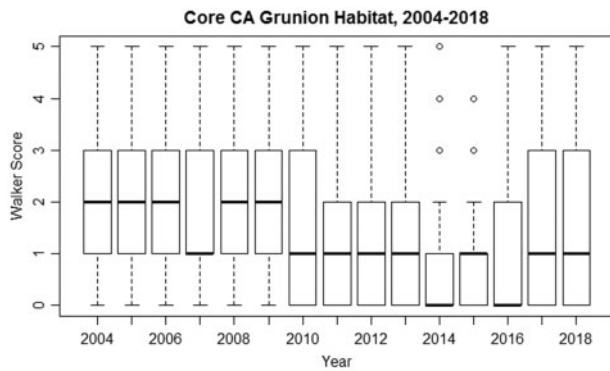


Figure 1. When the Grunion Greeters started, median (heavy bars) run size was a moderate but effective W2 in the core species habitat of southern California. Since 2010, the median of runs reported has been no higher than W1, meaning that at least 50% of the runs observed do not hold significant spawning activity. In two years (2014 and 2016) the median was W0, meaning that >50% of the time runs were predicted, few or no spawning fish were present. From 2011 to 2018, the median across the traditional habitat range typically was W1 and twice was W0. $N = 3462$.

65.4% of reports in the 5 years from 2014 to 2018. The proportion of runs at the W5 level has remained low and fairly consistent over the years, $1.58 \pm 0.76\%$ of reports in a given year.

Runs north of the core habitat seem to be increasing according to our reports, although not yet significantly (Figure 5). The areas of northward range extension around San Francisco Bay underwent local extirpation in 2008 (Martin et al., 2013) but have been re-colonized in 2014. Runs in locations in and around San Francisco Bay start later, in May rather than March, and continue into August, with the largest runs usually in July and August.

Grunion Greeters reported poaching (catching out of season, without a license, or with the use of any gear) in ~20% of reports during closed season, and hunting or poaching for 93% of reports during open season. California fishers are not required to display a license while fishing. Informal questioning indicated that many adults hunting grunion during runs did not purchase a fishing license. Game Wardens were rarely observed during runs, <5 instances out of 5133 reports. Active hunting was often accompanied by loud, raucous crowds and high disturbance and prevention of spawning (Table 2).

Clutches of eggs are buried 10–20 cm deep in beach sand in a band no >1–3 m wide parallel to shore on the upper beach in the mid to high intertidal zone. Considering a narrow strip on average ~3 m wide along 483 km of sandy beaches in southern California results in a total spawning habitat area of 1.45 km² for *L. tenuis* in its core primary habitat at the current time.

Discussion

California Grunion spawning runs can be assessed with the help of citizen scientists; in fact this may be the only way to obtain these extensive, hyperlocal data. The Walker Scale is currently used by professional resource biologists to monitor grunion runs for agencies such as US Army Corps of Engineers, California Department of Fish and Wildlife, California Coastal Commission, National Marine Fisheries Service, and California State Parks, as well as for public educational programs at Cabrillo Aquarium and Birch Aquarium at Scripps, among others (Martin et al., 2011). The Walker Scale is an effective, accurate, non-invasive

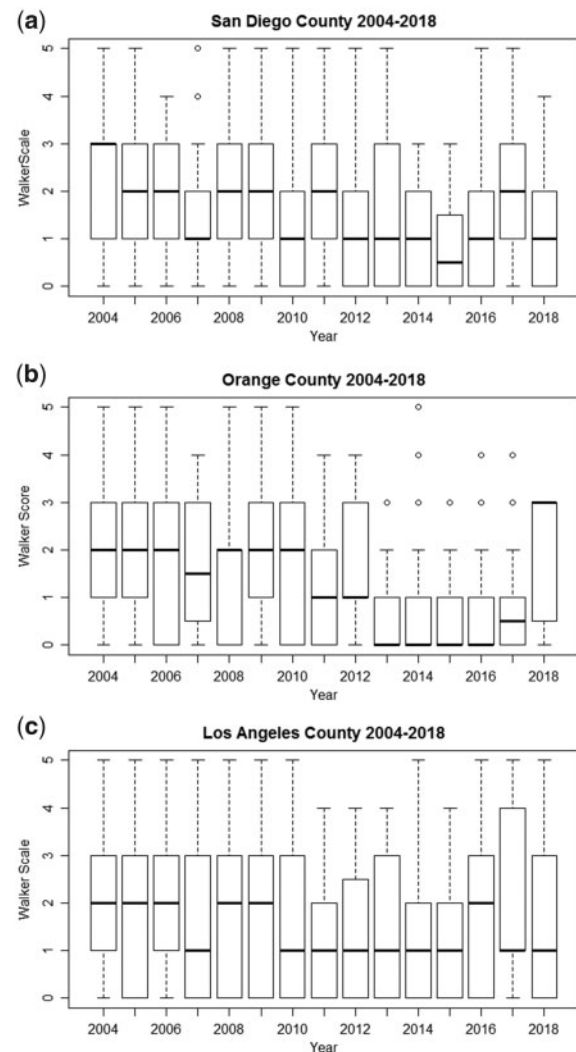


Figure 2. Reports from Grunion Greeters indicate that median (heavy bars) run size based on the Walker Scale have significantly decreased over time for each of the three southern counties. (a) San Diego, (b) Orange, and (c) Los Angeles.

although labour-intensive method for assessment of this species and other beach-spawning fishes. While the data from professional biologists monitoring grunion runs for coastal projects are certainly reliable, the number, locations, and frequency of these short-term projects are small relative to the substantial, long-term efforts of volunteer Grunion Greeters.

Even though large runs can still be observed, the median Walker Score for California Grunion spawning on shore has declined significantly across much of the core habitat range in the past ten years (Figure 1). This pattern is consistent for this endemic fish across the three coastal counties constituting its core habitat (Figure 2) and within individual beaches known historically for large spawning runs of grunion (Figure 3). The occasional presence of large spawning aggregations may create the illusion of abundance even when a population is depleted (Erisman et al., 2011). These occasional large runs may tempt resource managers to believe that these kinds of runs are both more common and more widespread geographically than is the actual situation (Figure 4, Sadovy and Domeier, 2005).

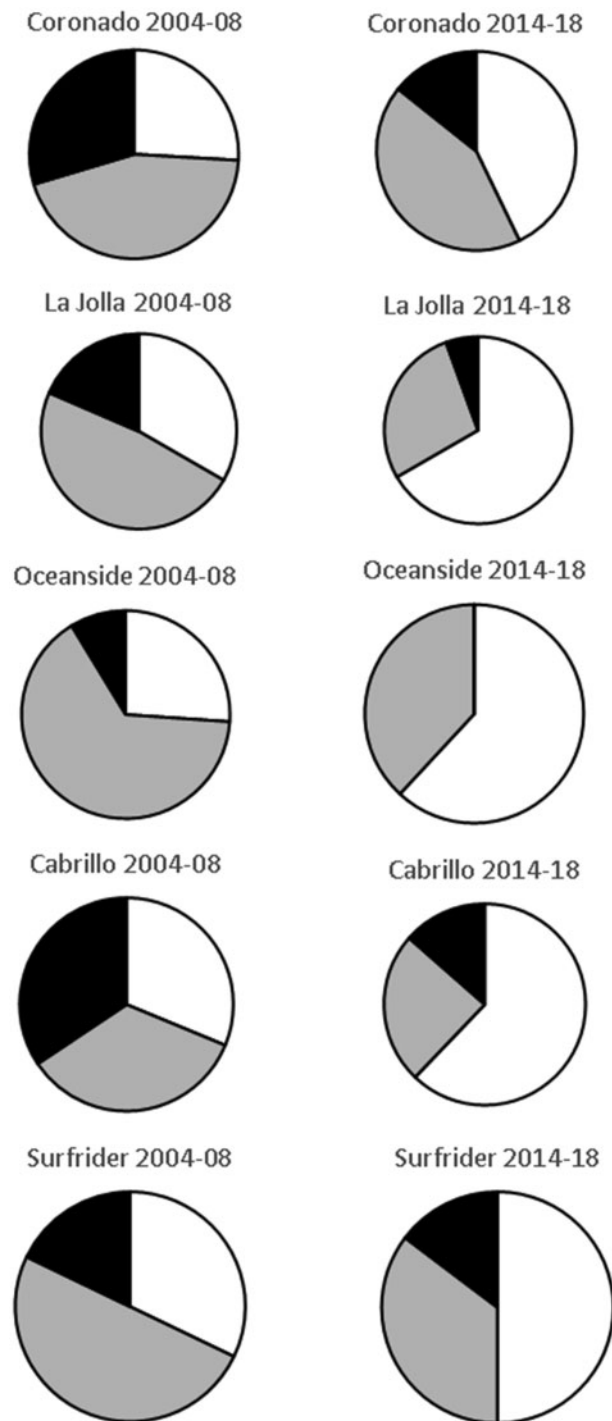


Figure 3. Proportions of runs that are small (W0 or W1), medium (W2 or W3), and large (W4 or W5) in five sentinel beaches in the core habitat range of southern California. Median runs dropped over the past decade and the likelihood of large runs decreased significantly in all cases.

On the basis of reports from Grunion Greeters and resource biologists, California Grunion appear to be both shifting their habitat range northward (Figure 5) and decreasing in numbers in the more southern habitats (Figures 1 and 2). Warming trends in ocean water and the atmosphere may be affecting this species

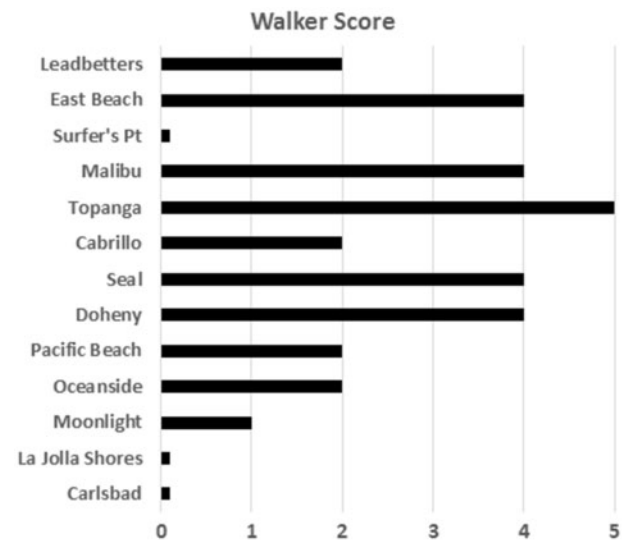


Figure 4. For one April night, beaches from San Diego, Orange, Los Angeles, Ventura, and Santa Barbara counties show the variability in run strength. The median run score is W2 for these 12 beaches.

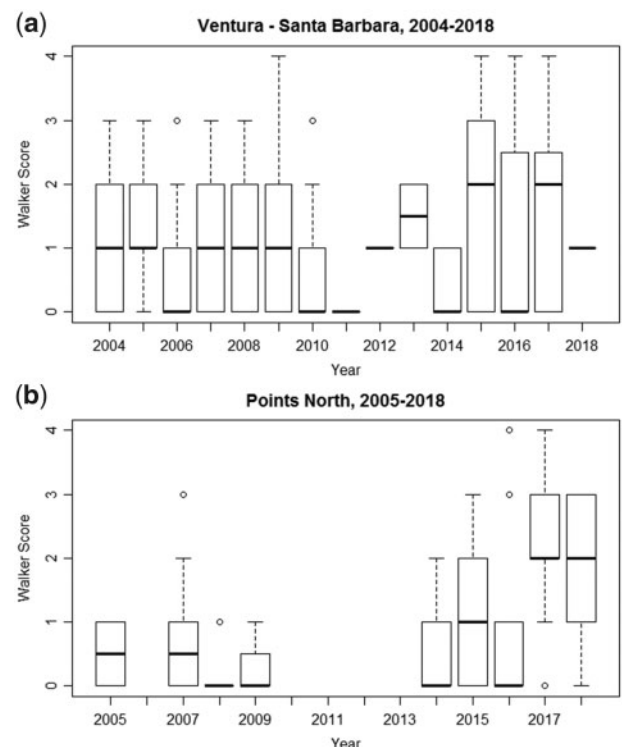


Figure 5. Runs appear to be increasing north of the core habitat range, but these differences are not significant. (a) Ventura and Santa Barbara Counties are north of the core habitat but within the traditional spawning range of *L. tenuis*. (b) *L. tenuis* colonized San Francisco Bay and points north in 2002, and then was locally extirpated by 2008. They returned in 2014 and runs are increasing in strength. Heavy line is median.

(Martin, 2015), along with ocean acidification (Tasoff and Johnson, 2019). There is an environmental component to sex determination of *L. tenuis*, so that warmer temperatures during

Table 2. Grunion Greeter reports indicate high levels of disturbance of spawning by people hunting.

<p>"Unruly THOUSANDS, some in water, all making noise. Looked like some sort of post-apocalyptic marine Mad Max."</p> <p>"The few grunion that actually came up onto the beach were automatically grabbed by poachers. There were probably 20–30 people taking the fish last night."</p> <p>"Hundreds of people on beach, many using buckets and strainers to collect fish; informed them of regulations." (report from a marine biologist with California Department of Fish and Wildlife).</p> <p>"A large group of people gathered at least 10 plastic grocery bags full of grunion and women were walking behind them laughing and kicking the grunion. Many people were taking several hundred grunion home in trash bags."</p> <p>"Over a hundred people in a frenzy to get the few fish that came in with each wave. Lots of screaming kids, dogs, and flashlights."</p> <p>"Three families harvested hundreds."</p> <p>"One goofy guy was running wildly up and down the beach with a flashlight and grabbing at any fish that started to spawn."</p> <p>"Hunting–Splashing into water, capturing in water or at surf's edge, noisy, yelling, screaming."</p> <p>"Lots of youngsters excited and splashing in the shallows chasing grunion. Probably they harvested 200 or 300. There were maybe 50+ in groups of 4–10 running to and fro."</p> <p>"There was a very rowdy group of ~10 people, catching and collecting the grunion during the entire run, yelling and chasing after the fish into the water, up to even waist deep!"</p> <p>"Bad behavior: Kicking fish, throwing, stepping, or jumping on them."</p> <p>"TONS of people. At the first big sighting of fish the people rushed the water & the grunion fled."</p> <p>"There was a pack of ~12–14 non-English speaking people stomping on and kicking fish on the beach. One run of grunion had started and when these people behaved in this way that run went back into the water and did not return to that location."</p> <p>"Poachers continuously ignored our information very frustrating. Picking them up filling buckets and stepping on them and ripping them in half."</p> <p>"Fish tried to come ashore but a crazy mob of people lined beach with buckets & lights."</p>
--

early life result in greater proportions of males (Brown *et al.*, 2014). Of more immediate concern, their critical spawning habitat is also declining (Dugan *et al.*, 2008; Vitousek *et al.*, 2017; King *et al.*, 2018), potentially concentrating the spawning population into fewer locations on shore. The spawning zone of *L. tenuis*, the upper beach between the mid and high intertidal zone (Martin *et al.*, 2006), is also the beach area that is most vulnerable to loss by coastal squeeze (Dugan and Hubbard, 2010; Schooler *et al.*, 2017). The core spawning habitat total area of 1.45 km² for *L. tenuis* is smaller than Dodger Stadium or the Los Angeles International Airport. The minimum size is 25 km² for one Marine Protected Area (MPA) in California (Botsford *et al.*, 2014), in a network of over 100 MPAs. This critical habitat for *L. tenuis* is likely to decrease, and is already <0.001% of the area of the California MPA network.

Even though the species has managed to shift its habitat and colonize some northern bays, the northern ecotype grows to a smaller adult size, spawns less frequently, and produces significantly fewer, smaller eggs per clutch (Johnson *et al.*, 2009; Martin *et al.*, 2013). For these reasons the northern populations are more vulnerable to ecosystem perturbations and local extirpation than the populations in the traditional habitat. In addition, the more northern populations spawn on a different annual schedule than the southern populations of this species, and therefore the peak run times of the northern populations are not protected by the current closed season of April and May. These northern fish are neither different genetically (Johnson *et al.*, 2009; Byrne *et al.*, 2013) nor are they different in physiological response to temperature (Brown *et al.*, 2012) from the southern grunion, so this habitat shift appears to be restricted to areas of bays that are warmer than the waters of the open ocean.

Fished species that form spawning aggregations face an increased extinction risk (Sadovy and Erisman, 2012). Modern conservation practices almost universally protect the reproductive period and spawning aggregations of species (Hutchings, 2001). The regulations for fishing on California Grunion do the opposite by specifically targeting the spawning aggregations, striking this

species at its most vulnerable and critical time, disrupting its ability to produce the next generations. Fishing on large aggregations can mask population declines or collapse (Erisman *et al.*, 2011).

Regulations put in place to protect the endemic California Grunion during spawning runs are rarely and unevenly enforced. Poaching during closed season is common on some urban beaches, and reported during ~20% of closed season observations. Collection of spawning fish by people with or without fishing licenses is nearly universal during open season, identified in the vast majority of open season reports, disrupting runs, and preventing reproduction while removing ripe adults from the population (Table 2). Many grunion hunters do not fish for any other species, and do not possess fishing licenses. Children, not required to have a license, are very effective hunters (see Supplementary Material). Thus the potential number of people hunting California Grunion is far greater than the 2.5 million sport fishing licenses that were sold in California in 2016 (<https://www.wildlife.ca.gov/Licensing/Statistics#SportFishingLicenses>).

Data from entrainment surveys are the only other long term dataset available for *L. tenuis*. The entrainment data conforms with CalCOFI nearshore trawl data pattern (Miller and McGowan, 2013). For California Grunion, usually less than one, or fewer than two individuals are seen per million cubic meter flow (E. Miller, pers. comm.). Compared with other local silverside fishes, for Topsmelt *Atherinops affinis* 14.6, and Jacksmelt *Atherinopsis californiensis* 39.4 are present per million cubic meters flow at a peak. Both *A. affinis* and *A. californiensis* are fished commercially and recreationally, with hundreds of thousands landed each year (Vejar, 2013). These fishery-independent surveys indicate at a minimum that *L. tenuis* abundance is substantially lower than its sister silverside species of similar size.

Trawl surveys of San Diego Bay (Williams *et al.*, 2016) and San Francisco Bay (Johnson *et al.*, 2009) show large population fluctuations from year to year. In 2016 Williams *et al.* suggested a stock estimate for *L. tenuis* in San Diego Bay of 785,183 fish, but 92% were juveniles in surveys taken during the spawning season. This suggests substantially fewer, only 62,815 adult grunion in

San Diego Bay in 2016. The human population of San Diego's metropolitan area is 3.1 million, <http://worldpopulationreview.com/us-cities/san-diego-population/> not including the city's 35 million tourist visitors per year (<https://www.sandiego.org/about.aspx>).

Because of the tendency of this species to aggregate, we hypothesize that even if fewer fish are present in the total population, large runs will still occur on occasion. Our observations suggest that it is likely that a minimum number of fish must be present for a spawning run to occur. Runs with fewer than a hundred individuals usually do not include spawning events or egg deposition. Therefore the presence of only small numbers of fish during a run suggests unsuccessful reproduction. As runs decline, fewer observations can be made. If the population declines, fewer locations will hold runs, and those runs will occur less frequently. The consistent pattern of decline in median run size is of great concern for this endemic indigenous species. We suggest it is possible that the numbers of adult fish could drop too low for successful spawning even when some members of the species are present and ripe.

The sister species, *Leuresthes sardina* the Gulf Grunion, is endemic to the northern Gulf of California (Bernardi et al., 2003). This species shares the beach-spawning habits of *L. tenuis* (Thomson and Muench, 1976). *Leuresthes sardina* appears on the IUCN Red List as "Near Threatened" because of potential habitat loss and human interference (Findley et al., 2010). The California Grunion *L. tenuis* may face even greater threats because of larger human populations and more coastal development in California compared with Mexico.

In summary, large spawning runs still occur for *L. tenuis*, but smaller runs have been much more common in the present decade than in the previous one in its core habitat range. There may be fewer California Grunion, or the fish may not be able to spawn as frequently as in the past. Either way, reproductive output appears to be lower. For those populations that have moved north, the shift in habitat comes at the cost of smaller size and reduced clutch size, as well as a shift in spawning season that is shorter and holds less frequent spawning.

We strongly encourage increased protection of the spectacular spawning runs for this charismatic indigenous endemic marine fish. Its status as a managed species and an indicator species for climate change warrant greater concern. At minimum, a return to closed season from April to June, as originally designated in 1927, would help protect the southern population from fishing pressure. We recommend that the *L. tenuis* population on the central coast, in Monterey Bay and around San Francisco Bay, should be completely closed to take, as the populations there appear to be too small to withstand any fishing pressure.

Outreach with the Grunion Greeters may help shift public perception of this species and their interaction with its runs. Greeters report with dismay that those hunting *L. tenuis* during its spawning runs exploit the vulnerability of these fish when out of water (Table 2). Unlike typical fishers who respectfully interact with the resource and take no more than they will use, grunion hunters often say they are following some sort of (perhaps misguided) cultural tradition. They scream and yell while running to wildly chase the fish that are trying to spawn. They sometimes step on the fish in their haste, breaking their backs; then toss them into buckets to expire. Instead, we hope that more and more people will come to quietly observe the run spectacle on its own terms, without disturbing the fish, as watchable wildlife. All should be

able to simply enjoy the amazing sight of California's original surfers dancing on the beach.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

Acknowledgements

We are thankful for funding from US Fish & Wildlife Service, "Connecting People with Nature," California Coastal Commission Whale Tail Program WT-13-22, National Science Foundation DBI 1062721, National Science Foundation, REU-1560352, USC Sea Grant College – Urban Oceans Program NOAA – NA14OAR4170089/Subaward 6094463, National Marine Fisheries Service, Southwest Region, Habitat Conservation Division Contract 8-819, National Geographic Society CRE 8105-07, and Pepperdine University. We are grateful to thousands of Grunion Greeters for their long walks on moonlit beaches. RD Martin provided helpful comments on the manuscript and C Davis, T Furlong, and M Perrault assisted with analyses.

References

- Allen, L. G., Findlay, A. M., and Phalen, C. M. 2002. Structure and standing stock of the fish assemblages of San Diego Bay, California from 1994 to 1999. *Bulletin Southern California Academy of Sciences*, 101: 49–85.
- Aryafar, H., Carrillo, A., Berquist, R., Frank, L. R., and Forsgren, K. 2019. Description of a male genital papilla in the California grunion, a beach-spawning marine silverside fish. *Bulletin of the Southern California Academy of Sciences*, in press.
- Barnhart, P. S. 1918. The spawning of the little-smelt *Leuresthes tenuis* (Ayres). *California Fish & Game*, 4: 181–182.
- Bernardi, G., Findley, L., and Rocha-Olivares, A. 2003. Vicariance and dispersal across Baja California in disjunct marine fish populations. *Evolution*, 57: 1599–1609.
- Botsford, L. W., White, J. W., Carr, M. H., and Caselle, J. E. 2014. Marine protected area networks in California, USA. *Advances in Marine Biology*, 69: 205–251.
- Brown, E. E., Baumann, H., and Conover, D. O. 2012. Absence of countergradient and cgradient variation in an oceanic silverside, the California Grunion *Leuresthes tenuis*. *Marine Ecology Progress Series*, 461: 175–186.
- Brown, E. E., Baumann, H., and Conover, D. O. 2014. Temperature and photoperiod effects on sex determination in *Leuresthes tenuis* (fish), Supplement to: temperature and photoperiod effects on sex determination in a fish. *Journal of Experimental Marine Biology and Ecology*, 461: 39–43.
- Byrne, R., and Avise, J. 2009. Multiple paternity and extra-group fertilizations in a natural population of California grunion (*Leuresthes tenuis*), a beach-spawning marine fish. *Marine Biology*, 156: 1681–1690.
- Byrne, R. J., Bernardi, G., and Avise, J. 2013. Spatiotemporal genetic structure in a protected marine fish, the California Grunion (*Leuresthes tenuis*), and relatedness in the genus *Leuresthes*. *Journal of Heredity*, 104: 521–531.
- Clark, F. N. 1925. The life history of *Leuresthes tenuis*, an Atherine fish with tide controlled spawning habits. Contribution No. 51, State Fisheries Laboratory. *Fish Bulletin Number 10*, California State Fish and Game Commission.
- Clark, F. N. 1926. Conservation of the grunion. *California Fish & Game*, 12: 163–166.
- Clark, F. N. 1938. Grunion in southern California. *California Fish & Game*, 24: 49–54.

- Defeo, O., McLachlan, A., Schoeman, D. S., Schlacher, T. A., Dugan, J., Jones, A., Lastra, M., *et al.* 2009. Threats to sandy beach ecosystems: a review. *Estuarine, Coastal and Shelf Science*, 81: 1–12.
- Dugan, J. E., Hubbard, D. M., Rodil, I. F., Revell, D. L., and Schroeter, S. 2008. Ecological effects of coastal armoring on sandy beaches. *Marine Ecology*, 29: 160–170.
- Dugan, J. E., and Hubbard, D. M. 2010. Loss of coastal strand habitat in southern California: the role of beach grooming. *Estuaries and Coasts*, 33: 67–77.
- Erisman, B. E., Allen, L. G., Claisse, J. T., Pondella, II, D. J., Miller, E. F., and Murray, J. H. 2011. The illusion of plenty: hyperstability masks collapses in two recreational fisheries that target fish spawning aggregations. *Canadian Journal of Fisheries and Aquatic Science*, 68: 1705–1716.
- Findley, L., Espinosa, H., Collette, B., and Rojas, P. 2010. *Leuresthes sardina*. The IUCN Red List of Threatened Species 2010: e.T183267A8083578. doi: 10.2305/IUCN.UK.20103.RLTS.T183267A8083578.en.
- Gregory, P. A. 2001. Grunion. In California's Living Marine Resources: A Status Report, pp. 246–247. Ed. by W. S. Leet, C. M. Dewees, R. Klingbeill and E. J. Larson. California Department of Fish and Game, Sacramento, CA. 592 pp.
- Higgins, B. A., and Horn, M. H. 2014. Suction among pickers: jaw mechanics, dietary breadth and feeding behavior in beach-spawning *Leuresthes* spp. compared with their relatives. *Journal of Fish Biology*, 84: 1689–1707.
- Hutchings, J. A. 2001. Conservation biology of marine fishes: perceptions and caveats regarding assignment of extinction risk. *Canadian Journal of Fisheries and Aquatic Science*, 58: 108–121.
- Johnson, P. B., Martin, K. L., Vandergon, T. L., Honeycutt, R. L., Burton, R. S., and Fry, A. 2009. Microsatellite and mitochondrial genetic comparisons between northern and southern populations of California Grunion *Leuresthes tenuis*. *Copeia*, 2009: 467–476.
- King, P. G., Nelsen, C., Dugan, J. E., Hubbard, D. M., and Martin, K. L. 2018. Valuing beach ecosystems in an age of retreat. *Shore & Beach*, 86: 1–15.
- Marine Protected Area Monitoring Action Plan. California Department of Fish and Wildlife and California Ocean Protection Council, California, USA. October 2018. <https://www.wildlife.ca.gov/Conservation/Marine/MPAs/Management/Monitoring/Action-Plan>
- Martin, K. L. M. 2015. Beach-Spawning Fishes: Reproduction in an Endangered Ecosystem. Taylor & Francis Group, CRC Press, Oxford, UK. 219 pp.
- Martin, K. L. M., Hieb, K. A., and Roberts, D. A. 2013. 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. *Copeia*, 2013: 729–730.
- Martin, K. L. M., Moravek, C. L., Martin, A. D., and Martin, R. D. 2011. Community based monitoring improves management of essential fish habitat for beach-spawning California Grunion. Sandy Beaches and Coastal Zone Management: Proceedings of the Fifth International Symposium on Sandy Beaches, Rabat, Morocco. Travaux de l'Institut Scientifique, 2011: 65–72.
- Martin, K., Speer-Blank, T., Pommerening, R., Flannery, J., and Carpenter, K. 2006. Does beach grooming harm grunion eggs? *Shore & Beach*, 74: 17–22.
- Martin, K., Staines, A., Studer, M., Stivers, C., Moravek, C., Johnson, P., and Flannery, J. 2007. Grunion Greeters in California: beach-spawning fish, coastal stewardship, beach management and ecotourism. In Proceedings of the 5th International Coastal & Marine Tourism Congress: Balancing Marine Tourism, Development and Sustainability, pp. 73–86. Ed. by M. Lück, J. Gräupl, J. Auyong, M. L. Miller and M. B. Orams. New Zealand Tourism Research Institute, Auckland, New Zealand.
- Miller, E. F., and McGowan, J. A. 2013. Faunal shift in southern California's coastal fishes: a new assemblage and trophic structure takes hold. *Estuarine, Coastal and Shelf Science*, 127: 29–36.
- Robbins, E. 2006. *Essential Fish Habitat in Santa Monica Bay, San Pedro Bay, and San Diego Bay: A Reference Guide for Managers*. MS thesis, Duke University, 129 pp.
- Roberts, D., Lea, R. N., and Martin, K. L. M. 2007. First record of the occurrence of the California Grunion, *Leuresthes tenuis*, in Tomales Bay, California; a northern extension of the species. *California Fish & Game*, 93: 107–110.
- Sadovy, Y., and Domeier, M. 2005. Are aggregation-fisheries sustainable? Reef fish fisheries as a case study. *Coral Reefs*, 24: 254–262.
- Sadovy, Y., Erisman, B. E., 2012. The social and economic importance of aggregating species and the biological implications of fishing on spawning aggregations. In Reef Fish Spawning Aggregations: Biology, Research and Management Edition, pp. 225–284. Ed. by Y. Sadovy de Mitcheson and P. Colin. Springer, New York. doi:10.1007/978-94-007-1980-4_8
- Sandrozkinski, A. 2013. California Grunion. Status of the Fisheries Report, an Update Through 2011. California Department of Fish & Wildlife, Sacramento, CA.
- Schoeman, D. S., Schlacher, T. A., and Defeo, O. 2014. Climate-change impacts on sandy-beach biota: crossing a line in the sand. *Global Change Biology*, 20: 2383–2392.
- Schooler, N. K., Dugan, J. E., Hubbard, D. M., and Straughan, D. 2017. Local scale processes drive long-term change in biodiversity of sandy beach ecosystems. *Ecology and Evolution*, 7: 4822–4834.
- Spratt, J. D. 1986. The amazing grunion. *Marine Resource Leaflet No. 3*, California Department of Fish and Game, Sacramento, California.
- Tasoff, A. J., and Johnson, D. W. 2019. Can larvae of a marine fish adapt to ocean acidification? Evaluating the evolutionary potential of California Grunion (*Leuresthes tenuis*). *Evolutionary Applications*, 12: 560–571.
- Thomson, D. A., and Muench, K. A. 1976. Influence of tides and waves on the spawning behavior of the Gulf of California grunion, *Leuresthes sardina* (Jenkins and Evermann). *Bulletin of the Southern California Academy of Science*, 75: 198–203.
- Thompson, W. F. 1919. The spawning of the grunion (*Leuresthes tenuis*). *California Fish & Game*, 5: 1–27.
- Vejar, A. 2013. Silversides. Status of the Fisheries Report, an Update through 2011. California Department of Fish & Wildlife, Sacramento, CA.
- Vitousek, S., Barnard, P. L., Limber, P., Erikson, L., and Cole, B. 2017. A model integrating longshore and cross-shore processes for predicting long-term shoreline response to climate change. *JGR Earth Surface*, 122: 782–806. <https://doi.org/10.1002/2016JF004065>
- Walker, B. W. 1949. The Periodicity of Spawning by the Grunion, *Leuresthes tenuis*, an Atherine Fish. Doctoral dissertation, University of California, Los Angeles.
- Walker, B. W. 1952. A guide to the grunion. *California Fish & Game*, 38: 409–420.
- Williams, J. P., Pondella, II, D. J., Williams, C. M., and Robart, M. J. 2016. Fisheries Inventory and Utilization Study to Determine Impacts from El Niño in San Diego Bay, *San Diego*, California for Surveys conducted in April and July 2016. Unified Port of San Diego, San Diego, CA.

Handling editor: Howard Browman