Once-iconic Pismo clams persist in southern California at low intertidal population densities and with variable recruitment

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FULL RESEARCH ARTICLE

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Abstract

The Pismo clam (*Tivela stultorum*) has experienced substantial population decline in California over the past century, extinguishing most public participation in a once-iconic recreational fishery before the end of the 20th century. A subsequent decrease in data collection has led to uncertainty about the current population status of this species. We conducted 6 years of intertidal Pismo clam population assessment surveys in Orange, San Diego, and southern Los Angeles Counties to provide a current dataset that could help guide research and management efforts in southern California. Pismo clams were observed at 19 out of 27 study sites during 57 days of surveys. Average clam bed density was low (mean 2.0 ± 1.1 clams/m^2, median 0.1 ± 0.7 clams/m^2, n = 21 sites), especially when considering larger clams ≥ 35 mm (mean 0.3 ± 0.1 clams/m^2, median 0.1 ± 0.4 clams/m^2), and varied greatly between sites (0.0–98.5 clams/m^2), with Orange County densities approximately one order of magnitude lower than those in San Diego County. Juvenile recruitment was generally low or undetectable, except for consistent recruitment within a < 10 km beach area in San Diego County and a much larger, widespread recruitment event in 2022. Multi-year observations at several sites failed to indicate any consistent seasonal or inter-annual population trends. Densities and abundances were similar to recent historic data (< 30 years old), but are substantially lower than populations prior to the 1980s. We conclude that the Pismo clam persists on many southern California beaches at generally low densities and that recruitment is occurring throughout the southern California region with high spatial and temporal variability. This study provides foundational data to help inform Pismo clam conservation management decisions and to which additional monitoring, ecological research, and fishery data collection should be added.

Key words: bivalve, Pismo clam, population density, recreational fishery, recruitment, southern California, *Tivela stultorum*

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Introduction

The Pismo clam (*Tivela stultorum*) is a large bivalve with a native range from Stinson Beach, California through Bahi Magdalena, Baja California Sur, Mexico (Coan et al. 2000). The species inhabits exposed, gently sloping, intertidal and subtidal sandy beach habitats, as well as entrances to sandy bays and estuaries (Shaw and Hassler 1989). Pismo clams typically burrow to a depth of 5–15 cm (Armstrong 1965), can live for decades, and can grow to exceed 180 mm in length (Fitch 1950). As a macrofaunal filter feeder, Pismo clams are capable of filtering large volumes of seawater (Coe 1947), and like other marine bivalves, may play an important ecological role in marine phytoplankton abundance, water clarity, and nutrient cycling (Strand and Ferreira 2018). The species is prey for a variety of predators such as fishes, gastropods, crustaceans, birds, and mammals, particularly the sea otter (Shaw and Hassler 1989; McLachlan et al. 1996). Humans have also utilized Pismo clams as a food source for millenia (Erlandson and Moss 1999; Thakar 2011).

The U.S. commercial Pismo clam fishery began in 1916 and produced peak landings of nearly 700,000 lbs in 1918 before rapidly declining until the commercial fishery was permanently closed in 1947 (Shaw and Hassler 1989). Following the closure of the U.S. fishery, California's remaining Pismo clam population supported a strong recreational fishery in central and southern California until precipitous declines in local populations occurred in the late 1970s and early 1980s (reviewed by McLachlan et al. 1996). The possible causes of Pismo clam population decline are unresolved; it has been suggested that the recovery of sea otter populations in central California may have contributed to the decline in those areas (Stephenson 1974; Miller et al. 1975; Wendell et al. 1986), whereas storms during the strong 1982–83 El Niño-Southern Oscillation event may have greatly impacted populations in southern California (McLachlan et al. 1996). However, multiple reports indicate that the recreational fishery continued to heavily exploit Pismo clam populations until at least the late 1970s (Frey 1971; Knaggs et al. 1977; McLachlan et al. 1996) and is likely to have contributed to the decline of Pismo clam populations (Pattison and Lampson 2008). The recreational fishery persists today, but the magnitude of recreational harvest is largely unknown.

The decline of this once-iconic recreational fishery was paralleled with a decline in standardized data collection, therefore our understanding of the current status of the Pismo clam population in California is limited. Literature reviews and summary reports are available, but often provide only summary statements about the population status (e.g., McLachlan et al. 1996; Pattison 2001; Pattison and Lampson 2008). For example, McLachlan et al. (1996) suggests that some populations may have recovered after successful recruitment events in the late 1980s, but no quantitative data is provided. Similarly, Pattison (2001) reports that large recruitment events occurred in central California in the late 1980s and an "abundance" of young clams were present throughout southern and central California in 1990 (up to ~280 clams/m^2), but limited information is provided to enable interpretation and comparison of data. Finally, the Pismo clam population on Coronado Beach was reported to be stable between 2000–2005, with recruitment occurring, and "significant numbers of Pismo clams [being] harvested from some of the beaches in southern California" (Pattison and Lampson 2008), but no data, summary statistics, or additional details were provided.

Recent studies provide informative data about Pismo clam populations but often lack methodological consistency or are of limited scope, making direct comparison difficult. Methods have included subtidal snorkel transect surveys used to estimate clam abundance and size distribution at Santa Rosa Island (Richards and Whitaker 2015), stratified random quadrat sampling to estimate clam density at Rincon beach in Ventura County (Evans and van Meeuwen 2013), and a combination of intertidal and subtidal transect surveys used to estimate the abundance of clams (but not population density specifically) at the same location (Greene 2015). Intertidal transects is the most consistently chosen method to survey Pismo clam populations and has recently been applied in central and southern California to estimate clam bed density (CDFW 2009, 2022) and abundance per meter of shoreline (Dugan et al. 2015). Most recently, researchers at California Polytechnic State University in San Luis Obispo (CPSLO) used intertidal transect methods to estimate clam bed densities across a wide geographic range (Monterey Bay to San Diego County) during 2018–2019 (reviewed by CDFW 2022). Such use of a standard methodology enables more direct comparisons between studies at different locations and times, which is necessary to better understand the current status or trajectory of the Pismo clam population. The objective of the present study was to produce a detailed multi-year assessment of intertidal Pismo clam populations in southern California that provides perspective on their present status and a strong foundation to inform future research and management efforts.

Methods

Study Area

We surveyed 27 study sites on 57 days between 2017–2022, spanning from the southern edge of Los Angeles County (LAC), through Orange County (OC), to the southern edge of San Diego County (SDC; **Fig. 1**). The distribution of study sites throughout these counties was not uniform nor an exhaustive sampling of locations with favorable Pismo clam habitat. Rather, we focused most of our effort on the beaches of OC and southern SDC due to their accessibility, proximity to human population centers, anecdotal reports of recreational fishery activity, and/or previously published data. We acknowledge that sampling in SDC was mostly limited to the southern margin of the county. Favorable study site characteristics included sandy habitat on gently-sloping beaches with unobstructed exposure to open ocean waves, consistent with the typical habitat of Pismo clams (Shaw and Hassler 1989). Sites were separated by 0.4–49 km (median 2.4 km) and we conducted surveys during summer months (May–Aug) and winter months (Dec–Mar). Repeated seasonal or annual sampling was only logistically possible at a subset of sites, therefore we selected sites that either had higher population densities, e.g., Bola Chica State Beach (BCSB) and Silver Strand State Beach (SSSB), or were generally representative of the local coastline, easily accessible, and could be surveyed frequently (e.g., NB Pier).

Figure 1. Maps of Pismo clam (*Tivela stultorum*) bed densities at (A) 27 survey sites throughout southern California and (B) 11 sites in Orange and Los Angeles Counties between 2017–2022. Los Angeles County (LAC), Orange County (OC), and San Diego County (SDC) are indicated and county lines are denoted with gray lines. Site names are provided. Mean bed densities for survey sites ranged from 0 to 20.3 clams/m^2. Data point size and color are formatted on a continuous scale according to bed density, with examples of size and color for specific increments provided in the legend.

Survey Protocol

We used a modified version of the California Fish and Wildlife *Protocol for conducting southern California Pismo clam surveys*, consisting of three transects per study site that were each separated by 10 m. Transects were excavated perpendicular to the shoreline during low tide cycles reaching at least –22 cm below mean lower low water (median low tide –38 cm). This method is intended to locate the inshore edge of the clam bed, if present, and then intensively sample within the clam bed. Therefore, we began each transect in the upper intertidal zone, higher than where we expected to find Pismo clams, then extended the transects into the water as far offshore as possible during low tide. Transects typically ended in ankle deep swash at low tide. Bean clams (*Donax gouldii*) were often present at our survey locations and formed dense beds that spanned several meters across-shore. These beds often coincided with the presence of Pismo clams and were sometimes used to estimate an appropriate starting point for the transects, approximately 15–20 m inshore of the bean clam beds. Excavation of the transect was completed using flat-blade transfer shovels to dig ~30-cm wide and ~20-cm deep trenches, a depth that should capture the majority of Pismo clams which reside in the top ~15 cm of sand (Armstrong 1965). We excavated transects in 3-m sections; this began at the inshore end of the transect and skipped every-other section until a clam was located, then we excavated the previously skipped section to ensure at least 6 m of transect was “cleared” above the upper margin of the clam bed. Subsequently, we excavated all 3-m transect sections on the seaward side of the first located clam. All the excavated sand was sieved with seawater through 0.6-cm steel mesh, enabling us to reliably capture clams as small as 10 mm in length, but occasionally as small as 5 mm. We recorded clam length to the nearest mm, their position along the transect, and the total number of excavated transect sections. Beach slope was measured using a sighting level and stadia rod at least once per study site (except Cabrillo Beach sites in 2022); in the case of repeated survey dates the beach slope was sometimes not remeasured if we observed a beach slope that was consistent with past surveys.

Occasionally, modifications to these methods were necessary. Many of our study sites had very few or no clams, in which case we would often excavate every 3-m section even if no clams were observed. Our use of this modification depended on field conditions and availability of fieldwork assistants, and was intended to increase sampling effort at sites where clam densities appeared to be very low. At times, field conditions and logistics affected the number of transects completed at a given study site; this rarely resulted in fewer transects and periodically resulted in additional transects (range 1–5). During 2022, a high abundance of young clams at Silver Strand State Beach necessitated that we estimate size in 5-mm increments for clams between five and 20 mm in length.

Data Analysis

“Bed density” was calculated using the total number of clams found on a transect, divided by the total area excavated within the “clam bed”; we considered the “clam bed” to begin at the most inshore 3-m section where a clam was observed and include all sections seaward of this. “Mature densities” were calculated in the same way but only included larger clams, either ≥ 25 mm or ≥ 35 mm in length. We chose ≥ 25-mm length as the boundary for one category of “mature” because this is generally attained by the second year after settlement for clams in southern California and clams of this size are large enough to be considered sexually mature (Coe and Fitch 1950), although reproductive maturity has recently been observed in smaller clams (Marquardt et al. 2022). We also included a ≥ 35 mm bed density category to enable direct comparison with similar data collected in 2018–2019 (reviewed by CDFW 2022). All clam bed densities (clams/m^2) were first calculated at the transect-level, then averaged across transects for each survey date, across survey dates for each site (when applicable), and across sites for broader geographical groupings.

Clam abundance per meter of shoreline was calculated to allow comparison to previously published abundance data (e.g., Dugan et al. 2015); the total number of clams was divided by the width of excavated beach (i.e., 30 cm per transect). Average size was calculated by pooling all clams for a given date, site, county, etc. Across-shore clam distribution was not formally analyzed because it was logistically difficult to standardize transect starting points according to across-shore location or elevation. All means are reported ± standard error (SE). Medians are reported ± interquartile range (IQR) when necessary to reduce the influence of skewed distributions.

Six sites in LAC and OC had high beach slopes (> 3.5°), and no other observations at the site suggested the presence of clams (e.g., shells, clams off-transect, clams present during repeated surveys, etc.). Although it is possible that low density populations of Pismo clams were present at these sites, we considered it unlikely and therefore attempted to avoid underestimating the regional density of clams by excluding data from these suboptimal sites when calculating any average density at a scale above site-level. The exclusion of these high beach slope sites is not meant to imply that they could not have previously supported a population of clams, but there is no data on the historic presence of Pismo clams with enough precision to make that determination. We included zero-density data in our calculations if a site had a more suitable beach slope or if the site was observed to have clams during subsequent surveys. Similar conditional exclusion of data is commonly used in two-part models for zero-inflated semi-continuous data (reviewed by Min and Agresti 2002). One site (NB N) had no clams and a beach slope > 3.5 during winter surveys, but clams were present with slopes ≤ 2.0 during summer surveys at this site, therefore data from NB N was included in our calculations.

Results

Population Density and Abundance

We observed 6,584 Pismo clams at 19 of 27 survey sites, and found no clams at eight sites, in southern

California between 2017–2022. Mean study site bed density ranged from 0.0–20.3 clams/m^2 (Fig. 1, Table 1, Appendix I (PDF)). Overall mean bed density in the southern California region was 2.0 ± 1.1 clams/m^2 (median 0.1 ± 0.7 clams/m^2, n = 21 sites) and mean ≥ 35 mm mature clam density was 0.3 ± 0.1 clams/m^2 (median 0.1 ± 0.4 clams/m^2). Pismo clam abundance followed similar patterns and was also highly variable, ranging from zero to over 4,000 clams/m of shoreline. Across all sites, mean abundance was 91.0 ± 50.2 clams/m (n = 21 sites) and median abundance was 3.3 ± 17.2 clams/m.

Mean and median bed densities were approximately one order of magnitude lower at OC sites (mean 0.5 ± 0.4 clams/m^2, median 0.1 ± 0.1 clams/m^2, n = 11 sites) compared to SDC sites (mean 4.5 ± 2.6 clams/m^2, median 1.0 ± 3.7 clams/m^2, n = 8 sites). Mean and median ≥35 mm mature clam densities followed a similar but less substantial pattern of differences between OC and SDC (means 0.1 ± 0.01 and 0.7 ± 0.2 clams/m^2, medians 0.1 ± 0.1 and 0.5 ± 0.6 clams/m^2, respectively). We detected the highest OC bed density at BCSB in the summer of 2022 (12.6 ± 1.0 clams/m2), but most OC sites had few or no detectable clams regardless of season. Conversely, we found clams at nearly all SDC sites in all seasons, with the highest bed density (98.5 ± 11.0 clams/m2) and ≥ 35 mm mature clam density (3.0 ± 0.5 clams/m^2) at SSSB survey sites during summer surveys in 2022 and 2019, respectively. The only times we were unable to detect clams in SDC was during two iterations of summer surveys at Imperial in 2018. Mean and median abundances at sites in OC (22.1 ± 19.0 and 1.7 ± 2.5 clams/m, n = 11 sites) were an order of magnitude lower than mean and median abundances in SDC (207.7 ± 122.6 and 32.2 ± 192.3 clams/m, n = 8 sites). Maximum abundance in OC was observed at BCSB (618.9 clams/m) and in SDC at SSSB (4032.2 clams/m) during surveys in summer of 2022. LAC results are only reported in Table 1 and Appendix I (PDF) due to the limited number of survey sites.

Density varied over time without consistent seasonal or inter-annual patterns at several study sites where repeated surveys were conducted (Fig. 2, Table 1). Temporal variability in clam bed density was especially notable during a high-recruitment event in 2022, which increased the mean bed density and abundance values reported above. However, the same pattern of differences between OC and SDC study sites persists when the influence of this event is minimized using median density and abundance values (medians 0.1 vs. 1.0 clams/m2 bed density, 0.07 vs. 0.5 mature clams ≥ 35 mm/m^2, 2.0 vs. 32.2 clams/m shoreline for OC and SDC, respectively). Densities calculated for clams ≥ 35 mm were not noticeably affected by variable recruitment events (e.g., Fig. 2). The across-shore distribution of clams was also variable, regularly overlapped with dense beds of *D. gouldii*, when present, and anecdotally appeared to be slightly higher in the mid- to off-shore regions of the Pismo clam bed.

Figure 2. Time series of Pismo clam (*Tivela stultorum*) mature clam bed densities (clams ≥ 35 mm length) at four southern California sites where at least three years of repeated surveys were conducted between 2017–2022.

Table 1. Summary data from 21 southern California intertidal beach survey sites considered to have suitable habitat (average beach slope < 3.5°) for Pismo clams (*Tivela stultorum*). Sites are listed in order from north to south, by date within site, and grouped by county. Site information includes the geographic coordinates, date(s) of survey(s), low tide value, beach slope, number of clams observed by size class (total, ≥ 25 mm, and ≥ 35 mm; Tot./25/35 # clams), mean length of all observed clams (Size), mean clam bed density (includes all clams), mean ≥ 25 mm mature clam bed density, mean ≥ 35 mm mature

clam bed density, and clam abundance per meter of shoreline. Summary means are provided for size, clam bed densities, and abundances at each site, for all sites in Los Angeles County (LAC), Orange County (OC), or San Diego County (SDC), and all sites combined (SoCal), with the total number of clams and survey sites indicated (n). All values are reported mean ± SE or median ± IQR.

Table 1a. Los Angeles County

Site Name	Lat. (°)	Lon. (°)	Date	Tide (cm)	Slope (°)	Tot./25/35 # Clams	Size (mm)	Bed Density (m^2)	≥ 25 mm Bed Density (m^2)	≥ 35 Bed Density (m^2)	Abundance (per m shore)
Cabrillo B	33.709	–118.283	16 Jul 22	–34	N/A	1/1/1	80	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	1.1
Cabrillo J	33.709	–118.280	16 Jul 22	–34	N/A	3/3/3	90.7 ± 10.5	0.5 ± 0.1	0.5 ± 0.1	0.5 ± 0.1	5.0
LAC Mean	—	—	—	—	—	—	**88.0 ± 7.9 (n = 4)**	**0.3 ± 0.3 (n = 2)**	**0.3 ± 0.2 (n = 2)**	**0.3 ± 0.2 (n = 2)**	**3.1 ± 1.9 (n = 2)**

Table 1b. Orange County

Site Name	Lat. (°)	Lon. (°)	Date	Tide (cm)	Slope (°)	Tot./25/35 # Clams	Size (mm)	Bed Density (m^2)	≥ 25 mm Bed Density (m^2)	≥ 35 Bed Density (m^2)	Abundance (per m shore)
Surfside	33.725	–118.082	3 Jul 19	–40	1.8	1/1/1	42	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	1.1
BCSB N	33.699	–118.052	13 Jul 18	–40	1.2	12/7/7	45.9 ± 9.5	0.3 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	10.0
BCSB N	33.699	–118.052	23 Jun 21	–47	1.2	5/5/5	68.4 ± 1.3	0.2 ± 0.05	0.2 ± 0.05	0.2 ± 0.05	5.6
BCSB N	33.699	–118.052	13 July 22	–49	1.2	557/11/10	13.9 ± 0.4	12.6 ± 1.0	0.3 ± 0.1	0.2 ± 0.1	618.9
BCSB N Mean	33.699	–118.052	—	—	—	—	*15.0 ± 0.5*	*4.4 ± 4.1*	*0.2 ± 0.02*	*0.2 ± 0.02*	*211.5 ± 203.7*
BCSB S	33.694	–118.048	12 Jul 18	–41	1.8	22/13/13	36.7 ± 4.6	0.5 ± 0.2	0.3 ± 0.1	0.3 ± 0.1	18.3

Site Name	Lat. (°)	Lon. (°)	Date	Tide (cm)	Slope (°)	Tot./25/35 # Clams	Size (mm)	Bed Density (m^2)	≥ 25 mm Bed Density (m^2)	≥ 35 Bed Density (m^2)	Abundance (per m shore)
HB T28	33.678	–118.032	2 Jul 19	–37	1.1	2/2/2	62 ± 10	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	2.2
HB T20	33.666	–118.017	19 Jan 19	–46	1.5	0/0/0	N/A	0 ± 0	0 ± 0	0 ± 0	0
HB Pier	33.659	–118.008	5 Dec 17	–39	1.5	3/3/3	47.7 ± 3.5	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	3.3
HB T3	33.654	–118.002	20 May 19	–30	1.1	3/3/3	37.3 ± 1.2	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	3.3
HSB T11	33.641	–117.980	11 Jul 18	–29	3.2	1/1/1	79	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.8
NB N	33.626	–117.954	11 Feb 17	–30	4.0	0/0/0	N/A	0 ± 0	0 ± 0	0 ± 0	0
NB N	33.626	–117.954	26 Jun 17	–40	1.3	2/1/1	28 ± 12	0.1 ± 0.1	0.03 ± 0.03	0.03 ± 0.03	3.3
NB N	33.626	–117.954	4 Nov 17	–22	4.0	0/0/0	N/A	0 ± 0	0 ± 0	0 ± 0	0
NB N	33.626	–117.954	17 May 18	–36	2.0	0/0/0	N/A	0 ± 0	0 ± 0	0 ± 0	0
NB N	*33.626*	*–117.954*	—	—	—	—	*28 ± 12*	*0.02 ± 0.02*	*0.01 ± 0.01*	*0.01 ± 0.01*	*0.8 ± 0.8*
NB Pier	33.608	–117.930	8 Feb 17	–37	0.3	0/0/0	N/A	0 ± 0	0 ± 0	0 ± 0	0
NB Pier	33.608	–117.930	29 May 17	–30	0.8	0/0/0	N/A	0 ± 0	0 ± 0	0 ± 0	0
NB Pier	33.608	–117.930	2 Dec 17	–30	1.4	7/6/6	66.9 ± 14.1	0.3 ± 0.1	0.3 ± 0.1	0.2 ± 0.1	5.8
NB Pier	33.608	–117.930	1 Feb 18	–46	1.3	0/0/0	N/A	0 ± 0	0 ± 0	0 ± 0	0
NB Pier	33.608	–117.930	13 Jun 18	–37	1.2	0/0/0	N/A	0 ± 0	0 ± 0	0 ± 0	0

Site Name	Lat. (°)	Lon. (°)	Date	Tide (cm)	Slope (°)	Tot./25/35 # Clams	Size (mm)	Bed Density (m^2)	≥ 25 mm Bed Density (m^2)	≥ 35 Bed Density (m^2)	Abundance (per m shore)
NB Pier	33.608	–117.930	16 Feb 19	–32	1.3	0/0/0	N/A	0 ± 0	0 ± 0	0 ± 0	0
NB Pier	33.608	–117.930	5 Jun 19	–34	1.7	1/1/1	45	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	1.1
NB Pier	33.608	–117.930	10 Jan 20	–40	1.1	1/1/1	62	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	1.1
NB Pier	33.608	–117.930	1 Aug 20	–25	1.5	1/1/1	71	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	1.1
NB Pier	33.608	–117.930	27 May 21	–52	N/A	0/0/0	N/A	0 ± 0	0 ± 0	0 ± 0	0
NB Pier	33.608	–117.930	15 July 22	–46	N/A	9/2/1	21.8 ± 3.3	0.3 ± 0.2	0.1 ± 0.04	0.03 ± 0.03	10.0
NB Pier Mean	*33.608*	*–117.930*	—	—	—	—	*69.6 ± 9.9*	*0.1 ± 0.04*	*0.05 ± 0.02*	*0.05 ± 0.02*	*1.7 ± 1.0*
Pelican Pt.	33.577	–117.846	14 Jun 18	–39	2.4	0/0/0	N/A	0 ± 0	0 ± 0	0 ± 0	0
OC Mean	—	—	—	—	—	—	**17.3 ± 0.6**	**0.50 ± 0.4**	**0.1± 0.03**	**0.1± 0.1**	**22.1 ± 19.0**
OC Median	—	—	—	—	—	—	**13 ± 4 (n = 627)**	**0.1 ± 0.1 (n = 11)**	**0.1 ± 0.1 (n = 11)**	**0.1 ± 0.1 (n = 11)**	**1.7 ± 2.5 (n = 11)**

Table 1c. San Diego County

Site Name	Lat. (°)	Lon. (°)	Date	Tide (cm)	Slope (°)	Tot./25/35 # Clams	Size (mm)	Bed Density (m^2)	≥ 25 mm Bed Density (m^2)	≥ 35 Bed Density (m^2)	Abundance (per m shore)
Oceanside	33.196	–117.386	25 Jan 20	–27	1.4	1/1/1	37	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	1.1
Mission	32.769	–117.254	12 Aug 18	–37	1.2	9/2/2	30.8 ± 8.1	0.5 ± 0.2	0.1 ± 0.1	0.1 ± 0.1	10.0

Site Name	Lat. (°)	Lon. (°)	Date	Tide (cm)	Slope (°)	Tot./25/35 # Clams	Size (mm)	Bed Density (m^2)	≥ 25 mm Bed Density (m^2)	≥ 35 Bed Density (m^2)	Abundance (per m shore)
Breakers	32.687	–117.203	3 Aug 19	–30	1.6	44/42/26	41.9 ± 2.1	1.1 ± 0.3	1.1 ± 0.3	0.7 ± 0.2	48.9
Coronado	32.682	–117.185	11 Aug 18	–42	1.9	55/45/40	36.5 ± 1.5	2.4 ± 0.3	2.0 ± 0.3	1.8 ± 0.3	61.1
Coronado	32.682	––117.185	11 Aug 18	–43	2.2	42/41/32	43.1 ± 1.9	1.6 ± 0.3	1.6 ± 0.3	1.2 ± 0.3	46.7
Coronado Mean	*32.682*	*–117.185*	—	—	—	—	*39.4 ± 1.2*	*2.0 ± 0.4*	*1.8 ± 0.2*	*1.5 ± 0.3*	*53.9 ± 7.2*
SSSB N	32.635	–117.143	31 Jul 19	–40	1.7	297/129/115	25.7 ± 0.08	7.6 ± 1.3	3.3 ± 0.4	3.0 ± 0.5	330
SSSB N	32.635	–117.143	3 Aug 20	–24	1.1	874/31/24	13.5 ± 0.3	14.0 ± 1.2	0.5 ± 0.1	0.4 ± 0.1	971.1
SSSB N Mean	*-117.143*	—	—	—	—	—	*16.6 ± 0.3*	*10.8 ± 3.2*	*1.9 ± 1.4*	*1.7 ± 1.3*	*650.6 ± 320.6*
SSSB HQ	32.632	–117.142	10 Aug 18	–40	1.4	97/3/1	17.8 ± 0.4	8.3 ± N/A	0.3 ± N/A	0.1 ± N/A	323.3
SSSB HQ	32.632	–117.142	1 Aug 19	–46	1.4	317/108/94	22.7 ± 0.7	6.0 ± 0.2	2.0 ± 0.1	1.8 ± 0.1	352.2
SSSB HQ	32.632	–117.142	2 Feb 20	-26	1.5	374/25/24	15.1 ± 0.6	7.1 ± 1.0	0.5 ± 0.02	0.4 ± 0.1	415.6
SSSB HQ	32.632	–117.142	27 Feb 21	-37	N/A	12/10/4	35.3 ± 4.4	0.4 ± 0.03	0.3 ± 0.1	0.1 ± 0.02	13.3
SSSB HQ	32.632	–117.142	23 Jul 21	–46	N/A	80/15/8	16.6 ± 1.6	1.7 ± 0.1	0.3 ± 0.1	0.2 ± 0.1	88.9
SSSB HQ	32.632	–117.142	14 Jul 22	-55	N/A	3629/183/24	14.5 ± 0.1	98.5 ± 11.0	4.8 ± 0.9	0.6 ± 0.2	4032.2
SSSB HQ Mean	*32.632*	*–117.142*	—	—	—	—	*15.3 ± 0.1*	*20.3 ± 15.7*	*1.4 ± 0.7*	*0.5 ± 0.3*	*871.0 ± 635.5*
SSSB S	32.624	–117.139	9 Feb 20	–52	1.6	14/9/8	36.8 ± 3.8	0.8 ± 0.3	0.6 ± 0.2	0.5 ± 0.5	15.6
Imperial	32.581	–117.133	7 Feb 17	–27	1.3	26/25/6	31.5 ± 0.9	1.5 ± 0.4	1.4 ± 0.4	0.4 ± 0.2	21.7

Site Name	Lat. (°)	Lon. (°)	Date	Tide (cm)	Slope (°)	Tot./25/35 # Clams	Size (mm)	Bed Density (m^2)	≥ 25 mm Bed Density (m^2)	≥ 35 Bed Density (m^2)	Abundance (per m shore)
Imperial	32.581	–117.133	27 Jun 17	–29	1.4	38/36/36	53.9 ± 4.3	1.1 ± 0.3	1.0 ± 0.3	1.0 ± 0.3	25.3
Imperial	32.581	–117.133	3 Dec 17	–45	1.3	16/16/16	64.6 ± 6.8	0.5 ± 0.1	0.5 ± 0.1	0.5 ± 0.1	13.3
Imperial	32.581	–117.133	15 Jun 18	–45	1.6	0/0/0	N/A	0 ± 0	0 ± 0	0 ± 0	N/A
Imperial	32.581	–117.133	9 Aug 18	–30	1.3	0/0/0	N/A	0 ± 0	0 ± 0	0 ± 0	N/A
Imperial	32.581	–117.133	17 Mar 19	–32	1.6	6/6/1	32.8 ± 0.7	0.5 ± 0.3	0.4 ± 0.3	0.1 ± 0.1	5.0
Imperial	32.581	–117.133	6 Jun 19	–30	2.3	4/4/3	37.8 ± 2	0.5 ± 0.3	0.5 ± 0.3	0.4 ± 0.2	4.4
Imperial	32.581	–117.133	11 Jan 20	–57	1.3	16/12/10	51.8 ± 9.1	0.6 ± 0.2	0.4 ± 0.2	0.3 ± 0.1	17.8
Imperial Mean	*32.581*	*–117.133*	—	—	—	—	*48.2 ± 2.6*	*0.6 ± 0.2*	*0.5 ± 0.2*	*0.3 ± 0.1*	*10.9 ± 3.5*
SDC Mean	**—**	**—**	**—**	**—**	**—**	**—**	**16.8 ± 0.1**	**4.5 ± 2.6**	**0.9 ± 0.3**	**0.7 ± 0.2**	**207.7 ± 122.6**
SDC Median	**—**	**—**	**—**	**—**	**—**	**—**	**15 ± 9 (n = 5953)**	**1.0 ± 3.7 (n = 8)**	**0.8 ± 1.1 (n = 8)**	**0.5 ± 0.6 (n = 8)**	**32.2 ± 192.3 (n = 8)**
SoCal Mean	**—**	**—**	**—**	**—**	**—**	**—**	**16.9 ± 0.1**	**2.0 ± 1.1**	**0.4 ± 0.1**	**0.3 ± 0.1**	**91.0 ± 50.2**
SoCal Median	**—**	**—**	**—**	**—**	**—**	**—**	**15 ± 8 (n = 6584)**	**0.1 ± 0.7 (n = 21)**	**0.1 ± 0.5 (n = 21)**	**0.1 ± 0.4 (n = 21)**	**3.3 ± 17.2 (n = 21)**

Recruitment and Size Distribution

The presence of first-year clam cohorts was generally low at most study sites, but highly variable between sites. The highest recruitment in southern California consistently occurred on SSSB (Fig. 3). During 2018–2022, first-year clams made up 81.3–96.5% of the total observed clams at two survey sites on SSSB (SSSB N and SSSB HQ). We also observed a relatively abundant second-year cohort (~30–50 mm length) at both sites during 2019, contributing to two of the highest ≥ 35 mm mature clam bed densities of all surveys (3.0 ± 0.5 and 1.8 ± 0.1 clams/m^2 at SSSB N and SSSB HQ, respectively). During the summer of 2022, recruitment of first-year clams at SSSB N was approximately 10-times higher than in previous years; we observed 3,446 clams < 25 mm, comprising over 50% of all clams observed during 6 years of surveys throughout southern California. Increased recruitment was also observed at two OC survey locations in 2022. Juvenile clams composed 98.0% of the 12.6 clams/m^2 bed density at BCSB N and 77.8% of the 0.32 clams/m^2 bed density at NB Pier, where we had previously observed only one juvenile clam. No juveniles were detected during the remaining 2022 surveys at two closely associated sites in LAC (Cabrillo Bathhouse and Cabrillo Jetty).

Figure 3. Bed density of Pismo clams (*Tivela stultorum*) per 5-mm size bin at one San Diego County study site (SSSB HQ) from 2018–2022. Recruitment of first-year clams (*c*. 5–25 mm) varied interanually and was an order of magnitude higher during 2022 compared to the previous 4 years. Y-axis scales are equivalent across all plots. The x-axis was truncated at 75 mm, excluding two clams: 150 mm observed in 2020 and 83 mm observed in 2021.

Recruitment was much lower at all other survey locations throughout the study. Three survey sites within 5–9 km on either side of the SSSB sites (Breakers Beach, Coronado, and Imperial) consistently had low or no detectable recruitment during seven summer surveys between 2017–2019 (**Table 1**). The highest recruitment we detected at these sites was at Coronado in 2018, when juveniles contributed 17.5% of the 2.4-clams/m^2 bed density. Recruitment at OC survey sites was consistently much lower than in SDC. We detected a low number of new recruits in 2018 during surveys at two closely-associated sites on BCSB (BCSB N and BCSB S; ~0.7 km apart); juveniles contributed only 41.9% and 42.9% of the relatively low 0.31 and 0.49 clams/m^2 bed densities at these sites, respectively. No recruits were observed on the transects during a repeated survey at BCSB N in 2021 (although several juveniles were found off-transect) and no other juvenile clams were detected in OC throughout the remaining 12 summer surveys conducted at seven sites between 2017–2021.

The length distributions of Pismo clams ranged from 6–131 mm in OC, 5–156 mm in SDC, and 71–110 mm in LAC (**Fig. 4**). Overall, clam length in OC was similar (mean 17.3 ± 0.6 mm; median 13 ± 4 mm, n = 627) to those in SDC (mean 16.8 ± 0.1 mm, median 15 ± 9 mm, n = 5953). Mean size of mature clams ≥ 25 mm was generally larger in OC than in SDC (OC mean 60.7 ± 2.9 mm, median 61 ± 28.8 mm, n = 58; SDC mean 39.6 ± 0.6 mm, median 38 ± 13 mm, n = 745), but SDC included a larger quantity of mature clams compared to OC. We observed a low number of clams with a mean length of 88.0 ± 7.87 mm during limited sampling on LAC beaches. Throughout all of southern California we observed 11 clams (0.2 % of all clams observed) that exceeded the 114-mm minimum recreational fishery size limit; 10 of 11 were observed in SDC and one was observed in OC.

Figure 4. Size frequencies of 6,584 Pismo clams (*Tivela stultorum*) observed at 19 southern California survey sites between 2017–2022. Clams ranged from five to 156 mm in length, with two peaks that represent a first-year cohort of recruits (*c*. 5–25 mm) and a second-year cohort of presumably mature clams (*c*. 25–50 mm). An enlarged inlay of frequencies for clams 60–160 mm is provided for clarity of less abundant size classes. The recreational fishery minimum size limit (114 mm) is denoted with a red dotted line. Approximately 5% more beach area was surveyed at sites where clams were observed in San Diego County (blue; 1,001 m^2) compared to sites where clams were observed in Orange County (green; 949 m^2). Los Angeles County (yellow) sites where clams

were observed included 36 m^2 of beach area.

Discussion

Patterns and Trends in Population Density and Abundance

We conclude that Pismo clam populations persist on many southern California beaches at low densities and abundances which can vary substantially over space and time. Clam bed densities during individual surveys ranged two orders of magnitude (0–98.5 clams/m^2), but averaged only 2.0 ± 1.1 clams/m^2 across all sites in southern California. Bed density was right-skewed by a small number of high-density study sites and a year of especially high recruitment in 2022, therefore, a better representation of average clam density in southern California is the median bed density (0.1 ± 0.7 clams/m^2). Bed densities were also variable between study sites when calculated for mature clams ≥ 35 mm (0–3.0 clams/m^2) but the southern California mean ≥ 35 mm bed density (0.3 ± 0.1 clams/m^2) was similar to the median ≥ 35 mm bed density (0.1 ± 0.4 clams/m^2). Clam abundance followed similar patterns of inter-site variability (0¬–4,032 clams/m), right-skew, and low median abundance (3.3 ± 17.2 clams/m).

Density and abundance also appeared to differ between the SDC and OC regions. Mean density and abundance values across sites in the SDC region were approximately seven to 9-times higher than those in OC; this pattern persisted for median values of density and abundance, which were five to 19-times higher in SDC than OC. These differences may be partially attributable to a more limited amount of sampling in SDC (8 sites) compared to OC (11 sites) and the presence of some anomalously high-density and high-recruitment study sites within the “Coronado Embayment” in SDC. Limited data collection in LAC prevented us from drawing any conclusions about density or abundance patterns in that region.

Temporal variability was also observed throughout southern California but there was no overall trend to Pismo clam density or abundance across the region between 2017–2022. Individual sites had generally consistent densities and abundances when repeatedly surveyed, i.e., no site with low density changed to have dramatically higher density, or vice versa. The most dramatic interannual difference we observed across the southern California region was a high recruitment event in 2022, which is discussed in more detail below. Although interseasonal differences were sometimes observed at individual sites, we did not detect any distinct patterns to suggest a consistent seasonal effect on bed density. However, seasonal trends could be possible, therefore it may be important to note the season of data collection when making comparisons.

Our data and comparable data collected by CPSLO in central and southern California provide moderate support of the generalization that southern California beaches have fewer Pismo clams than central California beaches (i.e., north of Point Conception; reviewed by CDFW 2022). Central California beaches had higher peak densities of clams ≥ 35 mm in 2018–2019 (up to 8.77 clams/m^2 in the Pismo Beach area; reviewed by CDFW 2022) than were observed at any point during our surveys (up to 3.0 clams/m^2). However, most sites north of Point Conception had lower population densities and variability between sites was similar to that observed in southern California; four sites had no clams, ~7 sites had densities < 1.47 clams/m^2, and only ~4 of ~15 sites (including three within ~ 3 km of coastline near Pismo Beach) had densities > 2.92 clams/m^2 (reviewed by CDFW 2022). Mean and median density values were not reported in the CDFW review of these data (2022), therefore it is difficult to make more generalized comparisons between these central California data and our data from southern California. Nonetheless, it is notable that the perception of relatively higher-density Pismo clam populations in central California may be primarily driven by localized high-density beaches (e.g., Pismo Beach) among a broader collection of typically lower-density beaches; this is the same general pattern we observed in southern California. In addition, the magnitude of differences between sites within the central or southern California region exceeds the magnitude of differences when sites are compared between these regions. This suggests that local factors, such as a concentrated spawning population, kilometer-scale differences in abiotic or biotic conditions, and localized predation or fishing pressure, may be more influential to Pismo clam populations than biogeographical differences in oceanographic conditions, anthropogenic disturbances, or other factors. It is unclear whether similarities or differences between sites or regions persist over time because large differences in Pismo clam population density can be observed during a single year or over many years at individual study sites (CADFW 2022).

CPSLO data overlapped with our study region in LAC, OC, and SDC between 2018–2019 and closely corresponds to our data. Several CPSLO study sites were located near our sites or were sampled simultaneously and in close proximity. In 2018, simultaneous sampling occurred at Huntington State Beach (HSB T11), Bolsa Chica State Beach (BCSB N), Coronado, Silver Strand State Beach (SSSB HQ), and Imperial Beach, with surveys separated by ~250 m. CDFW (2022) reviewed the corresponding 2018 CPSLO density values (≥ 35 mm) numerically or graphically, depending on the location. In OC, CPSLO observed 0.45 clams/m^2 at BCSB and we observed slightly lower density of 0.1 clams/m^2, whereas we observed clams at HSB T11 (0.1 clams/m^2) where CPSLO observed none. In SDC, CPSLO and the present study report nearly identical clam density at Coronado Beach (1.79 and 1.8 clams/m^2, respectively) but densities differed at Imperial Beach; CPSLO reported < 1.47 clams/m^2, but we found no clams despite having previously observed 1 clams/m^2 at the same site in 2017. CDFW (2022) also reviewed CPSLO data from an unspecified location on SSSB in 2019 (2.93 clams/m^2). We surveyed two locations on this beach less than one month later and observed slightly lower density at SSSB HQ (1.8 clams/m^2) but nearly identical density (3.0 clams/m^2) at SSSB N. The overall correspondence of these two datasets strengthen our confidence in the patterns we report, but the differences observed during simultaneous surveys highlights the spatial variability that can exist along individual beaches. Uneven distribution of clams has previously been described in detail along Rincon Beach (Evans and Van Meeuwen 2013) and was recently observed and quantified along BCSB (N. Caruso et al., Get Inspired Inc., unpublished data).

Comparison of our data to older Pismo clam population data suggests that densities and abundances of Pismo clams in southern California are approximately consistent with those recorded during the last 25 years. The strongest evidence to support this conclusion is provided by direct comparison of clam bed density with CDFW data from winter of 2008–2009 at corresponding SDC study sites. CDFW (2009) reported clam bed densities of 2.4 and 1.25 clams/m^2 during surveys at Coronado and Imperial, respectively. This is comparable to our two-summer mean of 2.0 ± 0.4 clams/m^2 at Coronado, but our four-year multi-season mean at Imperial (0.6 ± 0.2 clams/m^2) was less than half the previously reported density at that site. However, densities at Imperial were variable between 2017–2021, and the highest density of 1.48 ± 0.4 during winter of 2017 is comparable to the CDFW report. There is less directly comparable historic data for most other sites in southern California, but previous reports generally support our conclusion of a stable population in recent decades. The bed densities we observed at multiple locations in Huntington Beach and throughout Orange County were typically lower than those reported for Huntington Beach in 1991 (1.32 clams/m^2; Togstad 1991) but were nearly 10-times higher at BCSB N when a large recruitment cohort appeared in 2022. Pismo clam abundance ranged from three to 107 clams/m of shoreline (maximum at Scripps Beach in SDC) at four study sites during 2012–2013

(Dugan et al. 2015) and 32–770 clams/m at ~11 mainland sites in the late 1990s (Dugan et al. 2000). Median abundance was not directly reported in either case, but in 2012–2013 it appears to have been approximately 10–20 clams/m (Dugan et al. 2015). These previous total clam abundance data are within the range of our abundance estimates from southern California (0–4032 clams/m), but our median abundance (3.3 ± 17.2 clams/m) is much lower and we did not observe abundant legal-size clams, which were reported to be as high as 3.3 clams/m in 2012–2013 (Dugan et al. 2015). Overall, our data suggest there has been no dramatic change in Pismo clams population density or abundance throughout southern California in recent decades.

Older historic data from southern California are not readily comparable to the present study because most data was reported as fisheries take (e.g., clams/hr), but a general comparison of our observations supports the previously reported lack of recovery following the decline of the Pismo clam population in the 1980s (e.g., McLachlan et al. 1996). Prior to the 1980s, Pismo clam populations in southern California supported a robust recreational fishery; clammers in OC were estimated to take ~2,000–5,000 or more legal-size clams each year during single-weekend surveys in 1975–1977 at rates of 1.03–4.28 legal clams/hr (Knaggs et al. 1977). Although our survey methods are not equivalent to recreational fishing methods, we found only one legal clam during 26 days of surveys in OC, a catch rate of approximately ~0.01 clams/hr. Low catch per unit effort (~0.03 legal clams/hr) was also recently been measured at BCSB (N. Caruso et al., Get Inspired Inc., unpublished data). Additional sampling is necessary to provide a better estimate of comparable catch per unit effort, but it seems clear that the the southern California Pismo clam population is much lower than it was 40 years ago. We qualify these conclusions with an acknowledgement that study sites were haphazardly selected and these data may not be representative of areas we did not sample.

Size Distribution and Recruitment

Intertidal Pismo clam populations in southern California include a wide size distribution that varies greatly between counties, individual study sites, and over time. Based on established size-age relationships, clams in our study likely ranged from less than one year old to more than 10 years old (Coe and Fitch 1950; Marquardt et al. 2022). We observed large adult clams in both regions, but only 11 clams were large enough to enter the recreational fishery (>114 mm). Overall, the majority of clams we observed in southern California (~88%) were presumably first-year clams (< 25 mm), given their size and the typical summer spawning season of Pismo clams (Marquardt et al. 2022). However, a winter spawning season has been documented in Pismo clam populations in Baja California Sur, Mexico (S. Curiel-Ramirez, Universidad Autónoma de Baja California, unpublished data), therefore it is possible that the smallest clams we observed (5–10mm) in mid-summer are as young as six months old. A second spawning season was not observed when Marquardt et al. (2022) sampled clams north of Point Conception, but Pismo clams in southern California may be more reproductively similar to populations in Baja California Sur than central California, due to oceanographic similarities with the former.

Young clams were not observed on all beaches during all years and most were observed in 2022. Prior to 2022, ~74% of clams in OC were ≥ 25 mm and over 72% of clams were ≥ 35 mm, therefore we conclude that at least some recruitment occurred in OC throughout the past decade, despite the overall low density of clams in the region. We could not identify specific strong or weak year-classes because of the low density of clams in OC, our dispersed sampling effort over several years and across multiple beaches, and the fact that we did not age clams directly. We are also not aware of comparable historic size distribution data for Pismo clam populations in OC. In contrast to OC, only 24% of clams in SDC were ≥ 25 mm prior to 2022, albeit with nearly 13-times the total quantity (~10-times the bed density). However, the composition on individual beaches varied substantially, for example, mature clams ≥ 25 mm composed only ~16% of total clams on Silver Strand State Beach and ~90% on all other SDC beaches prior to 2022. During the mid-20th century, the demographic composition on La Jolla Beach, SDC, included ~30% mature clams (Coe and Fitch 1950), which is comparable to the overall composition in SDC prior to 2022. Likewise, Pismo clam populations at Imperial and Coronado Beaches were dominated by young clams in 2008, with a substantial number of large clams (> 110 mm) also present only at Coronado (CDFW 2009). This corresponds with our observations of high between-site variability in demographic composition.

Some of the most remarkable observations throughout the duration of our study are the magnitude of spatial and temporal variability of Pismo clam recruitment in southern California. During most years, newly recruited juvenile Pismo clams were undetected or only present in very low numbers at nearly all survey sites throughout southern California, except for what appeared to be consistent and anomalously high recruitment on SSSB between 2018–2021. However, our understanding of “high recruitment” changed in 2022 when we observed up to 36-times greater recruitment than ever before at beaches in SDC and OC. There is no record of Pismo clams having such high abundances as were observed in 2022 on SSSB, over 4,000 clams per meter of shoreline, composed of 95% small juveniles. These observations underscore what Tomlinson (1968) and others have described as the sporadic recruitment of juvenile Pismo clams, with substantial recruitment events occurring on the order of two decades (Shaw and Hassler 1989). The duration of our study falls well within this two-decade range, therefore we are uncertain whether 2022 represents a rare pulse of high recruitment, 2017–2021 represents a period of anomalously low recruitment at most sites, or if there is the possibility of even larger recruitment events. However, these six years of recruitment data allow us to conclude that substantial spatial and temporal variability in Pismo clam recruitment magnitude is still possible in southern California.

We tentatively conclude that the high recruitment detected in 2022 is indicative of a widespread recruitment event that may have occurred on beaches throughout much of southern California. We qualify this conclusion as tentative because we surveyed a limited number of long-term monitoring sites in 2022. However, we detected a clear signal of recruitment at two sites where we have repeatedly seen little or no recruitment in past years (BCSB N and NB Pier), and a corresponding increase in recruitment at our high-recruitment study site, SSSB HQ. We have not yet analyzed specific factors that could have influenced this recruitment pattern, but a spatially broad recruitment event may require favorable oceanographic conditions throughout southern California. We only failed to observe first-year clams in 2022 at two closely associated sites in LAC (Cabrillo Bath and Jetty), which were located on Pt. Fermin and experience different oceanographic conditions than beaches in Orange County (Noble et al. 2009). This widespread recruitment event was also notable because the first-year clams we observed in July 2022 likely settled as juveniles in late summer or early fall of 2021, following the summer spawning season (Marquardt et al. 2022). These juvenile clams were potentially exposed to oil contamination from the Pipeline P00547 Incident in October 2021, which spilled nearly 25,000 gallons of crude oil into San Pedro Bay (near the LAC–OC county line) and was then dispersed along the southern California coastline (CDFW 2021). It is unknown whether oil contamination impacted the southern California Pismo clam population, but comparison of 2022 data to our baseline data from previous surveys at BCSB N, NB Pier, and SSSB HQ (**Table 1** and **Fig. 2**), suggests little or no acute negative impact of this incident. Continued surveys at these and other sites will help us better understand the magnitude and breadth of the 2022 recruitment event and monitor potential long-term impacts of the Pipeline P00547 Incident.

Pismo clam recruitment to the intertidal beach habitat can also be localized at on smaller scales. The high density of adult clams at multiple study sites along ~16 km of coastline within the Coronado Embayment (i.e., Breakers, Coronado, SSSB N, SSSB HQ, SSSB S, and Imperial) provides indirect evidence of previous high recruitment throughout this area. Consistent high recruitment (or high survival of recruits) is likely influenced by several factors. One ultimate factor may be the oceanographic characteristics present in the lee of the Point Loma headlands, where the divergence of prevailing southerly currents causes upwelling, decreased temperatures, and increased productivity (Roughan et al. 2005). Also, highly restricted coastal access along the Naval Amphibious Base located immediately north of SSSB may protect large unfished Pismo clam beds that could be a local source of larvae and recruits. These factors may explain the general pattern of high recruitment and abundance of Pismo clams in this area of SDC.

Pismo clam recruitment can also vary in an even more localized manner, at the one to 10 km scale, even if that area is centrally located along a continuous stretches of suitable beach habitat. We observed high levels of recruitment within a ~0.5-km stretch of beach on SSSB during 2018–2020 while observing very few juvenile clams during nearly simultaneous surveys on three Coronado Embayment beaches that lie within 6.5–8.5 km to the north and 5 km to the south of SSSB. This was a surprising pattern because all these sites share the same littoral cell (Patsch and Griggs 2006) and the mean density of mature clams in the intertidal zone of SSSB (1.4–1.9 clams/m^2) was similar to the nearby low-recruitment beaches (0.5–1.8 clams/m^2) between 2018–2022. However, intertidal clam bed density may not provide an appropriate estimate of a Pismo clam population's reproductive capability.

It has been suggested that recruitment of Pismo clams is unrelated to stock size (McLachlan et al. 1996), but that may be a misinterpretation of Tomlinson's (1968) conclusion that recruitment was independent of the "stock size *subjected to sampling*". The fact that our sampling was limited to the intertidal beach area is an important caveat in this respect, because we did not assess subtidal clam beds (discussed more below), which can be home to a large number of adult clams (Fitch 1965). Differences in offshore clam abundance could contribute to the disparity in recruitment between specific beaches, especially if dispersal dynamics differ among the beaches. Nearshore circulation patterns and beach hydrodynamics can influence the spatial and temporal variation in larval recruitment (Shanks et al. 2010, Morgan et al. 2018). For example, benthic streaming can be an important cross-shore transport mechanism for negatively buoyant larvae and may differ between beaches (Morgan et al. 2017). Pismo clam larvae have also been described as negatively buoyant and "benthic or near-benthic" by three days post-fertilization (Shaw and Hassler 1989), which corresponds with recent observations of Pismo clam larval development and metamorphosis (I. Jacobson, et al., Holdfast Aquaculture LLC, unpublished data). In addition, the general pattern of water circulation in the Coronado Embayment is anti-cyclonic and of low magnitude (Roughan et al. 2005), which could carry larvae from protected naval waters southward to SSSB without advecting them away from the Coronado Embayment. These are speculative hypotheses, but the magnitude and variation in recruitment within the Coronado Embayment presents an opportunity to further investigate these processes.

Monitoring Considerations

The task of monitoring infaunal clams includes inherent challenges, weaknesses, and strengths, regardless of which monitoring method is applied. The standard CDFW survey method we employed during the present study is labor intensive; we estimate our field volunteers excavated, transported, and sieved over 2.5 million lbs of sand during the 6-year study period. This provides a logistical challenge when attempting to monitor a large number of beaches across the region. However, the wide geographic extent of our study and the study by CPSLO can serve as a foundational “snap-shot” that can be built upon with repeated sampling of “indicator” beaches and other occasional surveys across the broader region.

The across-shore transect method we employed also has an inherent weakness if used to survey low-density Pismo clam populations; it is difficult to delineate the inshore edge of a clam bed, which is necessary if calculating bed density for comparison to historic data. This weakness likely impacted our estimates of bed density at many low-density beaches in southern California but may not have been a problem on high-density beaches. Protocol modifications that increase sampling effort (i.e.,additional excavation) can help mitigate this weakness while surveying low-density beaches, but alternative methods of sampling may be necessary to effectively assess the presence and density of Pismo clams on some beaches. For example, Miller et al. (1975) combined transect sampling and 15-minute timed-digs to improve their ability to assess the abundance of rare large clams in the lower intertidal zone. Alternatively, this weakness can be minimized if the data is converted to clam abundance per meter of shoreline instead of bed density, as used in other large-scale beach monitoring projects (e.g., Dugan et al. 2015). Therefore, we recommend future studies that use similar transect methods report abundance statistics in addition to bed density.

The greatest weakness associated with this and nearly all previous assessments of Pismo clam populations is the failure to survey subtidal clam beds, although rare exceptions to this weakness exist (e.g., Greene 2015; Richards and Whitaker 2015). Miller et al. (1975) quotes a 1975 personal letter by J. Fitch describing offshore Pismo clam beds throughout central and southern California that are “so dense they represent nearly virgin stocks”. However, the current extent of subtidal Pismo clam beds along mainland southern California is undescribed. We presume at least some subtidal beds exist because we have received anecdotal reports of subtidal clam beds from local citizens and we observed recreational clammers collecting legal-size clams just outside the surfzone on some beaches. Further description of these beds will be necessary to fully understand the Pismo clam population status because they could be a source of reproductive output or a sink for larval settlement or ontogenetic transport.

Despite the fact that large subtidal beds of adult clams do not necessarily equate to high levels of local recruitment, as was previously observed in Zuma Beach (Fitch 1965), their potential as a source of reproductive output necessitates consideration. Also, subtidal beds could directly receive recruitment of young clams or be a sink to which clams are slowly transported after beginning their benthic life in the intertidal zone. Year-over-year reduction of Pismo clam cohorts in the intertidal zone has been previously attributed to mortality (e.g., Coe and Fitch 1950; Fitch 1950) and others have suggested a process of ontogenic offshore transport of Pismo clams (Herrington 1929), but no clear evidence has been presented to support either claim. In the present study, large recruitment cohorts were sometimes recognizable as a distinct size class within the intertidal zone at the end of their second-year (e.g., on SSSB in 2018–2019), while in other years second-year cohorts were not easily distinguished. We do not know whether these “missing” cohorts had been transported offshore or died, and therefore cannot know their potential contribution to the adult population. The role subtidal beds play in the ecology and life history the Pismo clam must be better known before the status of the Pismo clam population can be thoroughly understood.

In contrast to the aforementioned challenges and weaknesses, the CDFW method is well-suited for monitoring Pismo clam recruitment; the intensive sampling and sieving through small mesh enables clams as small as 5 mm to be observed. It is not known if recruitment is limited to the intertidal zone being surveyed, but we are hopeful that intertidal surveys provide an accurate indication of recruitment at the beach being surveyed, or possibly more broadly. This method is also valuable because it can be used to track intertidal population trends at repeatedly-surveyed study sites and enables comparisons across several recent studies. Given these strengths, we encourage the continued use of the CDFW transect methods to provide comparable long-term monitoring data, but we also suggest additional methods be used to supplement its inherent weaknesses.

Management Considerations

Managers face a difficult task when attempting to determine the status of the Pismo clam population, the sustainability of the current recreational fishery, or the effectiveness of current management strategies. Challenges include but are not limited to the sparse availability of population status data, unknown population connectivity, and minimal fishery data. Here, we reflect on these challenges and provide thoughts and recommendations to help guide efforts to conserve the Pismo clam.

As previously discussed, collection of Pismo clam population status data has been limited in recent decades. A combination of the data presented here and data reported by CPSLO (reviewed by CDFW 2022), should help fill this gap and provide a strong foundation upon which future population assessment plans can be built. Spatial and temporal variability in population density and recruitment will be a necessary consideration when planning future monitoring. We recommend that a subset of high-density and low-density locations from multiple regions be included in any monitoring plan; this should include locations in each region or county, at sites where past data is available for comparison. The CDFW transect protocol should be used to monitor the intertidal population and recruitment annually during the summer months (to minimize the influence of any seasonal varability). It will also be helpful to use alternative survey methods to more effectively assess the abundance and size distribution of larger clams which occur at lower densities and may be under sampled by the CDFW transect method. Large-clam surveys could occur less frequently (e.g., every five or more years) as long as the sampling method enables the identification of peaks or gaps in the size distribution throughout the time period between surveys. The location, description, and monitoring of subtidal clam beds should also be considered a high priority. This combination of monitoring efforts should be coordinated between management agencies and academic researchers and will enable the identification of trends or acute changes that may necessitate management changes and will inform our overall understanding of the species.

Our limited understanding of the early life history and population connectivity of Pismo clams is another major knowledge gap. Pismo clam life history includes a pelagic larval stage that lasts approximately three weeks, which led Coe (1947) to suggest possible dispersal distances as far as 150 km. However, the behavior of larvae has the potential to greatly influence larval dispersal and population connectivity (Cowen and Sponaugle 2009), and the “benthic or near-benthic” behavior of larvae (Shaw and Hassler1989) may substantially reduce dispersal distances. The demographic connectivity and population genetic structure of Pismo clams is currently unknown, but we suspect limited demographic connectivity between regions, especially where oceanographic conditions may limit exchange (e.g., north and south of Pt. Conception). A good understanding of metapopulation structure, especially demographic connectivity, is necessary for effective spatial management of fishery species (Kritzer and Sale 2004), and Pismo clams are no exception. Therefore, we recommend additional research be directed towards filling the knowledge gap of Pismo clam early life history and population connectivity.

Finally, managers are also challenged by the general scarcity of Pismo clam fishery data. The limited stock of legal-size clams in southern California could quickly become diminished without the knowledge of managers because recreational fishing can rapidly deplete Pismo clam stocks (Fitch 1950). Therefore, we recommend managers attempt to collect data on legal and illegal fishery catch. It may be feasible to use catch “report cards”, similar to other recreational fishery species (e.g., spiny lobster). We also suggest that managers reconsider the bag limit for this species because there is clear evidence that Pismo clam populations still have not recovered after major population declines of the late 20th century, yet bag limits (10 clams per person) have not changed since 1948 (McLachlan et al. 1996). Together with continued monitoring and improved understanding of Pismo clam population connectivity, the collection of additional Pismo clam fishery data and a cautious management approach may help ensure the conservation and sustainability of this once-iconic fishery species.

Conclusion

Our objective was to gain insight into the present day status of the Pismo clam, a once-iconic recreational fishery species whose presence has diminished in the scientific literature and the minds of Californians over the past several decades. After six years of surveys, we conclude that the Pismo clam is still present in the intertidal zone of many beaches in southern California, but typically at very low densities. Population trajectories were difficult to assess during the study period, but appear generally stable when compared to limited data reported over the past three decades. There is also ample evidence that recruitment has been occurring throughout southern California, with great variability between regions, sites, and years. However, our observations also suggest the Pismo clam population in southern California is still greatly reduced compared to the pre-1980s population. Continued monitoring, additional life history and population connectivity research, and increased collection of fishery data are needed to better understand Pismo clam populations and help support their conservation in southern California.

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