

PISMO CLAMS (*TIVELA STULTORUM*) IN CALIFORNIA: POPULATION STATUS, HABITAT
ASSOCIATIONS, REPRODUCTION, AND GROWTH

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Population Status, Habitat Associations,
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ABSTRACT

Pismo Clams (*Tivela stultorum*) in California: Population Status, Habitat Associations, Reproduction, and Growth

Alexandria Rebeckah Marquardt

Marine shellfish play a vital role in intertidal ecosystems and coastal communities, but many of these fisheries are small-scale and lack the necessary monitoring to ensure long-term sustainability. Effective management often requires information on key demographic parameters, such as population status, reproduction and growth. Pismo clams (*Tivela stultorum*) are a culturally important and iconic species in California, which supported a thriving commercial and recreational fishery throughout much of the 1900's. However, Pismo clam populations have declined statewide in recent decades and are attributed to human harvest and predation by California sea otters (*Enhydra lutris*); However, no studies have examined their populations, population drivers, or life history for at least 40 years. Managers require updated and expanded information on populations, habitat associations, reproduction and growth rates to effectively manage, regulate, and recover Pismo clam in California.

In Chapter 1, we investigated current Pismo clam population levels in California and examined the role of abiotic and biotic factors as correlates of clam abundance. We quantified Pismo clam presence, density and biomass at 38 sites in California during 2018 and 2019. Our results indicate that while human population density does not appear to drive clam populations, median sediment grain size is an important predictor for Pismo clams on open coast beaches. As median grain size increases, the probability of clam presence, density, and biomass decreases, suggesting that the composition of beach habitat is a critical factor regulating Pismo clam populations. Additionally, clam density and biomass are significantly higher on beaches north of Point Conception compared to beaches south. This suggests that Pismo clam population declines are more complicated than conventional wisdom suggests. Overall, Pismo clam densities are lower and size structures are shifted towards smaller sizes than historical accounts. This study is the most comprehensive set of population surveys to date and identifies key factors associated with Pismo clam abundance, which may be used to inform management and guide restoration and recovery of this once iconic species.

In Chapter 2, we examined life history characteristics of Pismo clams in California. Specifically, we investigated the annual reproductive cycle of Pismo clams in California, pairing multiple metrics within a single study to describe the sex ratio, gonad development stages, body condition index, and length at sexual maturity. Further, we examine age-length relationships across California to provide estimates of age structure and growth rate, which will better inform recovery timelines for the recreational fishery in California. Our results indicate that the sex ratio is 1:1, peak spawning occurred in late summer, and clams can spawn in their first year (<20 mm). Cycles of body condition were influenced primarily by mean monthly sea surface temperature, but mean monthly chlorophyll-a concentration, photoperiod, clam size, and year were also important. Body condition was significantly correlated with the proportion of clams in the Ripe stage. Thus, body condition has the potential to be a rapid, inexpensive proxy for monitoring reproduction in Pismo clams, potentially providing useful information about changes in reproductive patterns. Finally, examination of age-length relationships for Pismo clams suggest that clams may require over 13 years to reach a legally harvestable size (114 mm across most of California). The estimated age at legal size is substantially older than historical estimates, which suggested that Pismo clams could reach legally harvestable size in as few as 6 years.

Collectively, this work represents a significant advance in our knowledge of the biology and ecology of this iconic and culturally important species. Furthermore, it provides vital information on the current population status, reproduction, and growth rates to inform management, regulation, and potential recovery of Pismo clams in California.

Keywords: Pismo Clam, Population Status, Reproduction, Histology, Growth, Management

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Research requires a community.

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Chapter 1

PISMO CLAM DISTRIBUTION, ABUNDANCE, AND DRIVERS OF POPULATION VARIABILITY ACROSS CALIFORNIA

1.1 INTRODUCTION

Marine shellfish play an integral role in intertidal ecosystems and coastal communities. Bivalve shellfish, in particular, provide important ecosystem services that improve water quality by filter feeding suspended particulates, regulating primary productivity and harmful algal blooms, and aiding nutrient cycling in marine systems (Newell 2004, Vaughn & Hoellein 2018, van der Schatte Olivier et al. 2018). Further, shellfish cultivation and harvest is central to many coastal communities on the West Coast of the United States (Norman et al. 2007). Harvest of wild shellfish stocks provide millions of dollars in revenue and jobs in coastal communities on the West Coast (Norman et al. 2007, Northern Economics, Inc. 2009, 2013, Dyson & Huppert 2010). Similar to finfish fisheries stocks, these wild caught shellfish need to be carefully managed to minimize overexploitation and fisheries collapse. Sustainable management of these fisheries therefore require accurate understanding of the population dynamics and habitat requirements, especially for small-scale fisheries which are particularly at risk of overexploitation and human disturbance (Perry et al. 1999).

Fishing pressure has shifted down food webs and made the harvest of invertebrates increasingly lucrative; however, emerging invertebrate fisheries are often data deficient, which complicates their long term sustainability (Pauly et al. 1998, Anderson et al. 2008, 2011, FAO 2009, Rogers-Bennett & Juhasz 2014). Though once considered resistant to overexploitation, there are many examples of overharvest and depletion of invertebrates (Jamieson 1993, Roberts & Hawkins 1999, Andrew et al. 2002, Kirby 2004, Berkes et al. 2006, Lotze 2006). Sustainable invertebrate fisheries management is hindered by data gaps on population trends, estimates of harvest pressure and catch, and basic life history parameters. Recreational fishing can negatively impact populations of targeted fisheries species, but often lack the data quantity and quality available for commercial fisheries, making it difficult to quantify impacts (Jackson et al. 2001, Cooke & Cowx 2004, 2006). In the absence of concrete data, recreational fisheries are often

managed with minimum size limits, theoretically allowing individual animals to spawn for several years before being harvested or by using information from similar species as a proxy (Jamieson 1993). Further, management decisions are based on the assumption that similar species and life histories are static. Without data on current population trends and life history traits, shellfish management efforts that seek conservation, restoration, and sustainability become more complicated and largely guesswork (Kraeuter & Castagna 1989, Dame 1996, Dame et al. 2002).

An excellent example of an iconic invertebrate fishery within California is the Pismo clam (*Tivela stultorum*). Pismo clams are found in sandy intertidal habitats from Monterey Bay, CA through Baja California, Mexico and were once a dominant macrofauna species (Fitch 1950). Pismo clams have been utilized for human consumption for thousands of years on the California coast, were harvested by coastal Chumash tribes for sustenance, and supported thriving commercial and recreational fisheries in California during the 1900's (Bureau of Marine Fisheries 1949, Frey 1971, Jones et al. 2002, Thakar 2012). An estimated 6.25 million pounds of Pismo clams were harvested for commercial sale in California from 1916 to the closure of the commercial fishery in 1947 and a strong recreational fishery was central to coastal communities in central and southern California until at least the 1980's (Bureau of Marine Fisheries 1949, Shaw & Hassler 1989). Efforts to manage this fishery included size limits (at least 114mm/4.5in), bag limits (10 per person per day), harvest closure zones, and out planting (Fitch 1950, 14 C.C.R. § 29.40). Despite these regulations, Pismo clam populations have declined statewide (Shaw & Hassler 1989).

Conventional wisdom and previous work posit that human exploitation and predation by California sea otters (*Enhydra lutris*) are the two primary drivers of Pismo clam population declines within California (Pattison & Lampson 2006). Total recreational take is unknown, however recreational harvest in the mid-1900's greatly exceeded historic commercial take (Frey 1971, Shaw & Hassler 1989). Intense recreational fishing has been documented on many beaches in California and could contribute to the decline of Pismo clams across their range (Knaggs et al. 1976, Shaw & Hassler 1989). In contrast, the impact of California sea otters is primarily limited to areas north of Point Conception. California sea otters recolonized the Pismo

Beach area in the late 1970's after being nearly hunted to extinction in the 19th century (Kenyon 1969). Their return was associated with a further decline in the abundance of Pismo clams in the region (Miller et al. 1975, Wendell et al. 1986). Numbers of recreationally harvested clams on Pismo Beach plummeted from an estimated 350,000 in 1978 to zero in 1983 following the return of otters (Wendell et al. 1986). Despite these findings, there is limited data to assess the hypotheses of human or sea otter driven decline, and little information on the current status of Pismo clam populations in California generally.

Historically, research and monitoring of Pismo clams in California has been limited spatially and temporally, and does not consider relevant environmental parameters in driving population trends. Past work focused on commercial and recreational fishing hot spots, such as Monterey Bay, Pismo Beach, and La Jolla, where clams were large and population sizes abundant. Nearly all published data is over 40 years old and comes from historically high density locations, which may not be representative of statewide trends (Weymouth 1922, Herrington 1929, Fitch 1950, Stephenson 1974, Knaggs et al. 1976, Steinbeck 1979). Furthermore, persistence of wild shellfish stocks are influenced by a combination of biotic and abiotic factors (Kraeuter & Castagna 1989). Oceanographic conditions, such as temperature, primary productivity, and local beach dynamics, interact with biological factors, such as predator presence and anthropogenic impacts, to influence successful recruitment, growth, and survival of many marine organisms, including native shellfish stocks (Miller et al. 1975, Wendell et al. 1986, Alexander et al. 1993, McLachlan et al. 1995, de la Huz et al. 2002, Blanckenhorn & Demont 2004, Manyak-Davis et al. 2013, Peterson et al. 2014, Fiori & Carcedo 2015, Schooler et al. 2019). In order to successfully develop a fisheries management plan for Pismo clams in California, it is necessary to understand the statewide population demographics and identify key factors associated with high densities and sizes of Pismo clams. Yet, to date, there has never been a state-wide survey for Pismo clams that includes low-abundance beaches and no studies consider the influence of factors aside from human harvest and otter predation in driving patterns of Pismo clam abundance. This limits our ability to understand the relative importance of other key factors that may influence population trends, which could inform management (e.g., updated

population data for accurate stock assessments) and conservation efforts (e.g., enacting harvest closures for beaches with important source populations, etc.). California Department of Fish and Wildlife has limited resources and personnel available to assess this fishery, thus management actions have remained static in the absence of recent biological, ecological, and fisheries information.

This study seeks to address these data gaps, which is necessary to inform Pismo clam management and conservation efforts. Specifically, this study aims to: 1) determine the status of Pismo clam populations across California; and 2) identify key factors associated with Pismo clam presence, abundance, and biomass.

1.2 METHODS

1.2.1 Study Areas

We conducted surveys at 38 different beach locations from Monterey Bay, CA to the California-Mexico border in 2018 and 2019 (Fig. 1.1, Fig. 1.2). The majority of surveys occurred in summer months from June to August during strong low tides (greater than -0.5ft/-0.15m mean low low water [MLLW]). We selected survey locations using several methods. Sites were chosen based upon 1) historical occurrence of Pismo clams; 2) recent documentation of Pismo clam presence on iNaturalist (<https://www.inaturalist.org>); 3) presence of appropriate sandy beach habitat based upon aerial imagery; and 4) even spatial distribution of sampling sites across their range in California, including many locations that had not been previously surveyed.

1.2.2 Survey Methodology

We used a modified version of the California Department of Fish and Wildlife's Pismo clam survey methodology (Evans & van Meeuwen 2013). At each location, the field crew generally surveyed three parallel transects (one site had two transects and four sites had four transects due to available personnel). We ran transects perpendicular to the ocean starting at the high water mark and extended transects as far into the surf as possible. Crews segmented each transect into 3 m sections, individually excavated each section in a 23 cm (9 in) wide strip, allowing us to estimate clam density per unit area. The inland end of the transect was defined by two consecutive sections (6 m) without clams. Crews sieved the sediment through ¼ in wire

mesh to capture all clams present (usually ≥ 10 mm). Density estimates incorporated sections starting at the first clam identified for each transect. As part of a related project, we also collected clams across a range of sizes from several sites and used these collections to generate a length-weight relationship. We used this relationship to estimate the average biomass of clams (g m^{-2}) for all clams present in each survey.

1.2.3 Abiotic and Biotic Factors

Anthropogenic impacts on beaches can have negative impacts on intertidal habitats via poaching, pollution, beach compaction, beach management practices, among many others (Defeo et al. 2009, Sheppard et al. 2009, Schlacher & Thompson 2012, Peterson et al. 2014, Schlacher et al. 2016, Schooler et al. 2019). Human population density is often used as a proxy for anthropogenic impacts in coastal systems, including harvest, pollution, and habitat modification (Steele 1998, Mora et al. 2011). Therefore, we obtained the human population density in a 10 km radius from each survey location from ArcGIS online (Esri Updated Demographics 2019). Human population density was transformed using a square root transformation to improve normality.

California sea otter predation may also influence Pismo clam population sizes (Miller et al. 1975, Wendell et al. 1986). To identify potential associations between the presence of California sea otters and clam populations, we split the survey area into two regions: north and south of Point Conception. Otters are typically only found north of Point Conception, except small populations in the westernmost part of the Santa Barbara Channel where we did not survey (Lafferty & Tinker 2014, Tinker et al. 2017). This regional delineation is also associated with differences in oceanographic conditions across the study area which influence patterns of species abundance (Hall 1964, Horn & Allen 1978, Blanchette et al. 2008). Otters can impact prey populations by decreasing overall abundance, as well as lowering median sizes through size specific predation (Stevenson et al. 2016).

Generally, sandy beaches range across a continuum of low energy, dissipative beaches (characterized by finer sediments and gentler slopes) to high energy, reflective beaches (characterized by coarser sediments and steeper slopes) (Short 1996, McLachlan & Dorvlo 2005,

Fiori & Carcedo 2015). Organisms in the sandy intertidal experience a stressful environment dominated by wave energy and sediment instability (Alexander et al. 1993, McLachlan et al. 1995, de la Huz et al. 2002, Fiori & Carcedo 2015, McLachlan & Defeo 2018). Since sediment characteristics influence sandy intertidal organisms, we collected a sediment sample from each site to measure median grain size (mm) following ASTM # D6913 (ASTM International 2004). Sediment samples contained a vertical strip of the top 20cm of sand, which corresponds to the typical burrowing depth of Pismo clams (Shaw & Hassler 1989).

Individuals at northern latitudes often reach older ages and larger sizes (Bergmann 1847), which has been documented in terrestrial and marine systems (Blanckenhorn & Demont 2004, Ruttenberg et al. 2005, Caselle et al. 2011, Manyak-Davis et al. 2013). While cooler waters typically have higher primary productivity and thus food availability for bivalves, warmer waters are associated with faster growth rates (Hall et al. 1974, Behrenfeld et al. 2006, Moura et al. 2013, van de Poll et al. 2013). To assess the influence of these factors on clam abundance, we obtained remote sensed satellite data for average Sea Surface Temperature (SST) and average Chlorophyll-a (Chl-a) concentrations in the nearest 4 km grid for each site from 2014-2018 (AVHRR Pathfinder, MODIS and NASA GES DISC 2015). Since the majority of clams identified during surveys were less than 5 years old (A. Marquardt unpub. data), this five year period represents typical conditions experienced by current clam populations.

1.2.4 Statistical Analysis

To examine the influence of abiotic and biotic factors on clam populations, we used a two-tiered approach utilizing generalized linear mixed effects models (GLMM). GLMMs are optimal for these analyses due to their ability to account for nested structure, such as transects within sites. First, we implemented a logistic mixed effects model to identify key environmental characteristics that best explain clam presence. The response variable was the presence or absence of Pismo clams for each transect within each site (n = 38 sites). The predictor variables included square root of human population density, region, median sediment grain size, average Chl-a and tidal height (ft). Tidal height was included to identify potential detection biases due to differences in accessible beach area. We considered average SST as a predictor variable, but

removed it from the models due to high correlation with Chl-a and region. Site was treated as a random effect.

Then, we used a GLMM to assess the relationship between environmental parameters and clam density and biomass at sites where clams were present. Using the same set of predictor variables, we ran a GLMM with the average density of clams (m^{-2}) at least 35 mm in length as the response variable. Clams 35 mm and larger have survived their first year and are generally reproductively mature (Coe 1947, A. Marquardt unpub. data). California sea otter minimum handling size for Pismo clams is estimated at 50 - 60 mm, however they are known to eat prey items as small as 10 mm (Estes & Vanblaricom 1985, Wendell et al. 1986, Tinker et al. 2008, Maldini et al. 2010). This size threshold conservatively includes all clams that are or may grow into a size class that is available for otter predation. We ran a second GLMM using the average clam biomass ($g\ m^{-2}$) using all clams at each site as the response variable. We used the natural log plus one of average clam biomass to improve normality in the biomass data. We selected the most parsimonious models using likelihood ratio tests and backward elimination (Zuur et al. 2009). Then, we compared models using Akaike's information criteria for small sample sizes, AICc (Burnham & Anderson 2002), and considered models within two $\Delta AICc$ to be strongly supported. For each supported model, we determined that a predictor variable had a strong effect if the 95% confidence interval (95% CI) did not overlap zero. Parameter estimates and 95% CIs in the results section are from the highest ranked model where the parameter had a strong effect. We calculated the marginal and conditional R^2 for the most parsimonious models to evaluate goodness-of-fit (Nakagawa & Schielzeth 2013). Marginal R^2 provides the percent deviance explained by both fixed and random effects (R^2_m) and the conditional R^2 provides the percent deviance explained by soley fixed effects (R^2_c). We calculated the intraclass correlation coefficient (ICC) for the most parsimonious model. The ICC is a repeatability index, which describes the accuracy and similarity of observations within groups (Nakagawa & Schielzeth 2010). Analyses were completed in the lme4 package and R Studio version 3.5.3 (Bates et al. 2015, R Core Team 2019)

1.3 RESULTS

1.3.1 Population surveys

Our surveys included 15 sites north and 23 sites south of Point Conception; 27 sites had clams present (Fig. 1.1). Average clam densities (≥ 35 mm) across sites was 1.1 clams m^{-2} (\mp 0.34 SE) and average biomass was 30.9 g m^{-2} (\mp 8.2 SE) however clam density and biomass varied considerably across the survey area (Fig. 1.1, Fig. 1.2). For example, we found higher average densities and biomass in the northern region compared to the southern region (Fig. 1.3). Since otter predation may impact the overall size structure of clam populations by preferentially removing larger individuals, we pooled all available clam size data for each region and subset the data to include only the upper quartile range (Choat & Robertson 2002, Ruttenberg et al. 2005). We did not find a significant difference in clam sizes between the two regions (Welch's T-test: $t = -0.54$, $df = 104.9$, $p = 0.6$).

1.3.2 Presence/Absence

Median sediment grain size had a significant effect on clam presence (Table 1.1). Our survey locations contained median sediment grain sizes ranging from 0.12 - 1.25 mm. Both strongly supported models included median sediment grain size as a significant parameter (Table 1.1). On average, we expect to see a 9.9% decrease in the odds of clams being present on a beach with a 0.1 mm increase in grain size ($\beta = -78.695$, 95% CI = -254.49, -21.85). As median sediment grain size increased, the probability of clams being present on a given beach declined sharply, especially at median grain sizes above 0.3 mm (Fig. 1.4). Clam presence was associated with higher concentrations of Chl-*a*, however this was not a significant parameter in our models ($\beta = 0.9784$, 95% CI = -0.889, 9.06).

1.3.3 Density

The top models for clam density indicate that median sediment grain size, region, and low tide value influenced density (Table 2). Similar to clam presence, clam density declined as sediment became more coarse ($\beta = -11.06$, 95% CI = -21.27, -0.84). Northern sites had, on average, higher clam densities than southern sites (region (ref. North): $\beta = -1.56$, 95% CI = -2.49, -0.617). Clam density was generally higher when surveys occurred during stronger, negative low

tides, but this effect was not significant ($\beta = -1.24$, 95% CI = -2.59, 0.11). Within sites there was a high degree of similarity in clam density between transects (ICC = 0.94). In the most parsimonious model, the fixed effects explained 30.3% of the variance observed and the entire model explained 95.5% of the variance observed ($R^2_m = 0.303$, $R^2_c = 0.955$).

1.3.4 Biomass

Among the top models for clam biomass, median sediment grain size, region, and low tide value influenced biomass (Table 3). Specifically, clam biomass decreased as sediment became more coarse ($\beta = -9.1867$, 95% CI = -16.87, -1.50). We expect to see a 9.9% decrease in clam biomass for each 0.1mm increase in median grain size. Southern sites typically had 77.9% less clam biomass when compared to northern sites ($\beta = -1.5089$, 95% CI = -2.22, -0.80). Clam biomass was generally higher for stronger, negative low tides, however low tide value did not have a significant effect on biomass ($\beta = -0.7297$, 95% CI = -1.76, 0.27). Within beach sites there was a low degree of similarity in clam biomass between transects (ICC = 0.36). In the most parsimonious model, the fixed effects explained 22.8% of the variance observed and the entire model explained 48.1% of the variance observed ($R^2_m = 0.267$, $R^2_c = 0.517$).

1.4 DISCUSSION

This study represents the first comprehensive examination of the status of Pismo clams across their range in California. We identify several factors that correlate with clam presence, density, and biomass. Our findings suggest that sand grain size has a strong effect on the probability of Pismo clam presence, such that beaches with larger grain sizes have lower probabilities of clams being present. Pismo clams appear to be absent on beaches with coarser grain sizes (0.5 - 1 mm). There are significant regional differences in clam density and biomass; beaches north of Point Conception typically have higher clam densities and biomass than beaches to the south. Our top GLMMs also included low tide value, however it was not a significant predictor of clam density or biomass.

1.4.1 Evaluating the Conventional Wisdom

The two leading hypotheses for Pismo clam declines in California have been predation by California sea otters (Wendell et al. 1986) and human harvest (Pattison & Lampson 2006). Our

final models found an effect of region, our proxy for otter presence, on clam abundance and biomass. However, our models indicated that beaches in the northern region, where otters are present, have higher clam abundance and biomass on average than beaches in the southern region, where otters are absent. Interestingly, across the species range in California, this pattern is the opposite of the conventional wisdom which predicts sea otter foraging reduces clam populations. Additionally, we did not find evidence that otter foraging north of Point Conception has caused a shift towards smaller Pismo clam sizes. Point Conception, the geographic delineation between the northern and southern regions, is associated with known differences in oceanographic conditions, where the temperature is generally lower and productivity higher in the northern region compared to the southern region (Hall 1964, Horn & Allen 1978, Blanchette et al. 2008). These regional patterns could influence clam abundance and biomass if colder, more productive waters increased clam abundance. However, some sandy beaches in central Baja California, Mexico have very high abundance of large Pismo clams (Ruttenberg, pers. commun.), where waters are warmer and productivity is typically lower than southern California (Hall 1964, Legaard & Thomas 2006, Blanchette et al. 2008). At broad scales our data suggests that oceanographic conditions across the range of the species may not be a major driver of Pismo clam presence, density, or biomass. Some localized areas in Baja California have intense upwelling similar to beaches north of Point Conception (Blanchette et al. 2008) and would be ideal locations to investigate the role of ocean productivity in driving Pismo clam populations within a region where other conditions are similar (e.g., human population and ocean temperature).

We did not find evidence that human population density, a proxy for human disturbance and other anthropogenic impacts, influences clam presence, abundance, or biomass on beaches in California. However, human population density may not necessarily capture the complexity of anthropogenic impacts in coastal systems. Urban ecology research often uses proxies and broad, aggregate variables to assess human impacts, nevertheless these parameters are unable to decipher underlying mechanisms, since anthropogenic impacts rarely occur in isolation (McDonnell & Hahs 2013, Schlacher et al. 2016). Coastal beach use varies spatially and different

types of anthropogenic disturbance can have distinct impacts on coastal ecosystems (Steibl & Laforsch 2019). For example, tourist inhabited islands and local resident inhabited islands both experience negative anthropogenic impacts, although the impacts differ. Tourist islands showed a decrease in abundance of hermit crabs (*Coenobita rugosus* and *C. perlatus*), whereas local resident islands showed a decrease in body sizes (Steibl & Laforsch 2019). The southern California region, specifically, is a highly urbanized area and nearly half of beaches are highly disturbed by regular, mechanized maintenance regimes (Dugan et al. 2003, Patsch & Griggs 2006). Central California is less urbanized and does not have the same intensity of beach disturbance, which may be driving the regional differences we observed in clam densities. Throughout Baja California human population densities are typically lower than central and southern California, and Pismo clam densities are high enough to support active subsistence and small-scale commercial fisheries (McLachlan et al. 1996). Together, these findings suggest that local scale anthropogenic impacts may be important, although we do not know the direct mechanisms driving the patterns observed in Pismo clams from this study. It is possible that different factors are controlling Pismo clam populations across regions (north vs. south of Point Conception and Baja California). Future research will need to address multiple spatial scales, both within regions and transboundary research comprising the entire range of the species, to disentangle regional effects controlling Pismo clam populations.

1.4.2 Sediment is Habitat

Our analyses identified that median sediment grain size is an important parameter for clam presence, density and biomass, as has been found for other sandy intertidal invertebrates (McLachlan 1996, Fiori & Carcedo 2015). Beach characteristics are influenced by a variety of factors including sediment regime, wave energy, currents, geology, and a range of anthropogenic impacts. For example, sediment grain size and wave exposure predictably influence beach slope, where larger grain sizes and higher wave exposure result in steeper beaches (Short 1996, McLachlan & Dorvlo 2005, McFall 2019). Physical conditions often act as a constraint for species, where sediment characteristics influence reburial time, survival and predation risk (Nel et al. 2001, de la Huz et al. 2002, Defeo & McLachlan 2005, Fiori & Carcedo 2015). Some species are

substrate generalists, able to persist across a range of sediment conditions, while others are substrate specialists, having a limited range of sediment conditions they can survive in (Alexander et al. 1993, Fiori & Carcedo 2015). For example, yellow clam (*Amarilladesma mactroides*) populations are absent at sites with high proportions of coarse sand and are most abundant at sites with fine sediments (Fiori & Carcedo 2015). Our results suggest that Pismo clams in the intertidal habitat prefer a specific range of sand grain sizes corresponding to beaches with moderate wave energy and median sediment grain sizes below 0.5 mm.

Furthermore, sediment characteristics on beaches can be heavily impacted by human alterations to beach habitats. Many beaches in Southern California undergo intensive, mechanized maintenance regimes, which negatively impact habitat quality (Dugan et al. 2003, Patsch & Griggs 2006, Peterson et al. 2014, Schooler et al. 2019). Urban beaches in California that undergo these intensive practices may have half as many macroinvertebrate species, reduced species richness, and reduced biomass compared to beaches that do not receive intensive management (McLachlan 1996, Schooler et al. 2019). Our data found lower clam abundance at more urbanized beaches in southern California than beaches in central California. Southern California beaches are more urbanized and experience a greater intensity and variety of anthropogenic impacts (e.g., beach maintenance, sand compaction, and pollution). However, we do not have information on the level of beach nourishment or intensive beach management practices across California and therefore cannot examine the impact of these specific activities on habitat quality for Pismo clams. Generally, these regional differences may be influenced by differences in anthropogenic impacts and management of sandy intertidal beach habitats, as well as the morphodynamic characteristics of the beachscape.

1.4.3 Fisheries Assessments and the Future of Pismo Clams

To put our data into a fisheries context, we sought to examine population abundance both by numerical density and biomass. Interestingly, models that examined density explained a larger portion of the variation among sites and had higher similarity among transects within sites compared to the model for biomass. This may be due to a small number of larger individuals at low density sites, which increase the variance in biomass among transects within sites. This

uneven distribution is different from the assumptions that underlie most traditional fisheries stock assessment models, making it difficult to apply to invertebrate fisheries, particularly sessile organisms that are patchily distributed (Perry et al. 1999). Furthermore, many invertebrate fishery species do not have the necessary quantitative information, such as growth rates, reproduction, population trends, catch and effort rates, or geographic ranges, to effectively conduct stock assessments (Anderson et al. 2008). The challenge is that data acquisition occurs slowly and is prioritized for economically and socially valuable species (Chen et al. 2003, Anderson et al. 2008), thus leaving low abundance, low value, or exploited species without active monitoring or management.

Pismo clam populations have declined throughout California despite a legal size that should significantly reduce fishing pressure. Unfortunately, historical records are not comparable to our current methodology and do not report clam population density estimates. However, we know that recreational harvest was intense on many beaches in California, indicating high densities of large individuals. For example, during a 2.5 month period in 1949, Pismo Beach had an estimated 5,000 recreational clammers per day with cumulative harvest estimated at 2 million legal sized clams (Fitch 1950). In contrast, our data suggest that legal sized clams are rare; in 115 transects over 38 surveys that counted 3,235 clams, we found no individuals above the legal size of 114 mm/4.5 in. Only 2% of clams were greater than half of legal size (56 mm) (Fig. 1.5) and represent a marked contrast to past decades (Weymouth 1922, Fitch 1950, Knaggs et al. 1976). Despite management efforts which effectively closed the intertidal fishery in much of California, Pismo clam populations have not recovered.

Invertebrates tend to have poor stock recruitment relationships, which complicates long term management (Caddy 1989, Magalhães et al. 2016, Timbs et al. 2018). Settlement and recruitment is temporally and spatially variable, and recruitment is thought to be independent of stock size (Coe 1953, Tomlinson 1968, Wendell et al. 1986). Previous and ongoing work found that Pismo clams may take 3-10 years to reach legal size, but may become reproductively mature in the first year at 15mm (Coe 1947, A. Marquardt unpub. Data). If these data are confirmed, current management should provide Pismo clams several years to spawn before reaching legal

harvestable size and recruiting to the fishery (Coe 1947, Fitch 1950). Even so, once a cohort reaches legal size and is fished down, the fishery may be effectively closed until the next cohort from a strong recruitment event reaches legal size (McLachlan et al. 1996). Across small-scale fisheries, minimum legal size regulations are rarely paired with catch quotas, which can result in the rapid harvest of most legal sized individuals upon recruitment into the fishery (Jamieson 1993). Management strategies may need to be reassessed in order to recover biomass, abundance, and subsequently, a sustainable Pismo clam fishery in California.

In the long term, management of invertebrate fisheries will require novel approaches (Perry et al. 1999, Winemiller 2005) and increased research and monitoring to avoid overfishing. Essential data include updated life history information (e.g. larval dispersal, population connectivity, reproduction, growth rates, mortality, etc.), spatial and temporal population data, and studies on drivers of populations across the species range to better understand the barriers to sustainability and recovery. While there is clearly a need for more information about the biology of Pismo clams, this study provides updated information on current population status throughout their range in California. Critically, this work identifies some of the key factors associated with clam presence, density, and biomass, thus setting a framework to inform management, restoration, and recovery of this iconic species.

Table 1.1. Model selection results from logistic mixed effect models for clam presence. Dashed line indicates threshold for candidate models ($\leq 2 \Delta AICc$). For candidate models, variables in bold indicate parameters with 95% confidence intervals which do not overlap zero.

Presence Model	No. fixed effects	AICc	$\Delta AICc$	AICc Weight
Sed50	1	73.99441	0	0.57
Sed50 + Chl-a	2	74.56039	0.57	0.43
Sed50 + Chl-a + region	3	76.52672	2.53	0
Sed50 + Chl-a + region + low tide value	4	78.75040	4.76	0
human + Sed50 + Chl-a + region + low tide	5	80.44800	6.45	0
null	0	80.21209	6.22	0

*Akaike's information criterion corrected for small sample sizes (AICc)

Table 1.2. Model selection results from GLMM for clam density. Dashed line indicates threshold for candidate models ($\leq 2 \Delta AICc$). For candidate models, variables in bold indicate parameters with 95% confidence intervals which do not overlap zero.

Density Model	No. fixed effects	AICc	$\Delta AICc$	AICc weight
Sed50 + region + low tide	3	149.8529	0	0.704
Sed50 + region	2	151.5782	1.73	0.296
Sed50 + Chl-a + region + low tide	4	154.0420	4.19	0
Sed50 + low tide	2	156.3700	6.52	0
region + low tide	2	156.6867	6.83	0
null	0	160.6184	10.77	0
human + Sed50 + Chl-a + region + low tide	5	167.3420	17.49	0

*Akaike's information criterion corrected for small sample sizes (AICc)

Table 1.3. Model selection results from GLMM for clam biomass (g). Dashed line indicates threshold for candidate models ($\leq 2 \Delta AICc$). For candidate models, variables in bold indicate parameters with 95% confidence intervals which do not overlap zero.

Biomass Model	No. fixed effects	AICc	$\Delta AICc$	AICc Weight
Sed50 + region + low tide	3	263.3414	0	0.474
Sed50 + region	2	263.4600	0.12	0.446
Sed50 + Chl-a + region + low tide	4	267.6465	4.31	0.055
region	1	269.6927	6.35	0.020
Sed50	1	272.4228	9.08	0.005
null	0	276.0359	12.69	0
human + Sed50 + Chl-a + region + low tide	5	281.4289	18.09	0

*Akaike's information criterion corrected for small sample sizes (AICc)

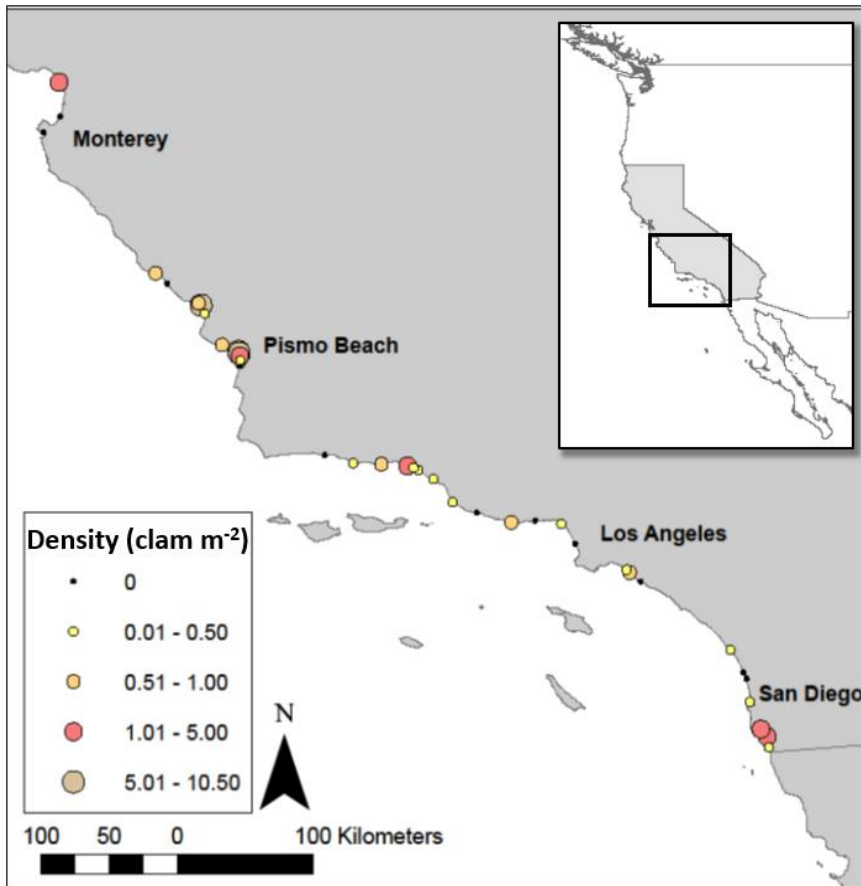


Fig. 1.1. Map of the study region displaying Pismo clam density (m^{-2}) for clams ≥ 35 mm length at surveyed sandy beach study sites (circles) on the coast of California, USA.

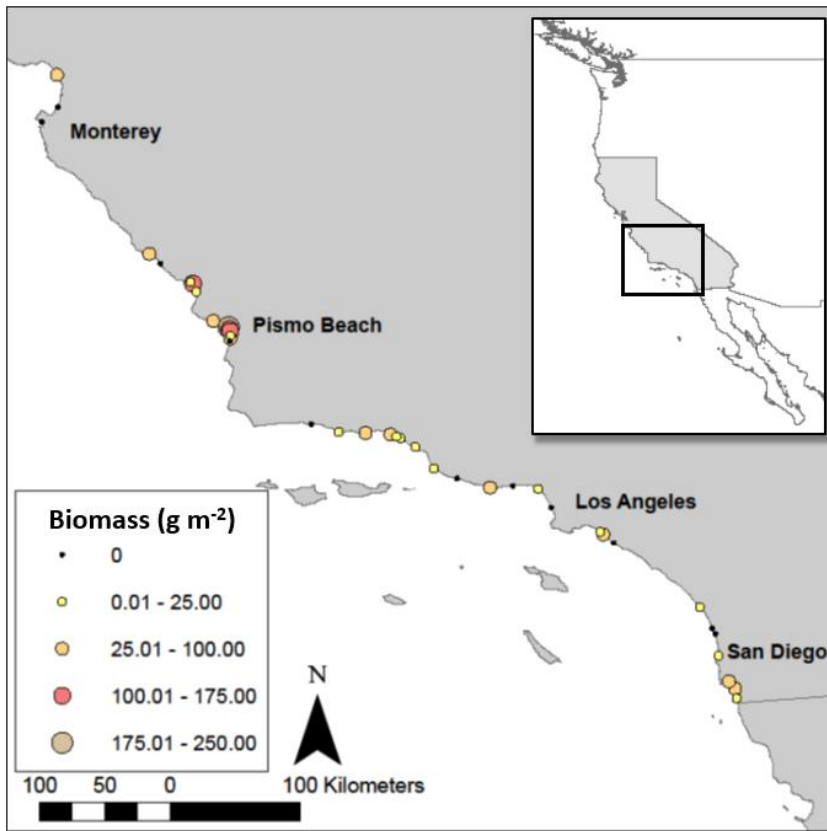


Fig. 1.2. Map of the study region displaying Pismo clam biomass (g m^{-2}) at surveyed sandy beach study sites (circles) on the coast of California, USA.

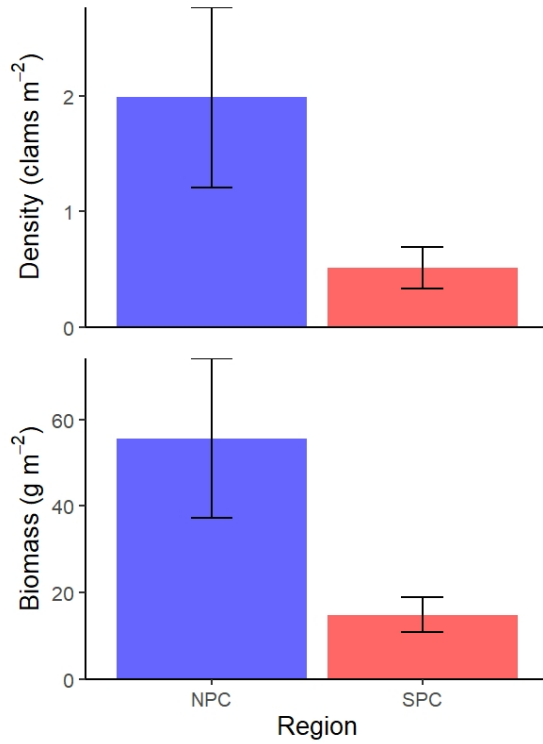


Fig. 1.3. Comparison of average Pismo clam density (≥ 35 mm length) and biomass documented in surveys north (blue) and south (red) of Point Conception. Bars indicate the standard error.

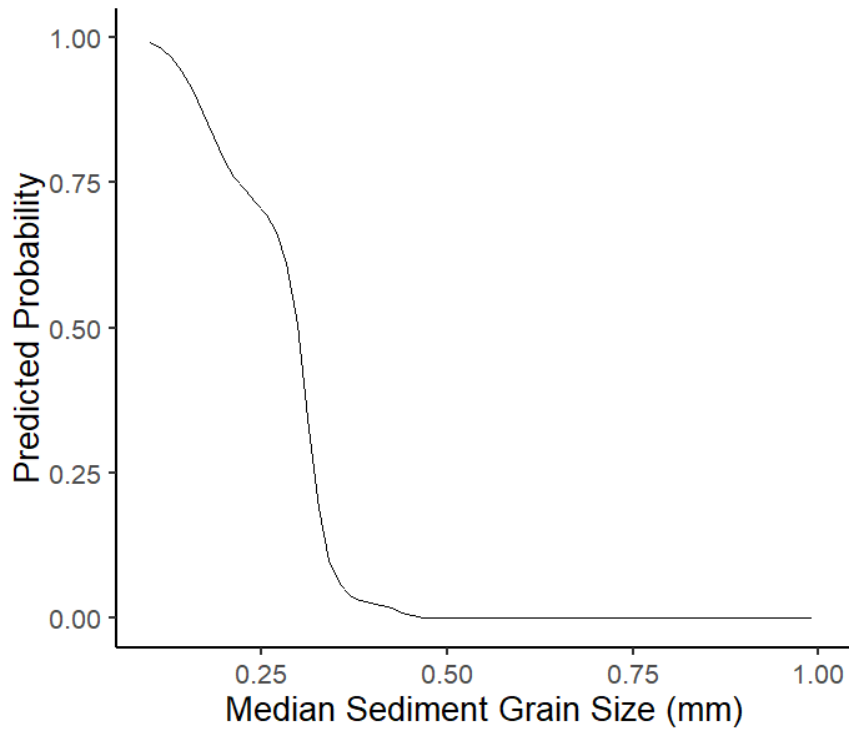


Fig. 1.4. Predicted probability of Pismo clam presence across median sediment grain sizes. Surveyed sites include median sediments ranging from 0.14 - 1.22 mm. We did not identify any clams at median sediment grain sizes >0.5 mm.

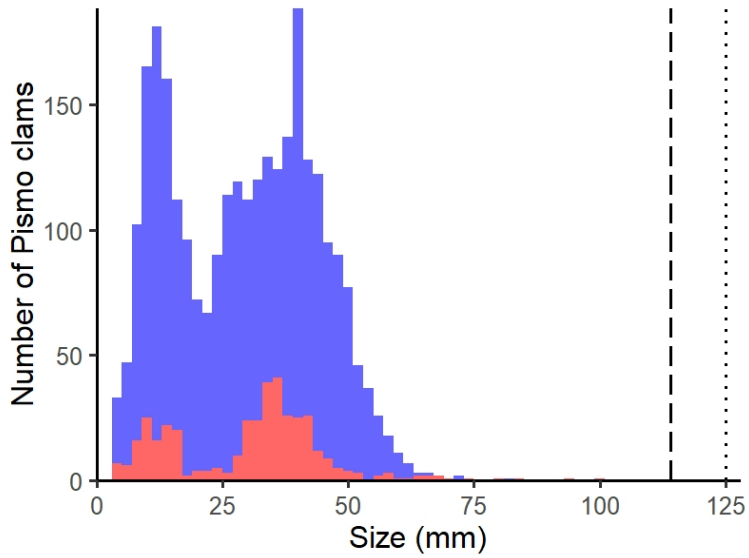


Fig. 1.5. Size distribution of all Pismo clams ($n = 3,235$) documented during field surveys north (blue) and south (red) of Point Conception. Vertical lines indicate legal size for harvest north (dotted: 125 mm/5 in) and south (dashed: 114 mm/4.5 in) of the Monterey/San Luis Obispo county boundary.

Chapter 2

PISMO CLAM REPRODUCTIVE CYCLES, BODY CONDITION, AND GROWTH

2.1 INTRODUCTION

Effective marine fisheries management requires information on key population parameters such as reproduction and growth rates (Perry et al. 1999, Anderson et al. 2008, Tirado et al. 2011). Unfortunately, many marine invertebrate fisheries often lack data on basic biological information, despite their cultural, economic, and ecological importance, (Anderson et al. 2008, 2011, Rogers-Bennett & Juhasz 2014). Even important and valuable commercial species have data gaps (Anderson et al. 2011, Purcell et al. 2013). Recreational fisheries, in particular, suffer from limited monitoring and harvest oversight (Cooke & Cowx 2004). Data acquisition to fill knowledge gaps is a slow process and favors economically and socially valuable species (Chen et al. 2003, Anderson et al. 2008), leaving low abundance, exploited, recreational fisheries without the information required for sustainable management.

Pismo clams (*Tivela stultorum*), a culturally important and iconic recreational fishery species in California, have been heavily exploited for many decades. Despite this long history of harvest, there are significant knowledge gaps in their basic biology and life history. Pismo clams inhabit sandy intertidal beaches from Monterey Bay, CA through Baja California, Mexico (Fitch 1950). Pismo clams were harvested by coastal Chumash tribes for millennia, and later supported thriving commercial and recreational fisheries in California during the 1900's (Bureau of Marine Fisheries 1949, Frey 1971, Jones et al. 2002, Thakar 2012). The commercial fishery was closed in 1947, but a strong recreational fishery persisted until at least the 1980's (Shaw & Hassler 1989, McLachlan et al. 1996). Efforts to manage this fishery included size limits, bag limits, harvest closure zones, and out planting (Fitch 1950, 4 C.C.R. § 29.40). Despite these regulations, Pismo clam population densities have declined throughout California in recent decades (Shaw & Hassler 1989, Marquardt et al. Unpub data). While recent work has examined patterns in abundance across the state (Marquardt et al. Unpub data), there have been no studies examining Pismo clam life history for many decades. Biological data on reproductive cycles and growth rates, critical for stock assessments and population modeling, is at least 40 years old (Coe 1947, Coe &

Fitch 1950, Hall et al. 1974, Stephenson 1974). Due to the lack of transparency in early methods and dramatic changes in coastal ecosystems over the last few decades, the existing biological information may no longer apply to current populations. Managers require updated and expanded information on reproduction and growth rates to effectively manage, regulate, and recover Pismo clams in California today.

Understanding reproductive cycles is essential for predicting recruitment, setting harvest quotas and regulations, and maintaining a sustainable population in the wild (Keck et al. 1975). Further, identifying the timeframe when clams spawn can aid in collections of mature clams to initiate lab based studies or captive rearing programs (Gomes et al. 2014). Reproductive timing is influenced by an array of factors, particularly exogenous conditions in the environment, such as temperature, food availability, and other factors (Gosling 2015). Early work on Pismo clam reproduction documented the species as broadcast spawners (Coe 1947), identified the major spawning period and sex ratio (Coe 1947, Coe & Fitch 1950), identified annual changes in body component indices for specific tissues (Giese et al. 1967), and examined female reproductive stages of clams in the northern extent of the range (Stephenson 1974). However, each of these examines only a single factor in isolation, is at least 40 years old, and pre-dates major population declines in the state. Successful management requires updated information on reproductive cycles to identify management goals (e.g. closing fishing seasons during reproductive times), particularly in the face of changing ocean conditions.

Growth parameters are a critical component of fisheries population modeling (Beamish & Mcfarlane 1983, Campana 2001). Age-based demographic information is essential to predict growth and mortality rates (Campana 2001, Moura et al. 2009), which may be used for population models that inform levels of sustainable harvest and other effective management efforts (Laudien et al. 2003, Leontarakis & Richardson 2005, Peharda et al. 2007, Katsanevakis 2007). Despite its importance, few published papers investigate age-size relationships in Pismo clams. Previous work examined external growth rings to estimate growth (Coe & Fitch 1950, Fitch 1950), identified daily shell increments (Hall et al. 1974), and determined Pismo clams produce one growth annuli per year (Bernal et al. 1989); however, none of these previous studies

estimated key growth parameters necessary for demographic modeling. An accurate characterization of current population age-size structures could be used to inform recovery timelines for the recreational fishery in California.

This study seeks to address knowledge gaps on Pismo clam life history and validate historical information in the context of current oceanographic conditions. Specifically, we investigated the annual reproductive cycle of Pismo clams in California, pairing multiple metrics within a single study, in order to describe their sex ratio, gonad development stages, body condition index, and length at sexual maturity. Further, we examined age-length relationships across California to provide accurate age and growth rate estimates, which will better inform recovery timelines for the recreational fishery in California. The intent of this study is to provide managers with the required information on Pismo clam reproduction and growth rates to effectively manage, regulate, and recover Pismo clams in California today.

2.2 METHODS

2.2.1 Survey and Collection Methods

From January 2018 to December 2019, we collected up to 70 Pismo clams per month from the intertidal zone on Pismo Beach, California (Fig 2.1). We targeted individuals of shell length ≥ 15 mm, the smallest size at maturity based on previous research (Coe 1947). We subsampled 30-40 clams per month from these collections for histological analyses of gonads and body condition (see Sections 2.3 and 2.4). In addition, we opportunistically collected Pismo clams from additional sites in California during the summer months of 2018 and 2019 as part of a related study on the abundance and distribution of Pismo clams (Marquardt et al Unpub Data). We used shells from all collected individuals for age analyses (see Section 2.5) (Fig 2.1).

2.2.2 Histological Techniques

From each monthly collection, 30-40 clams were used to assess reproductive stage. We measured the length of each clam (mm) and removed the tissue from the shell by severing the adductor muscle. We removed a portion of gonad tissue from the dorsal portion of the foot and fixed it in 10% formalin. Then, we processed tissues using standard histological procedures (dehydrated in an ethanol series, cleared in xylene, embedded in paraffin wax), sectioned tissues

to 5µm using a KD-2258 microtome, and stained with haematoxylin-eosin (Howard et al. 2004). Using a Leica DM500 compound microscope at 100x and 400x magnification, we identified the sex of each individual and categorized reproductive stages as inactive, early active, late active, ripe, partially spent, or spent (Table 2.1, Fig 2.2). Reproductive stages were based upon previous studies of bivalves (Power et al. 2005, Popović et al. 2013). If more than one developmental stage was identified, clams were categorized to the stage with the majority of follicles present.

2.2.3 Body Condition Index

Gametogenesis is an energy intensive process and requires the use of stored energy reserves (Gosling 2015). Body condition indices reflect nutritive states in bivalves and closely match reproductive cycles for some species (Crosby & Gale 1990, Ojea et al. 2004, Peharda et al. 2007, Moura et al. 2008). Approximately 30 clams per month were used for a body condition index (BCI). We measured the length of each clam (mm) and then removed the soft tissue from the valves. We rinsed any excess sand and dried the specimens at 60°C for 48 hours to obtain the dry shell and dry tissue weights. The body condition index was measured as: $BCI = [\text{dry tissue weight (g)} / \text{dry shell weight (g)}] \times 100$ (Walne 1976, Mann & Glomb 1978, Drummond et al. 2006).

2.2.4 Age-Length Relationships

To examine age-size relationships, we used 165 clams collected from locations in southern California, and 467 clams from our monthly collections on Pismo Beach and other locations in central California (Fig. 2.1). We found no live individuals larger than 91 mm in central California. As such, we opportunistically collected an additional 30 large (>100 mm), empty shells (from previously living clams) from areas near Pismo Beach in central California. Only shells that had a fully intact valve and could be accurately aged were included. Given the lack of living clams <100 mm in this area, these larger shells allowed us to estimate ages of larger individuals and estimate asymptotic size. We measured the length of each individual (mm) along the anterior-posterior axis, then removed the tissue and allowed shells to air dry so they could be used for subsequent age determination.

Counting external annuli on the exterior of the shell is an efficient method to age bivalves (Richardson & Walker 1991, Moura et al. 2009); However, age determination is challenging for species without external bands, where the first year is difficult to identify, or for long lived species where old individuals have tightly packed growth rings along the shell margin (Richardson et al. 1990, Gosling 2015). Examining internal growth rings in shell cross sections can help overcome these issues (Richardson 2001, Gosling 2015). Previous work has validated that Pismo clams produce annual growth rings (annuli) in their shells, and that these are interpretable both internally through shell cross-sections and externally (Bernal et al. 1989). To count internal annuli, we cut the shell from the ventral margin to the umbo using either a low-speed saw (clams <5 cm; 11-1180 ISOMETTM Low Speed Saw) or a tile saw (clams >5 cm; Kobalt 7-in wet tile saw). We ground and polished the cut surface with successively finer sandpaper (220, 330, 400, 600 grit) to remove abrasion marks from cutting and to improve clarity of annual rings. We counted the number of annuli within each shell using a Leica EZ4D stereo microscope and complemented internal annuli counts with an examination of the external shell surface, since Pismo clams produce thin, light biochecks during the first two to three years of life, which are better differentiated on the exterior surface of the shell (Bernal et al. 1989).

2.2.5 Environmental Parameters

Ocean temperature, food availability and photoperiod are associated with growth and reproductive patterns of other bivalve species (Navarro et al. 2000, Fabioux et al. 2005, Popović et al. 2013, Gosling 2015). To assess the influence of these factors on annual cycles in Pismo clams, we obtained mean monthly sea surface temperature (SST) and chlorophyll-a (Chl-a) concentration from the California Harmful Algal Bloom Monitoring and Alert Program (CalHABMAP). CalHABMAP collects weekly measurements for SST and Chl-a off the Cal Poly Pier in San Luis Bay (35.17°, -120.741°), which is 9.8 km from our study location. Further, we obtained the mean monthly photoperiod for Pismo Beach, CA (Forsythe et al. 1995, Hijmans 2017).

2.2.6 Statistical Methods

We used a Chi-square test to determine if the sex ratio for all specimens where sex was successfully determined differed from a typical 1:1 ratio.

We investigated the relationship between reproductive stage and BCI by performing a correlation analysis between the proportion of clams in the Ripe stage and the BCI across months. To evaluate the role of abiotic factors as drivers of annual BCI cycles, we used a general linear model (GLM) with BCI as the response variable and mean monthly SST, mean monthly Chl-a, mean monthly photoperiod, clam size and year as predictor variables.

To investigate growth parameters for Pismo clams in California, we used the von Bertalanffy growth function (VBGF). The VBGF has been used to describe growth in a range of marine species (Ruttenberg et al. 2005, Palomares & Pauly 2009, Chute 2016, Bradley et al. 2017) using the function:

$$L_t = L_r + (L_{inf} - L_r)[1 - e^{-k(t-t_r)}],$$

where: L_t is shell length at age t , L_r is the specific mean length, L_{inf} is the asymptotic maximum shell length, k is the rate at which clams grow to the asymptotic size, t is age in years, and t_r is the time required to reach size r (Ogle & Isermann 2017). We ran a pooled VBGF for all individuals collected that were ≥ 1 year old and included the larger shells collected on beaches north of Point Conception, because live-collected individuals had not achieved asymptotic size. Further, we ran separate VBGFs for central and southern California to explore potential differences in growth parameters across the state. We used parameters from the VBGFs to predict growth rates in different regions, as well as the expected age at legal size (4.5 in / 114 mm) from San Luis Obispo county to the US border with Mexico. All statistical analyses were completed in R Studio version 3.5.3 (R Core Team 2019).

2.3 Results

2.3.1 Histological Analysis

Of the 785 clams examined histologically, 361 (45.9%) were female, 383 (48.8%) were male and 19 (5.3%) were sexually undifferentiated. Mean size was 41 mm (± 12 mm SD) in

length. The overall female:male sex ratio of 1:1.07 was not statistically different from a 1:1 ratio ($\chi^2 = 0.65$; $df = 1$; $p = 0.42$).

Progression of the gonadal cycle was synchronous between the two sexes and similar across the study period (Fig 2.3). Gametogenesis was initiated in the spring (February - April) when the majority of individuals were in Stage 1 Early Active. Clams reached peak maturity, Stage 3 Ripe, in late summer (July-August). Clams transitioned to Stage 4 Partially Spent from August-September, which is an indication of successful completion of spawning for an individual. We observed clams < 20 mm in all reproductive stages and the smallest clam observed in any reproductive stage was 14 mm (Fig 2.4).

2.3.2 Body Condition Analysis

Clams reached peak BCI during August of both years (Fig 2.5), which coincided with months with the highest proportion of Stage 3 Ripe individuals. Specifically, we found that BCI was positively correlated with the proportion of clams in Stage 3 Ripe ($r = 0.69$, $p < 0.01$, $R^2 = 0.48$).

We considered mean monthly SST, mean monthly Chl-a, mean monthly photoperiod, clam size and year as predictors of Pismo clam BCI. In the full linear model, all parameters were significant predictors of BCI ($p < 0.001$). Our model explained 39.9% of the variance in BCI and was a significant predictor of BCI ($F(5, 640) = 86.76$, $p < 0.001$, Adjusted $R^2 = 0.399$). For each 10 mm increase in clam length, there is an almost 1% decrease in BCI on average ($\beta = -0.09$, $p < 0.001$). With a one degree increase in ocean temperature ($^{\circ}\text{C}$), there is an average ~0.3% increase in BCI ($\beta = 0.33$, $p < 0.001$). For each additional hour of daylight, there is a 0.14% increase in BCI ($\beta = 0.136$, $p < 0.001$). For every one mg/m^3 increase in Chl-a, there is a 0.05% increase in BCI ($\beta = 0.05$, $p < 0.001$). On average, clams in 2019 had ~0.5% lower BCI than clams in 2018 ($\beta = -0.53$, $p < 0.001$).

2.3.3 Age-Length Relationships

Our collections included live specimens from central and southern California, as well as large shells opportunistically found in central California. Live specimens from central CA were on average 41 mm (± 12 SD) and ranged from 14 - 91 mm and specimens from southern CA were

on average 38 mm (± 22 SD) and ranged from 13 - 142 mm (Fig 2.6). Large shells found in central CA were on average 129 mm (± 12 SD) and ranged from 104 - 153 mm (Fig 2.6). Overall, 85 of 632 individuals collected live had not deposited their first year band (average length 19 mm ± 4 SD) and were excluded from analyses.

We pooled all clams \geq one year old ($n = 577$) and fit a von Bertalanffy growth function. Shell ages ranged from 1 y to 21 y for live specimens; However, we documented clams that had lived up to 34 y in age in our sample of non-living shells. We estimated the VBGF as $L_{inf} = 148$ (± 3.0 SE) and $K = 0.1$ y⁻¹ (± 0.005 SE) for all samples. Based on the VBGF, we expect present-day clams to reach a legally harvestable size (114 mm) in 13.2 years (± 3.3 SE).

Additionally, we ran separate VBGF analyses for central ($n = 459$) and southern CA ($n = 118$) (Fig. 2.7). Growth parameters for central CA were $L_{inf} = 149$ (± 2.8 SE) and $K = 0.095$ (± 0.005 SE). We estimate clams in central CA will reach legally harvestable size in 13.5 years (± 0.03 SE). Growth parameters for southern CA were $L_{inf} = 164$ (± 15.8 SE) and $K = 0.11$ (± 0.02 SE). We estimate clams in southern CA will reach legally harvestable size in 9.6 years (± 0.68 SE).

2.4 Discussion

This study provides critical, updated data on Pismo clam reproduction, body condition, and growth. We confirmed that Pismo clams have an equal sex ratio, identified a peak spawning period in late summer (July - August), and found a significant correlation between gonadal development of Stage 3 Ripe and BCI. BCI peaked in August in both 2018 and 2019. Seasonal patterns in BCI are influenced by a combination of mean monthly SST, mean monthly Chl-a concentration, clam size, photoperiod, and year, but SST was the strongest predictor. Our age data suggest that populations in central and southern California grow at similar rates and that Pismo clams reach a legally harvestable size (114 mm throughout most of CA) in 13.2 years.

2.4.1 Reproduction and Body Condition

The reproductive cycles and sex ratios we document are similar to historical Pismo clam studies. We observed a 1:1 sex ratio on Pismo Beach, which matches Pismo clam sex ratios documented at other beaches in CA (Coe 1947, Stephenson 1974). Further, we documented that

gametogenesis begins in the spring (February - April), with the primary spawning period in July and August. While this finding is consistent with the earliest work on Pismo clam reproduction, which reported that the principal spawning period occurred from July to September, this early work did not use histological methods to examine gonad tissue, and also incorrectly concluded that the species was hermaphroditic (Weymouth 1922). Subsequent work in La Jolla, CA reported that Pismo clams are dioecious and spawn from July to November, with limited spawning during July (Coe 1947). On Pismo Beach, spawning was thought to occur primarily in September (Stephenson 1974). Our findings and previous work agree that spawning on the central coast occurs in late summer, despite some variation in peak months. During our two year study, we saw interannual variation in peak spawning periods, with spawning in 2019 peaking one month earlier than 2018. Variation in exogenous conditions, such as oceanography, upwelling, and food supply may contribute to the interannual variation in peak spawning, but additional studies are needed to confirm the relative importance of each of these factors. Finally, we documented clams < 20 mm in all reproductive stages, which supports that Pismo clams mature in their first year (Coe 1947, Stephenson 1974).

No previous studies document annual cycles of body condition in Pismo clams; However, body condition indices have been used to monitor spawning in other bivalves, which suggests BCI may be effective for Pismo clams as well (Ojea et al. 2004; Peharda et al. 2006; Moura et al. 2008). One study used Pismo clam wet weights to observe changes in specific tissues and found increased gonad tissue in the summer (Giese et al. 1967). However, wet weights are less accurate than dry weights for these types of indices, since water content varies seasonally and by tissue type (Gosling 2015). For these reasons, we believe that our standard measure of BCI (Walne 1976, Mann & Glomb 1978, Drummond et al. 2006) more accurately reflects actual cycles in energy storage. BCI and Stage 3 Ripe are significantly correlated, with both peaking in August. Thus, BCI has the potential to be a rapid, inexpensive proxy for monitoring reproduction in Pismo clams, potentially providing useful information about changes in reproductive patterns to inform management.

Reproduction in bivalves is influenced by a variety of exogenous factors, such as

temperature (Chávez-Villalba et al. 2002, Philippart et al. 2003, Herrmann et al. 2009, Popović et al. 2013), food availability (Sastry 1966, Navarro et al. 2000), and photoperiod (Fabioux et al. 2005). Further, young bivalves focus energy into growth and shift towards greater reproductive effort as they age (Gosling 2015). Our results found that all of the parameters we included (SST, chl-a, photoperiod, and clam size) are significant predictors of clam BCI. There is evidence that salinity (Gomes et al. 2014, Adkins et al. 2016), physical stimulus (Seed & Suchanek 1992), and chemical regulation within clams (Gosling 2015) also influence reproductive cycles, but we were unable to evaluate these factors. Future lab based studies could help tease apart the relationship between environmental conditions and Pismo clam reproductive cycles, spawning success, and larval life stages. Understanding drivers in the environment will improve our understanding of Pismo clam recruitment and population recovery.

2.4.2 Age-Length Relationships

VBGF for Pismo clams in California showed that growth in the first 4 years is relatively rapid and then gradually slows, a pattern that is typical of many marine invertebrates (Rogers-Bennett et al. 2007, Palomares & Pauly 2009, Moura et al. 2009). Our pooled VBGF estimates Pismo clams may reach the legally harvestable size of 114 mm at 13.2 years. The current estimated age at legal size is substantially older than historical estimates in California, which determined that Pismo clams reach a 127 mm in shell length between 6 and 9 years old (Coe 1947, Coe & Fitch 1950, Fitch 1950). These differences in the age-length relationship between the past and current day could be explained by selection for smaller individuals by fishery pressure, environmental change, or differences in the methodology used for aging. We discuss each of these possibilities below.

Fisheries pressure can influence the genotype and phenotype of harvested species (Law 2000, Dunlop et al. 2009). Fisheries-induced phenotypic changes can influence growth and body size (Conover & Munch 2002, Swain et al. 2007, Nusslé et al. 2009, Olsen et al. 2009, Kendall et al. 2009) in populations. Further, these changes can have lasting impacts on the population even if harvest stops (Allendorf & Hard 2009, Enberg et al. 2009). For shellfisheries specifically, there are documented population size shifts attributed to human harvest pressure (Silva-Cavalcanti &

Costa 2009, Rick et al. 2016, Peters et al. 2017, Hesterberg et al. 2020). Intense commercial and recreational harvest of large Pismo clams in the early 1900's may have decreased population sizes and the sizes of individuals (Marquardt et al. Unpub Data), but given that Pismo clams mature at sizes far smaller than the size at legal harvest, it seems unlikely that fisheries harvest pressure has resulted in selection for smaller individuals.

Climatic changes may also explain the differences between historical and observed age-length relationships. Climate warming has altered species ranges and phenology (Walther et al. 2002). Additionally, there is increasing evidence that climatic warming also decreases body size across species (Daufresne et al. 2009, Gardner et al. 2011, Ohlberger 2013). Relationships between climate warming, physiological mechanisms, and body size are complex and can vary considerably between species and across life stages (Thresher et al. 2007, O'Gorman et al. 2012, Radchuk et al. 2013, Ohlberger 2013). Climate change induced stressors may have altered vital rates in Pismo clams, resulting in the slower growth rates and increased age at size we observed. However, our data does not have a large enough temporal window to understand how changes in the environment may impact Pismo clam vital rates. Long term monitoring of ocean conditions and Pismo clam vital rates in situ or lab based studies on specific stressors, in isolation or combination, will help tease apart these relationships.

Finally, methodological limitations in previous attempts to age Pismo clams may have led to an underestimation of age. Previous work exclusively used external bands and only provided descriptive statistics for growth (Coe 1947, Coe & Fitch 1950, Fitch 1950). Earlier work therefore may have underestimated ages of individual clams, leading to errors in growth rates and subsequent age at legal size. Our models estimated Pismo clams take nearly twice as long to reach legal size than historical descriptions. VBGFs, and nonlinear functions generally, are sensitive to missing data at the edges of the distribution (Haddon 2011). Therefore, it is important to note that our data set has low representation of large individuals, which could impact our age at size estimates. Southern California, in particular, we only found three individuals >100 mm and had less certainty in our parameter estimate for asymptotic size; However, our data set is still the most representative of current populations in California, uses an improved aging technique, and

provides a foundation for future Pismo clam growth studies. Critically, Pismo clams appear to take longer to reach legal size than previously thought, which will have important implications for Pismo clam management.

2.4.3 Management Implications

Pismo clam populations have declined throughout California and there are fewer large individuals in the population than were present historically (Fitch 1950, Knaggs et al. 1976, Marquardt et al. Unpub Data). Indeed, our surveys detected no clams larger than 92 mm in central California, and only 6 clams in southern California. Despite these limitations, this study provides valuable information on reproduction and growth which can be used to enhance management and restoration of Pismo clams. Life history information is critical to set appropriate regulations, such as size limits or season closures, which support sustainable harvest (Tirado et al. 2017). Current regulations limit harvest to 10 clams per person per day and require a minimum size of 114 mm (4.5 inches) south of the Monterey/San Luis Obispo county line or 127 mm (5 in) north of the county line (4 C.C.R. § 29.40). Pismo clams reproduce in their first year at sizes < 20 mm, which allows individuals to reproduce for multiple years, possibly for more than a decade, prior to growing to the legal harvestable size of 114 mm. Spawning typically occurs in late summer and is synchronized between the sexes, so implementing a seasonal closure during peak spawning periods may enhance spawning success and provide additional protection should the fishery recover. Seasonal closures to protect peak spawning periods, minimum size limits to ensure individuals have an opportunity to spawn, and harvest limits to control exploitation are in effect for other shellfish species and have resulted in more sustainable shellfisheries (Lochead 2012, Tirado et al. 2017). Although added conservation measures may help boost population numbers in California, Pismo clams in this study exhibited slower growth rates and required 14.5 years to reach legal size, which is substantially longer than historical estimates. Understanding the mechanisms underlying slower growth will be critical for restoration of a Pismo clam fishery in California. While additional research on Pismo clam life history is needed, this work provides vital information on reproduction and growth rates to inform management, regulation and potential recovery of Pismo clams in California.

Table 2.1. Appearance of gonad stages from histological specimens (adapted from Power et al. 2005, Popović et al. 2013).

	Female	Male
Inactive	Small undifferentiated germ cells. Sex determination difficult.	Small, undifferentiated germ cells. Sex determination difficult.
Early Active	Monolayer of developing, small oogonia and germ cells attached to follicle walls. Abundant connective tissue.	Small follicles filled with dark and large germ cells and first spermatogonia. Abundant connective tissue.
Late Active	Oogonia attached to follicle wall in less number.	Spermatogonia on periphery. Spermatocytes in follicle center.
Ripe	Larger, concentrated follicles. Most oocytes free in the lumen. Small numbers of vitellogenic oocytes.	Spermatozoa with tails pointing towards center of lumen
Partially Spawned	Small number of free oocytes per follicle, with some empty follicles.	Partially empty follicles filled with mature spermatozoa.
Spent	Few residual oocytes remaining. Loose, abundant connective tissue.	Some basally located spermatozoa remaining. Many phagocytes.

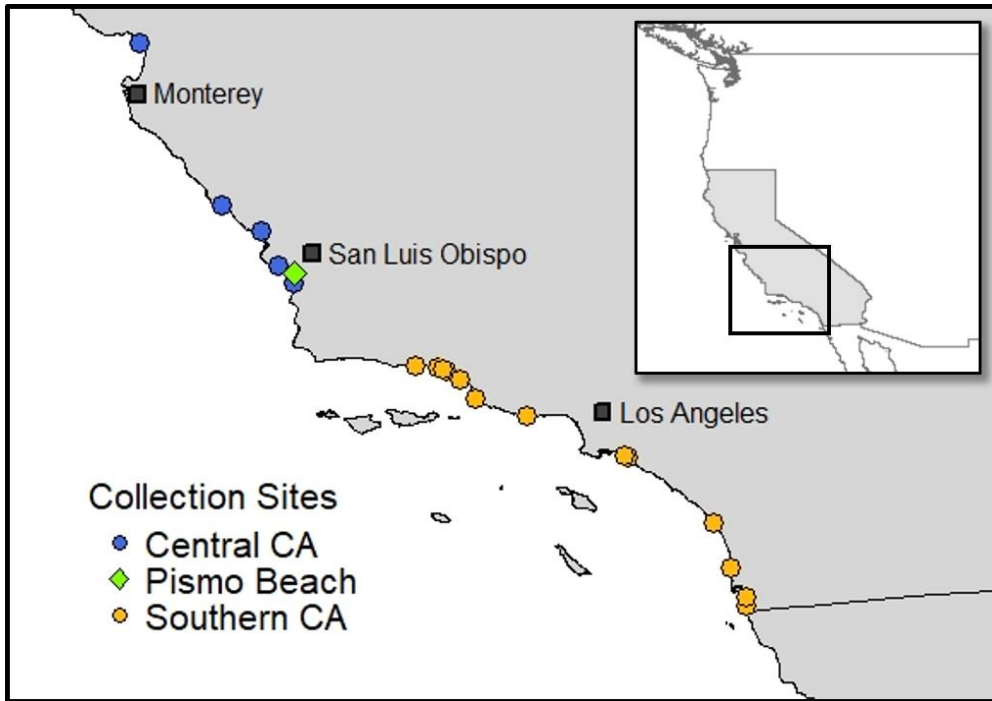


Fig. 2.1. Map of the study region displaying collection sites on the coast of California, USA. Collections from Pismo Beach (green diamond) were used for histology, body condition index, and age-length studies. Opportunistic collections for age-length studies occurred at sites in central (blue circles) and southern (yellow circles) California.

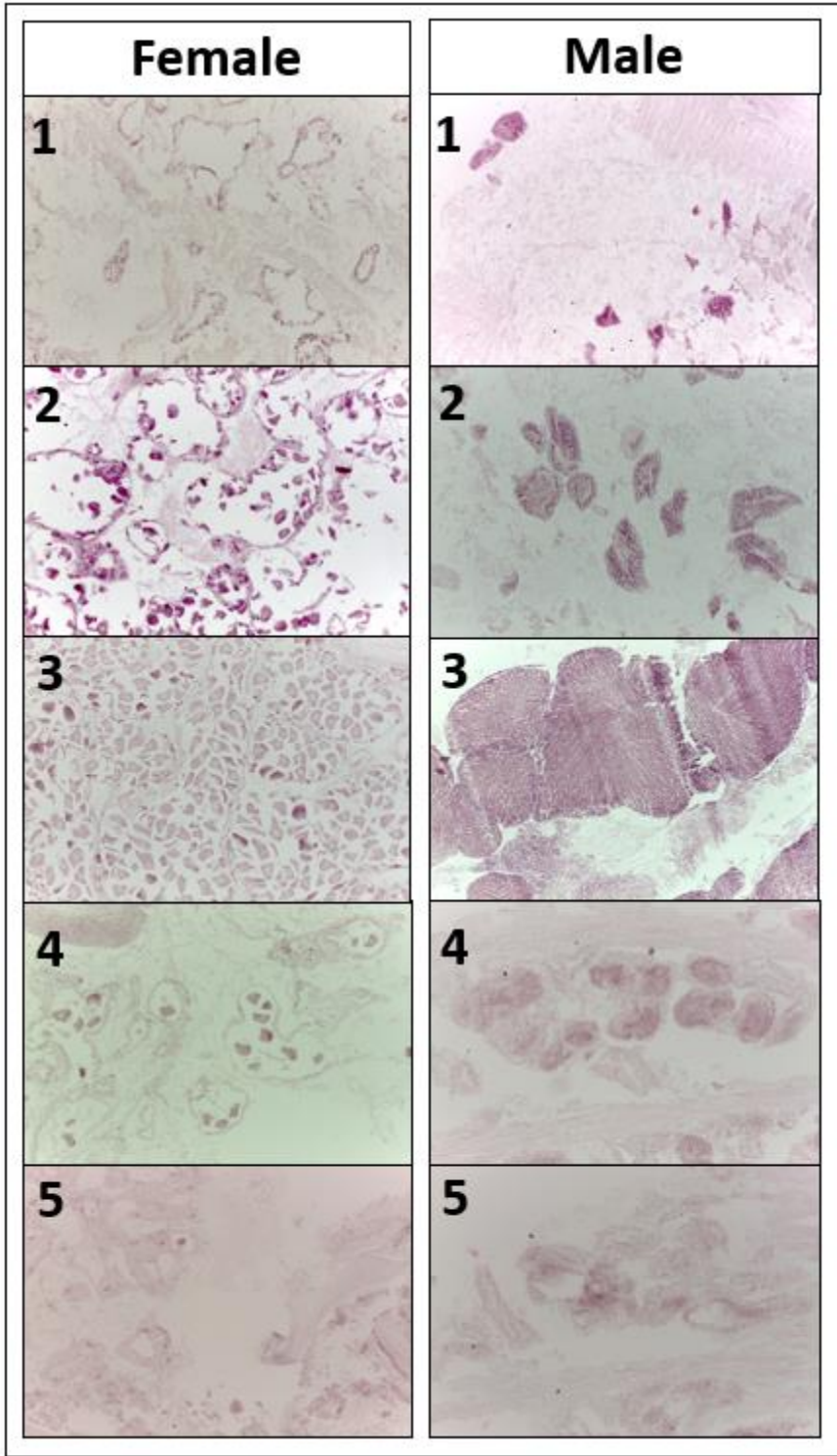


Fig. 2.2. Photomicrographs showing developmental stages (1, Early Active; 2, Late Active; 3, Ripe; 4, Partially Spent; 5, Spent) of *T. stultorum* female and male gonad tissue.

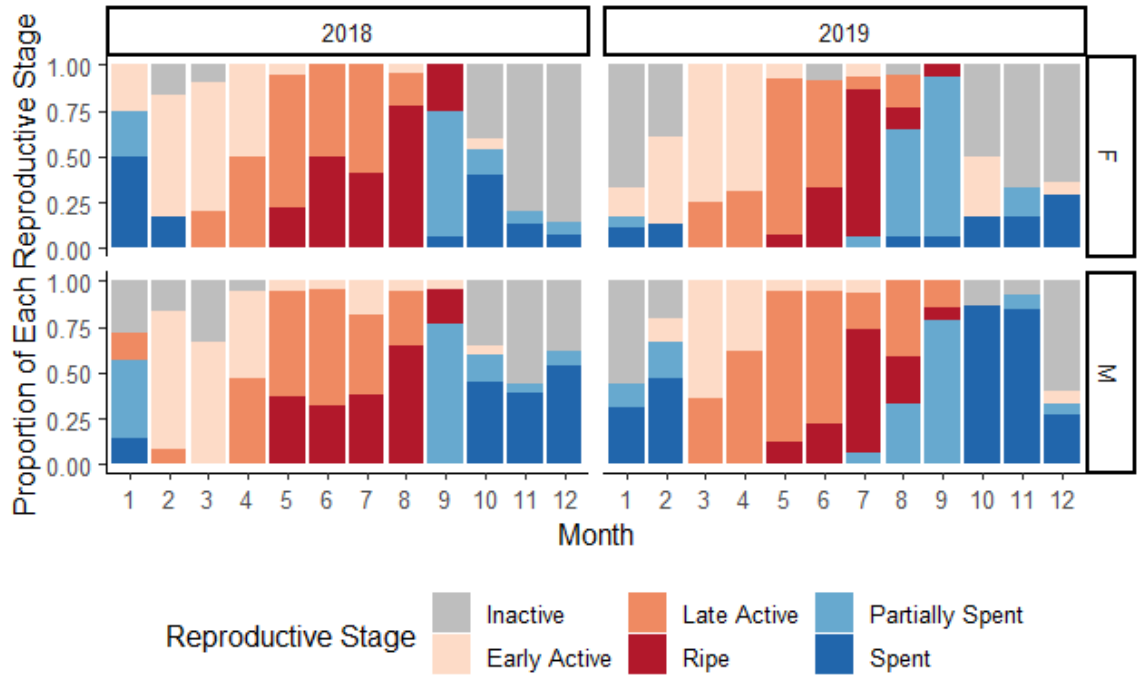


Fig. 2.3. The proportion of female (F) and male (M) clams in each reproductive stage from January 2018 to December 2019.

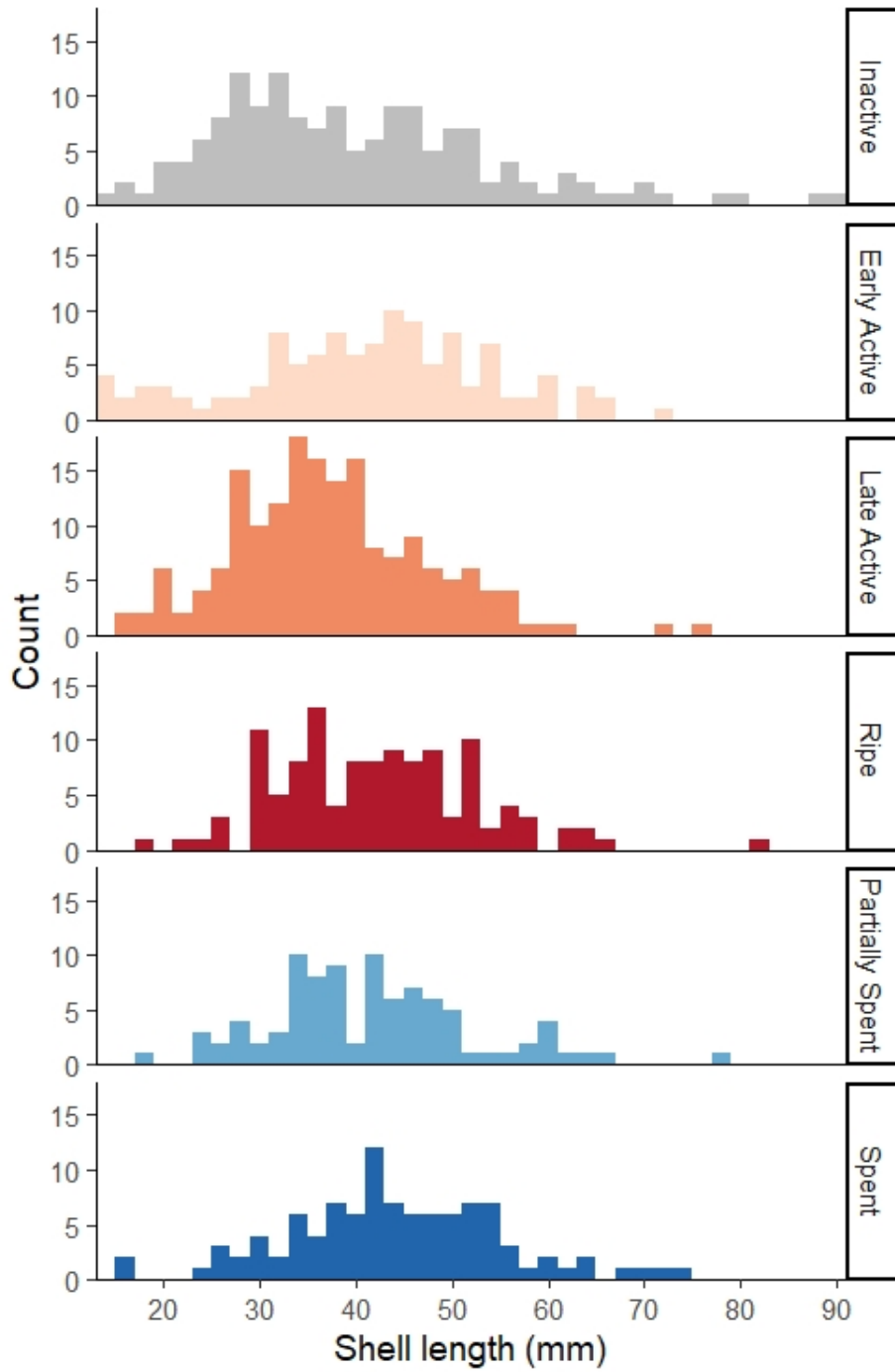


Fig. 2.4. Pismo clam length frequency for each reproductive stage. Clams < 20 mm were observed in all reproductive stages.

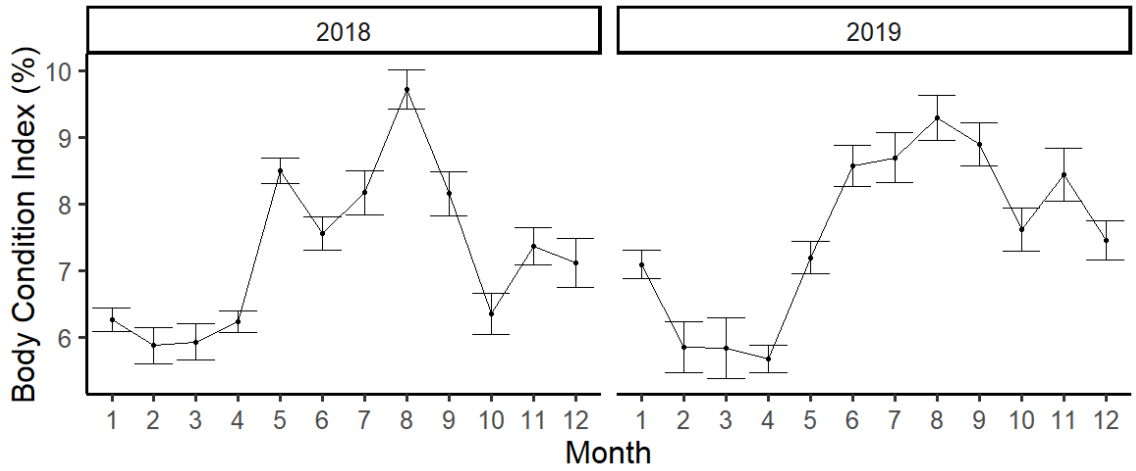


Fig. 2.5. Body condition index (BCI) of Pismo clams on Pismo Beach, CA from January 2018 to December 2019. Bars indicate standard error.

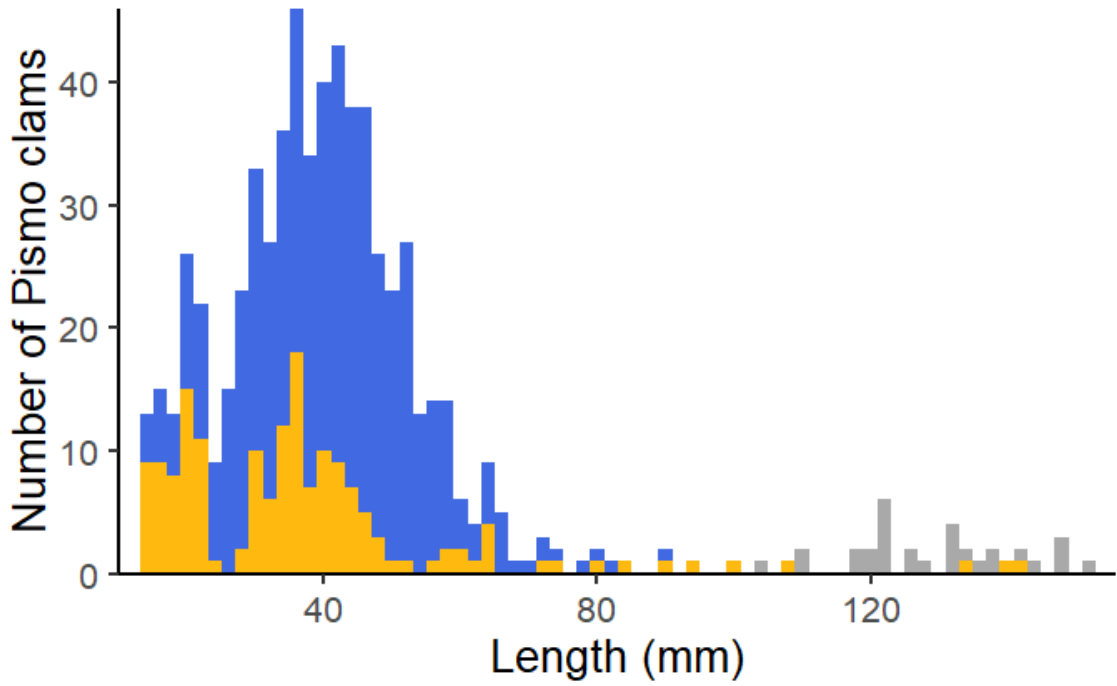


Fig. 2.6. Overlaid size distribution of Pismo clams collected for use in von Bertalanffy growth functions. Collections included live specimens from central (blue) and southern (yellow) California, and large shells collected in central CA (grey).

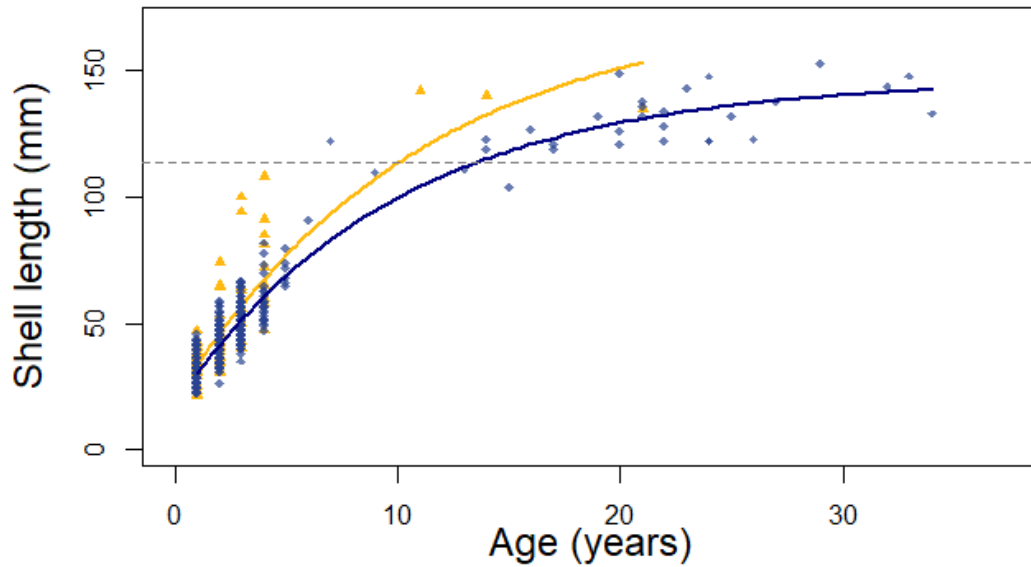


Fig. 2.7. Pismo clam age-length data for central (blue) and southern (yellow) California. von Bertalanffy growth curves are fit to each data set. VBGF parameters for central California are $L_{inf} = 149 (\pm 2.8 \text{ SE})$ and $K = 0.095 (\pm 0.005 \text{ SE})$, whereas southern California is $L_{inf} = 164 (\pm 15.8 \text{ SE})$ and $K = 0.11 (\pm 0.02 \text{ SE})$. Legal harvest requires clams to be at least 114 mm (dotted line).

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