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Reproduction, body condition, age, and growth of a large sandy intertidal bivalve, *Tivela stultorum*

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ABSTRACT: The iconic Pismo clam *Tivela stultorum* (Mawe, 1823) once supported a thriving commercial and recreational fishery in California, but populations have declined statewide in recent decades, in part due to overfishing. To manage and restore populations, fishery managers need accurate life history information, but critical data on reproductive cycles, maturity, and growth rates is either unknown or many decades old. This project aimed to (1) determine annual reproductive cycles and body condition of Pismo clams; (2) identify environmental drivers of reproduction and body condition; (3) determine size–age relationships among clams in California; and (4) estimate growth rates. Up to 70 clams mo^{-1} were collected from Pismo Beach, CA, for histological analysis to determine reproductive stage, measure a body condition index, and estimate ages from shells. Additional clams and shells were collected from sites north and south of Point Conception to compare growth and age at legal size between these 2 major oceanographic zones. Data suggests that reproductive timing deviates only slightly from historical records, with clams spawning later in the year than decades ago. Body condition indices correlate with reproductive stage 3 Ripe, providing an inexpensive proxy to monitor Pismo clam reproduction. Growth was faster in warmer Southern California compared to Central California, but still substantially slower than historical estimates; we estimate that Pismo clams reach the current legal size (114 mm) in 11.1 yr, several years later than previous estimates. Collectively, these data are critical to improve and guide management decisions for this once-abundant species.

KEY WORDS: Reproductive cycle · Body condition · von Bertalanffy · *Tivela stultorum* · Pismo clam

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). Despite their cultural, economic, and ecological importance, many marine invertebrate fisheries lack data on basic biological processes, likely in part because of the challenges in collecting these data for a diverse set of fisheries (Anderson et al. 2008, 2011, Rogers-Bennett & Juhasz 2014). Even valuable commercial species, such as spiny lobster, Dungeness crab, and sea cucumbers in California (CA), have significant data gaps (Anderson et al. 2011, Cope et al. 2011, Purcell et al. 2013, ODFW 2014) and many recreational fisheries suffer from limited monitoring of harvest pressure, population status, and key life history parameters (Cooke & Cowx 2004). Since generating these important data is expensive and time-consuming, resources are often allocated towards economically and socially valuable species (Chen et al. 2003, Anderson et al. 2008), leaving lower value, recreational fisheries without the information required for sustainable management.

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Pismo clams, *Tivela stultorum* (Mawe, 1823), an iconic recreational fishery species in CA, exemplify many of the challenges of managing recreational invertebrate fisheries. Pismo clams were culturally important and heavily exploited for many decades in CA (Shaw & Hassler 1989). The species inhabits sandy intertidal beaches from Monterey Bay, CA, through Baja California, Mexico (Fitch 1950). Coastal Chumash tribes harvested Pismo clams for millennia, and during the 1900s, the species supported thriving commercial and recreational fisheries in CA (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 1980s (Shaw & Hassler 1989, McLachlan et al. 1996). Efforts to manage this fishery included size and bag limits, harvest closure zones, and out-planting (Fitch 1950, 14 CCR § 29.40). Despite these regulations, Pismo clam populations have declined throughout CA in recent decades (Shaw & Hassler 1989, A. Marquardt unpubl. data). While recent work has examined patterns in abundance across the state (A. Marquardt unpubl. data), no studies have examined Pismo clam life history for many decades, and there are significant knowledge gaps in the species' basic biology. Biological data on reproductive cycles and growth rates, critical for stock assessments and population modeling, is at least 40–60 yr old (Coe 1947, Coe & Fitch 1950, Hall et al. 1974, Stephenson 1974). The lack of methodological transparency in many of these early studies and dramatic changes in coastal ecosystems over the last few decades cast doubt on the ability to use existing and outdated information to manage current populations (Doney et al. 2012, Beas-Luna et al. 2020). Managers require updated and expanded information on reproduction and growth rates to effectively manage, propagate, regulate, or restore harvested species (Ojea et al. 2004, Moura et al. 2008, Tirado et al. 2011, Chute et al. 2016).

Understanding reproductive cycles and reproductive output is essential for the long-term sustainable management of fisheries. Information on reproduction helps to predict annual recruitment, set harvest quotas and seasons, adapt management to changing conditions, and enhance aquaculture (Keck et al. 1975, Gomes et al. 2014). 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). Histological techniques are the most reliable method to determine reproductive stage and annual cycles in bivalves (Gosling 2015), but these approaches can be time-intensive and costly. Because gametogenesis is an energy-intensive process and requires the use of stored energy reserves, body condition indices can reflect nutritive states in many shellfish and track reproductive cycles for some species (Barber & Blake 1981, Crosby & Gale 1990, Ojea et al. 2004, Peharda et al. 2006, Moura et al. 2008, Gosling 2015). Thus, body condition indices can be a useful and inexpensive proxy to monitor reproductive cycles. Determining annual cycles and the environmental conditions which drive them is increasingly important to evaluate shellfish management strategies 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 necessary to estimate growth and mortality rates (Campana 2001, Moura et al. 2009), which may be used to predict population trajectories, determine levels of sustainable harvest, and identify potential management strategies (Laudien et al. 2003, Leontarakis & Richardson 2005, Katsanevakis 2007, Peharda et al. 2007). Some species create hard structures that deposit annual rings, such as otoliths in fish or shells in many molluscs (Campana 2001, Black 2009). For bivalves, age can be estimated by examining external surface rings or internal microstructure; however, the accuracy of age estimates among methods can vary by species and the age of specimens (Richardson 2001, Gaspar et al. 2004, Morsan & Orensanz 2004, Moura et al. 2009).

The objective of this study was to address knowledge gaps on Pismo clam life history and validate historical information. We examined several key reproductive metrics including sex ratio, gonad development stages and seasonality, and a body condition index (BCI) as a proxy for monitoring reproduction. Further, we examined size–age relationships across CA, estimated growth rates and age at legal size, and compared these parameters to historical estimates from decades ago. Furthermore, we compared internal and external aging techniques to investigate potential methodological biases from historical studies. Cumulatively, this study provides the first updates to key life history parameters for Pismo clams in many decades, generating current estimates of processes that are critical to inform management, regulation, and assist recovery of depleted Pismo clam populations in CA.

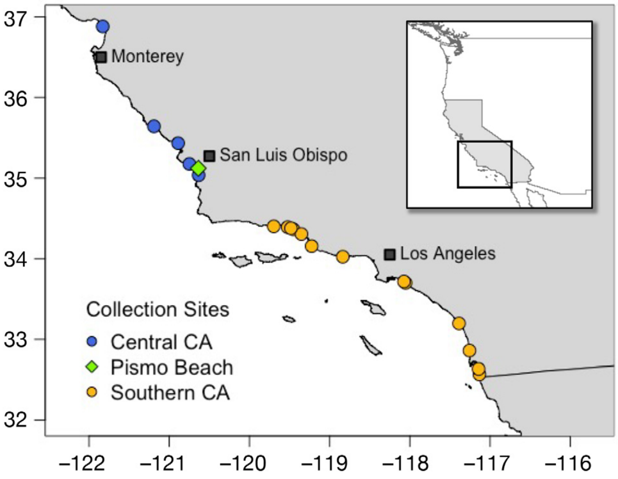

Fig. 1. Study region, displaying collection sites on the coast of California, USA. Collections from Pismo Beach (green diamond) were used for histology, body condition index, and size–age studies. Opportunistic collections for size–age studies occurred at sites in Central (blue circles) and Southern (yellow circles) California

2. MATERIALS AND METHODS

2.1. Survey and collection methods

From January 2018 to December 2019, we collected up to 70 Pismo clams mo^{-1} from the intertidal zone on Pismo Beach, CA (Fig. 1; Table S1 in the Supplement at www.int-res.com/articles/suppl/b031p019_supp.pdf). We targeted individuals of shell length ≥15 mm, the smallest size at maturity based on previous research (Coe 1947), and our collections were generally representative of the size structure we observed in our surveys. We haphazardly subsampled 30–40 clams mo^{-1} from these collections for histological analyses of gonads and body condition (see Sections 2.3 and 2.4), ensuring that subsampled clams spanned the range of sizes from each collection. In addition, we opportunistically collected Pismo clams from additional sites in CA using the same approach during the summer months of 2018 and 2019 as part of a related study on the abundance and distribution of Pismo clams. We used shells from all collected individuals for age analyses (see Section 2.5) (Fig. 1).

2.2. Histological techniques

From each monthly collection, we used up to 40 clams to assess reproductive stage (Table S1), measured the length of each clam (mm), and removed the tissue from the shell by severing the adductor muscles. Technicians removed a small portion of gonad tissue from the dorsal portion of the foot and fixed it in 10% formalin. We processed tissues using standard histological procedures (dehydrated in an ethanol series, cleared in xylene, embedded in paraffin wax), sectioned tissues to 5 µm using a KD-2258 microtome, and stained with haematoxylin-eosin (Howard et al. 2004). Using a Leica DM500 compound microscope at 100× and 400× magnification, we identified the sex of each individual and categorized reproductive stages as Inactive, Early Active, Late Active, Ripe, Partially Spent, or Spent (Table 1, Fig. S1). 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 as the stage with the majority of follicles present.

2.3. Body condition index

From each monthly collection, we used up to 30 clams mo^{-1} for a BCI (Table S1). 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 h to obtain the dry shell and dry tissue weights. We report BCI as: BCI = [dry tissue weight (g) / dry shell weight (g)] × 100 (Walne 1976, Mann & Glomb 1978, Drummond et al. 2006).

2.4. Size–age relationships

To examine size–age relationships, we used 165 clams collected from locations in Southern CA, and 469 clams from our monthly collections on Pismo Beach and other locations in Central CA (Fig. 1). We found no live individuals larger than 91 mm in Central CA. As such, we opportunistically collected an additional 30 large (>100 mm), empty shells (from previously living clams) from areas near Pismo Beach in Central CA. We only included shells that were fully intact and could be accurately aged. 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, but we are uncertain how recently these clams died. 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.

Table 1. Appearance of Pismo clam gonad stages from histological specimens (adapted from Power et al. 2005, Popović et al. 2013)

Stage	Female	Male
Inactive	Small, undifferentiated germ cells on follicle wall. Sex determination difficult. Abundant connective tissue	Small, undifferentiated germ cells on follicle wall. Sex determination difficult. Abundant connective tissue
Early Active	Monolayer of developing, small oogonia and germ cells attached to elongated follicle walls. Dense connective tissue	Small, compact follicles filled with large, dark germ cells and first spermatogonia. Dense connective tissue
Late Active	Oogonia attached to follicle wall in less number. Some larger free oocytes in the lumen, of similar abundance to attached oocytes	Larger, densely-packed follicles. Small, round, and dark spermatogonia on periphery. Spermatocytes in follicle center
Ripe	Larger, concentrated follicles with thin walls. Most oocytes free in the lumen. Small numbers of vitellogenic oocytes	Larger, elliptical follicles packed with mostly mature spermatozoa with tails pointing towards center of lumen. Some basally attached spermatagonia and spermatocytes
Partially Spent	Lower number of free oocytes per follicle, with some empty follicles. Follicle walls breaking down	Partially empty follicles filled primarily with mature spermatozoa. Loose, abundant connective tissue
Spent	Few residual oocytes remaining in broken, scattered follicles. Loose, abundant connective tissue. Many phagocytes	Some basally located spermatozoa remaining in mostly empty follicles. Compact connective tissue. Many phagocytes

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 annuli along the shell margin (Richardson et al. 1990, Gosling 2015). Examining internal annuli in shell cross sections can help overcome these issues (Richardson 2001, Gosling 2015). Previous work has validated that Pismo clams produce annual growth rings in their shells and that these are best interpreted by combined examination of internal shell cross-sections and external rings (Searcy-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 <40 mm; 11-1180 ISOMET^{TM} Low Speed Saw) or a tile saw (clams >40 mm; 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 improve the clarity of annual rings. Two independent readers counted the external surface annuli for each individual and, following a minimum of 1 wk interval, counted annuli with combined examination of external and internal annuli, as recommended by Searcy-Bernal et al. (1989), using a Leica EZ4D stereo microscope. In the event of a discrepancy in age estimates between readers, the readers reanalyzed the shells and determined a common age estimate.

2.5. Environmental parameters

Ocean temperature, food availability, and photoperiod are often associated with growth and reproductive patterns of bivalves (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*) concentrations 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° N, 120.741° W), which is 9.8 km from our primary study location. Chl *a* measurements were log transformed to improve normality. We obtained the mean monthly photoperiod (hours) for Pismo Beach, CA, based on latitude (Forsythe et al. 1995, Hijmans 2019).

2.6. Statistical methods

We used a chi-squared test to determine if the sex ratio differed from a typical 1:1 ratio, including all specimens where sex could be determined. We investigated the relationship between reproductive stage and BCI by examining the correlation 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 multiple linear regression with BCI as the response variable and mean monthly SST, log-transformed mean monthly chl *a*, mean monthly photoperiod, clam size, and year as predictor variables. Year was incorporated as a categorical variable in the model. Collinearity between predictors was assessed using correlation coefficient ($|r| > 0.7$) and tolerance (<0.1) thresholds (Dormann et al. 2013).

To determine growth rates for Pismo clams in CA, we used the internal age readings and performed a 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 et al. 2016, Bradley et al. 2017) using the function:

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

where L_t is shell length at age t, L_r is the specific mean length (which we set to legal size at 114 mm), 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). This parameterization is algebraically equivalent to the traditional VBGF and was used to estimate the time to legal size (t_r) with a confidence interval. We ran a pooled VBGF for all individuals collected that were ≥1 yr old (n = 592) 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 CA to explore potential differences in growth parameters in these regions. 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]) for both regions and all samples combined.

To investigate potential methodological biases in aging techniques, we compared external and internal age estimates for all shells that had reader consensus using paired *t*-tests. We conducted tests using the entire data set and subsequent analyses using specific size classes (≤100 and >100 mm) to determine if the accuracy of aging methods varied between smaller and larger individuals. All statistical analyses were completed in R version 3.5.3 (R Core Team 2021).

3. RESULTS

3.1. Histological analysis

Of the 785 clams examined histologically, 361 (45.9%) were female, 383 (48.8%) were male, and 41 (5.3%) were sexually undifferentiated. Mean (±SD) length was 41 ± 12 mm. 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). Monthly collections included an average of 33 ± 7 clams and ranged from 17 to 40 individuals mo^{-1}.

Progression of the gonadal cycle was synchronous between the 2 sexes and similar across the study period (Fig. 2). Gametogenesis was initiated in the spring (February–April) when the majority of indi-

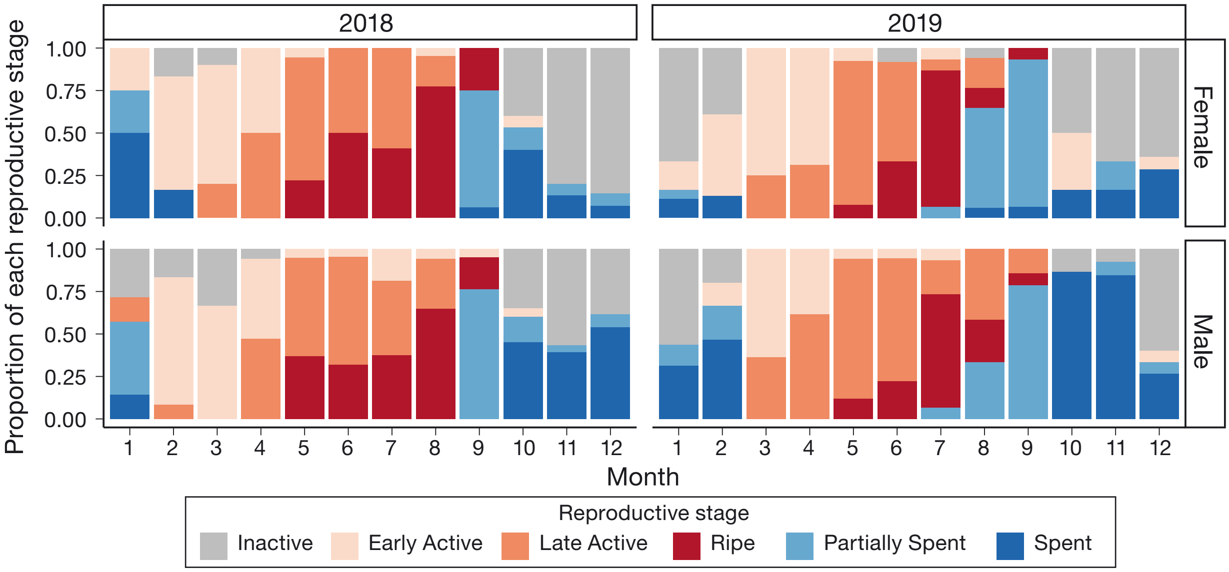

Fig. 2. Proportion of female (n = 361) and male (n = 383) Pismo clams in each reproductive stage from January 2018 to December 2019

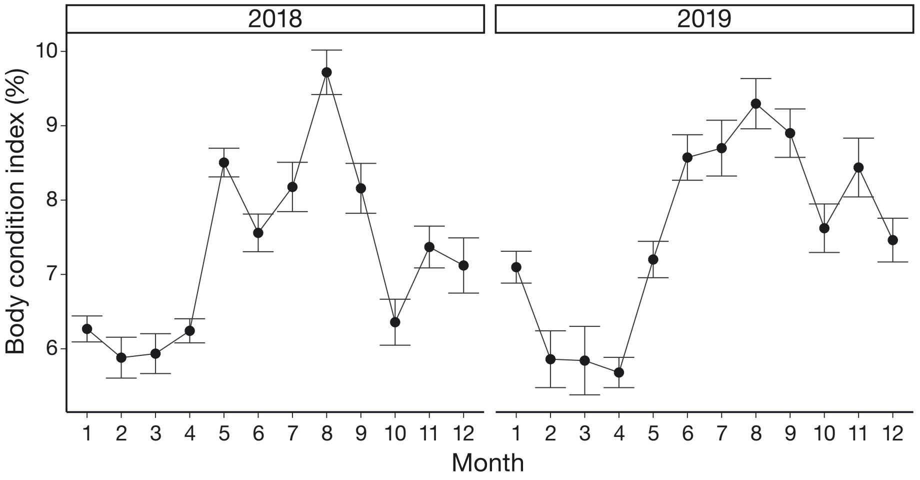

Fig. 3. Mean (±SE) body condition index of Pismo clams (n = 646) on Pismo Beach, CA, from January 2018 to December 2019

viduals were in Stage 1 Early Active. Clams reached peak maturity, Stage 3 Ripe, in mid to 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; the smallest clam observed in any reproductive stage was 14 mm (Fig. S2).

3.2. Body condition analysis

Clams reached peak BCI during August of both years (Fig. 3), which coincided with the 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, log-transformed mean monthly chl *a*, mean monthly photoperiod, clam size, and year as predictors of Pismo clam BCI. There was no evidence of collinearity between predictors ($|r| < 0.7$ and tolerance >0.1 in all cases; Dormann et al. 2013). All parameters were significant predictors of BCI ($p < 0.001$). Our model explained 40.2% of the variance in BCI and was a significant predictor of BCI ($F_{5,640} = 86.76$, $p < 0.001$, adjusted $R^2 = 0.4023$). On average, clams in 2019 had approximately 0.5% lower BCI than clams in 2018 ($\beta = -0.49$, $p < 0.001$; Table 2). Clam body condition increased with warmer mean monthly SST, increased mean monthly chl *a*, and longer day lengths (Table 2). Clam body condition decreased with increasing clam size (Table 2). Monthly collections included an average of 27 ± 5 clams and ranged from 15 to 30 individuals mo^{-1}.

Table 2. Linear model parameter estimates for Pismo clam body condition. SST: sea surface temperature

Parameter	Estimate	SE	95% CI	*t*	p
Intercept	4.58	0.809	2.99, 6.18	5.66	<0.001
Length	−0.09	0.005	−0.10, −0.07	−15.24	<0.001
log(average monthly chl *a*)	0.65	0.116	0.42, 0.87	5.628	<0.001
Average monthly SST	0.26	0.049	0.17, 0.36	5.326	<0.001
Year (2019)	−0.49	0.138	−0.75, −0.21	−3.544	<0.001
Day length	0.13	0.038	0.06, 0.20	3.408	<0.001

3.3. Age–length relationships

Our collections included live specimens from Central and Southern CA as well as large shells opportunistically found in Central CA. Live specimens from Central CA were on average 41 ± 12 mm and ranged from 14 to 91 mm while specimens from Southern CA were on average 38 ± 22 mm and ranged from 13 to 142 mm (Fig. 4). Large shells found in Central CA averaged 129 ± 12 mm and ranged from 104 to 153 mm (Fig. 4). Overall, 72 of 634 individuals (11.4%) collected live had not deposited their first-year band (average length: 18.5 ± 2.8 mm) and were excluded from analyses.

We pooled all clams aged ≥1 yr (n = 592) and fit a VBGF using the internal age estimates. Shell ages ranged from 1 to 21 yr for live specimens; however, we documented clams that had lived up to 32 yr in our sample of non-living shells. We estimated the

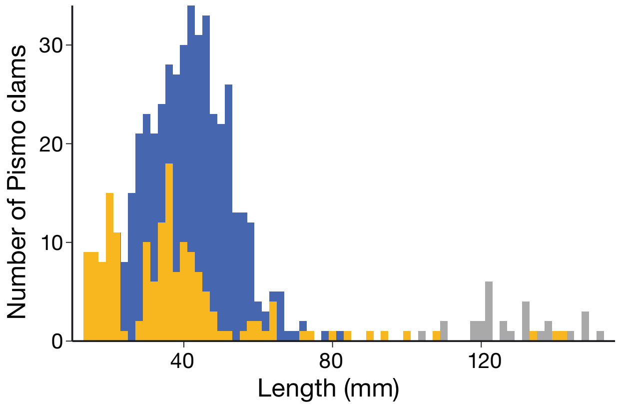

Fig. 4. Size distribution of Pismo clams collected for use in von Bertalanffy growth functions. Collections included live specimens from Central (blue; n = 437) and Southern (yellow; n = 125) California, and large dead shells collected in Central CA (grey; n = 30)

VBGF as L_{inf} = 152 ± 2.8 (mean ± SE) and K = 0.1 ± 0.005 yr^{-1} for all samples. Based on the VBGF, we expect present-day clams to reach a legally harvestable size (114 mm) in 11.1 ± 0.22 yr. We estimated that Pismo clams reach the historical legal size (127 mm) in 14.7 ± 0.40 yr.

We also ran separate VBGF analyses for Central (n = 437) and Southern CA (n = 125) (Fig. 5). Growth parameters for Central CA were L_{inf} = 151 ± 2.9 and K = 0.11 ± 0.005. We estimate clams in Central CA will reach legally harvestable size (4.5 in [114 mm]) in 11.4 ± 0.25 yr. Growth parameters for Southern CA were L_{inf} = 166 ± 11.1 and K = 0.11 ± 0.01. We estimate clams in Southern CA will reach legally harvestable size (114 mm) in 9.6 ± 0.44 yr.

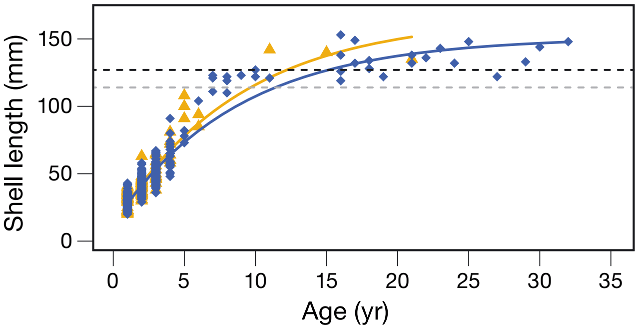

Fig. 5. Pismo clam age–length data for Central (blue; n = 437) and Southern (yellow; n = 125) California. von Bertalanffy growth curves (VBGF) are fit to each data set. VBGF parameters (mean ± SE) for central California are L_{inf} = 51 ± 2.9 and K = 0.11 ± 0.005, whereas Southern California is L_{inf} = 166 ± 11.1 and K = 0.11 ± 0.01. Upper dashed line: historical legal size (127 mm [5 in]); lower dashed line: current legal size (114 mm [4.5 in])

3.4. Comparison of aging techniques

Across all specimens successfully aged using both methods (n = 654), we documented a statistical difference between the internal and external aging techniques (t = −5.67, p < 0.001; Fig. S3); however, the internal method only estimated clams as 0.151 yr older than the external method. Age estimates for shells larger than 100 mm (n = 28) were statistically significantly older using the external aging method, but only by 0.154 yr (t = −6.79, p < 0.001). For shells smaller than 100 mm (n = 626), there was no difference between the 2 aging methods (t = −0.39, p = 0.702).

4. DISCUSSION

This study provides the first updates in many decades of key life history parameters for Pismo clam reproduction, body condition, and growth. We confirmed that Pismo clams have an equal sex ratio, identified a peak spawning period in mid to late summer (July–August), and found a significant correlation between gonadal development of Stage 3 Ripe and BCI. Seasonal patterns in BCIs are related to a combination of mean monthly SST, mean monthly chl *a* concentration, clam size, photoperiod, and year. Our age data suggest that populations in Southern CA, where water temperatures are warmer, grow more quickly than those in Central CA, where waters are cooler. Possibly as a result of this trend, Pismo clams in Southern CA reach legal size ~2 yr earlier than those in Central CA. Aging methods (internal vs. external) were statistically different, but not biologically meaningful. Thus, age estimates between the 2 methods are functionally similar. Additionally, our analyses revealed a ~5–9 yr older estimate for age at the previous legal size (127 mm) compared to historical accounts, which has important implications for recovery timelines.

4.1. Reproductive cycles, body condition, and the environment

This study documented a 1:1 sex ratio, which matches previous observations of sex ratios in Pismo clams (Coe 1947, Stephenson 1974). A 1:1 sex ratio is common for venerid species, such as *Mercenaria mercenaria* (Eversole 2001), *Tivela mactroides* (Denadai et al. 2015), *Callista chione* (Moura et al. 2008), and *Venus verrucosa* (Popović et al. 2013), among others. We did not observe hermaphrodites in any of our specimens. Prior work documented <1% of Pismo clams are hermaphroditic and contain a small number of follicles of the opposite sex (Coe 1947, Stephenson 1974). Since we examined a small section of the gonad, we may have missed hermaphroditic individuals, but if they are present, they are likely to be uncommon.

Previous studies documented broader spawning periods and variation in peak months (Weymouth 1922, Coe 1947, Stephenson 1974), but our 2 yr study on Pismo Beach showed a consistent peak in late summer (Fig. 2). Peak summer temperatures associated with spawning are common for venerid species, such as *M. mercenaria* (Keck et al. 1975), *Mesodesma mactroides* (Herrmann et al. 2009), and *Ruditapes philippinarum* (Drummond et al. 2006). Reproductive timing in bivalves can be influenced by a variety of environmental factors, but additional studies are needed to confirm their importance in driving Pismo clam reproduction.

BCIs have been used to monitor spawning in other bivalves, and we found a significant positive relationship between BCI and reproductive Stage 3 (Ripe) in Pismo clams, with both peaking in August. Since BCI correlates well with reproductive stage, BCI may provide a rapid, inexpensive proxy that would facilitate tracking reproduction in Pismo clams over large spatial and temporal scales. Furthermore, we found that SST, chl *a*, photoperiod, and clam size are significant predictors of BCI, suggesting that both environmental and demographic factors impact condition. Future laboratory studies could help tease apart the relationship between ocean conditions and Pismo clam reproductive cycles, spawning success, and larval life stages. Understanding how the environment influences Pismo clam reproduction and recruitment can help predict how reproduction, and ultimately population size, will respond in the future as oceanographic conditions change with the climate.

4.2. Accurate age–length estimates are critical for management

We observed spatial differences in Pismo clam growth rates across CA, with slower growth in Central CA than in Southern CA, consistent with previous findings (Coe & Fitch 1950). Previous bivalve studies suggest that many temperate species exhibit faster growth in warmer waters across latitudinal gradients (i.e. *Tivela stultorum*, Searcy-Bernal et al. 1989; *M. mercenaria*, Ansell et al. 1964; *Crassostrea virginica*, Lord & Whitlatch 2014; *Mytilus californianus*, Blanchette et al. 2007). In contrast, some species exhibit reduced growth and signs of stress at warmer temperatures at the edge of their geographic range (Weinberg et al. 2002, Narváez et al. 2015, Munroe et al. 2016, Hornstein et al. 2018). Since the range of Pismo clams extends south to at least Baja California Sur, Mexico, we would not expect Pismo clams to show a thermal stress response as far north as California.

Our estimates for Pismo clam age at legal size differ considerably those of previous decades. Studies from the 1940s and 1950s reported that Pismo clams require 6–9 yr to reach the previously larger legal size of 127 mm (5 in) (Coe 1947, Coe & Fitch 1950, Fitch 1950), whereas our data suggest that Pismo clams require 14–15 yr to reach an equivalent size today. Previous literature suggested that Pismo clam populations were skewed towards large, old animals due to low recruitment success and long lifespans (McLachlan et al. 1996), but our monthly survey data from the last several years suggest a different pattern (A. Marquardt unpubl. data). Our data from Central CA show a population dominated by small, young individuals and with an average internal age of only 2.5 yr. This pattern suggests relatively consistent recruitment in Central CA, with possibly low survival to older size classes. Though the death year is unknown for the 30 non-living shells, they provide crucial size–age information for larger size classes, which are absent from current populations in Central CA and very rare in populations in Southern CA.

Potential mechanisms underlying the observed change in growth rates are poorly understood, but likely involve a combination of factors. One possible explanation for the observed difference in growth rates is methodology, which we addressed by estimating both internal and external ages for each specimen. Our aging techniques were based, in part, on photos of aged specimens published by Fitch (1950). Historical estimates may have consistently underestimated age for a given clam since the first and second annuli tend to be faint on the external surface of the shell (Searcy-Bernal et al. 1989); however, even a consistent 1–3 yr difference in age estimates caused by methodology does not account for the 5–9 yr difference in age at legal size that we observed. While we believe our external aging technique is comparable to historical methods, there may be some unknown discrepancy. In addition, VBGFs and other nonlinear functions are sensitive to low sample sizes at the edges of the distribution (Haddon 2011). We included age estimates for only 34 individuals over 100 mm, 30 of which were non-living shells. The year of death and growth conditions for these non-living shells are unknown and may not be representative of current populations. To understand if the observed difference in growth is due to methodology or an actual change in life history, future work could examine archived museum collections to directly compare growth rates across decades with consistent methods and readers.

Other potential mechanisms to explain changes in growth include fishery harvest or changes in ocean climate. Intense harvest of large Pismo clams in the early 20th century may have altered size structure or growth rates. Though evidence for fishery-induced changes in growth rates is limited, fishing pressure can alter size structure, maximum size, and longevity in venerid species (Nakaoka 2000, Dalgiç et al. 2010, Munroe et al. 2016) and other molluscs (i.e. *Lottia gigantea*, Kido & Murray 2003, Erlandson et al. 2011; *Halitotis rufescens*, Rogers-Bennett et al. 2013). Change in maximum size or longevity may simply reflect the harvest of the largest and oldest individuals in a population, but it is possible that such changes may reflect phenotypic plasticity or even fisheries-induced evolution (Fenberg & Roy 2008, Munroe et al. 2016). Since Pismo clams reach sexual maturity at small sizes and fecundity increases with size (Coe 1947, 1953, Fitch 1950), individuals have multiple opportunities to spawn prior to reaching a harvestable size, such that fisheries-induced evolution seems unlikely. Changing oceanographic conditions can also impact growth rates of marine species. Global ocean temperatures have warmed over the last few decades (EPA 2021), and warmer temperatures often lead to faster growth for many invertebrates, including Pismo clams (Coe 1947, Fitch 1950, Searcy-Bernal et al. 1989). Therefore, warming waters should lead to faster growth rates in the modern day compared to historical accounts — the opposite of what we observed in this study. It is possible that some other small-scale oceanographic variability has led to a net decrease in growth rate, but we are unable to evaluate any potential links to climate factors with our current data.

4.3. Management implications

Pismo clam populations have declined throughout CA, and there are fewer large individuals in the population than were present historically (Fitch 1950, Knaggs et al. 1976, A. Marquardt unpubl. data). Our surveys detected no clams larger than 91 mm in Central CA, and only 6 clams larger than 90 mm in Southern CA, suggesting that Pismo clam abundance, particularly large and legal-sized individuals, has declined statewide. Despite these limitations, this study provides valuable information on reproduction and growth which can be used to enhance current management and restoration of Pismo clams.

Since Pismo clams reproduce in their first year at sizes <20 mm, they have ample opportunities to spawn prior to recruiting to the legal recreational fishery. Spawning is synchronized in late summer, so 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 have been effective in improving sustainability in other shellfish species, such as the Atlantic sea scallop *Placopecten magellanicus*, cardid clam *Acanthocardia tuberculata*, and Pacific geoduck *Panopea generosa* (Myers et al. 2000, Hart & Rago 2006, Lochead 2012, Tirado et al. 2017). Using BCIs as an inexpensive proxy for reproduction can provide cost-effective information to improve our understanding of Pismo clam reproductive cycles across regions in CA. Combined with population surveys, this information could be used to better understand potential stock–recruit relationships throughout their range.

Recovery timelines based on historical Pismo clam growth rates may be too optimistic. Our data suggest that Pismo clams may require 9–12 yr to reach the current legal harvest size of 4.5 in (114 mm), much longer than previously thought. Pismo clams may persist on CA beaches, but restoring a substantial population of harvestable individuals may require decades. Future work could explore growth and size–age relationships in Baja California, Mexico, where Pismo clams are abundant and individuals are large (B. Ruttenberg unpubl. data). Since populations in Baja California are closer to the southern extent of the Pismo clam range, information from this region will enhance our understanding of Pismo clam growth rates for larger size classes and provide context for how warming ocean conditions may impact Pismo clam populations in the future in CA.

Understanding the mechanisms underlying demographic processes will be critical for improved management, recovery, and restoration of a Pismo clam fishery in CA. While additional work is necessary to better understand additional aspects of Pismo clam biology (e.g. larval dispersal and population connectivity, fecundity and recruitment, mortality), this work represents an important advance, generating vital information on reproduction and growth rates of Pismo clams in CA.

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