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ABSTRACT Understanding spatial and temporal patterns in the recruitment of marine invertebrates with complex life histories remains a critical knowledge gap in marine ecology and fisheries. As marine invertebrates are facing multiple stressors from overfishing and climatic stress, it is important to evaluate the conditions that facilitate recruitment in low-density populations. The red abalone *Haliotis rufescens* historically supported an economically important fishery in California, but the fishery was sequentially closed as stocks declined, and the last fished area was closed in 2018 following the collapse of the kelp forests in Northern California. Here, red abalone recruitment was evaluated annually from 2012 to 2016 and monthly from 2016 to 2017 in Central California where red abalone naturally occur in highly aggregated but low-density populations because of sea otter predation. Trends in wind-driven upwelling, temperature, wave forces, and food resources (kelp) were evaluated over the same time period as factors that could affect recruitment patterns. Recruitment was annually consistent except in 2015, when recruitment declined by 76%, likely because of reproductive failure during the second year of the North Pacific marine heat wave. The monthly recruitment assessment was the first field assessment of red abalone recruitment over a full year, and it showed that red abalone can recruit year-round. There were no clear recruitment patterns associated with seasonal wind-driven upwelling or relaxation patterns, and kelp density was constant over the study period; however, conditions at the study sites included three key features that may provide optimal conditions for consistent recruitment: (1) spatial abalone aggregation, (2) a sheltered embayment that may retain larvae, and (3) persistent algal food resources. These results can inform statewide and global abalone recovery and management programs.

KEY WORDS: larval settlement, recruitment, population dynamics, marine heat wave, restoration, fisheries, invertebrate

INTRODUCTION

Marine species are in decline globally as a result of multiple stressors including overfishing (Myers & Worm 2003, Pauly & Zeller 2016, Kroodsma et al. 2018), climatic stress (Allison et al. 2009, Cheung et al. 2010), and disease (Harvell 2019). Nearshore benthic marine invertebrates are particularly susceptible to overfishing (Hobday et al. 2001, Uthicke et al. 2009), and recruitment dynamics can be difficult to predict. Marine invertebrates typically have benthic adult stages with a dispersing larval stage that can decouple local adult population abundance from larval settlement and recruitment spatially and temporally (Hughes & Tanner 2000, Kinlan et al. 2005). Furthermore, changing environmental conditions and oceanographic processes can affect the recruitment of benthic invertebrates in seemingly unpredictable or nonlinear ways (Myers 1998, Przeslawski et al. 2008, Menge et al. 2011, Phelan et al. 2018).

Worldwide, abalones represent high-value fisheries, but populations are vulnerable to extirpation (Shepherd & Brown 1993, Roberts & Hawkins 1999, Rogers-Bennett et al. 2019). Most abalones are long-lived, relatively slow-growing species with delayed sexual maturity (Day & Fleming 1992, Nash 1992,

Rogers-Bennett et al. 2007, Leaf et al. 2008). Adult abalones may not move far from their natal habitat, as was observed in the pink abalone *Haliotis corrugata* in Southern California (Coates et al. 2013) and are typically found in nearshore environments easily accessible to fisheries. Abalone reproduction is subject to the Allee effect (Allee 1931) at low densities, and adult spacing greater than 4 m greatly reduces fertilization of broadcast gametes (Babcock & Keesing 1999). Larval duration is known to be relatively short (1–3 wk; Roberts & Lapworth 2001, Takami et al. 2002, Miyake et al. 2017), and dispersal can be over long or short distances (Miyake et al. 2017). It is thought that settlement and survival may be higher if larvae are retained on their natal reef (McShane et al. 1988), which can limit connectivity and increase the risk of recruitment overfishing (Strathmann et al. 2002, Rogers-Bennett et al. 2004). Although the number of larvae that travel long distances may be small, in California, there appears to be enough dispersal to create large-scale genetic connectivity among populations of red abalone (Gruenthal et al. 2007). Abalone populations have declined dramatically in many parts of the world including Southern California (Karpov et al. 2000), Mexico (Morales-Bojórquez et al. 2008), Australia (Shepherd et al. 2001), New Zealand (Andrew et al. 2002), and South Africa (de Moor et al. 2015), and most recently, in Northern California (Rogers-Bennett et al. 2019).

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The seven species of California abalones once supported major recreational and commercial fisheries. Abalones in Southern California were depleted between the 1960s and 1990s because of overharvesting and disease, and the commercial and recreational fisheries for all abalone species were closed south of San Francisco in 1997 (Rogers-Bennett et al. 2002). Black abalone (*Haliotis cracherodii* Leach, 1814) and white abalone (*Haliotis sorenseni* Bartsch, 1940) are now endangered, and pink (*Haliotis corrugata* Wood, 1828), green (*Haliotis fulgens* Philippi, 1845), and pinto (*Haliotis kamtschatkana* Jonas, 1845) abalones are species of concern (Rogers-Bennett et al. 2016). Southern California red abalone (*Haliotis rufescens* Swainson, 1822) populations remain very low with few signs of recovery (0–0.18 abalone/m^2; CDFG 2012). In Central California, red abalone populations remain persistent at densities less than or equal to 0.20/m^2 (Rogers-Bennett 2007, Micheli et al. 2008) because of predation by sea otters (*Enhydra lutris* Linnaeus, 1758), and population increases are unlikely under otter predation (Hines & Pearse 1982, Leet et al. 2001). Until recently, red abalone in Northern California supported a recreational free dive–only fishery valued at up to $44 million USD per year (Reid et al. 2016). Following the North Pacific marine heat wave from 2014 to 2016 (Di Lorenzo & Mantua 2016, Gentemann et al. 2017), Northern California abalone populations declined from between 0.44 and 1.01 abalone/m^2 before 2014 to between 0.01 and 0.24 abalone/m^2 currently (Rogers-Bennett et al. 2019). As a result of the mass mortality event, the Northern California fishery was closed in 2018.

Despite the decline in abalone populations, little is known about field conditions conducive to abalone reproduction and recruitment. In Northern California, when abalone abundance was formerly high (mean 0.44–1.01 individuals/m^2), recruitment varied temporally with good and bad recruitment years (Rogers-Bennett et al. 2016). In the present study, red abalone recruitment was evaluated annually over 5 y (2012 to 2016) in naturally low-density and aggregated populations in Monterey Bay (Central California). Recruitment was expected to be highly variable and lower than recruitment in Northern California because of lower population density. Monthly recruitment has not been previously examined for California abalone and was assessed in Monterey Bay between July 2016 and June 2017. Annual and monthly recruitment trends were evaluated in relation to wind-driven coastal upwelling, temperature, wave forces, and kelp density. Coastal upwelling is the dominant driver of seasonal physical and biological variability in Central California and the California Current System (Checkley & Barth 2009, Walter et al. 2018, Barth et al. 2020) and, thus, could influence abalone recruitment. Temperature can have impacts on multiple aspects of recruitment, and warm water (>2°C above ambient) has been shown to negatively affect red abalone larval production, settlement, and recruit survival (Searcy-Bernal 1999, Vilchis et al. 2005, Rogers-Bennett et al. 2010), although one study found increased fertilization during warmer nonupwelling periods (Boch et al. 2017). It was expected that Central California abalone recruitment would show distinct seasonality with peaks corresponding to the strongest wind-driven upwelling in the spring when waters are cooler (Pennington & Chavez 2000, Walter et al. 2016, 2018). Surface wave forcing was evaluated because previous studies found that increased wave forcing could serve as a trigger for spawning in some abalone species (Sasaki 1985, Onitsuka et al. 2007);

however, other studies found that decreased wave forcing enhanced reproduction (Campbell et al. 2003, Zimmer & Riffell 2011), making impacts of variation in wave forcing hard to predict. Kelp density was evaluated in relation to abalone recruitment because food availability was a major driver of the abalone population decline in Northern California (Rogers-Bennett et al. 2019), and changes in kelp density could have implications for recruitment. Furthermore, kelp can serve to retain abalone larvae near natal habitats (McShane et al. 1988). Trends in annual and seasonal recruitment in Central California and correspondence with the physical and biological factors mentioned earlier are discussed in terms of implications for abalone recovery and management.

MATERIALS AND METHODS

Sampling Newly Settled Abalone Recruitment

Newly settled abalone (<1.5 mm size) were assessed by collecting crustose coralline–covered cobbles in rocky subtidal kelp forest habitats. As a first assessment of abalone settlement in Central California, abalone were collected from 33 cobbles per site at three sites in southern Monterey Bay in November 2012: Hopkins Marine Life Refuge (HMLR; 36° 37′ 12″ N, 121° 54′ 8″ W), Lovers Point (36° 37′ 30″ N, 121° 54′ 56″ W), and Point Pinos (36° 38′ 17″ N, 121° 56′ 2″ W). All three sites are in marine protected areas: HMLR and Lovers Point are in the Lovers Point State Marine Reserve, and Point Pinos is in the Pacific Grove Marine Gardens State Marine Conservation Area. In the following years (2013 to 2016), 30–33 cobbles were collected annually in the fall (September and October) at HMLR to allow for an annual recruitment assessment across 5 y (2012 to 2016). To investigate seasonality in recruitment, 30–37 cobbles were collected monthly at HMLR between July 2016 and June 2017 (except in March 2017 when storms and large waves prohibited diving).

Cobbles were collected and processed following established methods from Rogers-Bennett et al. (2016). Scuba divers targeted cobbles between 4- and 6-cm diameter and with a high cover of crustose coralline algae (CCA, >50%), as CCA is a known settlement cue for abalone (Morse et al. 1979, O'Leary et al. 2017). Cobbles were collected across three kelp forest depths (3, 6, and 9 m), representing the depth range of kelp at the collection sites, and 10–14 cobbles were collected per depth during each collection period. Although cobbles were targeted with high CCA cover and uniform size, over the course of the monthly sampling, there was variation in the cobble size and CCA cover. Collected cobbles ranged in size from 40 to 4,353 cm^3 (maximum length of each cobble was measured with a ruler along three dimensions, and values were multiplied to obtain approximate volumes) and visually ranged from 0% to 97% CCA cover. Because cobbles were the unit on which recruitment was assessed, to understand possible effects of variation in the cobble size and CCA cover on recruitment counts, abalone recruits/cobbles were graphed by cobble size and by CCA cover and evaluated with a linear regression. Abalone recruits were evenly distributed across various cobble sizes and CCA percent cover (Appendix 1A and B). On collection, divers immediately bagged cobbles underwater at the collection site in two zipper-top bags, gently transported them to the surface, and

maintained cobbles in their bags in ambient seawater temperature until processing was completed within 3 h.

To remove abalone from cobbles, each cobble was placed in an individual 5-gallon (approximately 18.9 L) bucket with enough seawater to cover the top of the cobble (8–11 L) and 120 ml of 95% ethanol, and then soaked for 10 min to anesthetize invertebrate settlers. Then, each cobble was scrubbed with a soft brush and rinsed with seawater over the bucket, and the contents were poured through an 80-µm mesh sieve. The sieve contents were stored in a sample jar with seawater, fixed with 40–45 mL of 95% ethanol, and kept in an –18°C freezer for 1–3 mo before sorting microscopically for newly settled abalone. Newly settled abalone were reported as mean abalone per cobble for each sampling period and site. Cobbles were transported and treated carefully to avoid crushing small abalone, newly settled abalone are fragile and it is possible that some were lost; however, if this is the case, the loss would be equal across samples in this study and in comparative studies in Northern California where the same methods were used.

Species Identification and Recruitment Age Determination

To identify newly settled abalone, the sieved samples were visually searched in an s-tray using an Olympus SZ61 dissecting microscope with 30× magnification. Morphological identifications were based on the presence of an extension of the radial lamellae underneath the spire (Fig. 1). For abalone less than 360 µm, however, the radial lamella extension was not fully developed. Because these small abalone could be misidentified as other species, two size classes were counted separately: less than 360 µm (possibly abalone) and greater than 360 µm (morphologically identifiable abalone). Each specimen was stored in a strip tube vial with 95% pure ethanol in a –18°C freezer for later genetic sequencing. To verify that morphologically identified specimens were red abalone, abalone from monthly recruitment samples collected between July 2016 and June 2017 were used. Twenty-three specimens were sequenced in the greater than 360 µm size class and 55 specimens in the less than 360 µm size class using the mitochondrial cytochrome oxidase I (COI) gene (see Appendix 2 for methods).
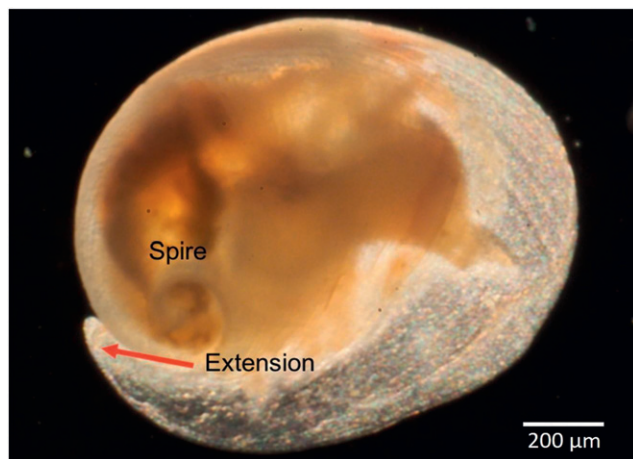
Figure 1. Extension of the abalone shell under the spire was characteristic of a newly settled abalone using morphological identification. This specimen is 1,276 µm.

To estimate abalone age, before sequencing, individuals in the greater than 360 µm size class were photographed and lengths measured using ImageJ1 software. Because there have been no field measurements for abalone age and size within the first few months of life, the literature was searched for laboratory studies on red abalone growth rates (Appendix 3). Among laboratory studies, there is high variability in early abalone growth rates, ranging from 4 to 63 µm/day (Appendix 3). The median growth rate was determined from each study (Appendix 3), and an average was created from the medians. This resulted in a mean growth rate which was used in estimating the age of newly settled abalone based on the sized individuals.

Kelp Surveys

Kelp is the major abalone food source, and availability of food may affect reproductive output, and hence abalone recruitment. In Northern California, loss of kelp has strongly affected abalone health and reproduction (Rogers-Bennett et al. 2019). Fluctuations in kelp availability could, therefore, lead to fluctuations in abalone recruitment. To assess kelp availability in Central California during the study period, *Macrocystis pyrifera* density was evaluated annually between 2012 and 2016 on scuba (at 36° 37′ 17″ N, 121° 54′ 5″ W), within 30 m of the HMLR cobble collection site. Scuba divers counted adult *M. pyrifera* with four or more fronds, either in circular plots (7.26 m² area) or in 10 × 2 m² transects, with 20–34 replicate counts per year. The placement of replicates was determined using random compass bearings and a number of fin kicks.

Temperature, Wave, and Upwelling Index Data

To evaluate possible physical factors that could affect patterns in annual abalone recruitment, temperature, wave, and wind-driven upwelling data were obtained from existing sources in Central California (Monterey Bay) as described in the following texts. For each of these data sets, monthly means were calculated between 2012 and 2016 and plotted with annual abalone recruitment from HMLR (Monterey Bay).

Seawater temperature data were obtained from the Monterey Bay Aquarium's intake pipe, located 17 m from water (at 36° 37′ 8″ N, 121° 54′ 5″ W) and in close proximity (approximately 150 m) to the HMLR collection site. Temperature was recorded every 5 min from a resistance temperature detector temperature sensor. Wave statistics were obtained every 30 min from the Cabrillo Point National Data Buoy Center buoy 46,240 (36° 37′ 35″ N, 121° 54′ 25″ W), 0.8 km from the HMLR cobble collection site. Continuous wind vector data were not available from Monterey-area buoys (e.g., National Data Buoy Center 46,042, 46,092). Therefore, the Bakun Upwelling Index was used, which provides estimates of offshore Ekman transport (Bakun 1975), from the grid point just offshore of Monterey Bay (at 36° N, 122° W; https://www.pfeg.noaa.gov/products/ PFELData/upwell/daily/p10dayac.all), 72 km from the HMLR cobble collection site. These data represent wind-driven cross-shelf transport per 100 m of coastline.

Data Analyses

Differences in recruitment among months, years, and sites were assessed in the Monterey Bay using separate models with R version 3.5.1 (R Core Team 2018). In each model, each cobble

was considered a sample, and the number of settled abalone per cobble was fitted as the response. The cobble surface area was not considered as a predictor because recruits were similarly distributed across cobble size, and there was a negligible relationship between recruitment and cobble size ($R^2 = 0.01$) based on a linear regression. To assess differences in recruitment between months sampled in 2016 and 2017, a generalized linear model (GLM) with a Poisson error distribution and log link was fitted, setting October (the month for which observed recruitment was highest) as the intercept. As no recruitment was observed in May and sampling was not feasible in March, these months were not considered in the analysis. The Poisson distribution is commonly used for discrete count data and is informed by a single parameter (λ) which is both the mean and the variance. The fit of this model was compared with a GLM with a negative binomial error distribution, which loosens the assumption that the mean and variance are equal, but comparison of model residuals suggested that the data did not deviate from the assumptions of the Poisson distribution. In addition, to test for zero-inflation (zeroes in excess of those expected from the Poisson distribution) in the count data, a likelihood ratio test was used to compare the fit of the Poisson model with a zero-inflated Poisson GLM, but the zero-inflated GLM was not a significant improvement (Neyman & Pearson 1933, Zeileis et al. 2008). Therefore, the Poisson distribution and log link were chosen for the models and pairwise comparisons on annual recruitment and between site recruitment.

To assess whether there were differences in annual recruitment during the fall (September–November) at HMLR among years, a GLM with a Poisson error distribution was fit, and the main effect of year with a was assessed with a likelihood ratio test (samples were pooled across months in each respective year at HMLR; see Table 1). Pairwise differences were assessed among years using the R package "emmeans" and adjusted for multiple comparisons using the Benjamini and Hochberg method for controlling the rate of false discovery (Benjamini & Hochberg 1995, Lenth 2019). A Poisson GLM was likewise used to assess differences among sites sampled along the Monterey peninsula in 2012 (Hopkins, Lovers Point, and Point Pinos).

RESULTS

Species Identification and Age

Of the 23 sequenced specimens in the greater than 360 μm size class (morphologically identified as *Haliotis rufescens*,

Fig. 1), 22 were identified as red abalone (>99% similarity *H. rufescens*) and one was identified as flat abalone (*Haliotis walallensis*; GenBank accession nos. MH304599.1–MH304626.1, Appendix 4). For smaller size classes (<360) that were suspected abalone but lacked the characteristic radial lamellae extension (Fig. 1), there was low success in extracting DNA because of the small specimen size, and only five of 55 individuals attempted were able to be sequenced. Only one of the five was a red abalone (>99% similarity *H. rufescens*). The other four were as follows: one flat abalone (>99% similarity *H. walallensis*), one opalescent nudibranch (>99% similarity *Hermissenda crassicornis*), and two brown turban snails (>99% similarity *Tegula brunnea*). Therefore, only the greater than 360 μm size class (which had distinct morphological cues, Fig. 1) was used in estimating recruitment. For the abalone measured in the greater than 360 μm size class, the size range was from 360 to 1,303 μm, with a mean of 790 μm. The age of abalone was estimated in this size class as between 2 wk and 2 mo. Thus, the methods used allowed for sampling of newly recruited abalones in very early size classes, and likely, only abalones in the first 2 wk after recruitment were missed.

Using these criteria, in total, 71 abalone were found from 207 cobbles during annual assessments at the HMLR between 2012 and 2016 (Table 1). In addition, in 2016, 29 abalone from 68 cobbles were found at two other Monterey Bay sites, Point Pinos and Lovers Point. During monthly assessments at the HMLR (July 2016–June 2017), 48 total abalone settlers were found from a total of 351 cobbles (Table 2).

Recruitment Patterns

Recruitment was not significantly different among samples collected at Lovers Point, HMLR, or Point Pinos in 2012 [χ^2 (2) = 0.48, $P = 0.79$; Fig. 2], suggesting that the data collected for intra-annual and interannual trends at the HMLR are largely representative of southern Monterey Bay. Annual fall (October–November) recruitment differed significantly among years [χ^2 (4) = 12.52, $P = 0.014$; Table 3, Fig. 2]. Abalone recruitment did not differ among sample years 2012, 2013, and 2014, with between 0.45 and 0.47 abalone per cobble each year (Table 3). Recruitment declined in 2015 to about 0.11 (±0.05) abalone per cobble and was significantly lower than in prior years (Table 3). In 2016, recruitment rebounded to about 0.29 (±0.07) abalone per cobble, and recruitment in 2016 did not differ significantly from 2012 to 2014 samples, but was also not

TABLE 1.

Summary of raw data from samples collected between 2012 and 2016 in the fall (September through November) on the Monterey Peninsula.

Year	Site	Collection interval	Cobbles collected	Abalone collected	Abalone per cobble (mean ± SE)
2012	HMLR	October 19–November 2	45	21	0.47 ± 0.14
	Lovers Point	October 20–October 29	32	12	0.38 ± 0.18
	Point Pinos	October 24–October 29	36	17	0.47 ± 0.14
2013	HMLR	September 2–September 3	29	13	0.45 ± 0.35
2014	HMLR	October 2–October 2	33	15	0.45 ± 0.13
2015	HMLR	September 8–September 8	37	4	0.11 ± 0.05
2016	HMLR	September 19–October 24	63	18	0.29 ± 0.07

HMLR, Hopkins Marine Life Refuge.

TABLE 2.

Summary of raw data from samples collected monthly between July 2016 and June 2017 at HMLR.

Collection date	Cobbles collected	Abalone collected	Abalone per cobble (mean ± SE)
2016			
July 18	37	6	0.16 ± 0.07
August 16	35	10	0.29 ± 0.1
September 19	30	6	0.2 ± 0.07
October 24	33	12	0.36 ± 0.12
November 18	31	3	0.1 ± 0.07
December 16	32	1	0.03 ± 0.03
2017			
January 27	31	1	0.03 ± 0.03
February 24	31	6	0.19 ± 0.11
April 21	30	2	0.07 ± 0.05
May 19	31	0	0 ± 0
June 23	30	1	0.03 ± 0.03

significantly different from 2015 recruitment (Table 3). Overall, recruitment at HMLR appears to have been consistently high between 2012 and 2014, declining in 2015 and rebounding to an intermediate level in 2016 (Fig. 2).

In monthly samples collected between July 2016 and June 2017, juvenile abalone were recruited during all sampled months except May (Table 4, Fig. 3). The highest recruitment was observed in October, but in general, recruitment was relatively high between July and October, as well as in February (Table 4, Fig. 3). Using October as the intercept (highest recruitment month), recruitment was not significantly different (based on Poisson GLM) between October and July, August, September, or February (Table 4). In contrast, recruitment was significantly lower in January, April, June, November, and December than that in October (Table 4).

Annual Patterns in Environmental Factors in Relation to Abalone Recruitment

Annual mean temperatures ranged from 11.7°C to 12.6°C (mean of 12.0°C) with maximums of 15.4°C–16.1°C in 2012, 2013, and 2016 (Fig. 4A). During the marine heat wave (2014 and 2015), the annual mean temperatures increased to 13.2°C and the maximum to 18.3°C in both years (Fig. 4A). Recruitment did not differ from previous years in the first year of high temperatures (2014) with 0.45 (±0.13) abalone per cobble in that year (Table 3, Fig. 4A). In the second year of the marine heat wave (2015), however, recruitment decreased to 0.11 (±0.05) abalone per cobble (Table 3, Fig. 4A). Kelp density consistently ranged between 1.0 and 3.4 plants per 10 m^2 (±0.22 and 0.40, respectively) at the HMLR from 2012 to 2016 (Fig. 4B), including during the marine heat wave, and did not appear to correspond to poor abalone recruitment in 2015.

The Bakun Upwelling Index showed a strong and persistent seasonal pattern every year in Central California. Upwelling followed the well-established seasonal pattern identified for the region (e.g., Pennington & Chavez 2000, Walter et al. 2016, 2018): upwelling increased during the early spring (April–May) and persisted until the relaxation season in fall months (September–November; Fig. 4C). Surface gravity waves consistently came from the north or northwest, with a distinct seasonal pattern of strong waves in the winter months (November–February), and weaker waves during the remaining seasons, a pattern consistent with long-term averages (cf.
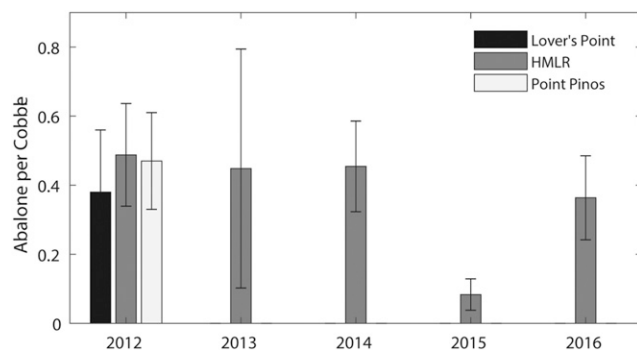

Figure 2. Average number of newly settled abalone per cobble (SE shown as error bars) collected annually at HMLR from 2012 to 2016. In addition to HMLR, newly settled abalones were collected at Lovers Point and Point Pinos in 2012.

TABLE 3.

Estimated annual mean recruitment (abalone per cobble) and corresponding confidence intervals (following a Poisson GLM) for samples collected between 2012 and 2016, with P values of pairwise comparisons adjusted using the Benjamini and Hochberg method.

Year	Fitted mean	Confidence interval		Contrast P values			
		2.5%	97.5%	2013	2014	2015	2016
2012	0.467	0.304	0.716	0.971	0.971	0.043	0.253
2013	0.448	0.260	0.772	–	0.971	0.043	0.308
2014	0.455	0.274	0.754	–	–	0.043	0.307
2015	0.108	0.041	0.288	–	–	–	0.197
2016	0.286	0.180	0.453	–	–	–	–

TABLE 4.

Estimated monthly mean recruitment (abalone per cobble) at HMLR for samples collected between July 2016 and June 2017, with corresponding confidence intervals (following a Poisson GLM).

| Month	Fitted mean	Confidence interval		Z-ratio	P value	
		2.5%	97.5%			
October (intercept)	0.364	0.207	0.640	–	–	–
January	0.032	0.005	0.229	–2.327	0.020	*
February	0.194	0.087	0.431	–1.261	0.207	–
April	0.067	0.017	0.267	–2.221	0.026	*
June	0.033	0.005	0.237	–2.296	0.022	*
July	0.162	0.073	0.361	–1.615	0.106	–
August	0.286	0.154	0.531	–0.563	0.573	–
September	0.200	0.090	0.445	–1.196	0.232	–
November	0.097	0.031	0.300	–2.051	0.040	*
December	0.031	0.004	0.222	–2.358	0.018	*

Months with P values below 0.05.
* Display significantly lower recruitment compared with October, the month for which recruitment was highest.

Woodson 2013, Fig. 4D). There was no clear correspondence between graphs of upwelling or wave forces and those of abalone recruitment (Fig. 4).

DISCUSSION

This is the first assessment of early (<2 mo) red abalone recruitment in the field in Central California where populations are at low densities but highly aggregated because of intense sea otter predation. This is also the first study to assess early red abalone (*Haliotis rufescens*) recruitment in the wild over an entire annual cycle examining recruitment seasonality. Red abalone were found to have consistent and moderate recruitment, despite the low population densities, and to be capable of reproducing and spawning year-round in the field in this region. Because warmer conditions are typically associated with reduced abalone recruitment (Searcy-Bernal 1999, Vilchis et al. 2005, Rogers-Bennett et al. 2010), it was expected that recruitment would be greatest during months of strong upwelling, when there is an influx of cool, nutrient-rich water in this region (Pennington & Chavez 2000, Walter et al. 2016, 2018).
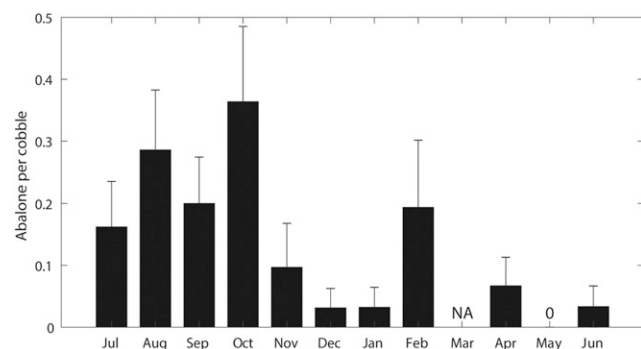
Figure 3. Average number of newly settled abalone per cobble (SE shown as error bars) collected monthly at HMLR from July 2016 to June 2017.

Instead, a bimodal recruitment pattern (with a broad peak from July to October and another in February) was observed, and there were no apparent seasons of higher or lower abalone recruitment that might correspond to typical upwelling seasonality (and the oceanic response) in Central California and the California Current System (cf. Pennington & Chavez 2000, Walter et al. 2018, Barth et al. 2020).

It was expected that like Northern California, Central California abalone recruitment would be highly variable year to year; however, annual recruitment was generally consistent across the years surveyed, with the exception of 2015, when recruitment dropped from 0.46 (±0.13) abalone per cobble to 0.11 (±0.05) abalone per cobble, a 76% decrease in recruitment. Coastal temperatures increased substantially in 2014 to 2015 in California during the North Pacific marine heat wave. In Central California, red abalone recruitment was similar to prior years in the first year of warming (2014) but declined dramatically during the second year of warming (2015). Other than temperature, none of the environmental factors that were evaluated (kelp abundance, upwelling, or waves) showed trends that might explain this decline. Increased sea surface temperatures during the heat wave began in the late summer of 2014 (Gentemann et al. 2017). Recruits collected in October 2014 would, therefore, have been exposed to the warm temperatures from the settlement date. As recruitment in 2014 was similar to prior years, these data suggest that warming may not have directly disrupted settlement or caused higher postsettlement mortality; however, as the warming trend continued through October 2015, prolonged heat stress may have caused adult abalones to reallocate energy resources away from gamete production to survival, leading to the low recruitment observed in the fall of 2015. Other studies in California have shown that increased temperatures (+5°C compared with ambient temperatures) caused reproductive failure in males and diminished fecundity in females (Rogers-Bennett et al. 2010), and that cooler waters (–2.5°C) promote higher gonadal development (Vilchis et al. 2005); however, another study in California showed that fertilization rates decreased during cooler periods associated with upwelling (–4°C; Boch et al. 2017). In the present study, prolonged temperature increases of 1.2°C in mean temperatures and 2.3°C in maximum temperatures during the marine heat wave appear to strongly negatively affect reproduction, as found in Rogers-Bennett et al. (2010) and Vilchis et al. (2005). It has been shown for other marine invertebrates that metabolic stress due to temperature changes causes an increased use of energy reserves, which diminishes the use of energy for other functions including reproduction (gametogenesis and spawning; Sokolova et al. 2012).

Thus, red abalone reproduction seems to be susceptible to increased temperature, and this will have implications for future ocean-warming scenarios predicted with climate change. The global abalone literature was reviewed on the impacts of temperature on recruitment (Appendix 5), and temperature increases as little as 2°C above ambient (mainly laboratory studies), consistent with the observed temperature increases during the marine heat wave, generally lead to reduced reproduction, larval transport, settlement, and postsettlement survival. In one study, red abalones exposed to warm water had poor gonad development, despite being fed abundant kelp (Rogers-Bennett et al. 2010).
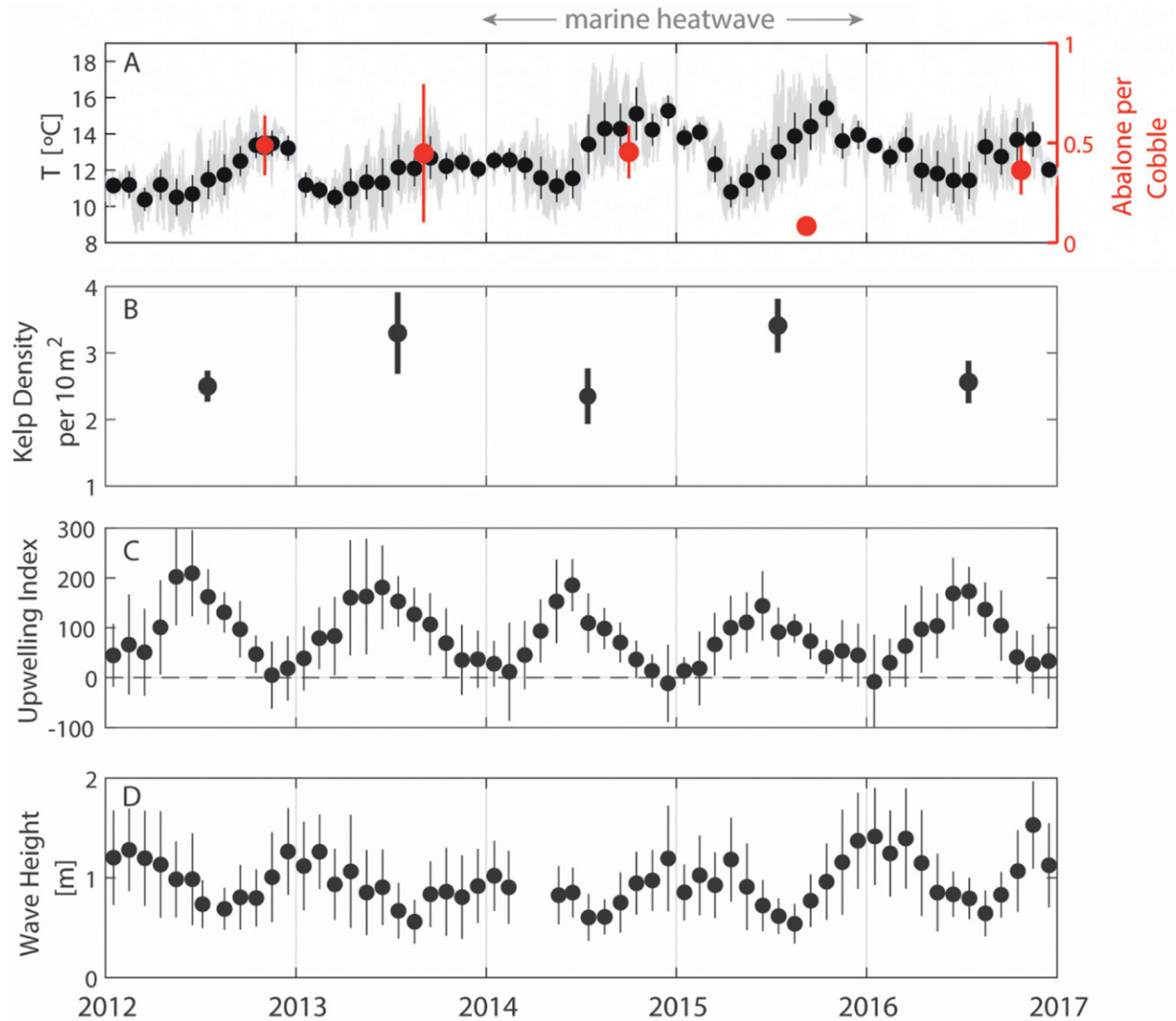
Figure 4. Time series of environmental conditions (left *Y*-axis) and annual abalone recruitment (red, right *Y*-axis on panel A) at HMLR. (A) Temperature with annual abalone recruitment, (B) kelp density, (C) Bakun Upwelling Index near HMLR, and (D) significant wave height. For temperature (A), upwelling index (C), and significant wave height (D), monthly means (gray dots) are shown with monthly SD. Temperature also shows the raw, 2-min data in light gray. For kelp (panel B, *Macrocystis pyrifera*), mean density per 10 m^2 collected annually in August is shown (gray dots) with SE. Annual abalone recruitment surveys are shown as averages (black dots) with SE (surveys done during 1 mo in the fall of each year, September–November). The time of the North Pacific marine heat wave is shown at the top (2014 and 2015).

Recruitment during "normal" years (i.e., 2012 to 2016 excluding 2015) in southern Monterey Bay in Central California [0.46 abalone per cobble (±0.13)] was about half that of recruitment during high recruitment years in Northern California (e.g., ~1 abalone per cobble; Rogers-Bennett et al. 2016). This was expected given that the population densities were ~2.7 times lower than those found in Northern California during past studies when recruitment was measured (Rogers-Bennett et al. 2016); however, recruitment in southern Monterey Bay (during this study period) appears to be more annually consistent than that in Northern California. In Northern California, before the post-2014 abalone decline, annual recruitment was typically very low (0–0.1 abalone per cobble), with occasionally high annual recruitment (e.g., approximately 1 abalone per cobble; Rogers-Bennett et al. 2016). There are several factors

that could contribute to the consistent recruitment in Central California. One possibility is that because abalone in Central California are highly aggregated in cracks and crevices because of sea otter predation (Lowry & Pearse 1973, Hines & Pearse 1982), abalone have localized areas of high density that overcome the Allee effect and increase fertilization success (Button 2008). Although densities are higher in Northern California, individual abalone may be more dispersed without otter predation, resulting in variable fertilization success. Another possible reason for different recruitment patterns between the Northern and Central California sites is differences in local oceanography and coastline features. Coastal embayments, such as Monterey Bay, have increased larval retention because of shielding from strong regional upwelling and less surface wave forcing (Graham & Largier 1997, Walter et al. 2016,

2018). In so-called upwelling shadow systems, increased retention allows for enhanced accumulation of buoyant organisms (Graham & Largier 1997, Ryan et al. 2014). Sheltered embayments along California's coast, and other upwelling systems (see recent review by Largier 2020), may provide larval retention sites that allow for increased abalone recruitment. A third possibility is that food resources are more abundant and seasonally consistent in Central California. Central California kelp forests are dominated by *Macrocystis pyrifera*, which is perennially present and continually releases large blades. By contrast, Northern California kelp forests are dominated by *Nereocystis luetkeana*, which dies each winter, leading to seasonal kelp shortages. Lack of food for part of the year can negatively affect abalone sperm and egg production (Rogers-Bennett et al. 2010), and loss of kelp was hypothesized as a major factor leading to low abalone recruitment in Northern California in recent years (Rogers-Bennett et al. 2016) and a cause of population declines post-2014 (Rogers-Bennett et al. 2019).

Although data from the present article provide high temporal resolution of abalone recruitment in the field, microscopically identifying new settlers is labor intensive (approximately 4 h per sample), making these methods challenging. In the future, new genetic techniques might allow for rapid processing of samples and facilitate frequent sampling (e.g., Shum et al. 2019). A limitation of this study was the inability to identify abalone less than 2 wk old (<360 μm). If, however, 20% of the specimen in this size range were assumed to be red abalones (based on the one red abalone of the five specimens sequenced), mean monthly recruitment would have increased only marginally from 0.13 (±0.04) to 0.18 (±0.04) abalone per cobble, and monthly trends appear robust to this omission. Although the inferences about dynamics in Central California are limited by spatially constrained sampling, recruitment was comparable between samples collected from the three sites in southern Monterey Bay in 2012. Thus, it seems likely that these results are representative of red abalone recruitment trends in southern Monterey Bay and give an indication of recruitment potential at low abalone densities under certain conditions.

The results from this work are broadly applicable to other marine invertebrates. Allee effects (Allee 1931) impact many free spawning marine invertebrates, and aggregation can improve fertilization success by decreasing nearest neighbor distance (Levitan 1995). Furthermore, prolonged heat stress may result in reallocation of energy resources away from gamete production (Sokolova et al. 2012). Impacts of heat stress on recruitment have been seen in multiple phyla (Shanks et al. 2020), and the observation in the present study of reduced recruitment after 2 y of heat stress indicates that decreased reproductive output may become an issue for other marine invertebrate populations. Although in the present study, food resources were not limiting, increased cellular energy demand when under stress (e.g., temperature) often leads to increased food consumption (Sokolova et al. 2012). Kelp forests are a major food supply for many marine invertebrates and have also been affected by warming and other ecosystem changes in California (Rogers-Bennett et al. 2019). Thus, wide-scale kelp loss in California may have further implications on energy reserves for marine invertebrates and affect reproductive capacity and population stability. Finally, in the future, use of genetic techniques (Shum et al. 2019) to more rapidly assess recruitment samples can broaden our ability to sample numerous marine benthic recruits and evaluate recruitment processes in warm and cool years for a suite of marine invertebrates.

Implications for Abalone Management and Conservation

California abalones were historically subjected to heavy fishing pressure and have experienced periodic fishing and disease-induced declines. Recently, Northern California red abalone populations experienced a mass mortality (Rogers-Bennett et al. 2019) because of warming-induced kelp loss and massive increases in sea urchins (Rogers-Bennett et al. 2019). The present study suggests red abalone may be susceptible to changing environmental conditions through reproductive failure under prolonged high temperatures, and more work is needed on this theme.

The findings presented here also indicate that low-density abalone populations can have moderate, consistent recruitment if animals are highly aggregated, in sheltered embayments, and have access to constant food resources. The creation of abalone aggregations may be an important conservation strategy to improve fertilization success (Taniguchi et al. 2013), and sheltered coastal embayments may represent optimal locations for restorative abalone stocking. In areas such as Northern California where the dominant kelp is annual and food limitation is more likely, ecosystem-based fisheries management may become critical to control algae competitors such as sea urchins. For example, sea urchins are currently being removed in Northern California to allow for kelp recovery, partly to alleviate competition for food with abalones (Hohman et al. 2019). With abalone now at low densities statewide, understanding where and when abalone recruit is critical as part of statewide abalone recovery and management. The sampling methods and results presented here provide essential fishery information and suggest conditions that could be critical to abalone recovery, informing statewide management and recovery programs.

ACKNOWLEDGMENTS

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APPENDIX 1

The number of newly settled abalone found per cobble at HMLR (all monthly samples from 2016 to 2017) as a function of (A) cobble size and (B) percent cover of CCA on the cobble
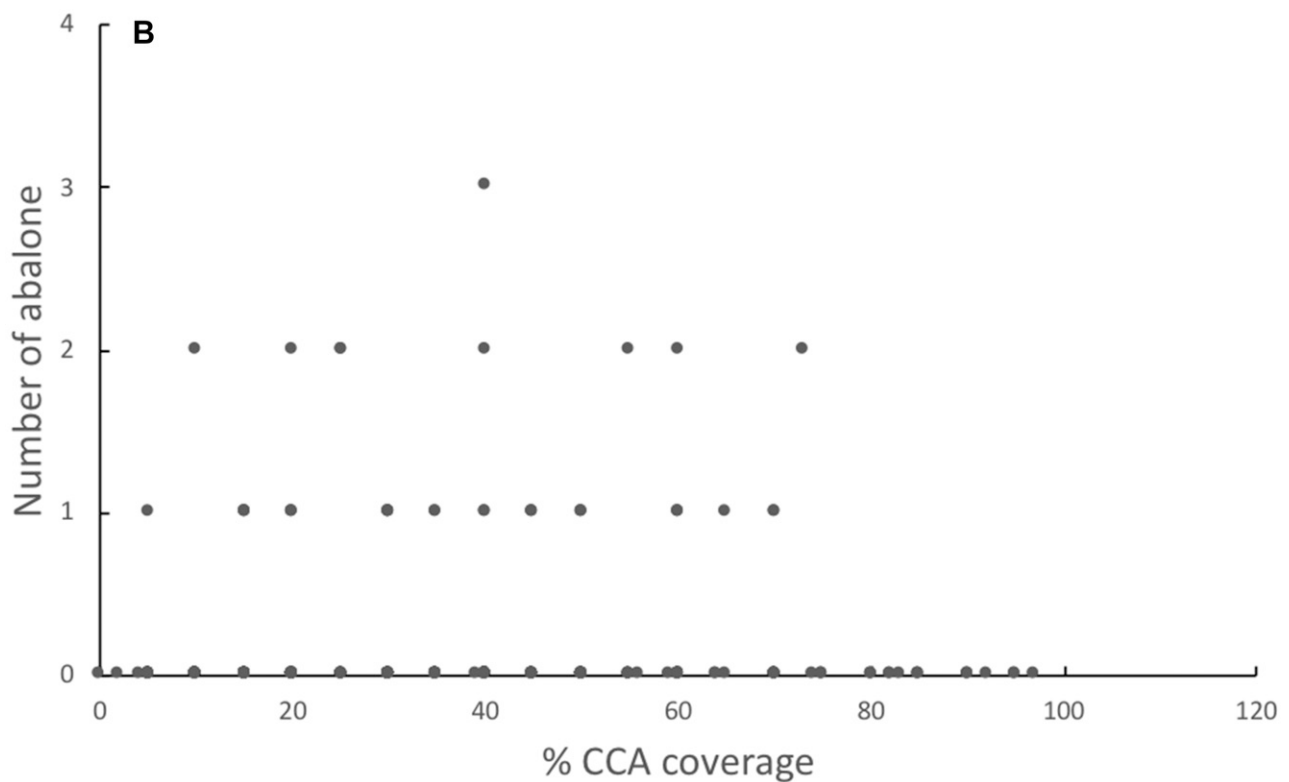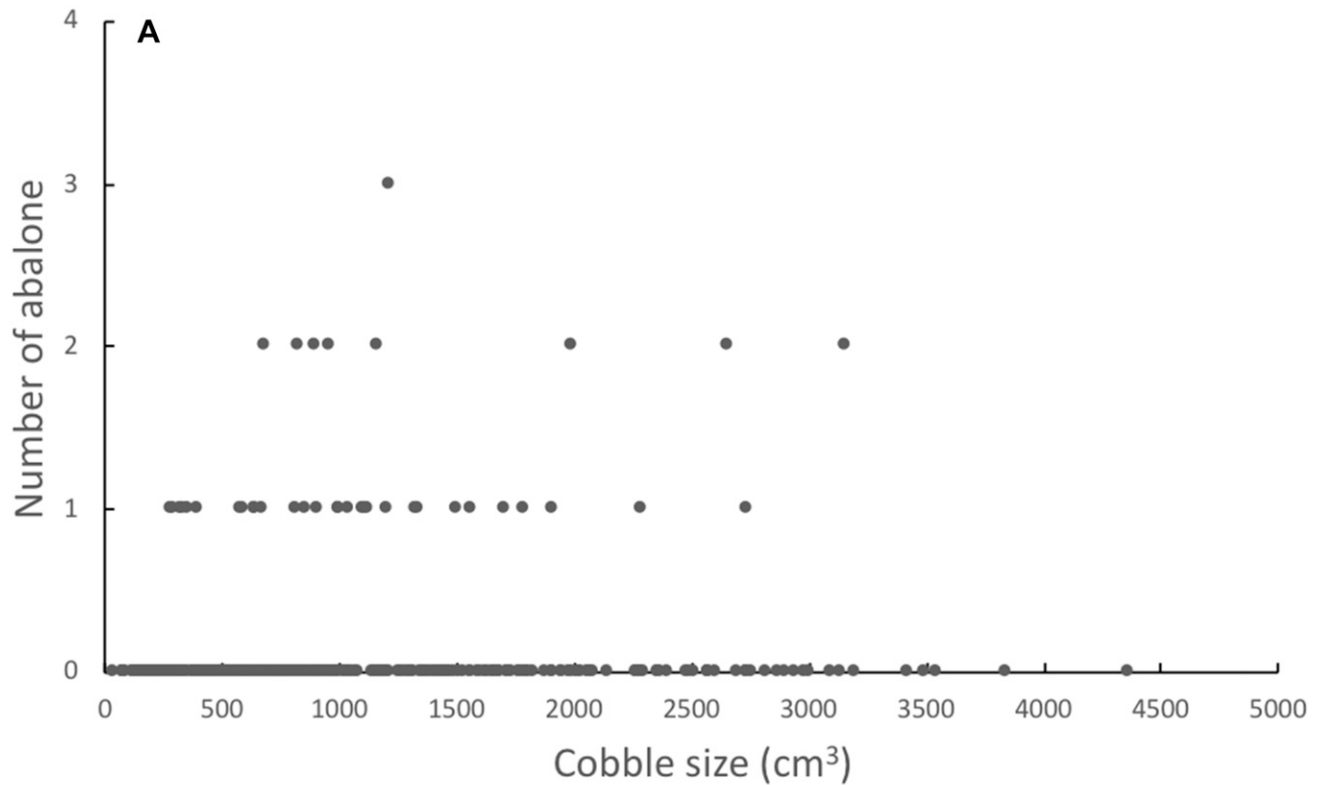
APPENDIX 2

Genetic Sequencing Methods Used to Verify That Identified Specimen Were Red Abalones Haliotis rufescens

Samples were pulse centrifuged, and ethanol was removed. We extracted DNA using a commercial kit NucleoSpin 96 (Macherey-Nagel GmbH & Co. KG, Düren, Germany). An approximately 650–base pair (bp) fragment of coding mitochondrial COI was amplified using degenerate Folmer primers (Folmer et al. 1994; LCO1490: 5′-TAA ACT TCA GGG TGA CCA AA-3′ and HCO2198: 5′-GGT CTA CTA ATC ACA AAG AYA THG G-3′). Reactions were carried out in 20 µL volumes containing $1\times$ PCR buffer, 2 mM MgC1$_2$, 4 mM dNTPs, 0.5 µM of each primer, 0.05 units Taq DNA polymerase, with 2 µL of DNA template. We performed amplifications in an Eppendorf Vapo Protect Thermocycler (Hamburg Germany) using the following temperature profiles: 94°C (2 min), 35 cycles of [94°C (30 sec), 50°C (30 sec), 72°C (60 sec)], followed by 7 min at 72°C. A positive and a negative control were included in all reactions. If the positive control failed to amplify or there was a visible band in the negative control, we reran the PCR. We subjected PCR products to electrophoresis through a 1% sodium borate acid ($1\times$ SB) gel stained with GelRed for visualization via a UV-transilluminator. PCR products were purified using magnetic beads ($0.5\times$) to remove unincorporated primers and deoxynucleotides in preparation to sequencing. Purified products were sequenced by ELIM BIOPHARM (ElM BIOPHARM; https://www.elimbio.com). We manually checked resulting sequences for quality, and edited, and trimmed sequences using Chromas Lite 2.1.1 (http://technelysium.com.au/?page_id=13).

We identified COI sequences using the Barcode of Life Data Systems online (BOLD, Biodiversity Institute of Ontario, University of Guelph, Guelph, Ontario, Canada; http://www.barcodinglife.org; Ratnasingham & Hebert 2007) using the species-level barcode database. We cross-referenced sequences using BLAST on GenBank (Basic Local Alignment Search Tool, National Center for Biotechnology Information, Bethesda, MD; http://www.ncbi.nlm.nih.gov/). We used a threshold of 99%–100% sequence similarities, above which identification of specimens was deemed reliable.

APPENDIX 3

Literature review of laboratory studies on the red abalone *Haliotis rufescens* postsettlement growth per day

Reference	Location	Temperature (°C)	Study duration (days)	Abalone growth (µm/day)	Influential factors
Searcy-Bernal et al. (2007)	Baja California, MX	14.3–15	100	37–63	Temperature/light intensity
Correa-Reyes et al. (2009)	Baja California, MX	18	50	18.5–34.2	Diet
Rogers Bennett et al. (2010)	Mendocino/Sonoma, CA	14	NA	7.14	NA
Muñoz et al. (2012)	Chile	13	30	16.8–21.2	Diet
Anguiano-Beltrán et al. (2012)	Baja California, MX	16–18	10	4.1–11.2	Diet
Anguiano-Beltrán and Searcy-Bernal (2013)	Baja California, MX	17.5	63	44.6–61.6	Water flow

APPENDIX 4

Identity of sequenced samples as determined by morphology and metabarcoding

Sample	GenBank accession	Date collected	Size (μm)	Morphological ID	GenBank (COI) >99%	BOLD (COI) >99%
H6_1	MH304599	October 2, 2014	1,084.00	*Haliotis rufescens*	*Haliotis walallensis*	*H. walallensis*
H6_3.1	MH304600	October 2, 2014	682.00	*H. rufescens*	*H. rufescens*	*H. rufescens*
H11_OCT	MH304601	October 2, 2014	812.00	*H. rufescens*	*H. rufescens*	*H. rufescens*
H33	MH304602	October 2, 2014	661.00	*H. rufescens*	*H. rufescens*	*H. rufescens*
H6_3.2	MH304622	October 2, 2014	782.00	*H. rufescens*	*H. rufescens*	*H. rufescens*
H35	MH304603	September 8, 2015	1,057.00	*H. rufescens*	*H. rufescens*	*H. rufescens*
H_29	MH304620	July 18, 2016	1,286.00	*H. rufescens*	*H. rufescens*	*H. rufescens*
H2_2	NA	July 18, 2016	300.00	Unknown settler	*Homo sapiens*	*H. sapiens*
Ab_H11_1	NA	July 18, 2016	300.00	Unknown settler	*H. sapiens*	*H. sapiens*
H1	MH304604	August 16, 2016	1,276.00	*H. rufescens*	*H. rufescens*	*H. rufescens*
H5_1	MH304605	August16, -2016	1,066.00	*H. rufescens*	*H. rufescens*	*H. rufescens*
H5_2	MH304606	August 16, 2016	825.00	*H. rufescens*	*H. rufescens*	*H. rufescens*
H7	MH304607	August 16, 2016	736.00	*H. rufescens*	*H. rufescens*	*H. rufescens*
H11_1	MH304608	August 16, 2016	848.00	*H. rufescens*	*H. rufescens*	*H. rufescens*
H11_2	MH304609	August 16, 2016	881.00	*H. rufescens*	*H. rufescens*	*H. rufescens*
H25	MH304610	August 16, 2016	775.00	*H. rufescens*	*H. rufescens*	*H. rufescens*
H28	MH304611	August 16, 2016	860.00	*H. rufescens*	*H. rufescens*	*H. rufescens*
Ab_H2	MH304612	October 24, 2016	280.00	*H. rufescens*	*H. rufescens*	*H. rufescens*
H27	MH304613	October 24, 2016	810.00	*H. rufescens*	*H. rufescens*	*H. rufescens*
Ab_H21	NA	October 24, 2016	270.00	Unknown settler	*H. sapiens*	*H. sapiens*
H16	MH304614	November 18, 2016	762.00	*H. rufescens*	*H. rufescens*	*H. rufescens*
H3	MH304619	November 18, 2016	800.00	Unknown settler	*H. rufescens*	*H. rufescens*
H19_1	MH304624	November 18, 2016	300.00	Unknown settler	*Tegula brunnea*	*Chlorostoma brunnea*
H19_2	NA	November 18, 2016	280.00	Unknown settler	*H. sapiens*	*H. sapiens*
H31_2	MH304625	November 18, 2016	280.00	Unknown settler	*H. walallensis*	*H. walallensis*
H_3	MH304623	November 18, 2016	260.00	Unknown settler	*T. brunnea*	No match
H_30	NA	November 18, 2016	800.00	Unknown settler	*H. sapiens*	*H. sapiens*
H18	MH304615	January 27, 2017	1,266.00	*H. rufescens*	*H. rufescens*	*H. rufescens*
H_21	NA	January 27, 2017	280.00	Unknown settler	*H. sapiens*	*H. sapiens*
H20	MH304616	February 24, 2017	530.00	*H. rufescens*	*H. rufescens*	*H. rufescens*
H_22_1	MH304621	February 24, 2017	530.00	*H. rufescens*	*H. rufescens*	*H. rufescens*
H21	MH304617	April 21, 2017	1,303.00	*H. rufescens*	*H. rufescens*	*H. rufescens*
H5	MH304618	June 23, 2017	495.00	*H. rufescens*	*H. rufescens*	*H. rufescens*
Ab_H30_2	MH304626	June 23, 2017	367.00	Unknown settler	*Hermissenda crassicornis*	*H. crassicornis*

APPENDIX 5

Literature review on the effects of temperature on abalone reproduction, transport, settlement, and postsettlement survival/growth.

Recruitment stage	Reference*	Species	Location	Study type†	Average ambient temperature (°C)	Temperature change‡	Factor evaluated	Effect: temperature increase	Comments
Reproduction	Vilchis et al. (2005)	*Haliotis fulgens*	Southern California	L	16	+2.5	Gonad development	−	Reproduction was more strongly influenced by abundance in food resources
Reproduction	Boch et al. (2017)	*Haliotis rufescens*	Central California	L	13	−4	Fertilization rates	+	Fertilization rates decreased during colder upwelling periods and near pH 7.55
Reproduction	Rogers-Bennett et al. (2010)	*H. rufescens*	Northern California	L	11	+5	Sperm production/fecundity	−	Reproductive failure in males and diminished fecundity in females
Reproduction	Vilchis et al. (2005)	*H. rufescens*	Southern California	L	16	−2.5	Gonad development	−	Cooler temperature promotes higher gonadal development
Larval development	Leighton (1974)	*H. rufescens*	Southern California	L	15	+1	Survival, growth	+	Most rapid growth and best survival at 15–18°C
Larval development	Searcy-Bernal (1999)	*H. rufescens*	Northern California	L	14	+2	Survival	−	Larval competency decreased
Larval development	McCormick et al. (2012)	*H. rufescens*	Southern California	L	14	0	Survival	NA	Larval competency periods were extended at 14°C in comparison with previous transport period estimations
Larval development	Leighton (1972)	*Haliotis sorenseni*	Southern California	L	16	+4	Larval development	+	Individuals did not survive once they settled at warmer temperature (20°C)
Larval development	McCormick et al. (2016)	*H. sorenseni*	Southern California	L	12	±3	Survival	−	Survival from fertilization to settlement was greatest at 12°C
Settlement	Rodriguez-Valencia et al. (2004)	*Haliotis corrugata, H. fulgens*	Mexico	F	19	+2	Settlement	−	Warm temperatures caused by ENSO conditions
Settlement	Guzmán del Proo et al. (2013)	*H. fulgens*	Mexico	M	21	±2	Settlement	−	Lower recruitment values were found at 19°C and 23°C
Settlement	Tegner et al. (2001)	*H. rufescens*	Southern California	F	16	+3	Settlement	−	Warm temperatures caused by ENSO conditions
Postsettlement	Searle et al. (2006)	*Haliotis iris*	New Zealand	L	8	+4–18	Growth/survival	±	Growth was higher; however, survival decreased (abalones were larger than those in this study: 10–60 mm)
Postsettlement	Britz et al. (1997)	*Haliotis midae*	South Africa	L	16	+5	Growth	−	Juvenile abalones tested were larger than those in this study: 17.5 mm
Postsettlement	Steinarsson and Imsland (2003)	*H. rufescens*	Central California	L	15	+5	Survival	−	Mortality increased at 20°C (abalones were larger than those in this study: 15.6–95.3 mm)
Postsettlement	McCormick et al. (2016)	*H. sorenseni*	Southern California	L	12	+3	Survival	−	Juvenile abalones tested were larger than those in this study: 29.8 mm

* Review includes multiple species globally because there were few publications on red abalone.
† Study type: L, laboratory; F, field; M, model.
‡ Temperature change: change in temperature from the average ambient temperature.