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TRACKING LARVAL, NEWLY SETTLED, AND JUVENILE RED ABALONE (*HALIOTIS RUFESCENS*) RECRUITMENT IN NORTHERN CALIFORNIA

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ABSTRACT Recruitment is a central question in both ecology and fisheries biology. Little is known however about early life history stages, such as the larval and newly settled stages of marine invertebrates. No one has captured wild larval or newly settled red abalone (*Haliotis rufescens*) in California even though this species supports a recreational fishery. A sampling program has been developed to capture larval (290 μm), newly settled (290–2,000 μm), and juvenile (2–20 mm) red abalone in northern California from 2007 to 2015. Plankton nets were used to capture larval abalone using depth integrated tows in nearshore rocky habitats. Newly settled abalone were collected on cobbles covered in crustose coralline algae. Larval and newly settled abalone were identified to species using shell morphology confirmed with genetic techniques using polymerase chain reaction restriction fragment length polymorphism with two restriction enzymes. Artificial reefs were constructed of cinder blocks and sampled each year for the presence of juvenile red abalone. Settlement and recruitment were found to vary with year and site from 2007 to 2015. In some years such as 2010 and 2013, there were many larvae and newly settled abalone, whereas in other years there were none. The two exceptionally poor years for larval and newly settled abalone were 2012 and 2015 (warm El Niño years). In 2013, there was spatial concordance between two sites 18 km apart with respect to the sizes of the newly settled individuals suggesting they were spawned and settled on the same day. The methods developed here, quantifying early life history stages, may shed light on the "black box" of recruitment and help address what are the drivers of good and bad recruitment years for red abalone in northern California.

KEY WORDS: early life history, recruitment, reproduction, settlement, spawning, spat

INTRODUCTION

Recruitment is a central question in population biology and fisheries science. Hjort (1914) proposed that strong year classes could be important drivers of marine populations that supported fisheries in northern Europe. Strong recruitment pulses of abalone *Haliotis laevigata* were observed twice over an 18-y period in South Australia (Shepherd 1990). The production of a strong year class requires that a number of stages in recruitment be successful. First, there must be gamete production indicating adults are getting enough food resources to spawn eggs and sperm. Second, the eggs must be successfully fertilized which requires spawning synchrony in time and space (Babcock & Keesing 1999). The larvae must survive the planktonic stage and return to suitable habitats, settle, metamorphose, develop a gut, and start first feeding. To ask questions about recruitment success or failure, early life history stages need to be detected and quantified to identify the mechanisms responsible for recruitment success.

Abalone species in southern California once supported important commercial and recreational fisheries, but today there are signs of recruitment failure (Rogers-Bennett et al. 2002, Rogers-Bennett et al. 2004). White and black abalone are endangered species, whereas pink, green, and northern abalone are species of concern. In 1997, abalone fishing was closed south of San Francisco leaving only a recreational skin diving fishery for red abalone (*Haliotis rufescens*) in northern California. The red abalone fishery in the north has 30–40,000 participants landing 200–310 mt/y and is closely managed (Kashiwada & Taniguchi 2007). Given the closure of multiple abalone fisheries as well as all of southern California, there is now enhanced focus on sustainably managing this resource.

Although there is interest in obtaining recruitment information for early life history stages of red abalone, these data are a challenge to obtain akin to searching for a "needle in a hay stack." Despite the challenges, several investigators have detected larval abalone from coastal waters surrounding Japan (Sasaki 1985, Tanaka et al. 1986, Sasaki & Shepherd 1995, Horii et al. 2006). Newly settled abalone (<1 mm) have been collected from crustose coralline algae and diatom covered substrates in Japan (Tanaka et al. 1986, Takami et al. 2006, Horii et al. 2006), New Zealand (Aguirre & McNaught 2011), Australia (Nash 1992, Keesing et al. 1995, Nash et al. 1995), and Mexico (Rossetto et al. 2013). To date, larval and newly settled abalone have not been detected in California as sampling is hindered by small larval size (290 μm), potential for low abundances, and a lack of information about where and when to sample. Furthermore, four species of abalone exist in northern California making species identification challenging.

Here a recruitment sampling program is developed to examine, larvae (290 μm), newly settled larvae (290–2,000 μm), and juvenile (2–20 mm) red abalone. From 2007 to 2015, these early life history stages are examined at multiple sites in the productive fishery region of Sonoma and Mendocino Counties in northern California. Plankton tows are conducted to sample larval abalone in the water column and cobble covered with crustose coralline algae are examined for newly settled abalone in the benthos. Larval and newly settled abalone are identified using morphological features and these identifications are confirmed using polymerase chain

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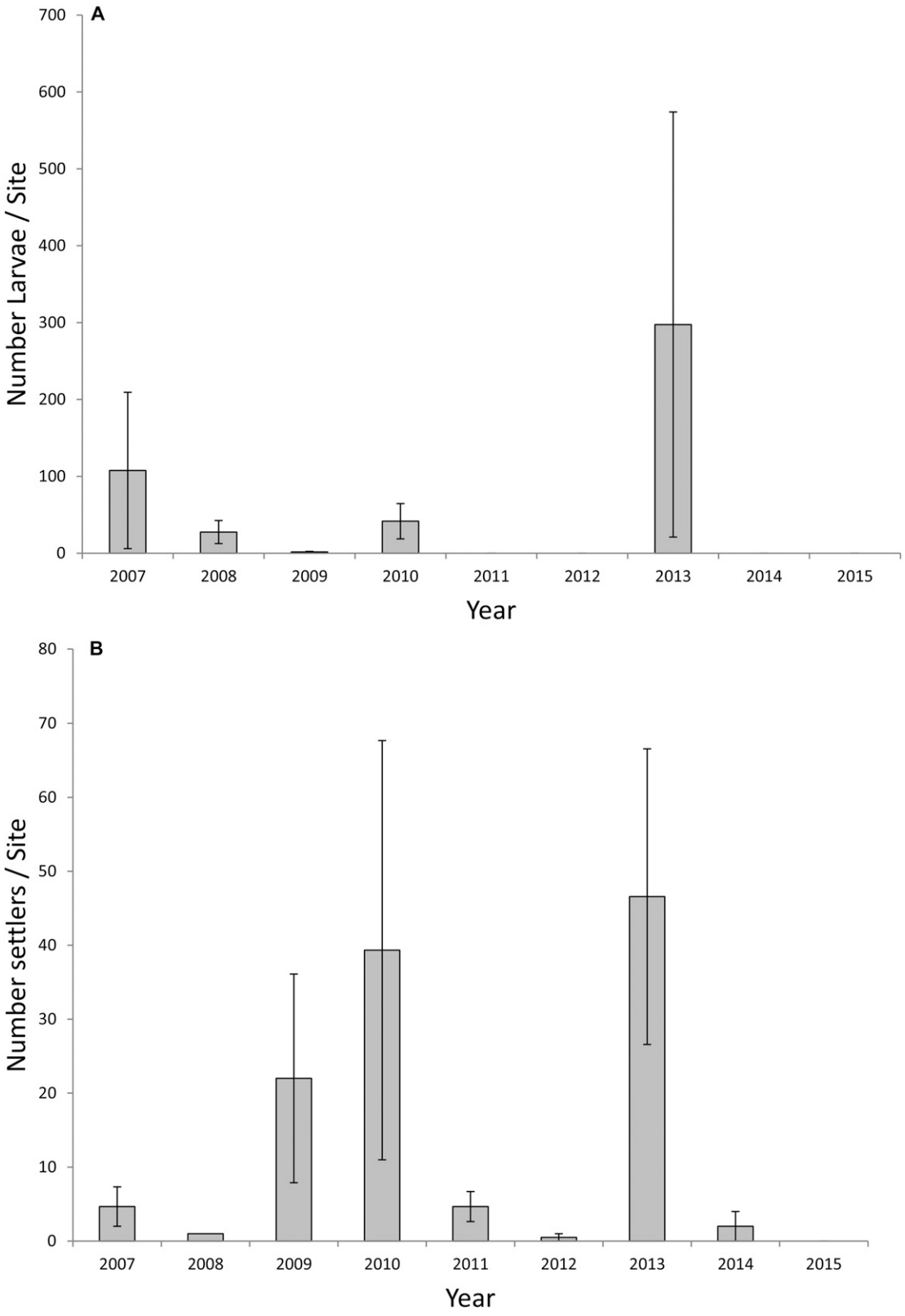

Figure 1. (A) The number of larval abalone captured in plankton tows per site from 2007 to 2015 in northern California showing standard error bars. (B) The number of newly settled abalone captured from cobbles ($n = 80$) covered with crustose coralline algae per site from 2007 to 2015 in northern California showing standard error bars.

TABLE 1.

Abundance of larval abalone captured in plankton tows from sites listed from north to south in northern California from 2007 to 2015.

Site	2007	2008	2009	2010	2011	2012	2013	2014	2015
Mendocino									
Todd's Point	–	64	3	–	–	–	574	–	–
Caspar	–	40	–	–	0	–	–	–	–
Van Damme	0	5	1	87	0	0	21	0	0
Stornetta	311	–	–	–	–	–	–	–	–
Point Arena	12	–	–	25	–	–	–	54	–
Sonoma									
Sea Ranch	–	–	–	–	–	0	–	–	–
Salt Point	–	1	–	–	–	0	–	–	–
Ocean Cove	–	–	–	13	–	–	–	–	–
Timber Cove	–	–	–	–	–	0	–	–	–
Fort Ross	–	–	1	–	–	0	–	–	0

TABLE 2.

Number of newly settled abalone (<1 mm) found on cobbles covered in crustose coralline algae ($n = 80$ per site) at sites listed from north to south in northern California from 2007 to 2015.

Site	2007	2008	2009	2010	2011	2012	2013	2014	2015
Mendocino									
Todd's Point	–	–	–	–	–	–	68	–	–
Cabrillo	–	–	–	–	–	–	6	–	–
Caspar	–	1	–	–	5	–	7	–	–
Van Damme	10	1	11	10	1	0	82	0	0
Stornetta	2	–	–	–	–	0	–	0	–
Point Arena	2	–	–	96	8	–	–	0	–
Sonoma									
Sea Ranch	–	–	–	–	–	0	–	–	–
Salt Point	–	1	–	12	–	0	–	–	–
Ocean Cove	–	–	–	–	–	–	–	–	–
Timber Cove	–	–	5	–	–	0	–	–	0
Fort Ross	–	–	50	–	–	3	–	–	0

reaction restriction fragment length polymorphism genetic methods. The size of the newly settled abalone is used to estimate spawning dates and model dispersal. These methods maybe used to develop a time series of larval and newly settled abalone abundance to identify good and bad recruitment years.

MATERIALS AND METHODS

Sampling Larval Abalone

Larval abalone were collected from the water column using plankton nets in August and September of each year. Plankton tows were conducted using CMS–O-type net 3 m in length with a 36 cm wide opening and 100 μm mesh. Plankton tows were 6-min integrated tows starting near the bottom for 2 min, at mid depth for 2 min, and then near the surface for the final 2 min. Three tows were done at two different depth strata, in deep water (33–45 m) and shallow water (10–15 m) for a total of six plankton samples per site. Flowmeter indicated that the volume of seawater sampled ranged on average from 5 to 25 m^3. Samples were collected avoiding kelp beds with the towing vessel traveling at speeds of less than 2 knots averaging 1.4 knots. Kelp and jelly fish were removed from the sample by hand when possible. Once the tow was completed, the net was rinsed down and the sample collected in a 1-l jar and then fixed with 5% ethanol. Samples were maintained in cold water for 1 h and then refrigerated or frozen to be sorted at a later date. Fresh or frozen samples were sorted using a dissecting microscope on a 1-cm^2 grid sampling dish. Larval abalone were enumerated and measured using an ocular micrometer.

Sampling Newly Settled Abalone

Plankton samples were coupled with sampling for newly settled abalone. Newly settled abalone from 290 μm to 2 mm were collected from crustose coralline algae (CCA)–covered cobbles and boulders. Cobbles and boulders ranged in size from 5 and 40 cm in length. Divers surveyed an area for the cobbles of the appropriate size with the highest percent of CCA and placed them carefully in large ziplock bags for transport to the surface. Once on the deck of the boat, cobbles were kept in cold seawater and then processed in less than 3 h to search for newly settled abalone. Cobbles were collected at depths ranging from 2 to 30 m. For each cobble, the depth of collection, cobble length, width, and height as well as percent cover of CCA were recorded. A total of 80 cobbles were sampled from preassigned areas that were randomly distributed throughout the site.

Boulders were processed by placing them in individual buckets in seawater with 5% ethanol and allowing the ethanol to anesthetize the invertebrates for 10 min. The cobbles were then gently washed in the seawater with soft brushes from the top to the bottom of the cobble brushing each surface. The invertebrate sample that had been washed from the cobbles was then collected on a 150-μm mesh sieve, rinsed into a sample jar, and fixed in 90% ethanol. The sample was later examined under the microscope for newly settled abalone and invertebrates. Newly settled abalone were enumerated using a dissecting microscope and measured with an ocular micrometer in the laboratory.

Spawning Dates and Dispersal Models

Estimated spawning dates were determined using the size of newly settled abalone found on the boulders from two

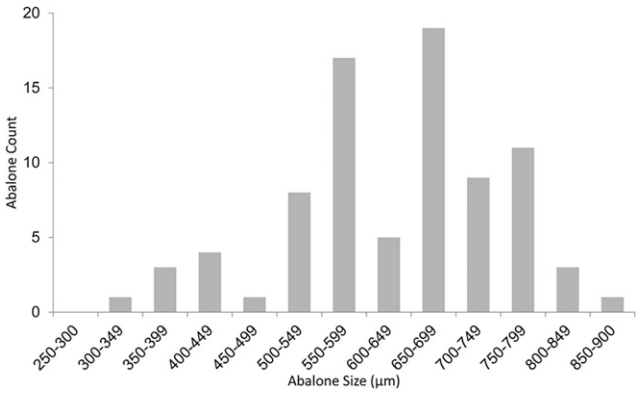

Figure 2. The size frequency distribution of newly settled abalone (<1 mm) found on crustose coralline cobbles ($n = 80$) at Van Damme State Park in 2013.

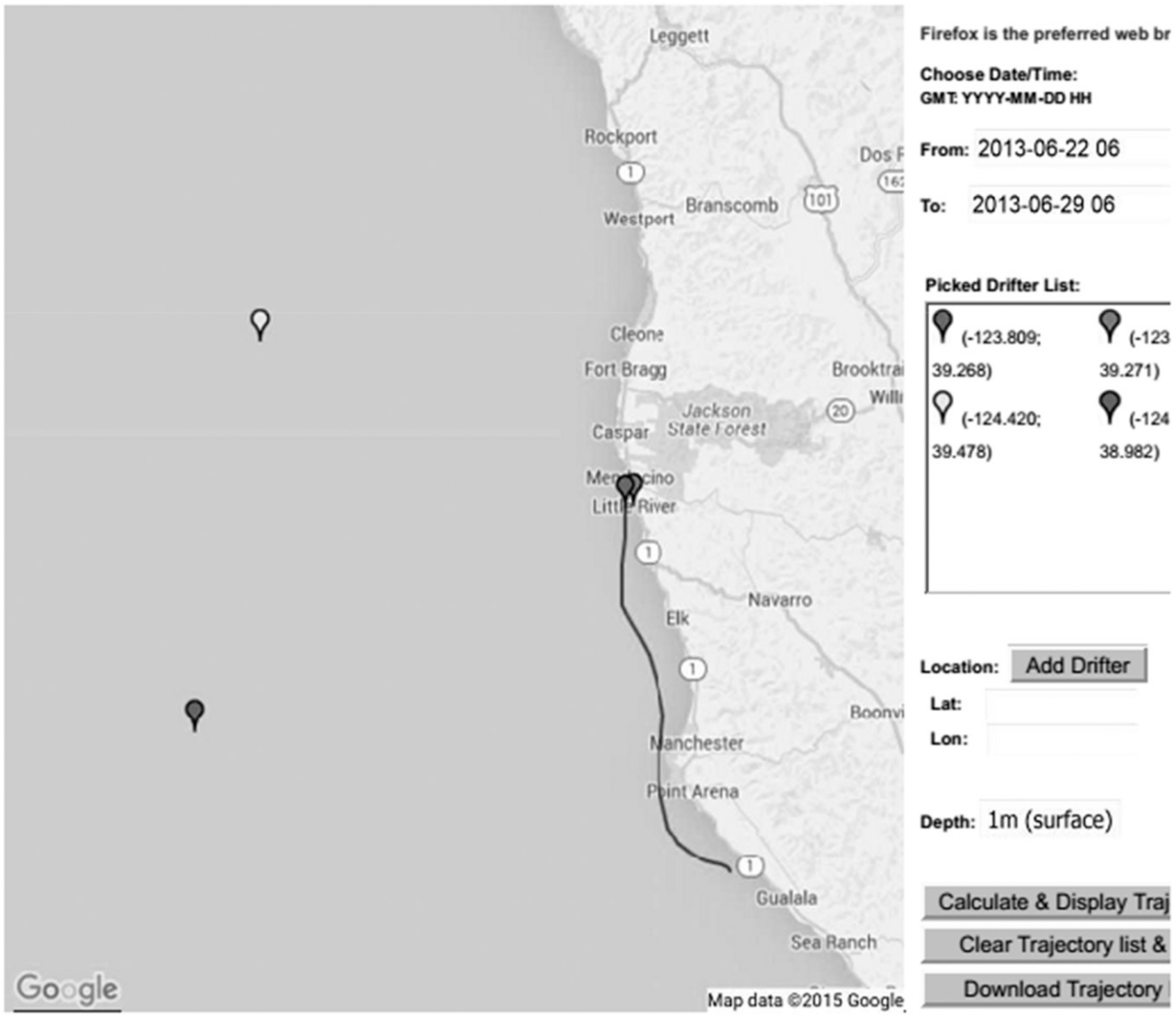

Figure 3. Dispersal track of larvae dropped into ROMS sea surface currents from June 22, 2013 to June 29, 2013.

Mendocino County sites in 2013 when numerous ($n = 150$) newly settled abalone were found.

The Regional Ocean Model System (ROMS) of surface currents was used to explore model dispersal for abalone larvae spawned from the sites in northern California. Adult abalone were assumed to spawn on estimated spawning dates (see above) and then a 7-day larval period from the spawning date was used as bounds for the dispersal calculations. The oceanographic tool "Drop Drifter" (developed by Dr. Yi Chao) was used to model the direction and distance traveled given the surface currents observed on that spawning date (http://www.cencoos.org/data/parameters/currents).

Identification Methods

Both morphological and genetic identification methods were used to identify larvae and newly settled abalone to species. To do this, novel genetic methods were used for identifying newly settled marine invertebrates to species (Hamaguchi 2009). Novel methods were needed as the amount of tissue material in a single larva is too small for traditional genetic techniques using adults. Polymerase chain reaction restriction fragment length polymorphism technology was adapted with two restriction enzymes; Fok I and Xba I for use with small quantities of abalone tissue samples.

Tissues from four species of abalone in northern California were examined: red, black (*Haliotis cracherodii*), flat (*Haliotis walallensis*), and northern abalone (*Haliotis kamtschatkana kamtschatkana*). The pattern of banding for these two restriction enzymes was examined for each of the four possible abalone species. Black, flat, and northern abalone are far less common than red abalone in the region.

Sampling Juvenile Red Abalone

Juvenile abalone were sampled inside artificial reefs at Van Damme State Park 39° 27.831 N, 123° 78.639 W in northern California. Juvenile abalone could reliably be detected by divers starting at 2 mm in shell length. Juveniles were defined as abalone 2–20 mm in shell length and are thought to be

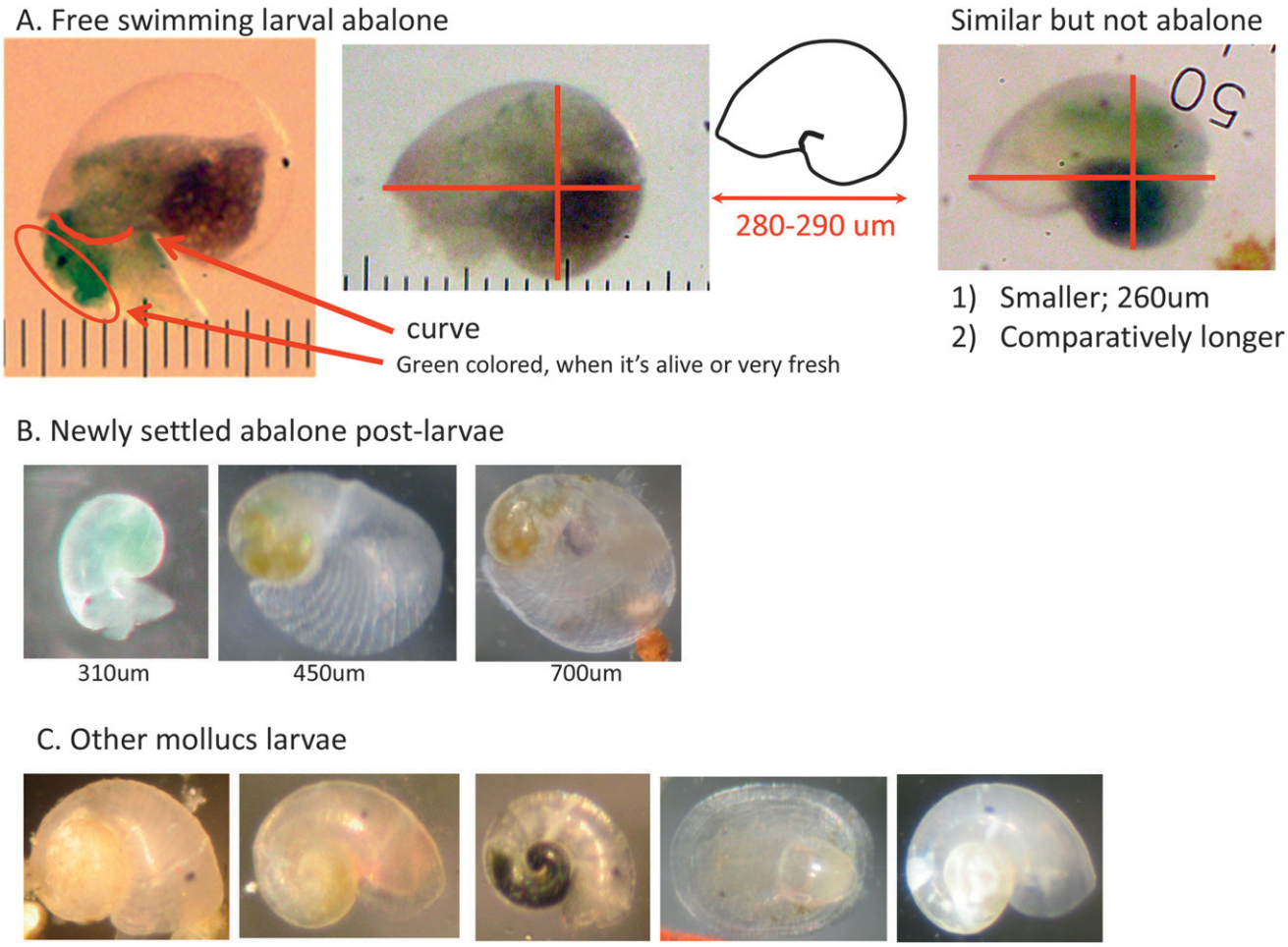

Figure 4. Images of larval abalone showing (A) the morphology near the opercular opening and the length width dimensions, (B) newly settled larvae, and (C) nonabalone mollusc larvae.

young of the year. Twelve artificial reefs made of metal cages with stainless wire mesh were filled with cinder blocks and bolted to the rocky substrate. Each reef had 9 cinder blocks cut in half for a total of 18 half bricks place cut side down in the shape of the letter "M" with approximately 2.6-m^2 sheltered surface area per reef (Rogers-Bennett et al. 2004). Reefs were

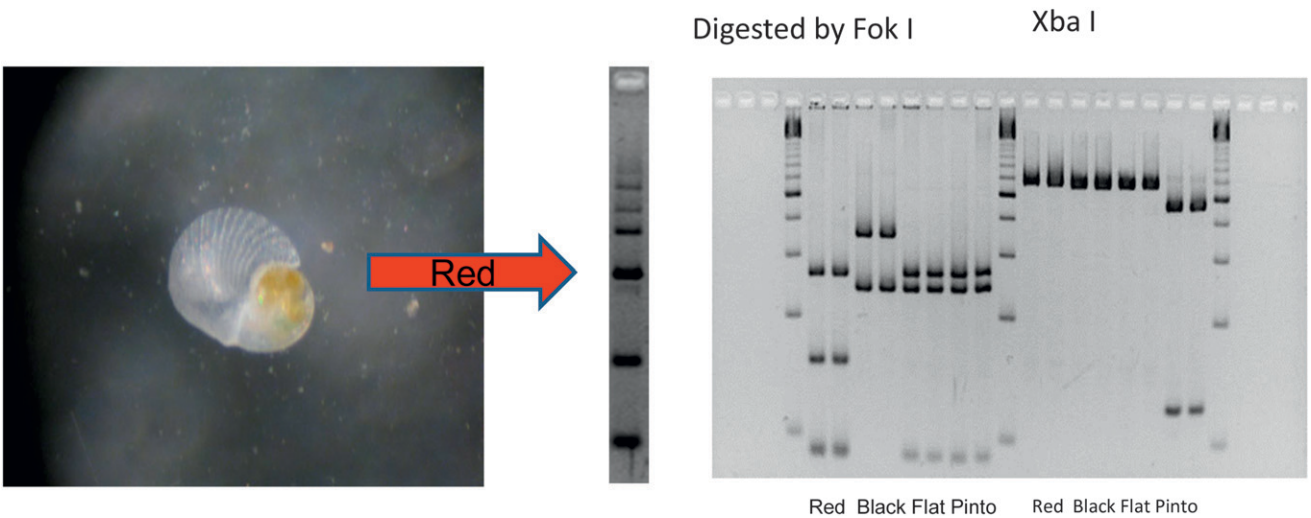

Figure 5. Restriction enzyme banding pattern for newly settled abalone indicating that the abalone matched the two band pattern associated with the red abalone banding pattern.

installed in three areas of the underwater park with four artificial reefs in each of the three areas. Reefs were located at the north, center, and south (inside the south island) at depths from 10 to 12 m. Artificial reefs were surveyed by dive teams once a year in mid-August from 2007 to 2015.

RESULTS

Larval Abalone

The number of larval abalone varied spatially and temporally indicating larvae are patchily distributed in northern California (Fig. 1A). There were a number of years with tows that were positive for red abalone larvae such as 2007, 2008, 2009, 2010, and 2013 (Table 1). The rest of the years did not yield any larvae in the plankton samples. Larvae appeared in both shallow and deep water tows, with the larvae in 2007 in deep tows and the majority of larvae recovered in 2013 from the shallow tows. In 2013, two sites that were 18 km apart had high numbers of larvae in the planktonic stage. In 2010, sites in both the northern and southern portion of the fishery had tows that were positive for abalone larvae (Table 1). No larval abalone were found at any of the three sites sampled in 2015, which was a warm El Niño year that immediately followed the anomalously warm 2014 y.

Newly Settled Abalone

The number of newly settled abalone varied between sites and years (Fig. 1B). In 2013, the most newly settled abalone were found (Table 2) and two sites had more than 65 newly settled abalone per site with Van Damme having close to one abalone per boulder. In 2010, Point Arena had more than one abalone per boulder, whereas in 2014 at the same site, no newly settled abalone were found. Similarly, newly settled abalone were not found at any of the three sites sampled in 2015 following the warm water fall of 2014 which was followed by the warm El Niño year in 2015.

Spawning Dates

Spawning dates were estimated using newly settled abalone found in 2013 at two sites ($n = 82$). The site Van Damme and the year were selected due to the large sample size of newly settled abalone. The size frequency distribution revealed three peaks indicating three possible spawning events (Fig. 2). A weekly growth rate of 50 μm was used based on laboratory growth rates of newly settled red abalone at 14°C to back calculate spawning date (L. Rogers-Bennett, unpublished data). Using this method, it was determined that the newly settled abalone sampled may have come from three separate spawning events in June 22, July 14, and July 25, 2013.

The ROMS model was used to explore how model larvae spawned on June 22, 2013 at Van Damme State Park disperse. Results show the model larvae traveled south in 10 out of 10 model runs. The distances varied widely from 20 to over 100 km. For many of the runs, the distance traveled was less than 70 km, which is north of the town of Gualala (Fig. 3). Model larvae ''dropped'' slightly further offshore tended to travel further south in the surface current patterns for that 1-wk period in June 2013. Summer is a period dominated by the California Current in which surface currents tend to flow south along the coast.

Species Identification

Larval shell morphology and size were used to distinguish larval abalone from other mollusc larvae in the plankton samples. The curvature of the larval shell at the opercular opening was used in combination with the total length of the shell (Fig. 4). These morphological identifications were used on a subset of larvae and newly settled individuals using genetic methods. The polymerase chain reaction restriction fragment length polymorphism techniques were successfully adapted to distinguish between the four possible abalone species in the region using two restriction enzymes, Fok I and Xba I. As shown in the plots, red and black abalone can be distinguished by the banding pattern for Fok I, whereas Xba I distinguishes flat from northern abalone. All the larval and newly settled abalone examined using Fok I and Xba I from 2007 to 2010 were consistent with the banding pattern for red abalone (Fig. 5). Once the species identifications were confirmed in the early years of this work, early life history stages of abalone from 2011 to 2014 were not genetically examined. No larval or newly settled abalone were found in 2015.

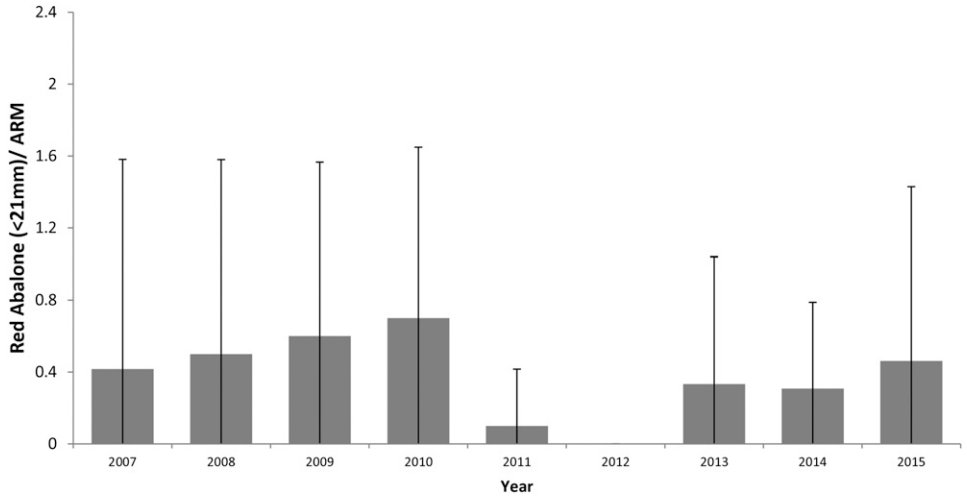

Figure 6. The number of juvenile (<21 mm) red abalone found inside 12 artificial reefs at Van Damme State Park from 2007 to 2015.

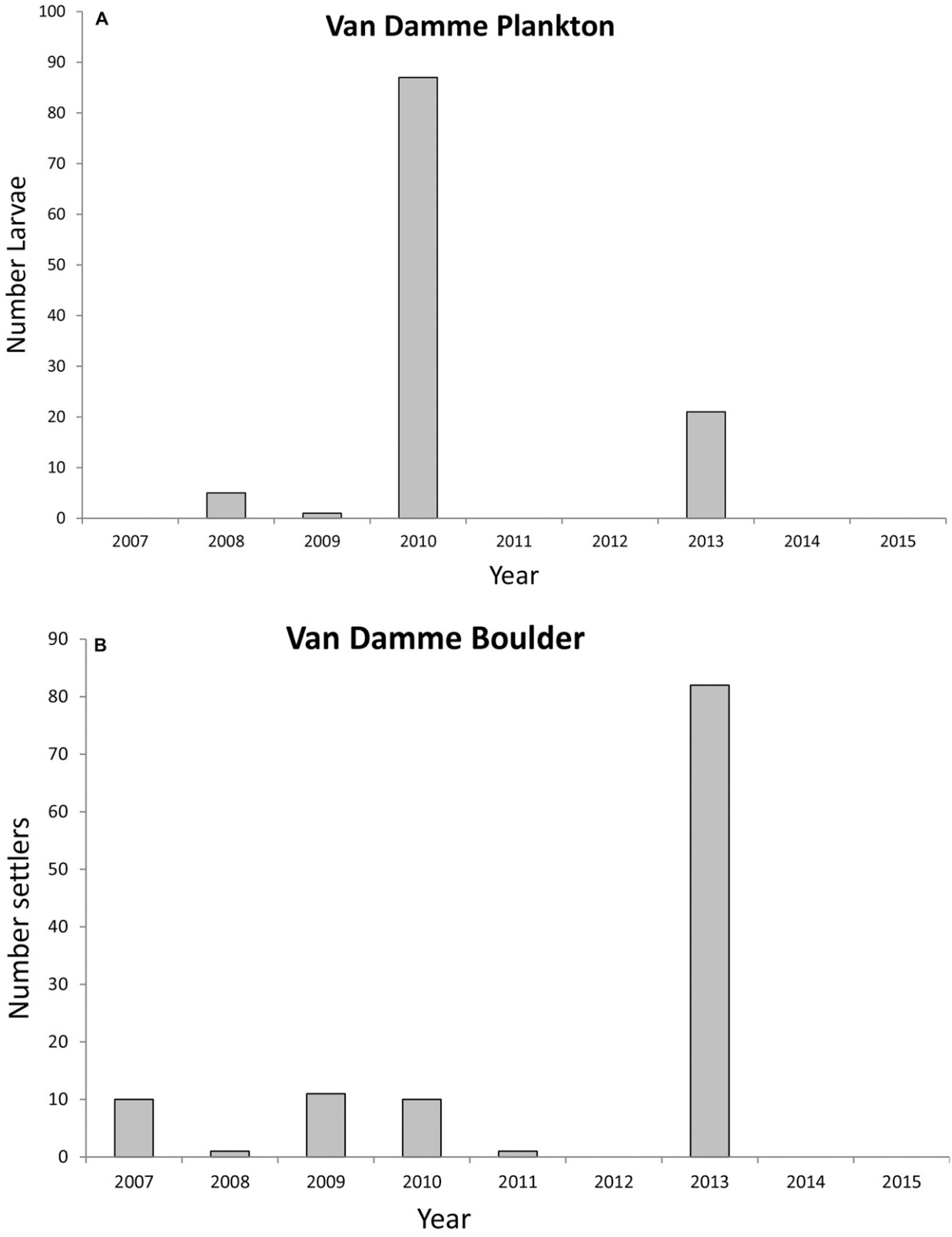

Figure 7. (A) The number of larval abalone captured in plankton tows from 2007 to 2015 at Van Damme State Park in northern California. (B) The number of newly settled abalone captured from cobbles ($n = 80$) covered with crustose coralline algae from 2007 to 2015 at Van Damme State Park in northern California.

Juvenile Red Abalone

The average number of young of the year (2–20 mm) juvenile red abalone found in the artificial reefs was 0.38 per reef or from 4 to 5 juveniles at Van Damme for the past 9 y (Fig. 6). The most juvenile abalone were observed in 2010 with 0.7 juveniles per reef. In 2012, no juvenile abalone were observed. At Van Damme, larval and newly settled abalone were also examined over each of the last 9 y (Fig. 7A, B).

Water temperatures in the artificial reefs at Van Damme at a depth of 12 m revealed that 2014 was the warmest year in the 9-y time series with a high of 16.9°C on September 24, 2014 (Fig. 8).

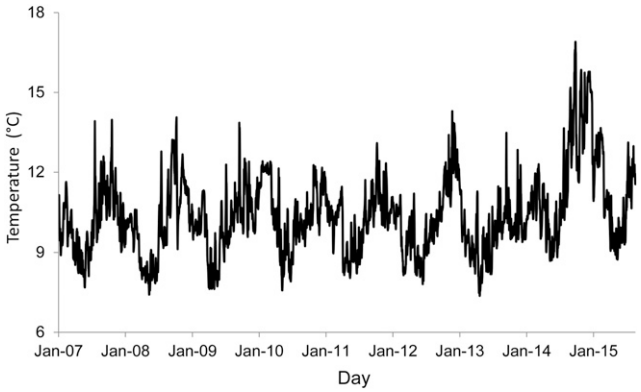

Figure 8. Sea water temperature at 10 m at Van Damme State Park from January 2007 to August 17, 2015.

DISCUSSION

Methods have been developed to sample larval, newly settled, and juvenile red abalone in northern California. The methods for finding these very small early life history stages have been successfully developed for wild red abalone. Morphological features can now be used to distinguish abalone larvae from other larval molluscs in the plankton. Furthermore, the morphological identifications have been confirmed using genetic techniques employing the restriction enzymes Fok I and Xba I. These methods can now be used to ask questions about settlement and recruitment of red abalone which are not only important members of kelp forest communities but also form the basis of the recreational fishery in northern California.

Sampling over the last 9 y suggests that abalone larvae are patchily distributed in northern California in space and time. Even at one site, Van Damme, where sampling was done the same week each year, some years had more larvae than others. This suggests that the production of larvae may also be variable between years. The abundance of newly settled abalone was also variable in space and time. These results show that 2012 was a poor year for abalone settlement and recruitment. In contrast, 2013 had the highest number of newly settled abalone. These methods are the first steps in developing the tools needed to answer future questions about abalone productivity, settlement, and recruitment in California.

Spawning Dates and Dispersal

These data support the hypothesis that there may be multiple spawning dates for red abalone in northern California. Other species such as white abalone *Haliotis sorenseni* spawn over a limited period primarily in the spring as seen in southern California (Tutschulte & Connell 1988) and in the laboratory (Rogers-Bennett et al. 2016).

There appeared to be synchrony in the spawning dates indicated by the size classes of the newly settled abalone at two nearby sites 18 km apart. This could arise from two possible scenarios: either the larval pool extended across the entire 18-km area depositing larvae at the same time at both sites or adults in both areas spawned at the same time (perhaps triggered by an environmental cue) and then the larvae settled in their respective sites on the same date. Either way, the abalone sizes at these two nearby sites corresponded to the same spawning dates in June and July of 2013. This is the first demonstration that abalone were spawning in July when there is a month-long closure of the recreational fishery, which was established to allow for spawning.

A number of environmental triggers for abalone spawning have been identified in Japan. Storms were observed to be an important cue for abalone *Haliotis discus hannai* (Sasaki 1985). Dramatic changes in sea temperatures appear to be the cue for spawning in abalone *Haliotis discus discus* (Tanaka et al. 1986). Typhoons triggered spawning in abalone *Haliotis diversicolor* (Onitsuka et al. 2007). Clearly, more work needs to be done to assess spawning dates and spawning cues for red abalone populations in northern California. The work here gives us some tools to address the question of what triggers spawning in red abalone in California.

With the advances in surface current models, such as the Regional Ocean Model System, it is now possible to ''drop'' model larvae at specific locations along coastal California on known spawning dates and run the model for the length of the larval period (in this case the length of the larval period was 7 days). It was found that the model larvae drifted south in 10 out of 10 model runs consistently predicting a southern transport of larvae spawned during the peak spawning event in June and July of 2013. The distances the model larvae traveled south depended to a large extent on the distance offshore the larval was ''dropped.'' It is suggested that these model runs are useful for thinking about dispersal, but nearshore topography, surface winds, vertical migration, larval behavior, and a suite of other variables will be important for predicting abalone larval transport (as opposed to model larval transport). More detailed work on particle tracking coupled with hydrodynamic modeling incorporating surface currents in the nearshore, as has been done to model larval abalone transport in Sagami Bay, Japan (Miyake et al. 2009), is needed in northern California.

Abalone Reproduction

After the warm fall of 2014, no larval or newly settled red abalone were found in 2015. This suggests that there may be reproductive failure in the red abalone at the sites sampled. The years 2014 and 2015 were characterized by warm ocean temperatures peaking in July and poor bull kelp *Nereocystis* growth which may have led to poor food conditions for mature adults. In the laboratory, the impacts of warm water and starvation were resolved showing that each negatively impacts reproduction of both sperm and egg production (Rogers-Bennett et al. 2010). The absence of larvae and newly settled

abalone may have been the result of warm water and poor food resources inhibiting successful reproduction.

The tools that have been developed in this work can be used to extend this 9-y time series of larvae and newly settled red abalone in northern California. The variability seen in the abundance of larvae, newly settled, and juvenile red abalone confirms that recruitment is dynamic in both space and time. For example, it was seen that there were no larvae or newly settled abalone after the warm water observed in September 2014. These methods can be used to better understand and identify the drivers of recruitment for the red abalone in northern California.

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