



Periodicity in *Chthamalus fissus* reproduction does not guarantee periodicity in settlement

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ABSTRACT: The timing of life history events can have profound implications for populations and communities, especially those events that influence species dispersal and recruitment. In benthic invertebrates, the majority of dispersal occurs during the larval phase of life. Yet the extent to which timing of reproduction (the beginning of the larval phase) directly influences timing of settlement (the end of the larval phase) is unclear, because biological and hydrodynamic processes can act to decouple these 2 events, and because reproduction and settlement are seldom studied together. Here, we used long-term (2014–2019) daily and weekly data from Bird Rock, La Jolla, California, USA, to look for lunar and seasonal cycles in reproduction and settlement timing of the acorn barnacle *Chthamalus fissus*, and we incorporated measurements of nearshore currents to examine the implications of reproduction timing on alongshore larval transport distances. We found evidence of lunar and seasonal cycles in reproduction but only limited cyclicity in settlement, possibly due to plasticity in larval development coupled with variable larval transport and dispersal. Our results demonstrate the complex nature of relationships between reproduction, larval transport, and settlement, which must be disentangled before accurate predictions can be made regarding the impacts of climate change on the population dynamics of marine species.

KEY WORDS: Lunar reproduction · Barnacle · Larval dispersal · Phenology

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1. INTRODUCTION

The timing of life history events can have major implications for the persistence of populations, species, and communities, but temporal coupling between one life history event and the next can be difficult to parse, partly because there are a plethora of biological and physical factors that can act as decoupling agents and partly because studying temporal processes is demanding. Many sessile and slow-moving marine invertebrates begin life as pelagic larvae, and the timing of reproduction and settlement (i.e. the beginning and end of the larval phase) can determine potential dispersal and ultimate recruitment into the benthic community (Cowen

& Sponaugle 2009, Pineda et al. 2009). Timing of recruitment, in turn, can impact intra- and inter-species interactions and subsequent community structure (Roughgarden et al. 1988, Connolly & Roughgarden 1998). The length of time between reproduction and settlement should theoretically correlate with the length of time required for larval development, which can range from minutes to months depending on the species (Shanks 2009), and indeed this has been used as a method to estimate larval duration in the field (Peterson 1966, Barbosa et al. 2016). In practice, however, out of 112 studies that examined both reproduction and recruitment in marine organisms (reviewed in Morgan 2021), roughly 38 % failed to find significant spatial or temporal coup-

ling between the two, with the exact proportion depending on pelagic larval duration (PLD), mode of reproduction (i.e. broadcast spawning versus brooding), and study methodology. Despite these challenges, there is broad interest in improving our understanding of the processes that contribute to decoupling, in order to better model population dynamics of marine species with pelagic larvae (Swearer et al. 2019) and, by extension, predict species response to local and global anthropogenic stressors.

In the study of population dynamics, often the most tractable place to begin is with evaluation of reproduction timing. Reproduction is often cyclical, and selective pressures to determine cycle timing may operate independently of population density (e.g. synchrony with environmental factors such as food availability for the benefit of adult or larval survival; e.g. Shima et al. 2020), or they may be density-dependent (e.g. synchrony with neighboring adults to maximize reproductive success; Korrynga 1947). In either case, reproduction events typically coincide with predictable patterns in the natural environment, commonly on semilunar (~14.8 d), lunar (~29.5; Korrynga 1947, Naylor 2001, Christy 2011, Collin et al. 2017), or seasonal cycles (~365 d; Strathmann 1987, summarized in Reitzel et al. 2004). Semilunar reproduction cycles in particular have been cited as a possible adaptation, in conjunction with tidal currents and larval vertical migration behaviors, to facilitate larval transport both to and from adult habitats (Zeng & Naylor 1996, Christy 2011, Collin et al. 2017, Tamaki et al. 2020). To achieve synchrony on lunar and tidal cycles, marine organisms may respond to exogenous cues such as salinity, moonlight, hydrostatic pressure, or (for intertidal organisms) immersion time (Morgan 1995). Alternatively, many species in temperate coastal oceans (e.g. the Baltic clam *Macoma balthica*) spawn in late spring in response to seasonal warming or the spring phytoplankton bloom (Philippart et al. 2003), and timing can vary between years and along a species' geographic range (e.g. Ropes & Stickney 1965, Newell et al. 1982), likely in response to variable temperature or food gradients over space and time. For species that respond directly or indirectly to temperature, it is expected that timing of reproduction will shift in response to ocean warming (Poloczanska et al. 2013), which may in some cases alter alongshore dispersal (Fuchs et al. 2020). For species whose reproductive timing coincides with environmental cues largely independent of temperature (e.g. the acorn barnacle *Semibalanus balanoides* releases larvae in response

to increased turbidity during winter storms; Gyory et al. 2013), reproduction timing may remain constant, and larvae may instead experience warmer water temperatures upon release. This is predicted to result in faster larval development, shorter dispersal distances, and reduced population connectivity (O'Connor et al. 2007, Gerber et al. 2014). Unfortunately, it is difficult to predict the full implications of consistent versus altered reproductive timing on ecosystems, in part because there have been very few studies that have followed reproduction events through to larval settlement.

Numerous studies have also reported cycles in larval settlement, but it is often unclear whether observed cycles are driven by physical transport mechanisms or cycles in reproduction, because few studies have measured both simultaneously. Some studies have reported tidal or semilunar periodicity in settlement time series (Shanks 1983, 1986, Morgan et al. 1996, Reyns & Sponaugle 1999, Tamaki et al. 2020), evoking transport via internal waves or tidal currents as the driving mechanism. In these studies, the authors argue that late-stage larvae are transported to the benthos in regular intervals through tidal forcing, but only one (Tamaki et al. 2020) of these 5 studies explicitly controlled for—and found—periodicity in reproduction. A sixth set of studies (Christy 1982, Christy & Stancyk 1982, Christy & Morgan 1998) found lunar cycles in reproduction and concentration of early-stage larvae in the water column but no lunar cycles in the delivery of late-stage larvae to adult habitat, leading the authors to conclude that reproductive timing was optimized for larval export away from adult habitat and not transport back. Ultimately, further study is needed to parse out the relative contributions of reproduction timing versus hydrodynamic phenomena on observed patterns in settlement.

Intertidal barnacles represent an excellent model system for quantifying the timing of reproduction and settlement, because reproductive adults are easily accessible, and settlement can be reliably monitored in the field. Here, we focus on *Chthamalus fissus*, the most abundant barnacle species in coastal southern California (Pitombo & Burton 2007, Wares 2020). Common in high and upper-middle rocky intertidal habitat, *C. fissus* are small (≤ 8 mm diameter), and individuals may produce >10 broods yr^{-1} (Hines 1978, Blower & Roughgarden 1988), though these estimates assume no recovery time between broods. Each brood develops over approximately 2 wk (Hines 1978) and produces 200–3000 nauplii (Newman & Abbott 1980).

Reproductive output is a function of food availability, body size, and habitat location relative to sea level (Hines 1978, Page 1984). Developing larvae pass through 6 naupliar stages and a final cyprid stage, at which point they return to the benthos to settle. According to laboratory trials conducted at 18°C, development to the cyprid stage can be achieved in as little as ~18 d (Miller et al. 1989). Settlement generally occurs year-round (Shanks 1986, Pineda et al. 2018), with settlers reaching reproductive maturity after ~2 mo and adults living ~3 yr (Newman & Abbott 1980).

Here, we analyzed daily and weekly time series of both embryonic development and settlement density of *C. fissus* over multiple years. Specifically, we tested (1) whether there was evidence of lunar or seasonal periodicity in *C. fissus* reproduction or settlement and (2) the degree to which periodic cycles in reproduction correlated with periodic cycles in settlement. To explore potential causes of decoupling, we also (3) calculated first-order estimates of along-shore larval transport. For evidence of semilunar, lunar, or seasonal cycles, we expected to see peaks in reproduction and settlement every ~14.8, ~29.5, or 365 d, respectively. For evidence of coupling between reproduction and settlement, we expected to see the same periodic cycles in both reproduction and settlement series, with high reproductive activity corresponding to high settlement ~18 d later. In the absence of such evidence, we expected that transport estimates might be large (>50 km), which would indicate the potential that incoming settlers were derived from more distant populations. With these

data, we shed light on the complex relationships between reproduction, larval transport, and settlement, which will be increasingly important to understand in order to better document and predict species responses to climate change.

2. MATERIALS AND METHODS

2.1. Data collection

Chthamalus fissus reproduction and settlement were measured in rocky intertidal habitat just above mean lower low water (MLLW) in Bird Rock, La Jolla, California, USA (32.8100° N, 117.2694° W). While *C. dalli* also occurs in southern California (Pitombo & Burton 2007) and is nearly indistinguishable from *C. fissus* in the field (Miller et al. 1989), the species is rare south of Point Conception (Wares 2020). Additionally, genetic assessment of both adult and larval barnacles in our study site found no *C. dalli* (Hagerty et al. 2019). Thus, we assume that all *Chthamalus* barnacles examined in this study were *C. fissus*.

To measure timing of reproduction, up to 100 adult *C. fissus* were collected daily (to assess semilunar or lunar periodicity; June to November 2016 and May to August 2017) or weekly (to assess seasonal periodicity; June 2016 to May 2018) (Table 1). Individuals were evaluated using a dissecting microscope and scored from 0 to 4, based on the stages of embryonic development described for other acorn barnacle species (Table 2). For all analyses, the number of adults per sample with each score was converted to propor-

Table 1. Summary of data series analyzed. Values in parentheses indicate number of interpolated points

Data description	Dates collected (mo/d/yr)	No. of samples	Analysis
Daily reproduction	06/11/2016 – 11/21/2016	164 (24)	Lunar/tidal periodicity
	05/31/2017 – 08/12/2017	74 (11)	
Daily settlement	04/24/2014 – 07/16/2014	84 (2)	Lunar/tidal periodicity
	10/06/2014 – 01/02/2015	89 (6)	
	04/23/2015 – 08/02/2015	102 (10)	
	09/22/2015 – 12/15/2015	85 (11)	
	04/06/2016 – 11/21/2016	230 (26)	
Weekly reproduction	06/12/2016 – 05/14/2018	103 (11)	Seasonal periodicity
Weekly settlement	01/11/2016 – 12/29/2019	208 (31)	Seasonal periodicity
Intertidal water temperature (daily)	04/22/2014 – 08/31/2018		Seasonal periodicity
NOAA sea level (daily)	01/01/2017 – 12/08/2018		Lunar/tidal periodicity
Alongshore currents (hourly)	04/19/2014 – 07/17/2014		Alongshore larval transport
	10/03/2014 – 01/03/2015		
	04/22/2015 – 08/03/2015		
	09/13/2015 – 12/17/2015		
	04/09/2016 – 11/20/2016		

Table 2. Description of scores used to rate embryonic development of *Chthamalus fissus*. Scores were modified from Crisp (1954) and Anderson (1994) by J. Pineda and V. Starczak (unpubl.) for examination of the acorn barnacle *Semibalanus balanoides*. See also Rognstad & Hilbish (2014) and Herrera et al. (2021) for implementation of similar scoring methodology

Score	Description	Stage
0	No eggs or tissue	Non-brooding
1	White mass/sac	
2	Eggs are visible but not developed	Early-stage embryos
3	Eggs are developed and naupliar eyespots are visible	Late-stage embryos
4	Nauplii are developed with visible body structure	

tion of adults by score, to normalize for sample size during weeks when 100 adults could not be collected due to low percent cover.

To measure timing of settlement, 6–12 polyvinyl chloride (PVC) plates were deployed in areas of dense adult *C. fissus* distributions (~0.3 to 0.6 m above MLLW). Plates were 11 cm long, 2.5 cm diameter, halved along the longitudinal axis, and with 3 grooves machined along the inner side (Fig. S1 in the Supplement; www.int-res.com/articles/suppl/m718p053_supp.pdf). These plates were swapped out either daily (2014 to 2016 in 5 discrete series; see Table 1 for dates) or weekly (January 2016 to December 2019), and number of settlers along the base of each groove was counted to determine the number of settlers per plate. Counts were divided by available settlement area along the base of the grooves (1.9 cm², as calculated in Pineda 1994b), converting settlement counts to densities, and densities for all plates collected on a given date were averaged to yield one mean value per sampling date.

While a portion of these settlement data have been previously published to examine how thermal stratification and large-scale oceanographic disturbances affect settlement (Pineda et al. 2018), data are used here to determine whether higher-frequency processes associated with lunar and seasonal cycles result in settlement periodicity. Additionally, measurements of both reproduction and settlement, collected simultaneously in 2016 (daily samples; n = 164) and 2016–2018 (weekly samples; n = 92) (Table 1), are used here to evaluate the extent to which settlement timing correlates with timing of population reproduction events.

In some instances, tide or weather conditions prevented the collection of adult barnacles or settlement plates. In these cases, embryonic scores were linearly interpolated using data from the nearest dates before and after the gap, and settlement density values were linearly interpolated and normalized to a 1 or 7 d value. In cases where settlement plates were collected for one time series and not the other (e.g. plates were only collected daily), values for the other dataset were estimated using the relationships between daily and weekly *C. fissus* settlement reported in Pineda et al. (2018). In instances where weekly settlement was measured at irregular intervals due to weather or tide conditions (e.g. plates were swapped out after 6 d, rather than 7 d), density values were normalized to a 7 d value.

Sea level data were also examined to determine how cycles in reproduction and settlement aligned to the tidal cycle. Hourly sea level data for 2017 and 2018 were obtained from the nearest NOAA tide station (ID 9410230) at La Jolla California (<10 km away from intertidal field site), and daily minimum, maximum, and range were extracted.

2.2. Assignment to the lunar cycle

To evaluate for lunar periodicity, all records (reproduction, settlement, and sea level data) were assigned to a lunar day (1 to 29, where Lunar Day 29 was the new moon) based on new moon times in La Jolla, California (timeanddate.com). This process excluded all interpolated points, so that only recorded data were considered. Daily reproduction data were averaged by lunar day. Settlement data were $\log(x + 0.04)$ transformed (equivalent to adding 1 settler to the total count across 12 plates, before converting counts to densities and averaging over the 12 plates), and all data points were plotted against lunar day. To visualize the alignment between biological, lunar, and tidal cycles, daily sea level range was also averaged by lunar day.

2.3. Statistical analyses

To determine if the reproduction and settlement time series exhibited lunar periodicity, a randomization test for periodicity (Manly 1998) was conducted on each daily series using MATLAB (R2021b). This process included interpolated points, because a continuous series was required. Periodograms were calculated for each daily time series (Table 1) and for

10 000 randomizations of each series. To identify statistically significant periodicity in the original series, we used a significance threshold of $\alpha = 0.05$ and applied a Bonferroni correction for repeat testing as follows: periodicity was significant when it was observed in fewer than αm^{-1} of the 10 000 randomized series, where m is half the number (n) of continuous observations in the timeseries (Manly 1998). With this approach, we can only resolve cycles of length kn^{-1} , where k is 1, 2, ... $m - 1$ (Manly 1998). This means that for short series, we can only resolve cycles that approximate the lunar cycle (e.g. 14 d instead of 14.8). Additionally, this approach is more effective when used with longer, continuous timeseries. Therefore, to create a longer series, each set of continuous data series was concatenated by lunar day to create 1 continuous series (e.g. the 2 continuous series of daily reproduction were concatenated by lunar day into 1 series), and each full series was re-analyzed using the same randomization procedure described above.

To describe seasonal patterns in reproduction and settlement, we analyzed the weekly data series, excluding interpolated data values. Because the sampling approach for weekly data did not control for lunar effects, we first accounted for variation on a lunar cycle, as follows. Proportions of late-stage brooding adults were arcsine transformed to better meet assumptions of normality (Zar 2010), and values were predicted using 3 nested linear models with harmonic predictor terms: (1) lunar day, with a periodicity of 14.5; (2) lunar day and day of year (DOY), with a periodicity of 182.5; and (3) lunar day, DOY, and their interaction. We used a lunar periodicity of 14.5 d here to align with our assignment of lunar day on a scale of 1 to 29. We compared the 3 nested models using the Akaike information criterion (AIC) (Burnham & Anderson 2002). If Models 2 or 3 were determined to be the best fit model, this would be taken as evidence that there was a seasonal cycle to reproduction in addition to the lunar cycles investigated using the methods above. Because there was no lunar cycle identified in daily settlement density series (see Section 3), weekly settlement densities were averaged by month to explore seasonal patterns.

2.4. Estimating larval transport

To explore potential causes for distinct cycles in reproduction and settlement, alongshore current data were used to calculate a first order approxima-

tion of larval transport distances. Current data were collected during 5 deployments of a 1200 kHz acoustic Doppler current profiler (ADCP; RD Instruments), which was bottom-mounted approximately 640 m from shore at 8 m depth. Deployments spanned 2014–2016 (Table 1). The ADCP recorded current velocities throughout the water column in 0.4 m bins, taking measurements every 2 s. Examination of signal strength, error velocities, percent good, and bin-to-bin velocity differences were used to remove measurements when kelp compromised the instrument. Remaining data were averaged over each hour and rotated along the main axis of variability for horizontal currents, which also aligned to the shoreline and roughly corresponded to north-south. Transport estimates were generated using alongshore current data for 4 m above the bottom (mab), because this corresponds to mean depth distributions for early-stage barnacle nauplii at this site (Hagerty et al. 2018). This required linear interpolation of currents using the bins immediately above and below 4 mab (3.9 and 4.3 mab). Current velocities were summed over a moving 18 d window to estimate alongshore larval transport over the approximate larval duration of *C. fissus* (Miller et al. 1989). Estimates are presented as monthly averages.

3. RESULTS

3.1. Reproduction of *Chthamalus fissus*

We found that *C. fissus* were moderately reproductive all year, with 0 to 50% of adults containing late-stage embryos on any given day (Fig. 1). Daily measurements of embryonic development indicated roughly 2 pulses of reproductive activity per month, though with substantial variation between days and weeks (Fig. 1A,B). When the proportion of adults containing late-stage embryos decreased substantially over a short time (e.g. 27 to 1% between June 11 and 12, 2016; Fig. 1A), this was taken as evidence that brooding adults released their larvae. Similar release events were observed throughout the daily series, though it varied whether a given release event occurred over 1 d (as in the example above) or over several days (e.g. 22 to 0% between June 28 and July 1, 2016; Fig. 1A).

In addition to the cycles observed in the daily data, weekly measurements of embryonic development yielded pulses of reproductive activity on longer (e.g. monthly and seasonal) timescales, with variation occurring both week to week and year to year (Fig. 1C).

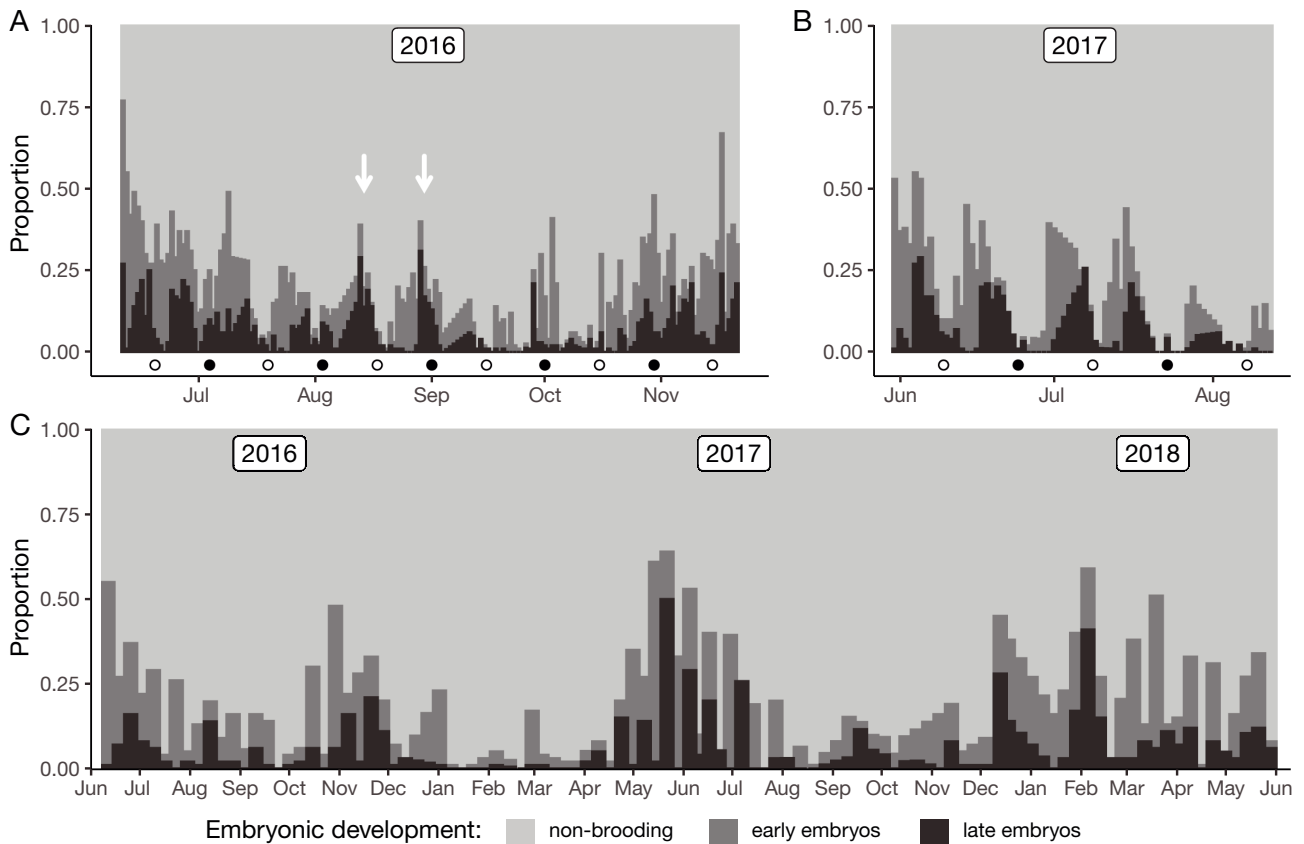


Fig. 1. Measurements of *Chthamalus fissus* embryonic development and reproduction over time. Samples were collected daily in (A) 2016 and (B) 2017 and weekly in (C) 2016–2018, and they were categorized by embryonic development stage as described in Table 1. Gaps in daily ($n = 34$) and weekly ($n = 11$) series were linearly interpolated. A rapid decrease in proportion containing late-stage embryos was taken as evidence of a reproduction event (e.g. the events marked with a white arrow in panel A), and therefore all subsequent analyses focused exclusively on this reproductive stage. Full and new moon dates are shown for daily data, with white and black circles, respectively

One such example of week to week variation occurred in 2017, when proportions containing late-stage embryos decreased from 50% on May 22 to 0% on May 29, then rose again to 29% by June 5. Such oscillations occurred throughout the weekly series, likely reflecting shorter-scale cycles observed in the daily data (see Fig. 1, as well as Section 3.2). Looking at the full 2 yr of weekly data, it was notable that both the timing and magnitude of reproductive pulses varied between years. In 2017, weekly measurements of proportions with late-stage embryos did not exceed 1% during January–March, but in the following winter there was a substantial pulse of reproductive activity, with 41% of adults containing late-stage embryos on February 5, 2018 (Fig. 1C). While it is possible that pulses of reproductive activity in 2017 occurred between weekly observations (e.g. there was at least 1 small pulse of adults containing early-stage embryos on February 28, 2017; Fig. 1C), it typ-

ically took >7 d in the daily series for a large number of adults to build up and then release late-stage embryos (Fig. 1A,B). Therefore, it is unlikely that weekly samples in winter of 2017 could have completely missed a similarly large pulse of reproduction as to what occurred in 2018.

3.2. Lunar and tidal cycles in sea level, reproduction, and settlement

To visualize how lunar and tidal cycles interact in La Jolla, California, daily sea level range was aggregated by lunar day (Fig. 2A). Our study site experiences mixed semidiurnal tides, and difference in daily sea level ranged from ~ 0.8 to 2.6 m. On average, there was no difference in sea level range during full versus new moons (Fig. 2A), though the timing of individual spring tides (i.e. the single maximum in sea level

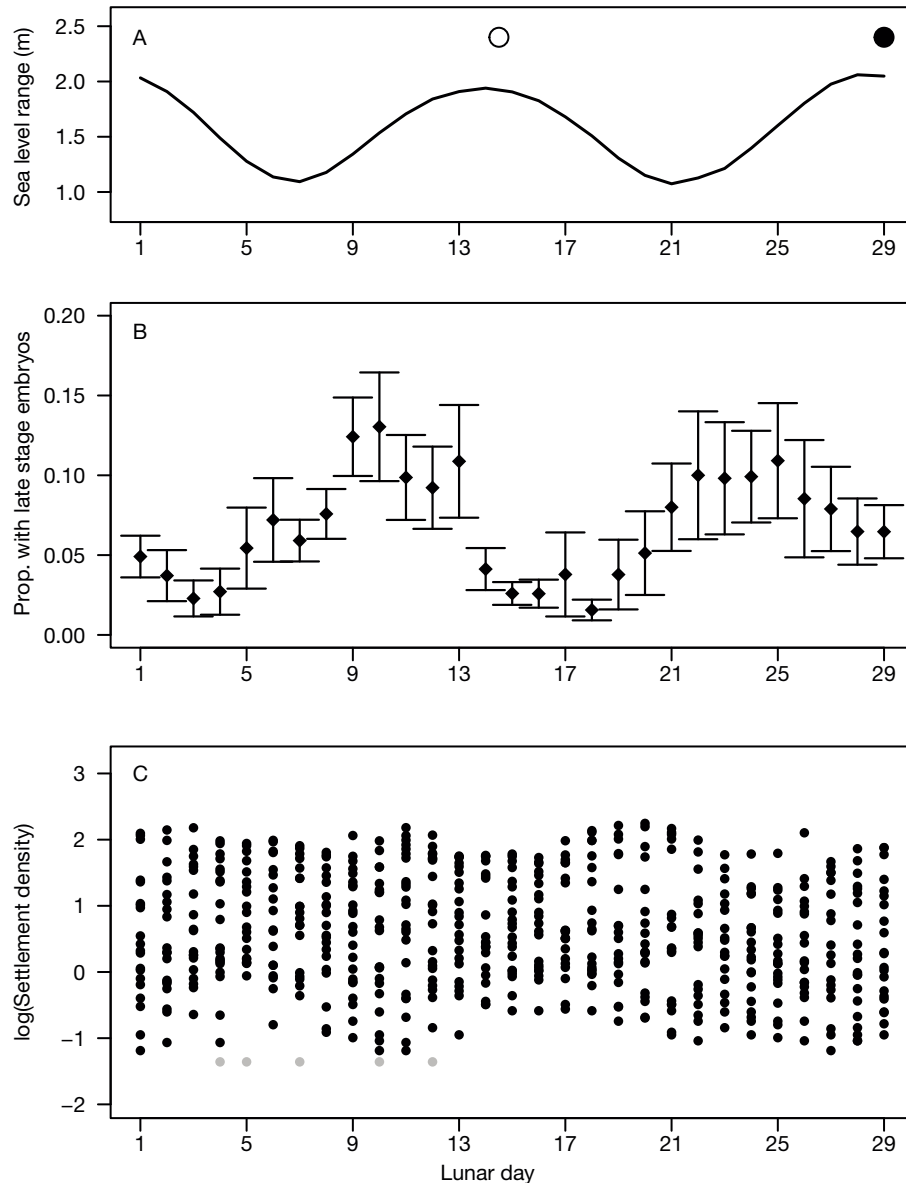


Fig. 2. Daily tidal range, *Chthamalus fissus* reproduction, and *C. fissus* settlement by lunar day. (A) Average daily tidal range per lunar day (with Day 14.5 representing the full moon and Day 29 representing the new moon), calculated from sea level data obtained from the nearest NOAA tide station (ID 9410230). (B) Average (\pm SE) proportion of *C. fissus* adults containing late-stage embryos per lunar day. (C) $\log(x + 0.04)$ -transformed daily settlement density (number of individual *C. fissus* settlers per cm^2) versus lunar day. Five data points with 0 settlement originally are shown in grey

range per lunar month) alternated between the full and new moons (e.g. in 2018, the greatest daily range in sea level occurred on January 3 [Lunar Day 15; a full moon] and July 13 [Lunar Day 29; a new moon]).

The highest levels of reproductive activity occurred on average roughly halfway between spring and neap tides, on Lunar Days 10 and 25 (Fig. 2B). Indeed, randomization tests conducted on each daily reproduction series identified significant periodicity of 14.8 d in the 2017 data ($p < 0.001$) as well as mar-

ginally significant periodicity of 14.9 d in the 2016 data ($p = 0.084$; Table 3). For the 2016 series, there was also significant periodicity identified at a cycle length of 16.4 d ($p = 0.008$; Table 3). When 2016–2017 reproduction data were concatenated by lunar day, creating a longer, continuous timeseries, randomization tests identified significant periodicity of 14.7 d ($p < 0.001$; Table 3; Fig. 3).

When daily settlement data were $\log(x + 0.04)$ transformed and visualized by lunar day, there was

Table 3. Results of randomization analysis. Values are shown for all cycles with a corrected p-value < 0.10. For reproduction series, only data for adults containing late-stage embryos (see Table 2) are presented, as proportions in each category are not independent of one another. Significant values ($p < 0.05$) are in **bold**. Values were omitted for cycles equal to or greater than half the length of the series. Dashes: no significant cycle matching these criteria

Data type	Series	Cycle (d)	Corrected p-value
Daily reproduction (late embryos)	2016 (n = 164)	82	0.066
		16.4	0.008
		14.9	0.084
Daily reproduction (late embryos)	2017 (n = 74)	14.8	<<0.001
Daily reproduction (late embryos)	2016–17 (n = 220)	14.7	<<0.001
Daily settlement	Spring 2014 (n = 84)	–	–
	Fall 2014 (n = 88)	–	–
	Spring–summer 2015 (n = 102)	34	0.026
	Fall 2015 (n = 84)	21	0.059
	2016 (n = 230)	–	–

at least a 2- to 3-fold difference on any given lunar day in the observed magnitude of settlement (Fig. 2C). The highest settlement densities generally occurred on Lunar Days ~2, 11, and 20. Excluding 5 dates when zero settlement was observed, the lowest settlement densities generally occurred on Lunar Days 2, 11, and 27 (Fig. 2C). However, randomization tests did not yield any significant semilunar or lunar periodicity, and cycles were not consistent between settlement series (Table 3).

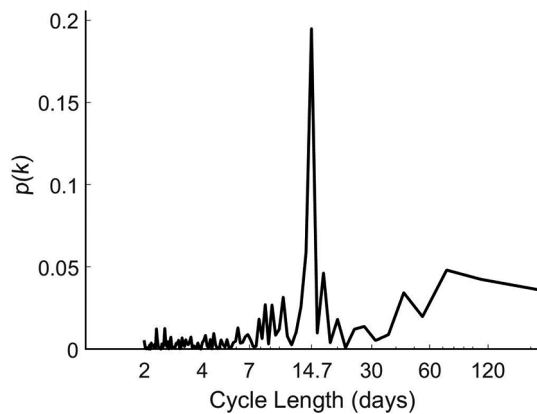


Fig. 3. Periodogram for daily samples of *Chthamalus fissus* adults with late-stage embryos. Periodogram for 2016–2017 series, concatenated into one series so as to be continuous by lunar day. The y-axis, $p(k)$, measures the proportion of variation in the series associated with each cycle period (shown here on a natural-log scale). The tallest peak in $p(k)$ occurs at 14.7 d and was highly significant ($p << 0.001$)

3.3. Seasonal cycles

During 2016–2017, adults were reproductively active during all seasons, though there was substantial variation between years (Fig. 1C). The best model of weekly reproduction included both lunar day and DOY as predictor variables, as well as their interaction (Table 4), indicating that both cycles are important in year-round *C. fissus* reproduction. The highest seasonal reproduction was predicted in mid-May and mid-November. It should be noted, however, that overall model fit was low (Table 4), indicating a high degree of variation remains unexplained. Settlement also occurred in all seasons during 2016–2019, and values tended to peak in April–May and July–December (Fig. 4).

3.4. Alongshore transport

In estimating how far larvae may be transported and, by extension, what degree of connectivity we might expect between our study site and others in the region, we found that average transport was likely limited to <50 km, and that there was no discernable pattern across years, months, or seasons (Table 5).

4. DISCUSSION

4.1. Cycles in reproduction

Results presented here are the first measures of high frequency cycles in the reproductive timing of *Chthamalus fissus*, and our data showed clear evidence of semilunar periodicity. While there were low numbers of brooding adults present in all months, we observed increased brooding activity midway between spring and neap tides (i.e. during waning gibbous and waxing crescent moons) when tidal range is increasing. Following these peaks in brooding is larval release, indicating that larvae are, on average, released into the water column roughly 3–4 lunar days before the spring tide.

Many intertidal and estuarine organisms undergo lunar or tidal reproduction. Reproductive cycles centered on spring tides have been identified in inter-

Table 4. Linear model comparison for cycles in weekly reproduction data. Both lunar day and day of year (DOY) were tested as explanatory variables for arcsine-transformed proportions of late-stage brooding adults. Lunar day was included within a sine term with 14.5 (half a lunar month) set as the periodicity. DOY was included within a sine term with 182.5 (half a year) set as the periodicity. AIC: Akaike's information criterion

Predictor variables	Adjusted R ²	df	p-value	AIC
Lunar day	0.084	90	0.003	-67.99
Lunar day + DOY	0.136	89	<0.001	-72.41
Lunar day + DOY + Interaction	0.198	88	<<0.001	-78.33

tidal barnacles (Macho et al. 2005), semiterrestrial and intertidal crabs (Flores et al. 2007, Christy 2011), and intertidal gastropods (Collin et al. 2017 and references therein), as well as some reef fishes (Robertson et al. 1990). This behavior has been postulated as an adaptation to maximize the time during which adult are underwater (particularly for intertidal and semiterrestrial species that live at or above high tide), as well as to facilitate larval transport away from the benthos on the spring ebb tide (Christy 1982, Christy & Stancyk 1982, Morgan 1995). Numerous other coastal species, however, demonstrate reproduction centered around neap tides (Reyns & Sponaugle 1999, Collin et al. 2017), indicating that factors influencing the timing of reproduction and larval release are complex. Additionally, many

Table 5. Estimated alongshore larval transport after 18 d. Values are reported in km, with south as the positive direction. Values in parentheses: number of days per month used in the transport estimates. Dashes: months with fewer than 15 d available data

Month	2014	2015	2016
April	-	-	33.7 (22)
May	9.74 (31)	18.2 (31)	-6.45 (31)
June	-4.89 (28)	-30.8 (30)	-18.4 (30)
July	-	-	-11.3 (31)
August	-	-	-
September	-	0.55 (18)	-
October	12.4 (29)	20.9 (31)	-
November	-15.8 (30)	37.5 (28)	-

species demonstrate a high degree of variability or spread in the exact date of population-wide reproduction (Robertson et al. 1990, Flores et al. 2007), suggesting that other high frequency processes may play a role in reproduction timing.

We observed substantial variation in the degree of reproductive synchrony of *C. fissus*, both in that population-wide timing of larval release was sometimes spread over several days (Fig. 1A,B) and in that reproduction peaks occurred over a range of days in the lunar cycle (evident in the SE bars in Fig. 2B). This may be a result of small-scale environmental heterogeneity; numerous environmental parameters (e.g. pressure, salinity) may serve as proximate cues for the tidal or lunar cycle, but the conditions that individual organisms experience may vary spatially

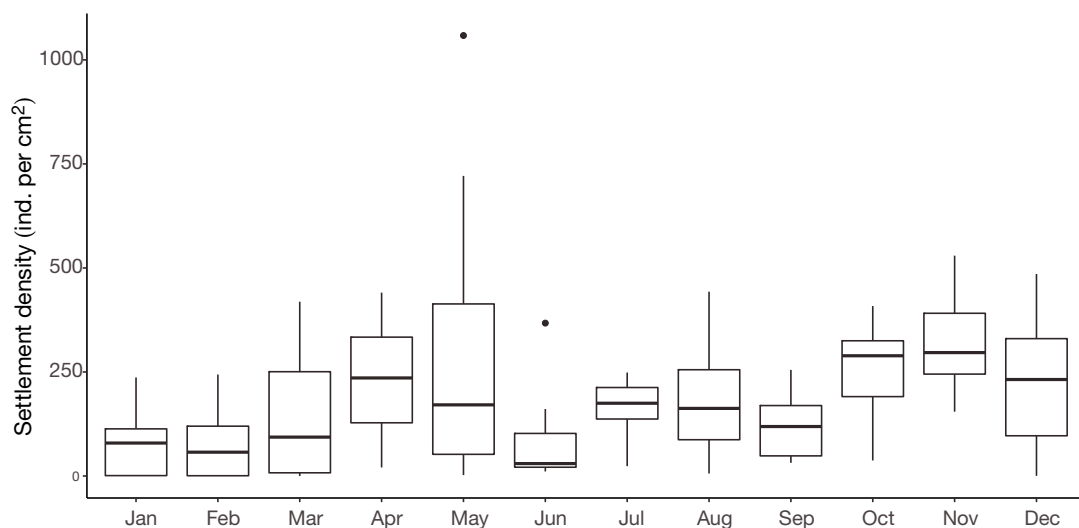


Fig. 4. Monthly averages of *Chthamalus fissus* settlement from weekly data series, to explore seasonal patterns. Box and whisker plots denote the median, first and third quartiles, and minimum/maximum values within 1.5× the interquartile range. Outlier points beyond these values denoted as black circles

over a population (e.g. Miller & Dowd 2019) such that it takes certain individuals longer to receive the cue to release larvae. Conversely, individuals may vary in sensitivity to particular environmental cues even with a uniform cue (e.g. Visser et al. 2011), creating a mosaic in individual responses. In all likelihood, individual timing is in response to multiple co-occurring cues (e.g. lunar and diel cycles; Jacinto & Cruz 2008), creating further opportunities for variation in individual sensitivity and experience.

Another possibility is that apparent asynchrony is observed due to multiple distinct breeding groups occurring within a population, such that portions of the population reproduce at most once per lunar month while the population overall undergoes reproduction twice as often (e.g. Christy 1978, Flores et al. 2007). Consistent with this, during our ~2 yr of sampling reproductive adults, there were only 2 sampling dates when we observed >33% of the population to be brooding late-stage embryos. Overall, our results highlight the importance of understanding such high-frequency reproductive cycles before evaluating lower frequency processes like seasonality: For this species in which proportions of late-stage brooding adults can vary between 0 and 50% over the year, variations on the order of at least 10–15% can be attributed solely to the lunar cycle (Fig. 2B).

After accounting for variation attributable to the lunar cycle, we also identified a seasonal cycle, though the timing of reproductive events differed from those reported for *C. fissus* at more northern locations. We found that *C. fissus* exhibited higher reproductive activity twice per year in mid-May and November. Hines (1978) monitored populations monthly over 2 yr at 2 sites >400 km northwest of our field site and found that a majority (60–90%) of each population brooded embryos from May to September (i.e. one long reproductive season). Blower & Roughgarden (1988) monitored populations every 4 wk over ~15 mo at 2 sites with varying degrees of parasitism ~600 km northwest of our study site and found that parasitism appeared to impact population-wide reproduction cycles. Adults at the site with low (<15%) prevalence of parasitism exhibited peaks in reproduction (60–100% of the population) during both March and September–November (i.e. 2 reproductive seasons yr⁻¹), while adults at the site with high (~10–30%) prevalence of parasitism exhibited a similarly large reproductive peak only in August–October and a much reduced reproductive peak (~40% of the population) in March (Blower & Roughgarden 1988).

Neither Hines (1978) nor Blower & Roughgarden (1988) controlled for the lunar cycle during sampling, which means that there may have been higher frequency reproductive cycles that were not captured in either study, or that may have dampened or inflated the signals observed. We found that the reproductively active portion of the population could vary by as much as 26% over 1 d and 50% over 7 d (Fig. 1), which means large reproductive peaks may have been missed by monthly samples. Still, there is precedent for species to exhibit multiple reproductive cycles across their range. In reefs off northwestern Australia, select colonies of 3 *Acropora* coral species demonstrated biannual reproduction, even while the majority of each species followed annual reproductive cycles, which was thought to be facilitated by particularly favorable environmental and food conditions (Gilmour et al. 2016). Along the US east coast, reproduction in the soft-shell clam *Mya arenaria* follows an annual cycle north of Cape Cod, while many populations south of Cape Cod exhibit biannual reproduction (Ropes & Stickney 1965). Cape Cod is a known oceanographic and biogeographic barrier (Pappalardo et al. 2015), so the differences could be driven by any number of environmental or biological factors.

4.2. Cycles in settlement

Interestingly, while visualization of all daily settlement data by lunar day yielded some apparent structure over a lunar month (Fig. 2C), there was no lunar cyclicity identified in individual settlement series (Table 3). This is in contrast to Shanks (1986), who reported lunar periodicity in settlement series of *Chthamalus* spp., measured ~7 km north of our field site. In this previous study, Shanks (1986) measured daily settlement at 3 heights in the barnacle zone (0.3, 1.0, and 1.5 m above MLLW) over 83 d in 1983, as well as at a single height (1.0 m above MLLW) over an additional 77 d later the same year. Because of the wide range in vertical height of settlement surfaces, Shanks (1986) normalized settlement densities by immersion time. While this was intended to control for settlement opportunity (given that settlement must occur underwater), this normalization may have inadvertently introduced a lunar/tidal cycle to the data. In our study, settlement plates were distributed along a narrower range of vertical heights (~0.3 to 0.6 m above MLLW), and there was no relationship between proportion of settlement per plate and plate elevation (Hargenrader 2018), similar to patterns

found in other barnacle settlement studies (Hatton 1938, Pineda 1994b).

In contrast, over the 4 yr of sampling, there were months with increased settlement (in April–May, and October–November), though this was against a background of nearly consistent settlement all year. These pulses of increased settlement, along with observed peaks in the daily series, could be caused by a variety of processes: (1) intermittent events of improved cross-shore transport, facilitating larval delivery to benthic habitat; (2) decreased availability of suitable settlement substrate, causing larvae to settle in higher densities on settlement surfaces; (3) lower water column mortality rates, allowing greater survival of larvae; and (4) increased reproduction, at this site or ‘up-stream’, leading to pulses of increased larval supply. Each of these processes is explored below.

4.3. Possible mechanisms for variability in settlement

Observed cycles in settlement series are often used as evidence of cross-shore delivery mechanisms, provided a mechanism can be found that operates on a similar timescale. Cross-shore larval transport in this region has been linked to internal tidal bores and internal waves (Pineda 1994a, 1999), particularly in conjunction with thermal water column stratification (Hagerty et al. 2018, Yamhure et al. 2021). However, these mechanisms cannot entirely explain observed settlement patterns here. Daily settlement series did not yield any consistent periodicity, and weekly series yielded particularly high settlement in fall months when stratification tends to be low (Hagerty et al. 2018). Previous analysis of the same daily settlement data presented here indicated that reduced settlement coincided with large-scale warm-water anomalies and reduced stratification (Pineda et al. 2018), but this cannot explain the biannual peaks in settlement observed in weekly data.

Pulses in settlement could also be driven by factors operating in the water column (driving variability in mortality) or on the benthos (driving variability in amount of suitable habitat). Increased settlement densities of *C. fissus* in this region have been linked to reduced available settlement habitat, as sections of rocky intertidal habitat are regularly inundated with sand, forcing settlers to concentrate in higher densities on any habitat remaining (Pineda 1994b, Hargenrader 2018). Variable mortality rates in the plankton could also lead to variable numbers of lar-

vae surviving to settle, though mortality in the plankton is notoriously difficult to quantify (Pineda et al. 2007). Food in the nearshore may impact survival of *C. fissus* larvae, but concentrations of phyto- and zooplankton in southern California tend to exhibit one spring peak with low concentrations in the fall (Loeb et al. 1983, Kim et al. 2009). Still, food can be incredibly patchy in the ocean (Dagg 1977), so variable mortality rates cannot be ruled out as a mechanism driving seasonality in settlement.

Increased settlement densities may also be linked to instances of higher larval supply, due either to higher average fecundity or higher overall reproductive activity. Fecundity in *C. fissus* is linked to body size (Hines 1978), and population-wide larval output should scale with population size overall. Population size of *C. fissus* varies throughout the year at this site (Hargenrader 2018), as does the size distribution of reproductive adults (N. Reyns pers. obs.), though the population at this site tends to be smallest in September–November (Hargenrader 2018). Given that there was consistently high settlement in the fall months, particularly November, fluctuations in population-wide larval output would seem an unlikely candidate for driving monthly differences in settlement unless settling larvae consistently originate from further sites with distinct population dynamics.

4.4. Lack of coherence between reproduction and settlement timing

Temporal patterns in settlement or recruitment are also sometimes used to estimate patterns in reproduction, particularly for habitats that are difficult to access. Examples include seasonal recruitment of corals in marine reserves (Harriott & Banks 1995, Mangubhai et al. 2007) and benthic invertebrates in Arctic systems (Kuklinski et al. 2013, Meyer-Kaiser et al. 2022). To overcome the fact that numerous biological and physical factors can act to decouple reproduction and recruitment, additional data are often collected, such as plankton samples of earlier-stage larvae (e.g. Kuklinski et al. 2013, Meyer-Kaiser et al. 2022) or opportunistic sampling of brooding adults (e.g. Meyer-Kaiser et al. 2022). When additional data are not available, settlement and recruitment data may instead be contextualized with prior studies that establish the reproductive biology of the species (e.g. Harriott & Banks 1995, Mangubhai et al. 2007), though this often means comparing reproduction and settlement from different sites or years. We observed distinct cycles in reproduction and settlement series,

even when data for each series were collected simultaneously at the same site (Table 3), indicating that the links between reproduction and settlement timing cannot be taken for granted. A variety of factors could be responsible for such a mismatch, and we discuss the most likely candidates for our system below, organized by the life stage that is impacted.

Before larvae can enter the water column, decoupling can occur due to processes that affect reproductive adults on the benthos. Other intertidal barnacle species have been shown to experience fertilization failure due to high temperatures (Crickenberger & Wetthey 2017), and other marine invertebrates potentially experienced similar failure due to extreme cold (Olive et al. 1981). Adult barnacles can also experience brood failure due to physical disturbance or predation, resulting in embryos that are released into the water column prematurely or that are trapped in the adult test, respectively (Branscomb et al. 2014). Parasitism may undercut predicted reproductive output, either through increased energetic costs that result in lower fecundity or through castration of the host directly. Many intertidal barnacle species, including *C. fissus*, may experience parasitism by the isopod *Hemioniscus balani*, which attaches to the host's ovaries and consumes the ovarian fluid (Goudeau 1977, Blower & Roughgarden 1988). This process functionally transforms the hermaphroditic barnacle hosts into males, thereby reducing the number of adults in the population that can brood and release larvae. We directly measured proportions of brooding adults, so these processes are unlikely to have driven the statistical decoupling we observed, but they may drive decoupling in other systems.

Even when larvae are successfully able to develop and enter the water column, they can encounter a range of conditions that impact their transport, development, and survival. Given sufficiently strong near-shore currents, larvae may be dispersed far afield, leading to open populations that only exhibit coupling if looked at in aggregate (reviewed in Morgan 2021). Dispersal can also vary over space and time (e.g. Barshis et al. 2011), making investigations into potential coupling extremely difficult without detailed knowledge and consideration of hydrodynamic processes. We estimated alongshore dispersal distances to be on the order of 50 km or less, assuming larvae only remain in the water column for their ~18 d development period. The population at this site is the largest for 10 km north and south (J. Pineda et al. unpubl.), but there are populations beyond this distance that could feasibly supply larval settlers to

our site. Additionally, our predicted transport distances varied between months and years, indicating that local retention of larvae (and, by extension, coupling between local reproduction and settlement cycles) may vary through time. Even if larvae are consistently retained close to their point of origin, larval development rates are typically affected by external factors including temperature (O'Connor et al. 2007) and diet (Stone 1989, Griffith et al. 2021), which can make it difficult to detect spatial or temporal coupling across a habitat mosaic. Similarly, delivery of competent larvae to adult habitat may rely on processes that do not occur on predictable cycles (e.g. Hagerty et al. 2018), thus forcing larvae to extend their time in the water column (increasing their realized PLD). Barnacle larvae can prolong their larval duration by relying on lipid reserves during the nonfeeding cyprid stage (Holland & Walker 1975), presumably to await better settlement conditions. *C. fissus* cyprids have been kept alive and swimming in the laboratory for 7 wk (N. Reyns pers. obs.), indicating that ours may be an underestimate of transport distances. Mortality in the plankton is also thought to be high (Pineda et al. 2007), and variable mortality rates over space or time could drown out evidence of correlation between reproduction and settlement.

In the event that coupling is maintained from reproduction through to larval delivery to rocky intertidal habitat, processes that occur during and after settlement can still drive apparent decoupling. Over short timescales, larvae arriving to adult habitat may fail to settle, due to a lack of settlement cues or a lack of available substrate (Pineda et al. 2010). While our site typically maintains ~20–60% free space in barnacle habitat, there is a seasonal drop to near 0% in September when algal growth increases (Hargenrader 2018). Additionally, free space at this site may be covered by sand, further reducing the amount of usable substrate available to barnacle settlers, causing higher settlement densities and increasing opportunities for statistical decoupling (Pineda 1994b). Following metamorphosis, settlers may undergo high rates of mortality (Pineda et al. 2006), resulting in much lower recruitment than expected. While we did not measure recruitment here, mortality may have impacted our weekly settlement series.

Overall, many of the processes described above are time-dependent, and the timing of adult reproduction may have evolved, at least in part, to maximize recruitment success and minimize larval and juvenile mortality (e.g. Shima et al. 2020, 2021). It has been noted, however, that in order for such multi-generational

selection to take place, selective pressures would have to be predictable and consistent (Morgan 1995), which is more likely in populations with high degrees of coupling (so that selected larvae return to habitat where those same selective pressures occur).

5. CONCLUSIONS

Despite the numerous decoupling factors described above, it was surprising to find such little coherence between reproduction and settlement, given our well-constrained system with data collected at high temporal resolution over multiple years. Although we observed significant semilunar and biannual reproductive cycles, and despite the relatively small magnitudes of estimated alongshore transport, we found little evidence of corresponding cyclicity in settlement on any timescale. Given the current knowledge of environmental and hydrodynamic processes in this region and at this site, the most likely causes for the decoupling of reproduction and settlement timing are (1) variability in cross-shore transport processes that deliver larvae back to adult habitat (e.g. Hagerty et al. 2018), (2) variability in alongshore transport processes that could demographically connect our study site with others in the region, and (3) plasticity in larval duration, particularly during the cyprid stage (e.g. Holland & Walker 1975).

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