

Local biological drivers, not remote forcing, predict settlement rate to a subtropical barnacle population

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ABSTRACT: In spite of growing evidence for potential larval retention close to parental populations, it is still commonly assumed that large-scale transport mechanisms overwhelm local reproductive patterns and control larval settlement. Here, we evaluated the likelihood of settlement rate regulation by local biological factors and remote physical transport in a population of the intertidal tropical barnacle *Chthamalus bisinuatus*. Results indicated that juvenile recruitment and larval settlement may be substantially regulated by local reproductive output and pelagic food supply. Seasonal reproduction, with peak activity during summer, is followed by juvenile recruitment with no apparent lag over successive (ca. 15 d) sampling dates. Likewise, high-frequency (1 d) time-series analyses connected the main steps of the process: naupliar release correlates to cyprid supply in nearshore waters 7 d ahead, and cyprid supply is followed by larval settlement after an additional 4 to 5 d. Positive correlations between residuals of release vs. settlement relationships and chl *a* concentration (a proxy of phytoplankton biomass) also suggest food limitation for late naupliar stages. Tidal and wind transport did not explain the temporal variation in larval supply, and larval settlement responded only weakly to the wind of the day, suggesting a modest and very local effect. Addressing transport hypotheses alone is likely an inadequate approach to understand the supply-side ecology of marine invertebrates living in meso-oligotrophic systems such as the one examined in this study. A better understanding of processes affecting reproductive output and pelagic larval survival in addition to transport mechanisms, is likely required.

KEY WORDS: Rocky shores · Self-recruitment · Larval behavior · Larval competency · Metamorphosis · Food limitation

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INTRODUCTION

It is often assumed that larval settlement of marine invertebrates is mostly controlled by physical transport mechanisms and largely decoupled from local reproductive output (Hughes 1990, Caley et al. 1996). Larvae advected offshore may face strong tidal and

wind-driven currents, which often override their swimming capacity and largely dictate their pelagic transport (see reviews by Shanks 1995, Queiroga & Blanton 2005). However, the release of larvae during periods of reduced advective potential (Shanks 1998, Bueno et al. 2010, Kasten & Flores 2013) and larval behavior in the water column (Shanks & Brink 2005,

Morgan et al. 2009) may greatly increase the chances of retention close to the shoreline. Such behavioral mechanisms may explain demonstrations of self-recruitment in different marine invertebrates and fish (e.g. Kingsford et al. 2002, Levin 2006, Jones et al. 2009), and downplay the importance of large-scale advection in the regulation of larval supply and settlement.

Under conditions of restricted transport and increased likelihood of population self-replenishment, biological processes that have been largely overlooked may actually control the settlement rate and benthic population dynamics of marine organisms which produce a pelagic propagule. One such process is obviously the reproductive output of source populations, but, surprisingly, studies attempting to find a link between high-frequency propagule release and settlement rate are rare (but see Robertson et al. 1988, Toupoint et al. 2012). The pelagic duration of propagules is usually in the range of a few days to a few weeks, but for most species temporal variation in reproductive output, as based on gonad maturation or the frequency of egg-bearing individuals, is usually examined at scales too coarse to test its correspondence to settlement rate. Although challenging, a metric of 'realized' fecundity, as *in situ* daily estimates of propagule release, should be attempted. Another important biological parameter is the pelagic food supply for developing larvae. Trophic limitation has clearly explained recruitment failure to fishery stocks for a long time (Cushing 1974, 1990, Beaugrand et al. 2003), but it has been vastly ignored in studies attempting to understand connectivity among discrete benthic habitat patches, such as rocky outcrops separated by long stretches of sandy beaches. In particular, a major trophic bottleneck may take place at the very end of the larval period if energetic reserves are insufficient to meet the demands of metamorphosis to the juvenile phase. Therefore, poor food supply may often greatly reduce, or even suppress, settlement rate.

In this study we addressed the supply-side ecology of the most abundant intertidal sessile invertebrate in southeastern Brazil rocky shores, the barnacle *Chthamalus bisinuatus* Pilsbry. We first regularly measured reproductive effort and juvenile recruitment over 1 yr to verify whether these 2 processes are coupled at the seasonal scale. We then obtained daily time series of 11 key parameters and used standardized statistical techniques to examine processes that take place over shorter time scales, within the main breeding season of this species. In particular, we were interested to identify major coastal processes

taking place at that time and evaluate, in this context, the likelihood of local biological drivers and remote forcing as main determinants of settlement rate.

MATERIALS AND METHODS

Seasonal reproduction and recruitment

A *Chthamalus bisinuatus* population along a 45 m coastline at Ilha Porchat, São Vicente, SP, Brazil (23° 58' 52" S, 46° 22' 03" W) was sampled regularly at approximately 15 d intervals, from October 2006 to October 2007. This is a steep shore with a clearly distinct and almost vertical chthamalid zone, approximately 30 cm wide.

Breeding activity. Eight 3 × 3 cm random squares were scraped over the entire target population and individuals were examined in the laboratory. Barnacles were counted, measured (opercular diameter, to the nearest 0.1 mm) and the development stage of their gonads classified as in O'Riordan et al. (1995). Monthly sample sizes varied between 94 and 392 barnacles. The percentage of mature barnacles with advanced or ripe gonads (Stage 2 or 3 ovaries) was used as an index of breeding activity. Because ovaries in chthamalids quickly refill after oviposition, most mature barnacles bear fully developed embryos ready to hatch (Burrows et al. 1992, O'Riordan et al. 1995). Barnacles smaller than 1.4 mm (the size of the smallest brooding individual) were excluded.

Juvenile recruitment. Fifteen 5 × 5 cm plates coated with gray 3M® safety walking tape were used as settlement surfaces. Groups of 5 plates were randomly allocated along the upper, the mid- and the lower edge of the barnacle zone. Plates were removed on each sampling date to count recruits and then replaced by new ones. Average estimates for all plates (n = 15) were used to describe seasonal recruitment variation. Settlement rates at the different vertical levels were compared using a 1-way analysis of variance, followed the SNK procedure for post hoc comparisons.

Within-season control of settlement rate

This part of the study was conducted at Baleeiro Head, located in the São Sebastião Channel, SP (23° 49' 45" S, 45° 25' 25" W), 100 km northeast of Ilha Porchat. This is also a steep rocky shore habitat with a clear *Chthamalus* zone. Within a coastline of ca. 200 m, we sampled daily 11 different physical and

biological variables, from 13 December 2008 to 17 April 2009 (126 d). Daily averages were calculated for variables measured automatically at higher frequencies. In the case of variables measured *in situ*, once per day, fieldwork was concentrated within 2 h around the diurnal low tide.

Physical variables. Seven meteorological and oceanographic parameters were monitored. Surface seawater temperature (1) was measured every 30 min using temperature loggers installed 1 m below the lowest tidal marks. Water salinity (2) was measured at 3 stations several tens of meters apart, using a portable conductivity meter (YSI 30). Sea surface level was measured at the time of diurnal low tide using a ruler installed at a sheltered spot within the sampled coastline. Differences between these readings and tidal chart data for São Sebastião Harbor were used to calculate sea level anomalies (3). Daily averages of tidal amplitude (4) were calculated using the same chart data. As in Kasten & Flores (2013), water flow over the shore (5) was estimated based on daily dissolution rates of plaster cylinders (4 cm diameter \times 6 cm height), which were totally varnished except the top, allowing gradual dissolution. Because of frequent rainfall, a cylinder placed above the high-water maximum served as control. A flow index (f_i) was then calculated as:

$$f_i = \bar{w}_b - \bar{w}_c t_e$$

where \bar{w}_b and \bar{w}_c are the average daily plaster dissolution rate (g d^{-1}) of 3 replicate cylinders installed in the barnacle and control zone, respectively, and t_e is the relative emersion time at the barnacle height, which varied from zero (constant emersion) to 0.95. Relative submersion times were estimated using sea-surface level data. Wind stress was calculated as in Queiroga et al. (2006) using wind velocity and direction data obtained at 10 min intervals from the meteorological station of the Center for Marine Biology of the University of São Paulo. In this case, wind stress was decomposed into along-shore (6) and across-shore (7) components (60° – 240° and 150° – 330° axes, respectively). Positive values were set at 60° and 330° .

Biological variables. Four biological parameters were quantified. Vertical walls with dense barnacle cover at the 3 Baleeiro Head sampling stations were selected to install traps measuring daily larval release (1). Trap specifics and sampling design are detailed elsewhere (Bueno & Flores 2008, Bueno et al. 2010). Briefly, 10 contiguous adjacent trap positions (9×9 cm) were set at each station, and a single position was randomly sampled with a single trap each day, without repetition, over blocks of 10 d.

Trap contents were examined under a dissecting microscope and released nauplii were counted. Larval supply (2) was estimated by processing samples obtained with an electrical submersible pump, installed 1 m below the lowest tidal mark and programmed to work for four 2 h periods daily (00:00–02:00 h, 06:00–08:00 h, 12:00–14:00 h, 18:00–20:00 h). Water (on average $49 \text{ m}^3 \text{ d}^{-1}$) was pumped into a $250 \mu\text{m}$ plankton net, the contents of which were collected daily. Cyprids were usually sorted and counted from whole samples, but a Folsom plankton splitter was used when necessary to process subsamples when larval numbers were exceedingly high. Larval settlement (3) was estimated by counting settling cyprids or first juveniles on 10 plates (10×10 cm), covered with safety walking tape, randomly spaced over the lower half of the sampled barnacle population. Plates were replaced daily. As a proxy of food resources for larvae, chl a concentration (4) was estimated at the 3 stations, using nearshore 2 l samples collected with black bottles. Filtration, extraction and fluorescence quantification were carried out following the protocols described in Kasten & Flores (2013).

Time-series analyses

We used independent evidence from standardized cross-correlation analyses between pairs of variables to investigate both seasonal (low frequency 15 d sampling) and within-season processes (1 d high frequency sampling). Namely, we used fortnightly data to (1) test for the seasonal correspondence between breeding activity (based on the percentage of barnacles with mature ovaries) and juvenile recruitment, and daily data to (2) describe coastal oceanographic characteristics at the study area, and (3) evaluate the likelihood of a set of mechanisms affecting settlement rate. Because most of the time series handled in this study are autocorrelated to some extent, direct significance testing of correlation coefficients (R_{XY}) is inadequate because actual Type I errors tend to be higher than the specified α . Rather than remove autocorrelation in these time series, which may render excessively conservative results (Pyper & Peterman 1998), we decided to adjust the procedures for hypothesis testing. The method consisted in correcting the degrees of freedom used to test the significance of R_{XY} . In 'Results', p_{adj} refers to p-values calculated for the corrected degrees of freedom. For that, we followed the guidelines proposed by Pyper & Peterman (1998), and used a modified version of

Chelton's method (Chelton 1984), which proposes a correction based on the sum of cross-products of the autocorrelations of tested variables ($R_{XX} \cdot R_{YY}$) over the examined lags. This corresponded in all our cases to the fifth of the entire length of the series ($N/5$).

RESULTS AND DISCUSSION

Correlational evidence for both the seasonal and the within-season temporal processes calls attention to a possible connection between local reproduction and larval settlement, or juvenile recruitment, in our study system. The breeding season at Ilha Porchat is very well defined, from mid January to late April, when more than 90% of the annual reproductive effort took place (based on the percentage of mature barnacles, Fig. 1). Juvenile recruitment follows a similar trend. Maximum correlation was positive and at no lag ($r = 0.854$, $p_{\text{adj}} = 0.0017$), indicating not only a close correspondence between both processes but also a relatively short pelagic phase. Average recruitment rate over the narrow vertical distribution of adult barnacles varied dramatically ($F_{2,327} = 8.89$, $p < 0.001$), with the highest rate at its lower edge (0.34 ind. plate $^{-1}$ d $^{-1}$), corresponding to almost 10-fold (0.039 ind. plate $^{-1}$ d $^{-1}$) and over 200-fold (0.0017 ind. plate $^{-1}$ d $^{-1}$) the rates measured at the mid position and the upper edge, respectively, resembling the patterns reported for other intertidal barnacle species (e.g. Bertness et al. 1992, Jenkins 2005).

Results obtained through higher frequency sampling, within the main breeding season, support a

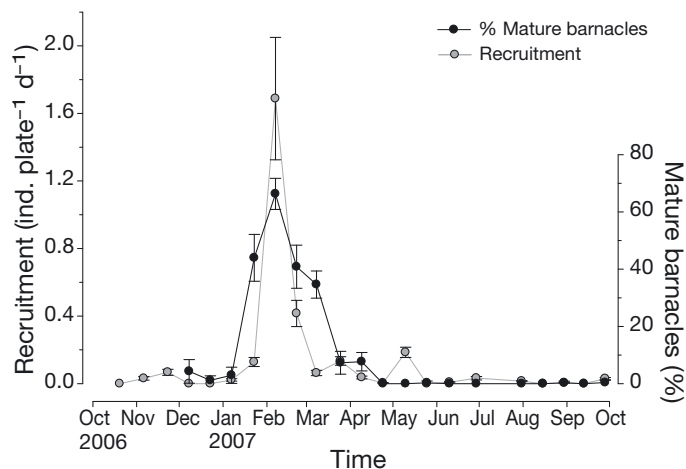


Fig. 1. Seasonal variation in breeding activity and juvenile recruitment of the chthamalid barnacle *Chthamalus bisinuatus* at Ilha Porchat, São Vicente, São Paulo, Brazil. Data are averages \pm 1SE

general connection between larval release by adults, cyprid supply to the nearshore and actual settlement rate (Fig. 2E-G). Cross-correlation analyses linked naupliar release to cyprid nearshore supply after 7 d, and cyprid supply to settlement after 5 d, summing up to a pelagic larval duration of 12 d (Table 1), shorter than reported for temperate congeners (Achtuv 1986, Burrows et al. 1999). A significant correlation connecting larval release directly to settlement in 11 d further suggests that reproduction is coupled to settlement at a local scale. One could argue that supply and settlement trends may also reflect release activity at many other places within the region, and therefore the relationships above would not represent a local connection. However, this does not seem to be the case. Kasten & Flores (2013) compared patterns of larval release in the São Vicente region and at Baleeiro Head, encompassing a 120 km coastline. The 2 sites sampled at São Vicente were 2.2 km apart but exhibited a remarkably similar pattern, following a sharp tidal-amplitude cycle, with maximum release at neap tides (Bueno et al. 2010). Food limitation for reproduction in these populations is unlikely since coastal waters are eutrophic due to urban pollution. Temporal trends in larval release are strikingly different, and far more erratic, at the more oligotrophic environment off Baleeiro Head, lacking any periodicity according to the neap/spring cycle, and reproductive output is near an order of magnitude lower. Populations in the São Sebastião Channel were proved capable of endogenous timing leading to neap-tide release, consistent with a retention strategy, but such a pattern is broken down in nature by stochastic environmental stressors, of which food supply and thermal stress seem particularly relevant (Kasten & Flores 2013). Because complex environmental triggers, coupled to barnacle physiological conditions (Freuchet et al. 2015), are expected to shape temporal larval release patterns rather locally, the correspondence between larval release and supply may reflect self-recruitment within a relatively short coastline, probably in the range of a few km or less. Additional work is, however, pending for a more precise determination of the spatial scale at which such irregular daily release patterns remain consistent. We also emphasize that our results should be interpreted as correlational evidence and constitute, by no means, proof of substantial self-replenishment. Specific tagging and recovery sampling protocols should be attempted to tackle this difficult task.

Although located in a relatively sheltered area, within the São Sebastião Channel, our study site is exposed to substantial physical forcing that could

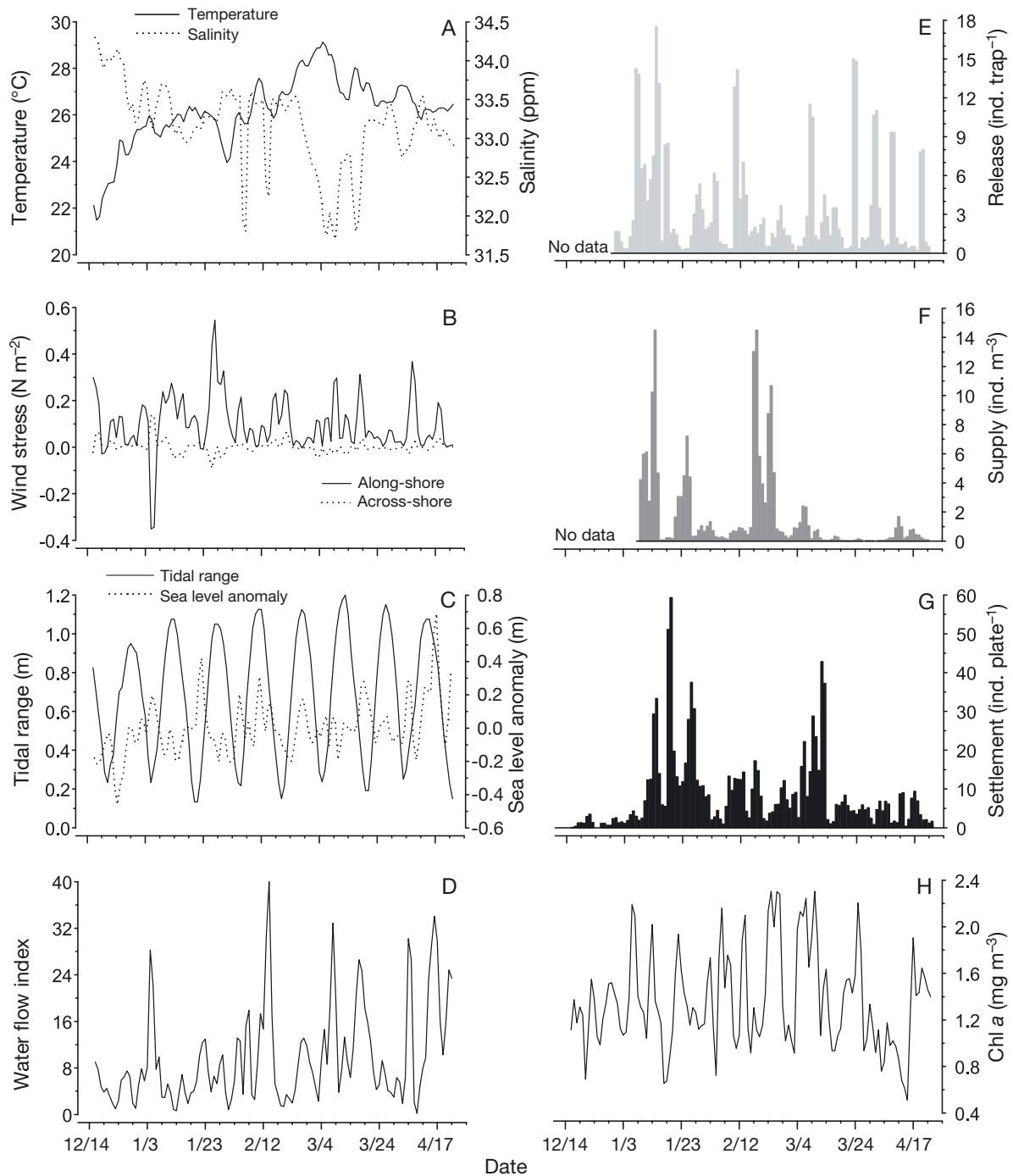


Fig. 2. Within-season time (mo/d) series of (A–D) physical and (E–H) biological variables potentially affecting settlement rate of the barnacle *Chthamalus bisinuatus*. The data shown for (C) water flow, (E) larval release, (G) larval settlement and (H) chl *a* correspond to average values calculated from 3, 3, 10, and 3 replicates, respectively, obtained along the target coastline. All series were smoothed by calculating 2 d moving averages

have blurred local reproductive trends. However, the only apparent and important effect of such an influence is the low settlement rate observed from the beginning of the study to mid-January (Fig. 2G), when unusually high salinity and low temperature

(Fig. 2A) suggest the occurrence of an upwelling event, similar to what has been previously documented in this study region (Aidar et al. 1993). This event may have caused substantial offshore movement of surface waters, and thus larval transport

Table 1. Cross-correlation analyses testing the association of biological and physical variables with the supply of late stage larvae in the nearshore and the effective settlement rate. p-values were calculated based on adjusted degrees of freedom accounting for the autocorrelation of time series (p_{adj}). In all cases, statistics are only shown for the lagged relationship rendering the highest correlation coefficient (r). –: Cases in which correlation coefficients were not significant at any of the tested lags; ns: not significant

	Larval supply			Larval settlement		
	Lag (d)	r	p_{adj}	Lag (d)	r	p_{adj}
Biological variables						
Larval release	7	+0.329	0.001	11	+0.261	0.016
Larval supply				5	+0.351	0.002
Larval flow				4	+0.450	<0.001
Physical variables						
Tidal amplitude	–	–	ns	–	–	ns
Along-shore wind stress	–	–	ns	0	+0.194	0.027
Across-shore wind stress	–	–	ns	0	–0.194	0.049

away from settlement grounds as reported in other studies (e.g. Farrell et al. 1991, Queiroga et al. 2006). Overall effects of along-shore wind stress on larval supply were, however, non-significant (Fig. 2B, Table 1), in spite of causing sea level anomalies (lag = 1 d; $r = -0.318$, $p_{adj} < 0.001$) of up to 60% of predicted tidal ranges (Fig. 2C), and therefore extensive horizontal flow. Sea level anomaly, not tidal range, was positively associated to water flow at the shore height sampled, with the highest correlation coefficient at no lag (Fig. 2C,D; $r = 0.548$, $p_{adj} < 0.0001$). Together with the weak, although significant, effect of wind stress at lag 0, a better prediction of settlement rate by correcting larval supply with flow estimates (by multiplying both variables, i.e. larval flow, Table 1) indicates that water motion positively affects larval settlement, probably by increasing the frequency of contacts with plates. Increased contact also explains the much higher settlement lower on the shore observed at Ilha Porchat.

While apparently playing a more important role than tidal and wind transport mechanisms, reproductive effort did not fully explain the daily variation of settlement rate. In particular, release pulses do not translate to obvious supply or settlement events over the last fourth of the examined time series (Fig. 2E–G). There were certainly other processes than those addressed in this study affecting settlement (e.g. predation), but chl *a* concentration, a surrogate of larval food supply, does partially explain residual variation after fitting release vs. settlement relationships (Fig. 3, see Table A1 in the Appendix for details of numerical procedures). A significant correlation was only found when residuals were paired with chl *a* averages 4 to 7 d after release ($r =$

0.304, $p_{adj} = 0.024$), when larvae would mostly consist of late naupliar stages. There were no significant correlations for the other 2 relationships (release vs. supply and supply vs. settlement) but it is interesting to note that coefficients were always positive and smallest p-values were consistently obtained for the late naupliar phase (Fig. 3). These findings support the results of Hentschel & Emlet (2000) on *Balanus glandula* showing that food restrictions to intermediate and late naupliar stages matter the most, reducing the time of metamorphosis and allowing larger accumulation of reserves, which will likely enhance settlement rate. The trends

reported in the present study suggest that trophic processes may be quite important in determining settlement success in coastal marine invertebrates, especially in oligotrophic conditions such as those prevailing in summer in our study region (Aidar et al. 1993). Proper experimental testing of explicit resource limitation hypotheses is underway.

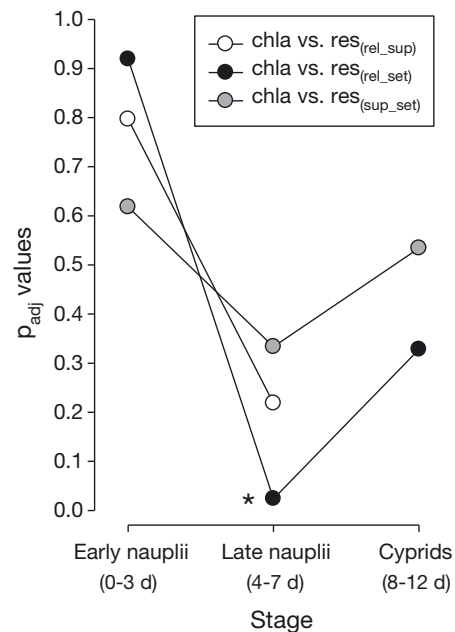


Fig. 3. Probability of adjusted Type I errors (α) in correlation analyses between chl *a* concentration (chl_a), a proxy for larval food supply, and residuals (res) of relationships linking larval release (rel), larval supply (sup) and settlement (set). Potential effects of pelagic food limitation were suggested by averaging chl *a* for different time intervals and lagging residual series based on the duration of larval phases (details are given in Table A1 in the Appendix). * $p < 0.05$

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Appendix.

Table A1. Numerical procedures to assess potential effects of food supply (as chl *a* concentration) on settlement rate of the barnacle *Chthamalus bisinuatus*. First, residuals (e_i) of relationships linking larval release, larval supply and settlement rate were obtained at the lags specified in Table 1. Second, variables were aligned to specific lags (d) as indicated by subscripts. Note that chl *a* conditions after the non-lagged variable (larval release) were used for the first 2 relationships (release vs. supply and release vs. settlement), while conditions before and after larval supply were used for the third one (supply vs. settlement), accounting for both past naupliar resources, and future conditions for cyprids while in the nearshore but before settling. Finally, moving averages of chl *a* data over periods estimated for the development of early nauplii (4 d), late nauplii (4 d) and cyprids (5 d) were used to test specific correlations for these 3 different phases

Day	Chl <i>a</i>			Residuals	
	x_i	Nauplii	Cyprids		
		Early (0–3 d)	Late (4–7 d)	(8–12 d)	
Larval release vs. larval supply (lagged 7 d)					
0	x_1	\bar{x}_{1-4}	\bar{x}_{5-8}	–	e_1
1	x_2	\bar{x}_{2-5}	\bar{x}_{6-9}	–	e_2
2	x_3	\bar{x}_{3-6}	\bar{x}_{7-10}	–	e_3
...	–	...
n	x_n	$\bar{x}_{(n-7)-(n-4)}$	$\bar{x}_{(n-3)-n}$	–	e_n
Larval release vs. larval settlement (lagged 11 d)					
0	x_1	\bar{x}_{1-4}	\bar{x}_{5-8}	\bar{x}_{9-13}	e_1
1	x_2	\bar{x}_{2-5}	\bar{x}_{6-9}	\bar{x}_{10-14}	e_2
2	x_3	\bar{x}_{3-6}	\bar{x}_{7-10}	\bar{x}_{11-15}	e_3
...	–	...
n	x_n	$\bar{x}_{(n-12)-(n-9)}$	$\bar{x}_{(n-8)-(n-5)}$	$\bar{x}_{(n-4)-n}$	e_n
Larval supply vs. larval settlement (lagged 5 d)					
0	x_1	\bar{x}_{1-4}	\bar{x}_{5-8}	\bar{x}_{9-13}	e_8
1	x_2	\bar{x}_{2-5}	\bar{x}_{6-9}	\bar{x}_{10-14}	e_9
2	x_3	\bar{x}_{3-6}	\bar{x}_{7-10}	\bar{x}_{11-15}	e_{10}
...	–	...
n	x_n	$\bar{x}_{(n-12)-(n-9)}$	$\bar{x}_{(n-8)-(n-5)}$	$\bar{x}_{(n-4)-n}$	$e_{(n-5)}$

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