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ORIGINAL RESEARCH

Early post-settlement events, rather than settlement, drive recruitment and coral recovery at Moorea, French Polynesia

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Abstract

Understanding population dynamics is a long-standing objective of ecology, but the need for progress in this area has become urgent. For coral reefs, achieving this objective is impeded by a lack of information on settlement versus post-settlement events in determining recruitment and population size. Declines in coral abundance are often inferred to be associated with reduced densities of recruits, which could arise from mechanisms occurring at larval settlement, or throughout post-settlement stages. This study uses annual measurements from 2008 to 2021 of coral cover, the density of coral settlers (S), the density of small corals (SC), and environmental conditions, to evaluate the roles of settlement versus post-settlement events in determining rates of coral recruitment and changes in coral cover at Moorea, French Polynesia. Coral cover, S, SC, and the SC:S ratio (a proxy for post-settlement success), and environmental conditions, were used in generalized additive models (GAMs) to show that: (a) coral cover was more strongly related to SC and SC:S than S, and (b) SC:S was highest when preceded by cool seawater, low concentrations of Chlorophyll a, and low flow speeds, and S showed evidence of declining with elevated temperature. Together, these results suggest that changes in coral cover in Moorea are more strongly influenced by post-settlement events than settlement. The key to understanding coral community resilience may lie in elucidating the factors attenuating the bottleneck between settlers and small corals.

Keywords Scleractinia · Recruitment · Demography · Recovery · Coral reef

Introduction

The demographic determinants of population growth are foundational to ecology (Chesson 1998; Hixon et al. 2002), and of great value in understanding ecosystem structure following disturbances (Symstad and Tilman 2001; Hughes et al. 2019). Demographic processes determine how predator abundances vary in concert with prey dynamics (Hixon et al. 2002), the capacity of strong competitors to translate resource acquisition into fitness (Chisholm and Fung 2020), the spread of pathogens through populations of host species (Gog et al. 2015), and the flow of energy among trophic levels (Ruttenberg et al. 2011; Stoner et al. 2017). Demographic traits cannot, however, regulate population size unless they operate with density-dependent feedback (Hixon et al. 2002). Such feedbacks operate in multiple systems (e.g., Ray and Hastings 1996; Courchamp et al. 1999; Sibly et al. 2005), including fruit flies (Mueller 1988), aphids (Agrawal 2004), tropical trees (Harms et al. 2000), large mammals (Fowler 1981), and coral reef fishes (Hixon and Carr 1997; Hixon et al. 2012).

There is a long history of studying recruitment as a factor causing population size to change in the marine environment (Keough and Downes 1982; Gaines and Roughgarden 1985; Caselle 1999). Recruitment describes the rate at which individuals are added to the population (Underwood and Fairweather 1989; Caley et al. 1996), and in benthic systems, this usually involves a combination of larval supply, settlement, and post-settlement processes. "Recruits" usually are somewhat arbitrarily defined by when they are first observed following settlement, which may be weeks or months later.

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An accurate understanding of recruitment requires, however, consideration of both adults and the propagules they produce (Grosberg and Levitan 1992; Hughes et al. 2000). Measurements of recruitment are dependent on the timing of surveys to quantify recruits, the rate at which recruits grow into subsequent age (or size) classes, and the challenges of quantifying small organisms (Caley et al. 1996; Hixon et al. 2002).

In benthic communities, recruits are often defined with the objective of estimating larval supply and settlement, which constitutes a shifting target dependent on the timing of observations. Analyses of recruitment over several weeks will generate results differing from those obtained over several months, thus highlighting the importance of early post-settlement events in modulating the distribution of settlers (Keough and Downes 1982). In most studies, recruits are operationally defined by the sampling schedules, or the capacity to identify small organisms (Caley et al. 1996). In fish ecology, for example, some studies quantify recruits that are millimeters long (Caselle and Warner 1996), others when they are centimeters long (Cargnelli and Gross 1996), and in the applied literature, when new individuals survive to a harvestable size (Frank and Leggett 1994). In coral biology, recruits often are defined as small settlers on tiles (Mundy 2000), or colonies ≤ 1-cm (Hughes and Jackson 1985; Price et al. 2019) or ≤ 5-cm (Moulding 2005; Holbrook et al. 2018) in diameter. A limitation of operationally defining recruits is an inability to attribute causation of changes in population size to larval supply, settlement, or post-settlement events.

While populations cannot grow without recruitment, recruitment alone does not ensure population growth if mortality at early life stages is high (e.g., Rumrill 1990), thus creating a recruitment bottleneck (Werner and Gilliam 1984; Doropoulos et al. 2016). Early life stages usually are more susceptible to mortality than adults (Hughes and Jackson 1985; Rumrill 1990; Przeslawski et al. 2015) and, therefore, have a high probability of succumbing to damage and slowing population growth, even if they are continually added through larval supply and settlement. The effects of high mortality early in life are relatively well known in the marine environment, where benthic and demersal habitats have provided tractable systems in which population dynamics have been studied for decades (Hixon 1998; Hughes et al. 2010). These habitats are dominated by organisms with complex life cycles, many of which include pelagic propagules that recruit following settlement, metamorphosis, and a period of post-settlement development (Grosberg and Levitan 1992; Pechenek 1999), before becoming adults. Here, recruitment has frequently been shown to have a strong association with benthic community structure (Roughgarden et al. 1988; Kinlan and Gaines 2003; Broitman et al. 2005).

Coral reefs provide a compelling system in which recruitment and population dynamics can be studied with relative ease (Sammarco and Andrew 1988; Jones 1990). In this ecosystem, the recent large declines in coral abundance (Hughes et al. 2018) highlight the value of understanding the conditions favoring recruitment and population recovery (Graham et al. 2011; Holbrook et al. 2018). In many tropical marine locations, disturbances including bleaching, diseases, and severe storms, have depressed coral cover to such an extent that population recovery is generally considered unlikely (Veron et al. 2009; Hooidonk et al. 2014; Hoegh-Guldberg et al. 2018), due mostly to low densities of coral recruits (Graham et al. 2011, 2015; Gilmour et al. 2013). Examples of recovery of coral communities following disturbances (Graham et al. 2011), provide opportunities to study the factors promoting population growth, with which high coral recruitment is often associated (Graham et al. 2011; Nakamura et al. 2022). Moorea, French Polynesia, provides an example of large-scale coral death through corallivory (by crown of thorns sea stars, *Acanthaster solaris*) and a cyclone, followed by rapid population recovery (Holbrook et al. 2018; Moritz et al. 2021). Here, measurements of coral recruitment on tiles (Edmunds 2022) and reef surfaces (Holbrook et al. 2018), support the conclusion that coral community recovery was driven by recruitment (Holbrook et al. 2018; Edmunds 2018). While the increase in coral cover in Moorea was associated with the arrival of small corals, particularly pocilloporids, the roles of settlement versus post-settlement events in driving recovery has not been determined. This limits the capacity to understand the general conditions under which degraded coral populations might recover.

The present study evaluates the roles of settlement and post-settlement events in causing changes in coral cover on an oceanic reef in the Indo-Pacific. Using 14 years of data from Moorea, where sampling took place every ~ 6 months (coral settlers) or year (small corals), we first test the hypothesis (H1) that temporal variation in coral cover is associated with coral settlement (i.e., corals usually < 2 mm diameter on tiles immersed for ~ 6 months), the density of small corals (≤ 4 cm diameter that have probably grown over several years) on reef surfaces, and post-settlement success estimated from the ratio of the densities of small corals (SC) and coral settlers (S) (i.e., SC:S). In this formulation, the ratio SC:S scales from 0 to 1, with 0 suggesting that none of the coral settlers survives to contribute to the small coral cohort, and 1 indicating that every coral settler survives to produce a small coral. These analyses evaluate the extent to which changes in coral cover since 2010 (Holbrook et al. 2018) are associated with coral settlement versus post-settlement events. Second, we describe how SC:S changed over time, and test the hypothesis (H2) that SC:S and S are associated with environmental conditions. The environment was characterized by seawater temperature because of its strong effects on coral metabolism (Carballo-Bolaños et al. 2019), seawater flow speed because of its role in dispersing larvae (Sammarco and Andrew 1988) and mediating benthic metabolism (Lowe and Falter 2015), and the concentration of subsurface Chlorophyll a because it is a proxy for productivity, seawater clarity, and the availability of primary consumers (e.g., copepods) that are food for corals (Sebens et al. 1998). Generalized additive models [GAMs (Wood 2017)] were used to test for non-linear relationships of the densities of small corals (SC), coral settlers (S) and the ratio of the two (i.e., SC:S) with environmental conditions. Finally, we combine the results of these analyses to revisit the causes of recent increases in coral cover on the reefs of Moorea with attention to the roles of settlement versus post-settlement events.

Materials and methods

The study utilized the time series of the Moorea Coral Reef LTER (Cowles et al. 2021), as they relate to coral community dynamics on the north shore fore reef. Annual measurements of coral cover, the density of coral settlers, and the density of small corals were used together with records of the environmental conditions to which they were exposed. Analyses focused on 2008–2021, which captured the final years of the last population outbreak of the crown of thorns (COTs) sea star (Kayal et al. 2012), the coral population recovery that took place between 2010 and 2019 (Holbrook et al. 2018; Edmunds 2018), and coral mortality attributed to bleaching in 2019 (Burgess et al. 2021). Biological data came from two sites (LTER1 and LTER2; Fig. S1 in Edmunds 2021) that are ~ 3 km apart, with environmental data from the same or similar sites (temperature), one of the two sites (flow at LTER1), or from 4.5 km resolution remote sensing data (Chlorophyll a as described below).

The ecological methods are described in detail elsewhere (Edmunds 2018, 2022), and are briefly summarized below. Coral cover was measured annually [April except for 2020 (August) and 2021 (May)] at 10-m depth along a 50 m, permanently marked transect at LTER 1 and LTER 2. Along each transect, 40 photoquadrats (0.5 × 0.5 m) were photographed at positions that were randomly selected in 2005, but fixed thereafter. Pictures were illuminated with strobes, and analyzed using CPCe (Kohler and Gill 2006) or CoralNET software (Beijbom et al. 2015) with manual annotation of 200 randomly located points on each image. Substrata beneath the points were categorized to coral genus (20 identified) and 1 family (Fungidae), and the percentage cover for all corals (scleractinians and *Millepora*) and *Pocillopora* spp. is reported. *Pocillopora*, *Acropora* and *Porites* accounted for a mean (± SE) of 79 ± 3% ($N=34$) of the coral cover at both sites over 17 years; *Pocillopora* accounted for 53 ± 4% of the coral cover. The changes in cover of corals (scleractinians and *Millepora*) provided a holistic summary of the coral community consistent with how we have described it elsewhere (Holbrook et al. 2018) and how it is described in the broader scientific literature on coral reefs. The separate summary for *Pocillopora* spp. provided a measure of coral cover that is the product of the most abundant coral settlers found on tiles deployed in the same habitat (i.e., pocilloporids). The density of small corals (≤ 4-cm diameter) was quantified in the field annually, shortly after the photoquadrats were recorded (but not in 2020 due to COVID-19), and was completed using quadrats (0.5 × 0.5 m) placed in the same positions as the photoquadrats. The benthos, including beneath branching corals, was inspected for small corals that were recorded to genus, and the densities of all corals and *Pocillopora* spp. are reported in units of corals 0.25 m^{-2}. Small corals were resolved to the same taxa as percentage coral cover, and *Pocillopora* accounted for a mean of 27 ± 4% ($N=32$) of all small corals (*Porites* = 22 ± 2%, *Acropora* = 8 ± 2%).

The density of coral settlers was measured using unglazed terracotta tiles (15 × 15 × 1 cm), seasoned (~ 6 months) in seawater beneath the marine laboratory dock, and then immersed on the reef at 10 m depth for ~ 6 months. Tiles were deployed from August/September to January/February and from January/February to August/September of each year at LTER1 and LTER2. Each tile was deployed independently and horizontally using a stainless steel stud with a ~ 1 cm gap beneath. Fifteen tiles were deployed at 10 m depth at each site, with tiles separated by a few centimeters to ~ 1 m. Upon retrieval, tiles were cleaned in dilute bleach, dried, and microscopically inspected (40× magnification) for coral recruits that were identified to family. The top, bottom, and sides of the tiles were inspected, and densities of settlers for all corals and pocilloporids are reported. Because ~ 82% of the settlers was found on the lower surface of the tiles (Edmunds 2021), densities (summed among surfaces) were expressed per 225 cm^2 of tile (i.e., the lower surface) and scaled linearly to settlers 0.25 m^{-2}. This assumption resulted in a slight upwardly biased estimate in the density of recruits (versus a downwardly biased estimate through consideration of the upper and lower surface at 450 cm^2), but it did not affect interpretation of settlement tiles as an assay for the density of settling corals. For each site, mean densities from both tile immersions each year were summed to estimate annual settlement.

A proxy for post-settlement success was generated from the ratio of the density of small corals (SC) and the density of settlers (S) (both scaled to 0.25 m^2), with SC:S approximating the number of small corals produced by each settler. Because settlers require time to grow into small corals, SC:S was calculated with settlers lagged by 1 year, 2 years, or 3 years relative to the year in which small corals were quantified. These lags capture the consequences of annual variation in coral growth (Pratchett et al. 2015), with values expected to be ~ 1–5 cm year^{-1} (linear extension) for the branching pocilloporids (Pratchett et al. 2015) dominating the coral recruits in Moorea.

Temperature was recorded with bottom-mounted sensors (Seabird SBE39, ± 0.002 °C) at 10-m depth, with one sensor at each of LTER2 and 300 m west of LTER1. Sensors recorded at 0.0008 Hz, and values were averaged by day. Bottom seawater flow (m s^{-1}) was recorded at 15-m depth at LTER1 using an Acoustic Doppler Current Profiler (RDI Workhorse Sentinel) sampling every 20 min and averaged by month. The yearly subsurface concentration of Chlorophyll a (mg m^{-3}) was determined by remote sensing from the MODIS level-3, monthly data (4.5 km resolution) for an area centered on Moorea (16˚S–19˚S/147˚W–151˚W) after the removal of the land pixels (Tahiti, Moorea, Maiao, Tetiaroa); yearly values were obtained by averaging the monthly data for each year.

Statistical approaches. For each site, coral cover and the density of small corals were displayed on line plots with time on the X-axis as means ± SE (*n* ~ 40 site^{-1}) by year, and the density of settlers was plotted as a single value generated from the summed averages of settlers recorded on tiles retrieved in January/February and August/September (each *N* ~ 15 tiles). Differences over time were not statistically evaluated as temporal effects were addressed through contrasts of SE bars (cover and small corals). Replicate determinations were not available when settlement was expressed by year, which required summation of mean settlement densities across settlement plates deployed from August to January and from January to August.

The relationships between coral abundances in different stages (overall cover of the coral community, settlers, and small corals; Hypothesis 1) were evaluated using Generalized Additive Models [GAMs (Wood 2017)] in which coral cover was the dependent variable, and the predictors were standardized values (i.e., as z-scores) of settlement, density of small corals, and SC:S. Analyses were repeated with settlers and small corals lagged by 1, 2, or 3 years to accommodate uncertainty in the time required for settlers to grow into small corals and contribute to coral cover; SC:S was computed with settlers lagged by 1, 2 or 3 years. Up to 24 sets of data from 2008 to 2021 allowed GAMs to be evaluated with two predictors, and the three possible predictors were evaluated in pairs to consider all combinations. Z-score standardization of predictors allowed their relative effects on the dependent variable to be directly compared in units of standard deviations of the predictor. Analyses were completed by combining results from LTER1 and LTER2 and testing for an effect of site, which was dropped from the model when not significant.

To test for the capacity of environmental conditions to explain variation in post-settlement success (i.e., SC:S) and settlement (Hypothesis 2), GAMs were used in which SC:S or the density of settlers were response variables, and flow speed, temperature, and Chlorophyll a were predictors. Flow speed and Chlorophyll a are each represented by a single series of values, which were used for both sites. Up to 26 replicate observations (consisting of both biological and physical environmental data) composed of annual sampling from 2008 to 2021 at two sites allowed GAMs to be evaluated with two predictors at once, and the three possible predictors were evaluated in pairs to consider all possible two-way interactions. For SC:S, GAMs were completed with lags of 1 year and 2 years in the denominator, and values were tested for an association with environmental conditions averaged over 2 years or 3 years, respectively. SC:S with settlement lagged by 1 year was tested with environmental conditions averaged over the year in which the density of settlers was measured, as well as the preceding year in which settlement was considered; settlement lagged by 2 years was tested with environmental conditions averaged over the year in which the density of small corals was measured, as well as the two preceding years capturing influences on settlers that arrived 2 years prior. For GAMs in which the density of settlers was the dependent variables, models were prepared with environmental conditions lagged by 1 year (i.e., averaged over the year in which settlement was recorded), 2 years (i.e., averaged over the year in which settlement was recorded and the prior year) or 3 years (i.e., averaged over the year in which settlement was recorded and 2 years prior).

GAMs were prepared using the mgcv package (version 1.8-34) in R (version 4.0.5), accessed through the XLSTAT (version 2021.2.1, Addinsoft, Paris) add-in to Excel 16.54 (Microsoft). Dependent variables were transformed as needed (logarithmic for counts and arcsine for coral cover) to restore normality, and models were run using Gaussian error distributions, cubic splines for smoothing, and variance components estimated by REML. Akaike Information Criterion (AIC_c) was estimated for all models that converged, and the best model was identified as having the lowest AIC_c. Significant smoothed effects for these models are displayed on plots of partial residuals against the predictor. Predictors were standardized (i.e., expressed as z-scores) where it was valuable to compare proportional effects on the response variable.

Results

Community structure. Coral community structure changed from 2008 to 2021, and the variation in coral cover and the abundance of coral settlers and small corals was similar at LTER1 and LTER2. For corals pooled among taxa (Fig. 1a, b), coral cover reached 0.4–3.0% following the COTs outbreak and Cyclone Oli in February 2010, but increased to

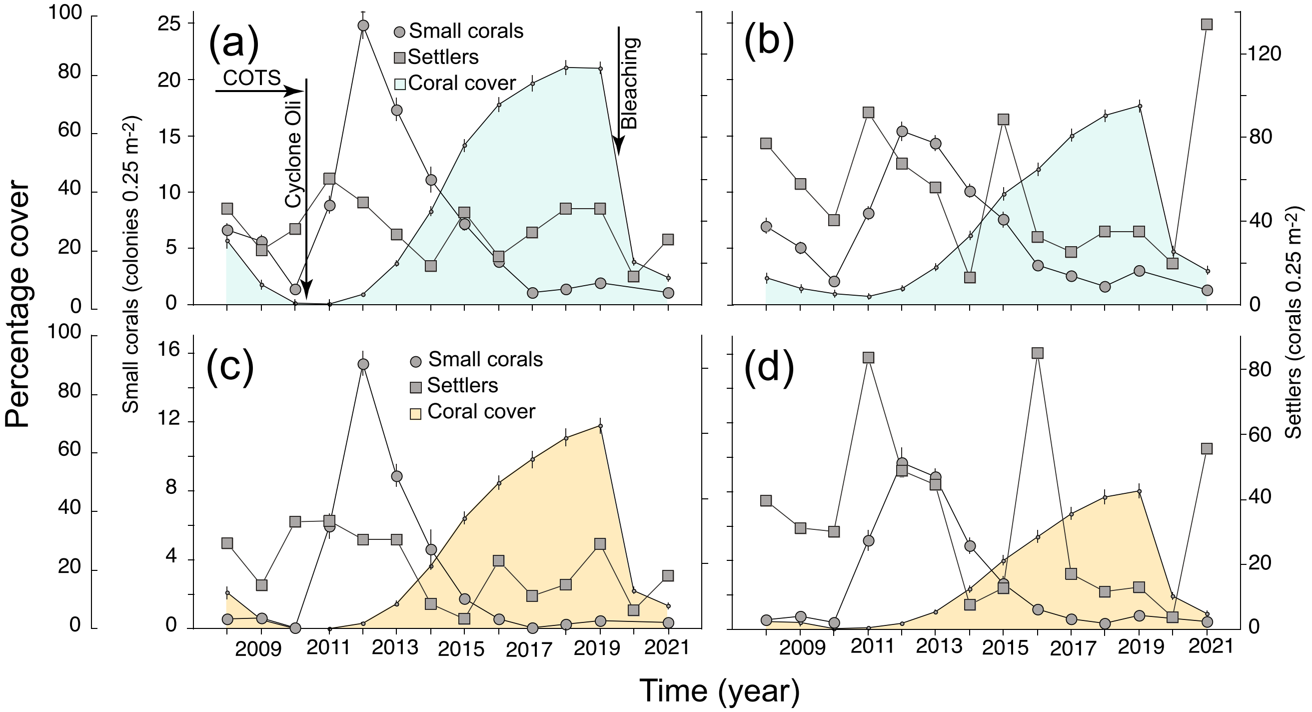

Fig. 1 Coral community structure at 10-m depth on the fore reef of Moorea [LTER1 (**a**, **c**) and LTER2 (**b**, **d**)] from 2008 to 2021. Panels display coral cover (% outer left ordinate, fill plot with symbols showing mean ± SE, $N = 37–40$ year^{-1}), density of small corals (colonies ≤4 cm diameter 0.25 m^{-2} inner left Y-axis, mean ± SE, $N = 37–40$ year^{-1}), and density of settlers (settlers 0.25 m^{-2}, right Y-axis, N = 1 yr^{-1} calculated from 26 to 31 tiles year^{-1}). **a**, **b** Scleractinians and *Millepora*, and **c**, **d** *Pocillopora* spp. Major disturbances (crown of thorns seastars [COTs] Cyclone Oli, and bleaching) shown in (**a**)

80.9% at LTER1 and 68.1% at LTER2 by 2019. Bleaching in April and May 2019 (Burgess et al. 2021) depressed cover to 9.4% at LTER1 and 11.9% at LTER2 by 2021. At LTER1, annual coral settlement (pooled among taxa) varied from 13.5 settlers 0.25 m^{-2} in 2020, to maxima in 2011, 2015 and 2019 (all 44.5–60.2 settlers 0.25 m^{-2}); at LTER2, there were four peaks of settlement in 2008, 2011, 2015, and 2021 (all 77.2–134.3 settlers 0.25 m^{-2}). The density of small corals varied from 1.1 ± 0.2 corals 0.25 m^{-2} at LTER1 (in 2017) and 1.4 ± 0.2 at LTER2 (in 2021) to a single maximum in 2012 of 24.8 ± 1.2 corals 0.25 m^{-2} at LTER1 and 15.4 ± 0.8 corals 0.25 m^{-2} at LTER2.

The temporal trends were similar for *Pocillopora* spp. (Fig. 1c, d), although they were more nuanced for settlers. At LTER1, the density of settlers was elevated from 2010 to 2013 (27.5–32.7 settlers 0.25 m^{-2}) and then was again high in 2016 and 2019 (both 21.2–26.1 settlers 0.25 m^{-2}). At LTER2, the 2015 peak in settlement for all corals (Fig. 1b) was decomposed into a peak of pocilloporid recruitment a year later in 2016 (Fig. 1d). Moreover, the difference between the lowest and the highest density of pocilloporid settlers in sequential years (e.g., at LTER 2, 2010 vs 2011, 2015 vs 2016 and 2020 versus 2021, Fig. 1d) was accentuated relative to the difference between low and high density of settlers in sequential years for all corals combined (Fig. 1d).

Relationships between coral cover and coral stages (Hypothesis 1). Changes in coral cover were associated with the number of settlers that developed into small corals, as well as the number of small corals, but were not associated with the number of coral settlers recorded on settlement tiles. The use of GAMs to test for relationships between coral cover and state variables quantifying early life stages revealed significant relationships from which the best-fit was identified using AIC$_c$ (Table 1, S1, Fig. 2). The best-fit model for coral cover (scleractinians + *Millepora*) included settlement 3 years before (S_3) and SC:S_3, and it revealed an inverse association with SC:S_3 but no relationship with settlers (Table 1, Fig. 2a). The model including small corals and settlers, both 3 years before, was only marginally less effective ($AIC_c = 2.450$), and revealed a positive association with the density of small corals 3 years before (Fig. 2b). Results were similar for *Pocillopora* spp. cover, for which the best model included settlers and SC:S, both 3 years before. This model indicated that cover increased with low values of SC:S_3 (Fig. 2c, Table 1). The models explained ≤41% of the variation in coral cover, and none displayed a positive association with settlement.

Table 1 Results of GAMs with two standardized predictors for coral cover (arcsine transformed) for (A) all corals, and (B) *Pocillopora* spp. Predictors were drawn from paired combinations of settler density, small coral density, and SC:S, with varying lags (1–3 years) (Table S1)

DV	Model	Type				
A) All corals	Settlers$_3$ + SC:S$_3$	*Parametric coeff*	Estimate	SE	*t*	*P*
		Intercept	0.624	0.064	9.814	< 0.001
		Smoothed terms	edf	Ref df	*F*	*P*
		Settlers$_3$	1.642	2.030	2.547	0.109
		SC:S$_3$	1.000	1.000	8.547	0.010*
		ΔAIC$_c$	0			
		R^2	0.329			
	Small corals$_3$ + Settlers$_3$	*Parametric coeff*	Estimate	SE	*t*	*P*
		Intercept	– 0.605	0.063	9.619	< 0.001
		Smoothed terms	edf	Ref df	*F*	*P*
		Small corals$_3$	1.000	1.000	6.103	0.024*
		Settlers$_3$	1.688	2.087	1.581	0.237
		ΔAIC$_c$	2.450			
		R^2	0.227			
B) *Pocillopora* spp.	Settlers$_3$ + SC:S$_3$	*Parametric coeff*	Estimate	SE	*t*	*P*
		Intercept	0.492	0.052	9.541	< 0.001
		Smoothed terms	edf	Ref df	*F*	*P*
		Settlers$_3$	1.000	1.000	0.979	0.337
		SC:S$_3$	1.980	2.223	6.886	0.007*
		ΔAIC$_c$	0			
		R^2	0.412			

ΔAIC$_c$ corrected AIC relative to lowest AIC$_c$

Parametric coeff. linear term in model, *SE* standard error, *t t* statistic, *P* probability, Smoothed terms fitted predictors in the model, *edf* effective degrees of freedom, *Ref df* reference degrees of freedom for computing test statistic, *F F* statistic

*significant smoothed terms displayed in Fig. 2. Subscripts in model column refer to lag applied

Environmental associates of SC:S and settlement (Hypothesis 2). Regardless of the time lag considered for recruitment, SC:S was persistently elevated from about 2013 to 2016, with this effect well developed at LTER1, and weakly expressed at LTER2. SC:S ranged from 0.004 (2018 at LTER2, with a 2 years lag in recruits, SC:S$_2$) to 0.943 (2012 at LTER1 with a 3 years lag in recruits, SC:S$_3$) for all corals, and for *Pocillopora* spp. it differed among years and varied inconsistently between sites (Fig. S2).

All three environmental conditions evaluated in the present study changed from 2008 to 2021 (Fig. 3). Yearly mean Chlorophyll a varied from 0.064 mg m^{-3} in 2009, to 0.045 mg m^{-3} in 2018, and differed among years ($F = 4.562$, $df = 12.143$, $P < 0.001$) and declined over the study ($F = 10.905$, $df = 1.10$, $P = 0.008$). Mean flow speed was high in 2008 (0.085 m s^{-1}), and declined nearly-monotonically ($F = 23.338$, $df = 1.13$, $P < 0.001$) to a minimum in 2021 (0.058 m s^{-1}). Mean temperature differed among years at LTER 1 ($F = 30.874$, $df = 12.4736$, $P < 0.001$) and LTER 2 ($F = 34.721$, $df = 12.4726$, $P < 0.001$), with 2011 the coldest year (mean = 27.2 °C), and the hottest years (28.1 °C) recorded in 2019 and 2020 at LTER1, and in 2016, 2019, and 2010 at LTER 2. Mean temperature slightly differed between sites.

GAMs revealed multiple relationships between SC:S and environmental conditions and, to a lesser extent, between settlement and environmental conditions (Table 2, S2, Figs. 4, 5, S2). For all corals, SC:S$_1$ (i.e., with settlers lagged by 1 year) declined with temperature (Fig. 4a). The relationship with Chlorophyll a was more complex, with SC:S$_1$ initially stimulated by rising concentrations but then depressed as concentrations increased further (Fig. 4b). SC:S$_2$ with recruits lagged by 2 years displayed a weak relationship of increasing with flow speed averaged over 3 years, at least to ~ 0.066 m s^{-1}, but with the relationship decaying at higher flow speeds due to sparse data (Fig. 4c). The density of settlers was associated with temperature averaged over 2 years, with a decline with increasing temperature both below ~ 27.6 °C and above ~ 27.8 °C, although sparse data between these extremes weakened the relationship described (Fig. 4d). Overall, SC:S (pooled among taxa) was elevated in cool years with low Chlorophyll a concentrations, and by moderate increased in flow speeds that mediated the effect of settlers lagged 2 years prior to the measurement of the density of small corals.

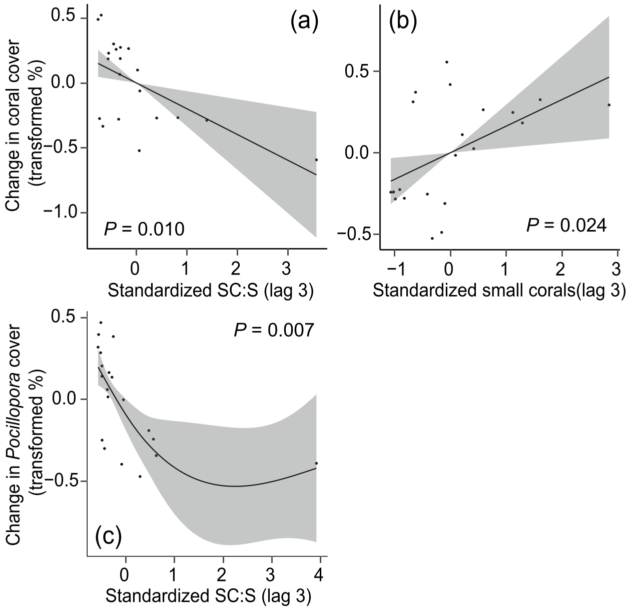

Fig. 2 Smoothed effects from GAMs testing for the influence of predictors: small corals, settlers, and SC:S on the percentage cover (arcsine transformed) of corals (scleractinians + *Millepora*) (**a**, **b**) and *Pocillopora* (**c**). Analyses completed with standardized predictors and varied lags in settlers and small corals (1–3 years). Shaded belts show 95% confidence intervals and dots show the partial residuals for all data; **a** $N = 20$, **b** $N = 22$, and **c** $N = 20$. Note transformed scale on Y axes

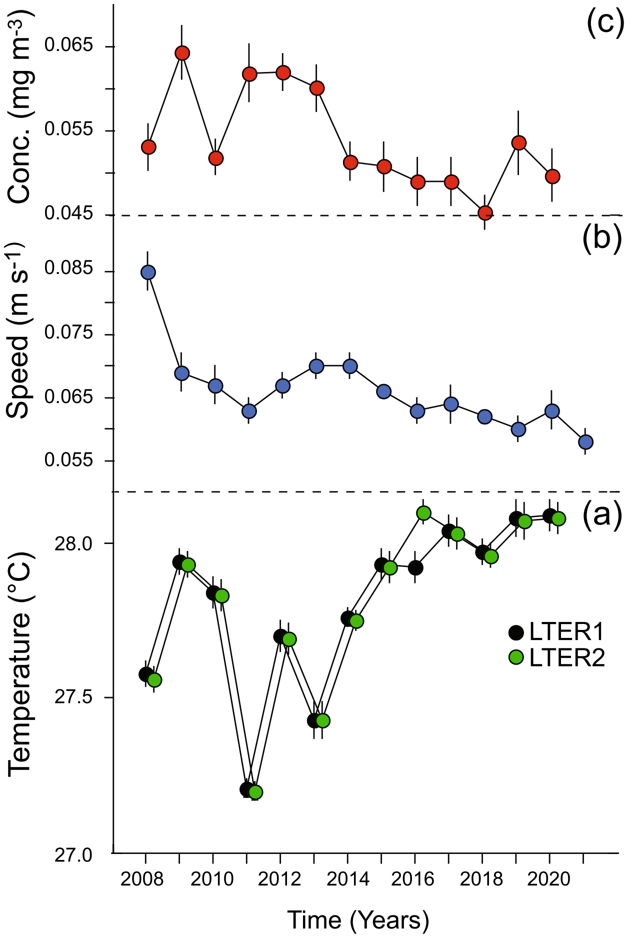

Fig. 3 Environmental conditions affecting LTER1 and LTER2. **a** Seawater temperature (mean ± SE, N = 365 days year^{-1}) was recorded at both sites, and **b** seawater flow (mean ± SE, $N = 12$ months year^{-1}) was measured at LTER1. **c** Sub-surface Chlorophyll a concentration (mean ± SE, $N = 12$ months year^{-1}) was evaluated by remote sensing

The results of testing for relationships between the density of settlers and environmental conditions, as well as SC:S and environmental conditions, were similar for *Pocillopora* spp. (Fig. 5). For SC:S$_1$, the ratio was elevated by low temperature, and initially stimulated by rising concentrations of Chlorophyll a, but then declining at higher concentrations, with both predictors averaged over 2 years (Fig. 5a, b). For SC:S$_2$ (i.e., with density of settlers lagged by 2 years), the relationships with temperature and concentrations of Chlorophyll a strengthened, in both cases declining with elevated temperature and more Chlorophyll a, as averaged over 2 years (Fig. 5c, d). The relationships between settlement and environmental condition were not as strong as those for SC:S (based on lower R^2 for settlers), and settlement was only related to flow averaged over 3 years. The relationship was positive at < 0.066 m s^{-1} but detection of effects of higher flow speeds was degraded by sparse data (Fig. 5e, f).

Overall, the proxy measure of post-settlement success (i.e., SC:S) was more strongly associated with multiple environmental conditions than was settlement, with these trends applying to all corals and *Pocillopora* spp. Post-settlement success was enhanced by preceding cool temperatures, by intermediate concentrations of Chlorophyll a, and slight increases in flow speed. Settlement was less strongly associated by environmental conditions, but there was evidence of enhancement by warm seawater and slight increases in flow speed at the low end of the range of mean flow speeds.

Discussion

Overview. Despite decades of research on recruitment in the marine environment, there remains much to learn about this process, and the incentive for so doing is intensified by the importance of recruitment in responding to the disturbances affecting present-day ecosystems (Harley et al. 2006; O'Leary et al. 2017). Yet, while recruitment continues to prominently feature in ecological research, the capacity to synthesize results on this topic is blunted by variation in life stages and processes to which "recruit" and "recruitment" can refer. The methodological limitations arising from inconsistent terminology are prominent for coral reefs, where many depleted coral populations (Riegl et al.

Table 2 Results of GAMs with two predictors for SC:S and settlers for (A) all corals, and (B) *Pocillopora* spp. Predictors were drawn from paired combinations of temperature, Chlorophyll a, and bottom flow speed, with varying lags included in dependent variables and predictors (Table S2)

Taxon	DV	Model	Type				
A) All Corals	Log(SC:S_1)	Temp$_2$ + Chl a$_2$	*Parametric coeff*	Estimate	SE	*t*	*P*
			Intercept	−0.917	0.043	−21.280	<0.001
			Smoothed terms	edf	Ref df	*F*	*P*
			Temp (°C)	2.329	2.894	7.020	0.003*
			Chl a (mg m^{-3})	3.114	3.589	3.568	0.020*
			ΔAIC_c	0			
			R^2	0.723			
	Log(SC:S_2)	Temp$_3$ + Flow$_3$	*Parametric coeff*	Estimate	SE	*t*	*P*
			Intercept	−0.921	0.034	−26.905	<0.001
			Smoothed terms	edf	Ref df	*F*	*P*
			Temp (°C)	1.000	1.000	1.108	0.313
			Flow (m s^{-1})	5.833	6.276	10.858	<0.001*
			ΔAIC_c	0			
			R^2	0.871			
	Log(Settlers)	Temp$_3$ + Flow$_3$	*Parametric coeff*	Estimate	SE	*t*	*P*
			Intercept	1.581	0.027	58.847	<0.001
			Smoothed terms	edf	Ref df	*F*	*P*
			Temp (°C)	6.553	7.496	5.486	0.002*
			Flow (m s^{-1})	1.000	1.000	0.193	0.666
			ΔAIC_c	0			
			R^2	0.633			
B) *Pocillopora* spp.	SC:S_1	Temp$_2$ + Chl a$_2$	*Parametric coeff*	Estimate	SE	*t*	*P*
			Intercept	0.128	0.018	7.200	<0.001
			Smoothed terms	edf	Ref df	*F*	*P*
			Temp (°C)	1.236	1.411	4.916	0.028
			Chl a (mg m^{-3})	3.334	3.934	3.206	0.036*
			ΔAIC_c	0			
			R^2	0.579			
	SC:S_2	Temp$_2$ + Flow$_2$	*Parametric coeff*	Estimate	SE	*t*	*P*
			Intercept	0.129	0.017	7.483	<0.001
			Smoothed terms	edf	Ref df	*F*	*P*
			Temp (°C)	1.000	1.000	42.011	<0.001*
			Flow (m s^{-1})	1.416	1.720	6.109	0.030*
			ΔAIC_c	0			
			R^2	0.703			
	Log(Settlers)	Temp$_3$ + Flow$_3$	*Parametric coeff*	Estimate	SE	*t*	*P*
			Intercept	1.257	0.051	24.416	<0.001
			Smoothed terms	edf	Ref df	*F*	*P*
			Temp (°C)	1.000	1.000	0.167	0.687
			Flow (m s^{-1})	4.882	5.528	4.409	0.007*
			ΔAIC_c	0			
			R^2	0.565			
	Log(Settlers)	Chl a$_3$ + Flow$_3$	*Parametric coeff*	Estimate	SE	*t*	*P*
			Intercept	1.257	0.052	24.341	<0.001
			Smoothed terms	edf	Ref df	*F*	*P*
			Chl a (mg m^{-3})	1.000	1.000	0.710	0.411
			Flow (m s^{-1})	4.752	5.401	4.041	0.011*
			ΔAIC_c	0			
			R^2	0.584			

Subscripts for S in DV column refer to lag in settlers; subscripts in Model column refer to number of preceding years over which predictors were averaged. Statistics as in Table 1

*Results of significant smoothed terms displayed in Fig. 4

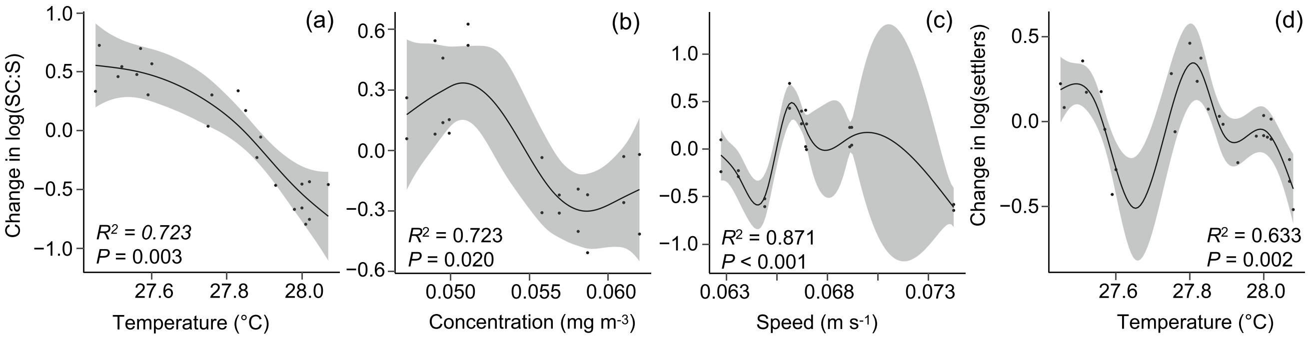

Fig. 4 Significant smoothed effects from GAMs testing for the explanatory capacity of three environmental conditions (Fig. 3) on all corals (scleractinians + *Millepora*) at 10-m depth (LTER1 and LTER) for the ratio of small corals to settlers (SC:S), and the density of settlers. **a** SC:S 1 year before versus conditions over 2 years: temperature* and chlorophyll, $N = 22$, **b** SC:S 1 year before versus conditions over 2 years: temperature and chlorophyll*, $N = 22$, **c** SC:S 2 years before versus conditions over 3 years: flow* and temperature, $N = 20$, and **d** settlers versus conditions over 2 years: temperature* and flow, $N = 26$; * indicating which significant predictor is displayed in each graph. Analyses of SC:S completed with log-transformed values and lags of 1 year (**a** and **b**), or 2 years (**c**), in the time required for settlers to grow into juveniles; analyses of settlers completed with log transformed values and lag of 2 years (**d**) with respect to capacity of previous events to affect settlement (Fig. S2). Full results in Table 2 and S2. Shaded belts show 95% confidence intervals and dots show the partial residuals for all data. Note log scale on Y axes

2013; Edmunds 2015; Hughes et al. 2017) motivate studies of recruitment. Coral recruitment, therefore, features in many studies of long-term changes in coral communities (e.g., Price et al. 2019; Edmunds 2023), but because most studies do not distinguish settlement from post-settlement events, and often quantify different life stages as recruits (e.g., Doropoulos et al. 2016 vs Holbrook et al. 2018), the causes of varying densities of recruits cannot be determined. It usually remains unknown, for example, whether variation in coral recruitment is a product of larval settlement and metamorphosis over weeks-months, or processes acting over months-years that determine the abundance of small corals. For contrast, barnacles (*Balanus glandula*) along the coast of California have provided an elegant model system in which it has been shown that larval settlement is the primary determinant of barnacle distribution (Gaines and Roughgarden 1985, 1987).

The present study focused on the fore reef of Moorea, where the last decade has brought large changes in coral cover, the density of small corals, and the abundance of coral settlers (Holbrook et al. 2018; Adjeroud et al. 2018; Edmunds 2021). The relationships between coral cover and paired combinations of settler density, small coral density, and the ratio of small coral density to settler density, did not support the hypothesis that coral settlement explains variation in coral cover, regardless of the time lag applied to settlement density. Instead, coral cover was best explained by a lagged estimate of post-settlement success (i.e., the ratio of small corals to settlers 3 years before, $SC:S_3$), and the lagged estimate of small coral density (i.e., 3 years before, SC_3) (Table 1). Coral cover was unrelated to the density of settlers, suggesting that settlement was not strongly associated with changes in adult abundance (cf. Gaines and Roughgarden 1985, 1987), even though new individuals cannot be added to the population without larval settlement. Coral cover rapidly increased 3 years after high densities of small corals were recorded (Figs. 1, 2b), with this effect intensified by low post-settlement success for settlers transitioning into small corals 3 years later (Fig. 2a, c). Presumably in these cases, the low proxy for post-settlement success was compensated by high densities of settlers, the product of which produced large numbers of small corals that contributed to coral cover. Post-settlement success was depressed by high temperature (Figs. 4a, 5a,c), possibly because it elevated mortality of small corals (reducing the numerator in the SC:S ratio) more than it depressed settlement (Fig. 4d, reducing the denominator in SC:S). Additionally, the proxy for post-settlement success showed a positive threshold response to the concentration of Chlorophyll a (Figs. 4e, 5b), and responded positively to increases in flow up to ~ 0.066 m s^{-1} (Fig. 4c). Values of the proxy for post-settlement success, approached unity in one year at one site (e.g., Fig. S2a,c), indicating that there were years when each settler had a high chance of growing into a small coral.

Interpretation of our results requires consideration of the state variables employed and their relationship to variation coral recruitment from 2008 to 2021. The recovery of the fore reef of Moorea has been remarkable since 2005 (Holbrook et al. 2018; Adjeroud et al. 2018; Moritz et al. 2021), with high coral cover in 2005 (40% at 10 m depth on the north shore) that declined through consumption by COTs (Kayal et al. 2012), and following a cyclone in February 2010 (Holbrook et al. 2018), reached nearly 0% across a seascape from which dead coral skeletons had been removed by Cyclone Oli (Edmunds 2018). High coral recruitment [i.e., settlers on tiles (Edmunds 2018) and small corals on

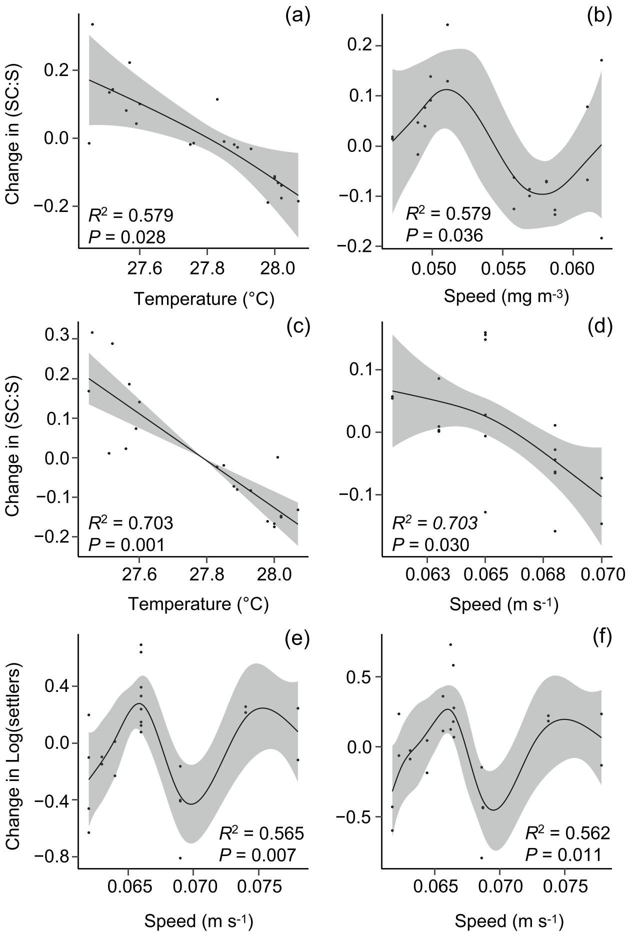

Fig. 5 Significant smoothed effects from GAMs testing for the explanatory capacity of three environmental conditions (Fig. 3) on *Pocillopora* spp. at 10-m depth (LTER1 and LTER) for the ratio of small corals to settlers (SC:S), and the density of settlers 2). **a** SC:S 1 y before versus conditions over 2 years: temperature* and chlorophyll, $N=22$, **b** SC:S 1 y before versus conditions over 2 years: temperature and chlorophyll*, N = 22, **c** SC:S 2 y before versus conditions over 2 years: temperature* and flow, $N=20$, **d** SC:S 2 years before versus conditions over 2 years: temperature and flow*, $N=20$, **e** Settlers versus conditions over 3 years: flow* and temperature, and **f** Settlers versus conditions over 3 years: flow* and chlorophyll, $N=24$; * indicating which significant predictor is displayed in each graph Analyses of SC:S completed on untransformed values with lags of 1 years (**a** and **b**), or 2 years (**c** and **d**), in the time required for settlers to grow into juveniles. Analyses of settlers completed with log transformed values and lags of 3 years (**e** and **f**) with respect to capacity of previous events to affect settlement (Fig. S2). Full results in Table 2 and S2. Shaded belts show 95% confidence intervals and dots show the partial residuals for all data. Note log scale on Y axes of (**e**) and (**f**)

reef surfaces (Holbrook et al. 2018)], particularly for *Pocillopora* spp. supported a high rate of increase in coral cover (cf Graham et al. 2011) that reached 75% (north shore) in early 2019; bleaching in April and May 2019 reduced cover to 11% by April 2021 (north shore) (Fig. 1). High densities of coral settlers on tiles in 2011 (92 settlers 0.25 m^{-2}, north shore), abundant small corals (i.e., ≤ 4 cm diameter) on reef surfaces over 2011–2013 (8–14 corals 0.25 m^{-2}), and density dependent *Pocillopora* spp. recruitment (Bramanti and Edmunds 2016; Edmunds et al. 2018), supported the conclusion that coral community recovery was driven by recruitment (Bramanti and Edmunds 2016; Edmunds 2018; Holbrook et al. 2018). Against this backdrop, the present results provide enhanced resolution of these events by demonstrating that coral cover from 2008 to 2021 was not associated with the density of settlers. Instead, it was associated with the density of small corals 3 years before, and the ratio of the density of small corals to settlers lagged by 3 years. Small corals (e.g., <3–5 cm diameter) can also be considered recruits (Moulding 2005; Holbrook et al. 2018), and their hypothesized role in supporting coral community recovery in Moorea (Holbrook et al. 2018) is consistent with the positive association between the density of small corals and coral cover (this study). The association of coral cover with the ratio of small corals to settlers suggests that post-settlement success modulates the capacity for rapid coral community recovery in Moorea (Speare et al. in review). Following a demographic analysis of the fate of 537 juvenile corals (<5 cm but >1 cm diameter) over 4 years at Palmyra Atoll, Northern Line Islands, Sarribouette et al. (2022) similarly concluded that a mortality bottleneck had a strong effect in determining recruitment into adult coral size classes.

Post-settlement success is determined by the events controlling the number of settlers that become larger and older. For corals, the high mortality of settlers drives the characteristic features of Type III survivorship (Vermeij and Sandin 2008; Doropoulos et al. 2016), which results in few of the larvae that settle recruiting into the population, thus creating a recruitment bottleneck (Arnold et al. 2010; Sarribouette et al. 2022). Because corals can settle in large numbers (Adjeroud et al. 2022), small changes in post-settlement success can result in large changes in the number of recruits, in which case, post-settlement success determines the size of the recruiting cohort. The quantitative aspects of these relationships can be expected to vary among reefs, but the relative meaning is robust for taxa exhibiting Type III survivorship. As changes in coral cover in Moorea are more strongly associated with our proxy for post-settlement success than the density of settlers, it might be timely to shift research attention from “recruitment” as a driver of coral community recovery (Edmunds 2019; Holbrook et al. 2018), towards the processes determining post-settlement success.

A wide diversity of biological and physical factors determines whether newly settled organisms grow into juveniles, and then adults (Pineda et al. 2009). Predation, disease, competition for space, and access to food determine whether settlers emerge as recruits from the gauntlet of post-settlement risks (Arnold et al. 2010, 2011). These effects can act independently of, or in synergy with, physical and chemical conditions that include temperature, flow speed, and concentrations of nutrients and organic carbon in seawater. The likelihood of succumbing to these effects is enhanced in delicate early life stages (Rumrill 1990; Pandori and Sorte 2019), although these risks can be reduced through maternal provisioning with information [e.g., trans-generational plasticity (Eirin-Lopez and Putnam 2019)] and resources such as food and protective metabolites (Hamdoun and Epel 2007). For reef corals, biological determinants of post-settlement success include corallivory, competition with other taxa for space, and the capacity to develop a complement of algal and microbial symbionts (Arnold et al. 2010; Doropoulos et al. 2016; vanOppen and Blackall 2019). Food supply is also likely to be important, either through the capture of plankton (Cumbo et al. 2012; Geertsma et al. 2022) or, for symbiotic corals, photosynthetically fixed carbon from their algal symbionts (Muscatine 1990). These effects operate in synergy with the physical and chemical conditions that modulate the success of coral recruits, notably through the effects of high temperatures that can cause bleaching and death (Mumby 1999; Bahr et al. 2020), flow speeds mediating heat flux (Jimenez et al. 2008), and the mass transfer of metabolites (Patterson 1992) and harmful chemicals (Maida et al. 1995). Light is likely to be particularly important for the success of symbiotic coral recruits by supporting photosynthesis (Muscatine 1990), and determining whether light exposure is harmful through excessive quantities (Mumby et al. 2001) or high levels of UV radiation (Gleason et al. 2006).

To gain insight into the factors causing the density of settlers and small corals to vary, GAMs were used to quantify the environmental conditions with the capacity to explain variation in the abundance of these life stages. Determining the mechanistic basis of the relationships so detected was beyond the scope of this study, but it is notable that several of the relationships are consistent with aspects of the biology of small corals. For post-settlement success, low temperature, for example, was a predictor of high values, with this effect integrated over 2 years. This relationship is consistent with the high thermal sensitivity of corals (Brown and Cossins 2011), and the benefits of low temperature in accumulating tissue energy reserves (Fitt et al. 2000). For Chlorophyll a, slight increases in concentration at the low end of the range of mean values were associated with increases post-settlement success (up to ~ 0.06 mg m^{-3}), possibly reflecting the value of Chlorophyll a as a proxy for planktonic food availability (Kürten et al. 2014). At concentrations greater than ca 0.06 mg m^{-3}, further increases were associated with lower post-settlement success, possibly reflecting the effects of higher light attenuation on photosynthesis (Maritorena and Guillocheau 1996). For flow speed, elucidation of associations with biological events was limited by sparse data above ~ 0.066 m s^{-1}, but up to this speed, increases were associated with elevated post-settlement success of all corals and *Pocillopora* spp. In Moorea, pocilloporids recruit at high densities when adults are rare [i.e., density dependence (Edmunds et al. 2019)], and under these conditions, high flow speeds might enhance larval supply and favor cosmopolitan settlement, with settlement on exposed surfaces where the risks of mortality are elevated. For coral settlers, there was some evidence that densities were (a) depressed by elevated temperature, perhaps because it reduced pelagic larval duration and limited dispersal to new locations (O'Connor et al. 2007; Figueiredo et al. 2014) or elevated larval mortality (Figueiredo et al. 2014), and (b) significantly, but equivocally, association with flow speed. Together, the aforementioned trends suggest that rapid increases in coral cover on the fore reef of Moorea are driven by conditions determining how many settlers grow into small corals and not through the arrival of settlers per se.

Caveats. There are two limitations of the present study. First, although our data extend over 14 years and originate from two sites at which coral abundance was estimated from replicate tiles, this large effort supplied ≤ 26 replicate values for hypothesis testing. The modest sample sizes limited the sophistication of the analyses that could be applied, as well as their capacity to resolve functional relationships between predictors and response variable. These challenges might be alleviated by sampling over multiple decades and, perhaps, through judicious substitution of space for time in key analyses (Damgaard 2019). Neither solution is likely to yield timely answers commensurate with the speed with which solutions are required to the ecological challenges affecting coral reefs.

Second, post-settlement success was evaluated from the quotient obtained by dividing the density of small corals by the density of settlers. While the numerator in this relationship probably is measured with accuracy (requiring that small corals are accurately counted in situ on reef surfaces), the denominator has equivocal meaning. The utility of the denominator relies on the extent to which settlement of corals on tiles reflects settlement of corals on reef surfaces, and with respect to this task, settlement tiles provide an assay for coral settlement. It is possible to count coral settlers (~ 1–2 mm diameter) on reef surfaces, for example, by using UV fluorescence (Zweifler et al. 2017), but such approaches are challenging to sustain for multiple years, they cannot distinguish coral taxa (which is possible with microscopic inspection of tiles), and are likely to generate false negatives in rugose habitats (where corals can "hide").

The relationships between the density and taxonomic composition of settlers on tiles versus on reef surfaces are unknown, but corals are well known to preferentially settle on the lower surface of tiles (e.g., Mundy 2000). This could reflect settlement choice (Babcock and Mundy 1996), or the removal of settlers from upper surfaces through grazing (Doropoulos et al. 2016) or smothering by sediments and algae (Birkeland et al. 1981). It is unclear, therefore, whether the use of horizontal tiles upwardly biases estimates of settlement density based on counts of corals on their lower surface. However, since the addition of refuges on the upper surface of tiles increases coral settlement tenfold relative to the upper surfaces of smooth tiles (Nozawa et al. 2011), and the lower surfaces of smooth tiles have ~ fivefold more settlers than the smooth upper surface (Edmunds 2021), the density of coral settlers on undersurfaces of tiles may be similar to that on upward-facing, rugose reef surfaces. Until more data becomes available, it is reasonable to conclude that the density of coral settlers on tiles is not greatly different from that on reef surfaces and, therefore, that the ratio of the density of small corals to coral settlers is an effective proxy for post-settlement success.

Finally, it is important to note that it is challenging to consider all potential biological and physical drivers of ecological change in a single analysis. In the case of the north shore fore reef of Moorea, annual records of several key environmental drivers that might influence the density and survival of coral settlers at LTER1 and LTER2, or the small corals they ultimately can produce, are not yet available. Several studies have highlighted the importance of spatio-temporal variation in seawater nutrients in driving benthic community dynamics in the backreef lagoon at Moorea (Donovan et al. 2020; Adam et al. 2021), and it is interesting to speculate whether similar effects might mediate post-settlement success of reef corals on the fore reef. Whether nutrients have an ecologically meaningful effect on the forereef is likely to be determined by the offshore hydrodynamic conditions that determines whether lagoon and island effects influences the nutrient regime on the fore reef, ~ 1 km from the shore. While the vigorous hydrodynamic regime and mixing on the fore reef of Moorea (Hench et al. 2008; Adam et al. 2021) could limit the effects of nutrients from the lagoon on the recruitment of corals on the fore reef, the existence of an island mass effect (IME) around Moorea (James et al. 2020) leaves open the possibility that nutrient availability could modulate coral recruitment in this habitat.

Summary. This study revisits coral community dynamics on the fore reef of Moorea from 2005 to present (cf. Holbrook et al. 2018; Moritz et al. 2021), and expands on the conclusion that the 2010–2019 recovery was driven by coral recruitment (Holbrook et al. 2018; Edmunds 2018; Moritz et al. 2021). While the recruitment of corals, particularly pocilloporids, supported the rapid increase in coral cover, an outstanding question has been whether recruitment was driven by larval settlement or post-settlement success. Adjeroud et al. (2018) indirectly addressed this issue by comparing coral recruitment from 2001 to 2014 on the fore reef of Moorea (two sites < 7 km from the present sites with tiles at 6, 12, and 18 m depth), and because the densities of recruits were low (< 140 settler m^{-2}) relative to other Pacific reefs, they suggested reef recovery in Moorea was favored by high post-settlement success rather than recruitment per se (see also Edmunds et al. 2015; Speare et al. in review). This conclusion is consistent with the present analysis, and while the mean densities of coral settlers reported here are higher than the benchmark of Adjeroud et al. (2018) (176 and 252 settlers m^{-2} at LTER 1 and 2, respectively) they are lower that the long-term regional average from 1979 to 2020 [633 settlers m^{-2} (Edmunds 2023)]. Resolving between the roles of coral settlement versus post-settlement success in determining rates of increase in coral cover is important for a more general understanding of the factors driving coral community resilience on present-day reefs. Variation in coral recovery driven by settlement would suggest a mechanistic origin in pelagic processes and the conditions enhancing fecundity, gamete quality, and larval competency. Conversely, variation in coral recovery driven by post-settlement success would suggest the underlying mechanisms are related to benthic processes that might, perhaps, mediate the physiological resilience of small corals. These conclusions indicate that it will be productive to focus future research more on the factors constricting the recruitment bottleneck for corals than the processes mediating settlement in order to understand where, when, and how coral communities can recover from disturbances.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00442-024-05517-y.

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Author contributions PJE conducted the fieldwork that generated the empirical biological data upon which this study is based. PJE conceived this study, PJE, SM, and SCB developed the analytical approaches, and SM advanced the remote sensing analyses. PJE prepared the first draft of the paper, PJE and SCB developed the graphic presentations of the data, and all authors contributed to editing and focusing the text.

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Availability of data and materials All data reported in this manuscript are available at www.bco-dmo.org. Data DOIs: https://doi.org/10.26008/1912/bco-dmo.918265.1, https://doi.org/10.26008/1912/bco-dmo.918299.1, https://doi.org/10.26008/1912/bco-dmo.918306.1, https://doi.org/10.26008/1912/bco-dmo.918312.1, https://doi.org/10.26008/1912/bco-dmo.918318.1, https://doi.org/10.26008/1912/bco-dmo.918324.1, https://doi.org/10.26008/1912/bco-dmo.918330.1.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Coral settlers were collected under permits issued by the Government of French Polynesia (Délégation à la Recherche) and the Haut-Commissariat de la République en Polynésie Francaise (DTRT), and the surveys was completed under the same authorization. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. No corals were exported from French Polynesia.

Consent to participate Not applicable.

Consent for publications Not applicable.

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