Settlement success and post-settlement survival of *Acropora* sp. aff. *tenuis* spat within a small bay in Japan

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ABSTRACT: The early life history of scleractinian corals is largely unknown. In this study, we compared the settler numbers and post-settlement survival of *Acropora* aff. *tenuis* larvae on a square hollow section (SHS) substrate at 10 stations and 2 depths (20 sites in total) from the mouth to the back of a small bay. The number of settlers tended to be lower at the back of the bay. Survival rates 15 mo after settlement were 2.5 times higher in the shallower waters at the back of the bay, and 2.5 times higher in the deeper waters at the middle and mouth of the bay. Water depth and temperature, photon flux, current velocity, sedimentation, water column and interstitial water nutrients, and algal cover were measured at each site, and a significant correlation was found between settler numbers and sedimentation. The best models of physical environmental factors affecting post-settlement survival in each monitoring period showed that daylight intensity on sunny days and algal cover had a negative effect on survival 3 and 15 mo after settlement. It is unlikely that light intensity would have a negative effect on corals, for which symbiosis with zooxanthellae is essential, but it is partly expected that the effects of algal cover and water depth on the light environment in the microhabitats within the SHS would vary with the environmental gradient in the bay. This study suggests that the relationship between environmental factors and juvenile coral survivorship is complex, even within a small bay.

KEY WORDS: Coral reef · Field experiment · Initial mortality · Environmental factors · Restoration

1. INTRODUCTION

The process of settling to the sea floor by the swimming larvae of marine sessile organisms involves important decisions, as the area in which they settle will be the habitat they reside in for the remainder of their lifetimes. A variety of environmental factors are associated with this important decision. Reports have indicated that larval settlement behavior is influenced by light, water currents, and temperature in some sponges (Maldonado & Young 1996), that light plays an important role in coral settlement (Mundy & Bab-

cock 1998), and that substrate material is used for settlement of sea cucumber larvae (Mercier et al. 2000). However, only a few studies have used field experiments to investigate the effects of the environment, including from the time of settlement to post-settlement survival (especially longer than 1 yr). In this study, environmental factors affecting the early life history of reef corals, a representative of the sessile organisms in tropical shallow waters, were thoroughly investigated in the field.

Unlike other marine organisms, scleractinian corals require light for photosynthesis, as they harbor sym-

biotic algae, in addition to prey such as small zoo-plankton. Indeed, most coral species uptake zoo-xanthellae at the larval stage and utilize their photo-synthetic products before settlement (Graham et al. 2008, Harii et al. 2010). This study, therefore, focused on the light environment as an important environmental factor for larval settlement and post-settlement survival of corals.

Larval recruitment is an important factor in coral recovery (Hughes & Tanner 2000, Lukoschek et al. 2013, Adjeroud et al. 2016, Harrison et al. 2021). Technology aimed at rapidly rejuvenating depleted coral populations by providing ample numbers of coral larvae or juvenile corals through artificial means is being developed (Heyward et al. 2002, Omori et al. 2004, Edwards 2010, Chamberland et al. 2015, 2017, Omori 2019, Suzuki 2021, Randall et al. 2021, 2023, Banaszak et al. 2023). For example, we have developed a system called the 'larval cradle' for collecting coral bundles, rearing larvae, and settling them while at sea (i.e. without land facilities), resulting in mass production of coral settlers (Suzuki et al. 2020). In addition, a square hollow section (SHS) substrate (i.e. a square-tube artificial substrate) was developed to increase the survival rate of post-settlement corals (Suzuki et al. 2011a, 2020). However, the feasibility of consistently increasing the survival rate for a period of 6 mo to 1 yr post-settlement and improving the efficiency of seedling production needs to be explored.

Several intermediate growth trials have indicated that the survival rate of post-settlement corals varies markedly according to settlement location, even on SHS substrate in larval cradles. Thus, identifying the best 'spawning hotspot' in which to place the larval cradle (Zayasu & Suzuki 2019) is important. In the present study, we compared the survival rates of larvae settled at the mouth and at the back of a small bay, which are environments commonly found in coral reef islands. We used an SHS settlement device, which allowed us to determine the post-settlement survival of coral juveniles because it prevents fish predation (Suzuki et al. 2011a), the most important factor in coral settler mortality (Baria et al. 2010, Penin et al. 2010). Moreover, the SHS device allowed us to evaluate the effects of environmental factors on post-settlement coral growth. Species (Suzuki et al. 2018a) and spatial (Suzuki et al. 2018b) differences in the post-settlement survival rates of *Acropora* corals have been identified using the lattice plate that was the prototype for the SHS. Suzuki et al. (2018b) compared survival rates inside and outside (i.e. outer reef slope) a relatively large lagoon and found that survival rates were higher inside the lagoon regardless of surrounding coral cover. Even within a smaller area, such as a small bay, the environmental conditions can vary greatly from shore to offshore, and this difference could affect the survival rates of juvenile corals.

To accurately assess juvenile coral recruitment (including the effectiveness of the larval cradle), it is necessary to separate settlement and post-settlement survival rates. Indeed, a simple comparison of juvenile coral densities between sites would not provide an accurate assessment of recruitment because larvae may fail to settle even when floating in the water, and post-settlement mortality may be high. Therefore, we conducted separate experiments in which the SHS substrate was conditioned at different sites to evaluate settlement, and at one site to evaluate post-settlement survival rates. In addition, physical and biological environmental factors were recorded at the sites, and the relationship between each factor and the settlement and survival rates of juvenile corals was analyzed.

This study is expected to improve our understanding of larval recruitment in coral, which remains largely unexplored. It has been difficult to monitor the survival of coral larvae in the field because they are almost invisible and hide in reef crevices. A fluorescence-based technique for detecting corals has been developed but finding larvae in the field remains challenging (Baird et al. 2006). Periodic monitoring of corals on artificial substrates from settlement onwards will facilitate accurate estimates of post-settlement mortality.

2. MATERIALS AND METHODS

2.1. Study site

The field study was conducted in Sakieda Bay, Ishigaki Island, Japan (Fig. 1). Ten study stations were established (Stns 1—10), with 2 depths (shallow and deep) at each station (20 sites in total) (Table S1 in the Supplement at www.int-res.com/articles/suppl/m728p015_suppl.pdf). Shallow depths were set in the range of −1.6 to −6 m relative to datum line, while deep depths were set in the range of −5.7 to −12.6 m. Stns 1, 2, and 3 were the closest to the mouth of the bay where water clarity and coral cover (rubble bottom) was high. Stns 4, 5, and 6 were in the middle of the bay where rubble bottom mixed with sand and where coral cover was high in the shallows, similar to the mouth of the bay. Stns 7, 8, 9, and 10 were located at the back of the bay and contained sandy bottoms with almost no *Acropora* corals.
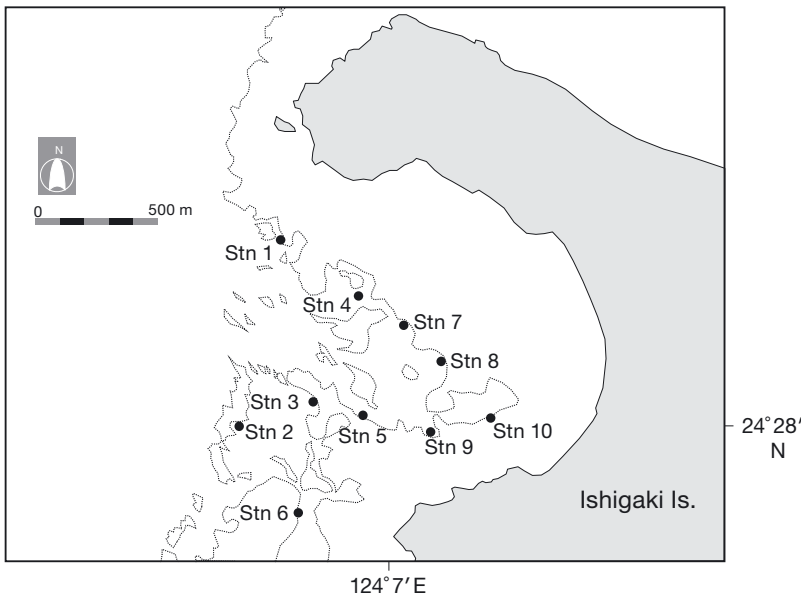
Fig. 1. Study sites at Sakieda Bay, Ishigaki Island, Japan. Dotted lines: reef edges

2.2. Settlement

In total, 1800 PVC SHSs (inner diameter: 32 mm; outer diameter: 40 mm; height: 40 mm) were prepared as substrates. In April 2018 (1 mo before coral spawning), 90 SHSs were conditioned at each of the 20 sites. They were placed in proximity on a PVC rack raised 50 cm above the sea bottom and covered with netting to prevent blowing away (Fig. 2). On 30 May 2018, around 20:00 h (immediately after sunset), 1 d after the full moon, approximately 0.3 million *Acropora* sp. aff. *tenuis* (this species has long been identified as the cosmopolitan species *A. tenuis* in this region, but Bridge et al. 2023 showed that it may be a different species in each region, so it is treated here as affinis of *A. tenuis*) bundles spawned from 20 mature colonies and were captured using the larval cradle (a large cylindrical net of 1.7 m diameter and 4 m height; see Suzuki et al. 2020). All conditioned SHSs were placed in the cradle 4 d after spawning. Prior to placing the SHSs, bubbling was used to stir the larvae in the cradle and remove their vertical bias. The SHS was set on a rack, and the entire rack was put into the cradle (20 racks in total). The racks were hung horizontally with ropes at the 4 corners and stacked about 20 cm apart. The order of stacking was random so that racks at close stations and sites would not be next to each other. After 48 h, the SHSs were removed from the cradle and placed back in the original 20 sites. However, 5 SHSs were randomly sampled at each site and brought back to the laboratory to count the number of *Acropora* settlers under a stereomicroscope. After 3 mo, the number of surviving settlers was estimated in the same manner. After 6 and 15 mo, the number of surviving juveniles was counted directly underwater to determine the survival rate.
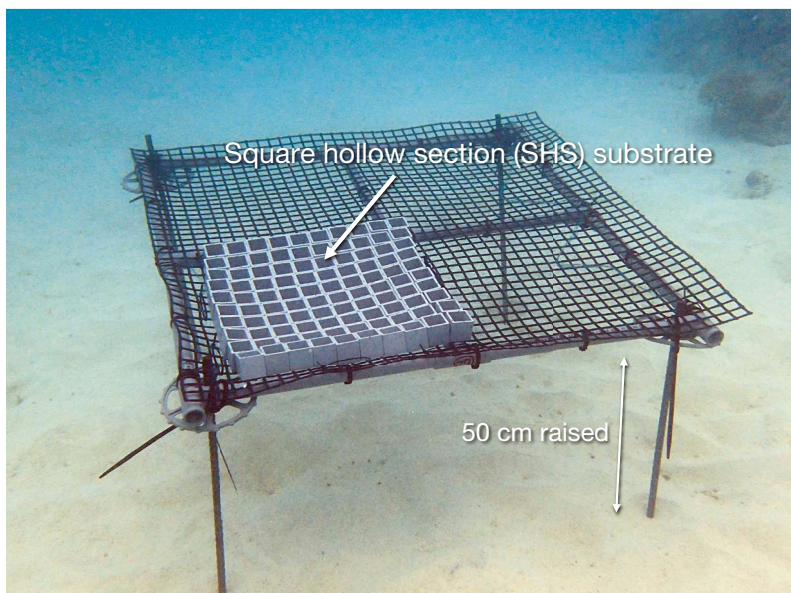
2.3. Post-settlement survival

In April 2019, 1800 SHSs were prepared using the same conditioning method as described above. However, in this experiment, all SHSs were conditioned together near Stn 2. On 18 May 2019, around 20:00 h (immediately after sunset), 1 d before the full moon, approximately 0.2 million *Acropora* sp. aff. *tenuis* bundles were trapped using the larval cradle. When the larvae were 4 d old, all SHSs were placed into the cradle after the larvae were well mixed by bubbling. Unlike the previous year, 45 SHS were packed in mesh bags (300 × 360 mm) of ~2 cm mesh (40 bags in total) and tied to a 4 m long rope hanging from a buoy. Each

Fig. 2. Square hollow section substrate on a PVC rack raised above the sea bottom

mesh bag was tied at ~50 cm intervals between 50 and 350 cm depth (6 ropes in total). Thus, all mesh bags were suspended from the buoys and inserted into the cradle. After 48 h, the SHSs were removed from the cradle and 90 SHSs (i.e. 2-bag equivalent) were randomly selected to avoid unbalanced positioning of the bag in the cradle and were placed on a rack raised 50 cm from the sea bottom at each depth at 10 sites (i.e. 90 × 20 = 1800 SHSs). A total of 20 SHSs were randomly sampled to estimate the average number of initial settlers. After 3 mo, 10 SHSs were collected at each site, and surviving juveniles and dead settlers that had become skeletons were counted under a stereomicroscope. After 6 and 15 months, survival rates were determined directly underwater as in the previous year. Two survival rate values were calculated: the percentage of juveniles surviving from the initial number of settlers per SHS and the percentage of SHSs with at least one surviving coral juvenile per site. The latter value is the yield measurement, which is a useful value for assessing the number of SHSs with living coral.

2.4. Environmental factors

Data on water depth, light quantum density, current velocity, sedimentation, algal cover, and nutrients (in the interstitial water of the sediment and the water column) were collected at each site. A dive computer was used to determine water depth as the depth under the datum line. Light quantum density was recorded every minute for 12 d in early August 2019 using a light quantum meter (DEFI2-L, JFE Advantec Co.), and data collected from 10:00 to 15:00 h were averaged to obtain the average light intensity per day. Measurements were also taken in the air (2 m above sea level), and the relative attenuation rate was calculated. Because there were many cloudy days during the period in which light intensity was measured, the average for the entire period and the average for only the sunny days were calculated. For current velocities, an electromagnetic current meter logger (Infinity EM, JFE Advantec Co.) was installed at each station and depth for 32 d (encompassing a lunar cycle) in August 2020, and data were recorded every 10 min (averaging every second value for 30 s in a single record) to determine the vector mean and maximum flow velocities. In addition, the average flow velocity for 2 d was estimated for all sites using plaster balls (the ball is a sphere with a diameter of 48 mm, made of calcium sulfate; Komatsu & Kawai 1992). Sedimentation was estimated from the total sediment volume over 30 d using sediment

traps (inner diameter: 50 mm; depth: 400 mm) in August 2020. All traps were set at the same height as the PVC rack (i.e. 50 cm from the seafloor) because the amount of sediment is affected by different heights from the seafloor (Ng et al. 2022). The trapped sediments were taken back to the laboratory and dried at 60°C for 48 h. Total weight of sediments was measured by removing large organisms that were visible to the naked eye but without removing any organic matter, and the sediment rate per day was estimated. Macroalgal cover was estimated by photographing the SHSs on the rack at each site at 3 mo post-settlement. A 1 × 1 m rack was photographed from directly above, and the percent cover on the rack was calculated visually (rounded to the nearest 5% increment) based on a 2.5 cm mesh size of the plastic net used for the rack. Macroalgal taxa were identified where possible to the family or genus level. We did not evaluate the correlation with the natural macroalgal flora at each site. Nutrients and sediment were collected from the water column at each site using a 20 ml plastic syringe, and 5 ml of water was immediately filtered using a syringe-connected disposable membrane filter unit (0.45 μm pore size; Dismic 25AS, Advantec). Filtered samples were transported to the laboratory in a cooler box and stored at −20°C in a freezer. Interstitial water in the sediment was collected by attaching an air stone to the tip of the syringe to avoid sucking in sand and mud where possible. The concentrations of nutrients, i.e. orthophosphate (PO_4-P), silicic acid (SiO_2-Si), nitrite (NO_2-N), nitrate and nitrite ($NO_2 + NO_3$-N), and ammonia (NH_4-N), in the samples were measured using an auto-analyzer (QuAAtro39, BLTECH). The minimum quantitation limits of PO_4-P, SiO_2, NO_2-N, $NO_2 + NO_3$-N, and NH_4-N were 0.04, 0.40, 0.02, 0.20, and 0.20 μM, respectively. The concentration of NO_3-N was calculated by subtracting that of NO_2-N from that of NO_2-N and NO_3-N. Artificial seawater, prepared by dissolving 40 g of sodium chloride in ultrapure water, was used as a blank sample.

2.5. Statistical analysis

First, statistical model analyses were conducted using a general linearized model (GLM) and a general linearized mixed model (GLMM) with the number of settlers and the number of surviving spats as objective variables. GLMs were conducted with station and depth as explanatory variables for the number of settlers. A negative binomial distribution was specified as the probability distribution model. For the number of surviving spats, a GLMM was conducted with time

of observation (3, 6, and 15 mo after settlement), water depth (shallow or deep), and area (the mouth of the bay, the middle of the bay, and the back of the bay) as explanatory variables, with station as a random effect. A zero-inflated negative binomial distribution was specified as the probability distribution model. To assess if there was a 3-way interaction, the chi-squared log-likelihood ratio test was conducted between Model 1 (the number of spats ~ time × depth × area + 1[|site]) and Model 2 (the number of spats ~ time + depth + area + time × depth + time × area + depth × area + 1[|site]). In both analyses, we also calculated a null model in which no variables were affected and compared the fitness of the models based on Akaike's information criterion (AIC). If the interaction was significant, a simple main effect determination was performed using the Mann-Whitney *U*-test. To determine the relationships between environmental factors and settlement and post-settlement survival, we performed a multiple regression analysis between all environmental factors and the average number of initial settlers (2018 experiment) and the surviving juveniles 3, 6, and 15 mo post-settlement at each location. In total, 25 variables were used as environmental factors: water temperature (average annual water temperature, September water temperature, and February water temperature), light intensity (short and long term), current velocity (short term, scalar average over the entire period, typhoon-excluded scalar average, maximum current over the entire period, and typhoon-excluded maximum current), macroalgal cover (total macroalgae, brown macroalgae, cyanobacteria, and turf algae), sediment abundance ($mg\,cm^{-2}\,d^{-1}$), and nutrient concentrations in the water column and interstitial water (nitrate, nitrite, ammonia, phosphate, and silicate). All environmental factors were used as explanatory variables. First, all factors were analyzed simultaneously, but the number of factors was too large so they were divided into 10 nutrient factors and 15 other physical factors. The analysis method used a model in which all explanatory factors (i.e. 10 nutrients or 15 physical factors) were employed as the initial model, and a stepwise method in both directions was used to increase or decrease the number of factors to obtain the optimal model based on the AIC. The optimal model was tested for multicollinearity using variance inflation factor (VIF) as an index,

and a model in which factors with VIF > 5 were excluded was adopted as the corrected optimal model. All analyses were performed using R version 4.2.3 (R Core Team 2022).

3. RESULTS

3.1. Settlement (2018 experiment)

In 2018, the number of settlers differed significantly on devices conditioned at different stations and depths (AIC of null model: 391.33; AIC of alternative model: 325.66) (Fig. 3), tending to be higher at the mouth (Stns 1—3) and lower at the back (Stns 7—10) of the bay. Post-settlement survival could not be assessed accurately in the inner part of the bay owing to the low number of settlers, but the post-settlement survival (yield) was more than 10 times higher at the mouth of the bay (59% on average) than that at the back of the bay (4%) (Fig. S1 in the Supplement).

3.2. Post-settlement survival (2019 experiment)

In 2019, the mean (±SE) number of settlers was 27.3 ± 2.1 individuals. Post-settlement survival differed significantly among stations and depths (AIC of null model: 6935.4; AIC of alternative model: 6759.6) (Fig. 4a). After 3 mo, the highest survival rates were 15.0% in the deep water at Stn 6 and the lowest survival rates were 0.4% in the deep water at Stn 7. After 6 mo, a similar trend was observed but the highest
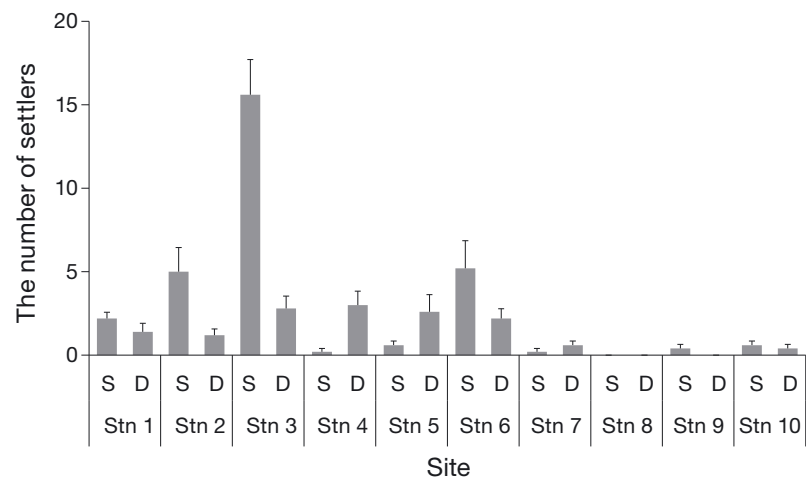

Fig. 3. Number of initial *Acropora* sp. aff. *tenuis* settlers (average ± SE) per square hollow section (settlement surface area: 48 cm²) at each station and depth (S: shallow; D: deep) in the 2018 experiment. Stn 1 is closer to the mouth of the bay; the larger the number, the closer to the back of the bay (same in subsequent figures)
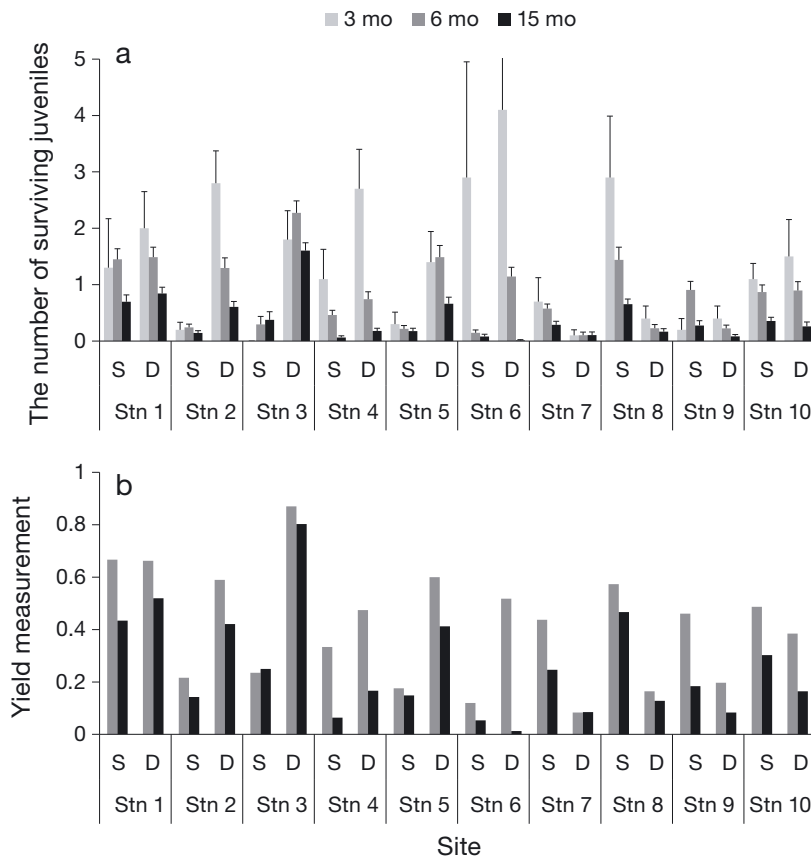
Fig. 4. Post-settlement survival of *Acropora* sp. aff. *tenuis* in the 2019 experiment. (a) Number of surviving spats (average ± SE) per square hollow section at each site and depth. (b) Yield measurement at each site and depth (rate at 3 mo post-settlement was not calculated because of small sample size)

Table 1. Summary results of the chi-squared log-likelihood ratio test between 2 generalized linear mixed models: Model 1 (the number of spats ~ time × depth × area + 1[|site]) and Model 2 (the number of spats ~ time + depth + area + time × depth + time × area + depth × area + 1[|site]). AIC: Akaike's information criterion; BIC: Bayesian information criterion

	df	AIC	BIC	logLik	deviance	χ^2	χ^2 df	Pr(>χ^2)
Model 2	17	6310.7	6413.3	−3138.3	6276.7			
Model 1	21	6308.4	6435.2	−3133.2	6266.4	10.247	4	0.036

factors of time, area, and depth was significant (Table 1); therefore, differences in post-settlement survival between depths were examined for each area and time as a simple main effect determination. Interestingly, at the back of the bay, the survival rate was 39% lower in deep water than in shallow water, whereas in the middle of the bay, the survival rate was 37% lower in shallow water than in deep water (Fig. 5). At the mouth of the bay, the survival rate was 40% lower in shallow water, the same as the middle of the bay in the 2019 experiments, whereas the survival rate was high in both shallow and deep water in the 2018 experiment.

At 3 mo post-settlement, the number of skeletons of dead individuals was higher at sites with high survival rates (Stns 1, 2, 3, and 6) (Fig. 6).

3.3. Relationships between environmental factors and post-settlement survival

All results of measured environmental factors are listed in Table S1. First, we analyzed the relationship between the number of initial settlers in 2018 and physical environmental factors and found that the best model was the one in which only sediment was significant (AIC: 108.42; Table 2). Indeed, sediment was significantly negatively correlated with the number of settlers, i.e. low sediment was associated with a high number of settlers (Fig. 7). Little or no settlement seemed to occur at a threshold sedimentation rate of 10 mg cm^{-2} d^{-1}. Examining the relationship between the number of settlers and nutrients, the model fit significantly better with a positive relationship with silicate in the water column and a negative relationship with phosphate in the interstitial water.

Next, the relationship between the number of surviving spats after 3 mo in 2019 and physical environmental factors was analyzed, and a model was adopted in which short-term light intensity acts negatively, maximum flow velocity except during typhoons acts positively, and cyanobacteria coverage acts negatively (AIC: −3.3725; Table 3). Negative effects of phosphate

survival rate was 8.3% in the deep water at Stn 3. After 15 mo, the highest survival rate was 4.0% in the deep water at Stn 3 and the lowest was 0.1% in the deep water at Stn 6. Notably, the survival rate in the deep water at Stn 6 fell from highest to lowest over the course of the experiment. A similar yield measurement trend was observed, indicating that no bias existed among SHSs in terms of the number of surviving spats within a single location (Fig. 4b).

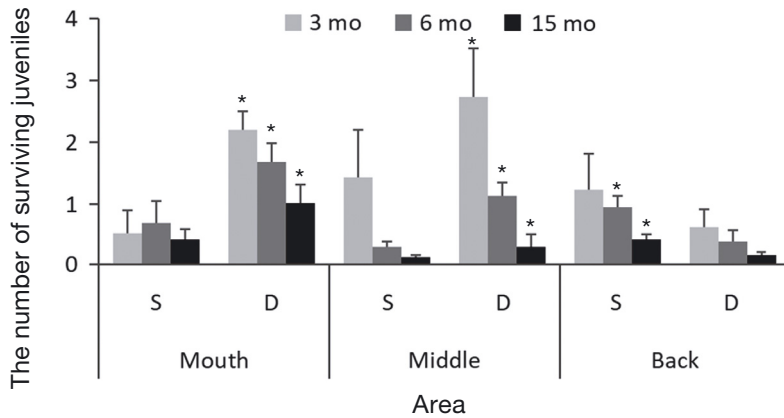A GLMM was conducted with time, area, and depth in the bay as factors, and the interaction between the 3

Fig. 5. Number of surviving *Acropora* sp. aff. *tenuis* spats 3, 6, and 15 mo after settlement in the 3 areas (mouth, middle, and back) of the bay. (*) denotes significantly higher (p < 0.05) value than the paired depth within each area (i.e. the deep [D] bar with asterisk is higher than the paired shallow [S] bar of the same area, and vice versa)
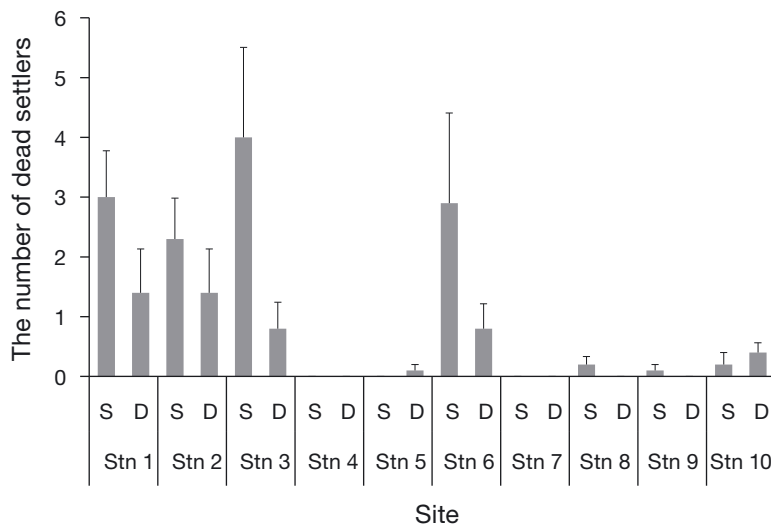

Fig. 6. Number of dead *Acropora* sp. aff. *tenuis* settlers (average ± SE) that became skeletons per square hollow section at each site and depth 3 mo postsettlement in the 2019 experiment

Table 2. Stepwise multiple linear regression analysis for the number of surviving *Acropora* sp. aff. *tenuis* spats at 3 mo after settlement. Depth: water depth; T_Feb: average water temperature during February 2020; Algal_turf: coverage of turf algae; Sediment: amount of sediment

	Estimate	SE	t	Pr(>|t|)
(Intercept)	−17.6	92.435	−0.19	0.852
Depth	−0.325	0.246	−1.319	0.207
T_Feb	1.117	3.862	0.289	0.776
Algal_turf	−0.081	0.071	−1.146	0.27
Sediment	−0.363	0.149	−2.445	0.027

and ammonia in the water column were suggested in relation to nutrients. In the regression analysis with survival at 6 mo, a model with no factors significantly affecting it was selected. For nutrients, the same model as at 3 mo was considered optimal. In relation to survival after 15 mo, a model was selected in which short-term light intensity and total algal cover were negatively affected (Fig. S2, Table S2 in the Supplement). On the other hand, a significant relationship with nutrients was no longer observed.

Finally, we determined the difference in the number of surviving spats after 3 and 6 mo and after 6 and 15 mo to determine the environmental factors that influenced each time period. For 3−6 mo, a model was adopted in which only the short-term light intensity was negatively affected among the physical environmental factors, but no factors had a significant effect for 6−15 mo. In relation to nutrients, the model adopted negative and positive effects of phosphate and ammonia in the interstitial water after 3−6 mo, respectively.

4. DISCUSSION

In the present study, we investigated the settlement and the post-settlement survival of *Acropora* sp. aff. tenuis larvae in a small bay. First, it was found that sedimentation was the only factor affecting their settlement. It is known that larvae are unwilling to settle in sediment-rich areas (Jones et al. 2015, Moeller et al. 2017). It is also known that coral larvae prefer to settle in areas with more calcareous algae and other organisms that attract coral settlers (Morse et al. 1988, Heyward & Negri 1999, Negri et al. 2001, Ricardo et al. 2017). The significant negative correlation found in this study between the amount of sediment and the number of settlers per site can be explained by the results of these previous studies. In relation to nutrients, the effect of silicate is unknown, but phosphate in interstitial water has been reported to inhibit the early growth of juvenile *Acropora* corals (Iijima et al. 2019) and may be avoided by coral larvae
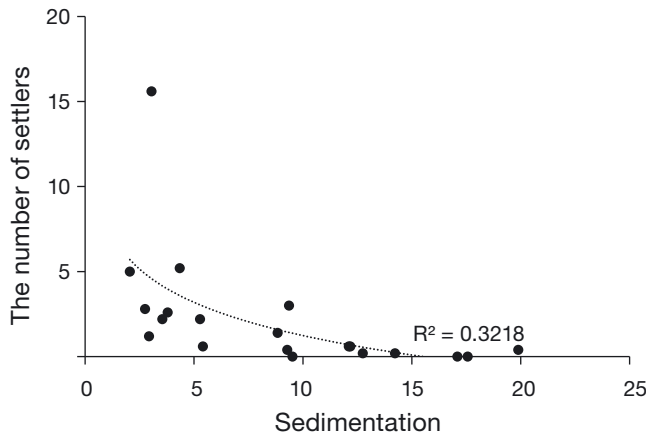
Fig. 7. Scatter plot of sedimentation (mg cm^{-2}d^{-1}) according to the number of initial *Acropora* sp. aff. *tenuis* settlers in the 2018 experiment

during settlement. It is also known that coral larvae avoid strong light exposure during settlement (Maida et al. 1994); however, in this study, there was no significant correlation between light and the number of initial settlers, possibly due to indirect effects via the epibenthic algae and/or bacteria on the SHSs.

In terms of the relationship between post-settlement survival, it appears that during the first 3 mo after settlement, low ambient light, high maximum current velocity, and low cyanobacterial abundance positively affect the survival of *Acropora* sp. aff. *tenuis* juveniles. Although the influence of physical environmental factors was obscured 6 mo after settlement, a negative relationship with light intensity and algae coverage was again suggested 15 mo after settlement. As a symbiotic organism with zooxanthellae, it is curious that it did

not show a significant correlation with the light environment, which might affect post-settlement survival. One of the expected causes from the observations made during this experiment is that the environment of the microhabitat (i.e. the inner surface of the SHS substrate) in which the corals settled is complex. For example, the light was stronger in shallow areas, but within 1 mo the SHSs were covered with macroalgae. Macroalgae are more abundant in shallow areas where the light is stronger than in deeper areas, so the light intensity inside the SHS where the corals were settled could have been equal to or darker than in the deeper areas. In addition, more sediment may weaken the light on the inner surface of the SHS more by being trapped by algae. Apart from these factors, the competitive relationship between algae and coral settlers is also considered to be complex. It is often assumed that too much algae kills coral settlers by directly covering them, but the relationship does not appear to be that simple. In fact, in the case observed in the present experiment, when macroalgae such as *Padina minor* grew on the upper surface of the SHS, smaller macroalgae and sediment decreased inside the SHS, creating an environment in which coral settlers could easily survive. Therefore, it is important to note that light intensity and algal cover, which were predicted to be negatively related to post-settlement survival in this study, are not simply associated with the growth of *Acropora* sp. aff. *tenuis*.

When the small bay was divided geographically, the survival rate of *Acropora* sp. aff. *tenuis* juveniles in shallow and deep water tended to be reversed from the back to the mouth of the bay within a single bay. Why does the relationship between water depth and juvenile coral survival change with location in a bay? No single environmental factor had a significant effect on survival, but the combination of light intensity, current velocity, macroalgae, sediment, and nutrients are likely to affect survival. At the back of the bay, more sediment is suspended, and turbidity is greater; thus, survival rates are higher in shallow water where light intensity is higher. In the middle of the bay, turbidity is weaker but sediment abundance is higher, and sediment tends to move easily during stormy weather, so shallow substrate is vulnerable to storm damage. In addition, a vast amount of macroalgae was covered in floating mud, and nutrients in the sediment may

Table 3. Stepwise multiple linear regression analysis for the number of surviving *Acropora* sp. aff. *tenuis* spats 15 mo after settlement. Light_S: daytime light intensity on a sunny day; *T*_Sep: average water temperature during September 2019; *T*_Feb: average water temperature during February 2020; Current_S_part: average scalar flow velocity during one month except during typhoons; Current_max_all: maximum flow velocity during one month; Current_max_part: maximum flow velocity during one month except during typhoons; Algal_brown: coverage of brown algae; Algae_cyano: coverage of cyanobacteria

	Estimate	SE	t	Pr(>|t|)
(Intercept)	−201.7	158.9	−1.269	0.231
Light_S	−0.006	0.002	−3.356	0.006
*T*_Sep	6.407	4.497	1.424	0.182
*T*_Feb	0.732	2.022	0.362	0.724
Current_S_part	0.193	0.934	0.206	0.84
Current_max_all	0.013	0.018	0.723	0.485
Current_max_part	0.53	0.192	2.765	0.018
Algae_brown	−0.01	0.009	−1.085	0.301
Algae_cyano	−0.074	0.028	−2.636	0.023

affect the growth of macroalgae. Coral survival rates were high at the mouth of the bay, regardless of water depth, because turbidity was low and light levels were sufficient even in deep water. However, the probability of physical damage to coral during a storm is higher in shallow water, as evidenced by the loss of 2 racks in Stns 1 and 2 during the 2018 experiment.

As we have discussed, considering the relationship between environmental factors and coral initial survival, it is necessary to observe this association at the microhabitat level. It should be noted that in this study, the coral larvae were settled on an SHS and then arranged on a rack raised 50 cm above the seafloor. In nature, larval settlement is difficult to visualize on natural substrate and survival is very low, making it difficult to obtain reliable data for field experiments, such as comparisons of post-settlement survival between habitats. Accordingly, we used an SHS that enhances post-settlement survival in this study, but this result may not be directly applicable when referring back to natural post-settlement processes. For example, phosphate, which inhibits juvenile coral growth (Iijima et al. 2019), had concentrations in the interstitial water that were several to dozens of times higher than in the water column at some locations but had no fatal harmful effects on the survival of juvenile corals on the SHS. However, even under natural conditions, they do not settle on sand (Hodgson 1990) and often settle in small holes and crevices on the reef substratum, so they would be subjected to stress similar to that inside an SHS device; for example, sunlight being blocked by algae or sediments being trapped by surrounding algae, and so on. Therefore, we believe that the results of this experiment roughly mirror the survival process of juvenile corals that naturally settle on natural substratum, although the absolute survival rate may be magnified by tens to hundreds of times.

Since this study was conducted using one species of *Acropora* corals, it is unknown to what extent it can be adapted to the more than 300 known species of scleractinian corals, even if limited to Ishigaki Island. However, in terms of coverage, most are dominated by the genus *Acropora*, which is certainly a representative coral. *Acropora* sp. aff. *tenuis* is one of the most common species of the *Acropora* genus often used in larval experiments; however, this species has a low bias in its range since it is found in many habitats, from shallow to deep and from outer to inner reef. Therefore, although not perfect, we believe it is suitable as a model species for inferring the ecology of *Acropora* corals, which are overwhelmingly dominant in this coral reef area.

This study improves our understanding of coral population recovery with respect to larval recruitment. We also sought to determine the habitat suitable for coral nurseries in small bays, commonly found in fringing reefs. The backs of bays are expected to contain fewer swimming larvae (Suzuki et al. 2012), but even if many swimming larvae arrive, reefs will not recover owing to low settlement rates. If larvae are artificially introduced into the back of a bay (e.g. Miller et al. 2022), recovery may occur only in shallow water. By contrast, from the mouth to the middle of a bay, recovery will proceed in deep water if larvae arrive, whereas recovery in shallow water may be difficult because of physical factors such as sediment. Furthermore, because larval recruitment rates tend to be lower in deep water than in shallow water (Suzuki et al. 2011b, 2012), artificially supplying larvae to areas of deep water could contribute to coral recovery.

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