

# Patterns of coral settlement in an extreme environment: the southern Persian Gulf (Dubai, United Arab Emirates)

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**ABSTRACT:** Coral settlement is a key ecological process in the maintenance, recovery and resilience of coral reef ecosystems. Coral reefs in the Persian Gulf survive in one of the world's most extreme environments, yet there remains limited knowledge of the role of coral settlement considered critical for maintaining population dynamics. Spatial and temporal patterns of coral settlement were examined at 6 sites in Dubai, United Arab Emirates, using settlement tiles deployed and collected every 3 mo from 2009 to 2011 following coral community surveys. Settlement was highly seasonal with the highest settlement rates between June and August ( $3.2 \text{ spat tile}^{-1} \pm 0.21 \text{ SE}$ ), when summer sea temperatures approached  $35^{\circ}\text{C}$ . There was a smaller settlement pulse between September and November, but no settlement between December and May. Settlement was observed 1 to 4 mo after the major spawning season (April and May), suggesting either delayed settlement of larvae, or spatial and/or taxonomic disparity between studies of reproduction versus settlement. Settlement rates varied significantly among sites, but spatial variation was consistent between the 2 years of the study, suggesting strong effects of local environmental conditions or local coral assemblages. Poritidae and Acroporidae comprised 27 and 11% of the spat respectively, there were no Pocilloporidae and the most abundant coral spat (61%) were from other, not identifiable, families. These data indicate that observed long-term shifts in the community structure of adult coral assemblages are being reinforced through a combination of settlement and post-settlement processes, such that there is limited scope for recovery of former *Acropora*-dominated coral assemblages in the Persian Gulf.

**KEY WORDS:** Coral reefs · Arabian Gulf · Coral settlement · Larval supply · Climate change

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## INTRODUCTION

Scleractinian corals are the primary habitat-forming species on coral reefs (Jones et al. 1994), but are declining in abundance in many coral reef provinces (e.g. Gardner et al. 2003, Bellwood et al. 2004). Sustained losses of scleractinian corals are attributed to multiple disturbances (e.g. over-fishing, coastal pollution and disease) that are being compounded by the more recent impacts of climate-induced coral bleaching from elevated temperatures (Hughes et al. 2003,

Bellwood et al. 2004). Aside from significant losses of live coral cover (Gardner et al. 2003, Bellwood et al. 2004), increasing frequency, severity and diversity of disturbances are likely to cause marked shifts in community composition (Pandolfi et al. 2011, Hughes et al. 2012). In light of these recent concerns, there is an urgent need to understand how increasing sea temperatures from ongoing climate change will affect early life history stages (Putnam et al. 2008, Albright & Mason 2013) and the capacity of coral populations to replenish themselves (Diaz-Pulido et al. 2009).

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For corals, most recent studies have focused on the effects of high sea temperature on the adult assemblage, with the goal of trying to understand the causes of thermal bleaching (Dove & Hoegh-Guldberg 2006) and differences in bleaching susceptibilities (e.g. comparative rates of mortality among adults; Marshall & Baird 2000). However, high sea temperatures caused by climate change are likely to affect biological and physiological processes that span multiple life history stages (Putnam et al. 2008, Albright & Mason 2013). Early life history stages of corals (i.e. larval development, survival and settlement) are extremely sensitive to environmental stresses, and especially high temperatures (Byrne 2011), the effects of which can have a greater biological significance than for adults (Gosselin & Qian 1997). Elevated temperatures, which cause bleaching, may also disrupt various early life history processes and greatly influence the number of individuals entering the adult population (McClanahan et al. 2009).

Population replenishment is an important demographic process for the persistence of all marine organisms (Gaines & Roughgarden 1985, Underwood & Keough 2001). The recovery of reefs following a disturbance (e.g. bleaching event) requires both the replenishment of coral populations by regrowth of surviving corals (Gilmour et al. 2013) and the arrival and settlement of coral larvae and their post-settlement growth and survival (Hughes 1994, Hughes & Tanner 2000). However, the only means of restoring both coral cover and the genetic diversity of coral populations is through sexual recruitment (Baums et al. 2006). Successful coral recruitment is dependent on many separate processes, including the fecundity of the local population (e.g. Hughes et al. 2000), rates of fertilization (e.g. Oliver & Babcock 1992), larval survivorship and dispersal (e.g. Graham et al. 2008), settlement (e.g. Hughes et al. 1999), and early post-settlement growth and survivorship (e.g. Penin et al. 2010). Of these processes, larval supply and settlement are recognized as one of the major determinants of adult assemblage structure, at least on some coral reefs (Caley et al. 1996, Hughes & Tanner 2000). Equally important are early post-settlement processes, such as differential growth and survivorship, which also strongly influence the local abundance and spatial distribution of adult coral populations (Edmunds 2000, Penin et al. 2010, Trapon et al. 2013). However, elevated temperatures can have dramatic effects on larval supply and settlement (Edmunds et al. 2001, Bassim & Sammarco 2003, Baird et al. 2006, Nozawa & Harrison 2007), which therefore can profoundly affect overall popu-

lation dynamics (Harrison & Wallace 1990, Connell et al. 1997). Given that global sea surface temperatures (SSTs) are predicted to increase 2 to 4°C within the next century (IPCC 2007), it is important to understand how coral settlement will likely be affected under more extreme environmental conditions.

The Persian Gulf provides a novel and important setting for studying coral settlement. Corals in the Gulf persist in a naturally extreme environment (Sheppard et al. 1992), at temperatures projected to occur on most tropical coral reefs by 2100 (IPCC 2007). SSTs can fluctuate >20°C over the course of a single year, with summer daily-mean temperatures of >35°C, while winter winds can chill water to <12°C (Sheppard et al. 1992, 2010). Furthermore, corals in the Gulf survive in a hypersaline environment year round with salinities regularly >42 ppt (Sheppard et al. 1992) with significant seasonal insolation fluctuations (Sheppard et al. 2010). While corals in the Gulf have clearly had many thousands of years to adapt to these conditions (Sheppard et al. 2010), nonetheless, studies in the Gulf can address the potential limits of adaptation in response to extreme environments. Indeed, adaptation can be surprisingly rapid (Parmesan 2006), even in organisms like corals (Guest et al. 2012). Moreover, corals in the Gulf are also subject to increasing pressure from anthropogenic impacts such as overfishing, large-scale coastal development (Sheppard et al. 2010, Sale et al. 2011) and bleaching events (Riegl et al. 2011). Minimizing or reversing the continuing degradation of these reefs is critical to prevent significant erosion of ecosystem services and goods (Sheppard et al. 2010), but the recovery and resilience of coral populations in the Gulf will be very much dependent on local levels of reproduction, pre- and post-settlement processes, and recruitment.

Research of coral settlement in the Gulf has been limited to a few small-scale studies conducted mainly in the United Arab Emirates (Burt et al. 2009, 2010). Burt et al. (2009) examined coral settlement at 4 sites (2 breakwaters and 2 patch reefs) over 1 yr in Dubai to determine whether the different construction materials commonly used to build breakwaters influenced settlement. Coral settlement varied by an order of magnitude among sites, ranging from <0.3 spat tile<sup>-1</sup> yr<sup>-1</sup> to 4.9 spat tile<sup>-1</sup> yr<sup>-1</sup>, possibly due to spatial variation in the abundance of adult corals and localized settlement (Burt 2009). However, there have not been any systematic studies of coral settlement to establish the seasonality in settlement, or explicitly testing for spatial variation in rates of settlement relative to local abundance and composition

of adult corals. The specific objectives of this study were to (1) examine the spatio-temporal variability of coral settlement at 6 sites for 8 seasons over 2 yr along the coast of Dubai (United Arab Emirates), (2) determine the taxonomic composition of coral spat and (3) explore the relationship between adult coral assemblages and coral spat among different families.

## MATERIALS AND METHODS

### Study area

This study was conducted in the southern basin of the Persian Gulf along the coast of Dubai (Fig. 1). Most of the sea floor in this area is shallow (<10 m) and dominated by sand and silt substrates, making it unsuitable for coral settlement (Sheppard et al. 1992, Riegl 1999). Suitable settlement substrate is restricted to small (<1000 m<sup>2</sup>), isolated areas of exposed limestone 'caprock', which occur mainly to the southwest of Dubai (Sheppard et al. 1992, Riegl 1999). In addition, breakwaters associated with coastal development in Dubai provide a substantial amount of hard substrate on which coral and other benthic fauna recruit (Riegl 1999, Burt et al. 2009). These breakwaters add over 65 km<sup>2</sup> of rocky subtidal habitat in an area where <10 km<sup>2</sup> of natural hard-bottom habitat occurs (Burt et al. 2008). To test for spatio-temporal variation in coral settlement, 6 sites (5 breakwaters and 1 natural reef site) were selected across ~45 km of coastline in Dubai (Fig. 1).

All sites had comparable water depths that did not exceed 8 m and similar exposure to environmental conditions (e.g. wind and waves). Throughout the Dubai coastline, winds and waves are predominantly from the northwest (Cavalcante et al. 2010), and settlement tiles were placed on exposed portions of the breakwaters and unsheltered coral patches. In Dubai, tides are mainly semi-diurnal and all sites experience similar tidal amplitude, ranging from 0.80 to 1.95 m (Cavalcante et al. 2010). The prevailing coastal currents move from west to east, are relatively slow (0.25 to 0.40 m s<sup>-1</sup>) and consistent throughout much of Dubai (Cavalcante et al. 2010).

### Settlement patterns

To measure settlement, 25 unglazed settlement tiles (10 × 10 × 1.5 cm) were attached to the substrate at each site. Five tiles were attached to each of five 2 m long PVC poles (2.5 cm diameter). Tiles were spaced ~50 cm apart, and held in place with stainless steel bolts and wing nuts. A plastic washer was used to maintain each tile 5 mm above the substrate, following Mundy (2000). At each site, poles were bolted directly to the substrate with the aid of a pneumatic drill at ~5 m depth, and separated by a distance of 1.0 to 1.5 m.

Settlement tiles were deployed in the field starting in March 2009 before the coral spawning season, which in the southern Gulf occurs predominately between April and May (Bauman et al. 2011). Tiles were replaced every 3 mo, thus defining 4 periods (hereafter referred to as seasons): March to May (spring), June to August (summer), September to November (autumn) and December to February (winter). This sampling procedure was repeated over a 2 yr study period (March 2009 to March 2011). Freshly collected tiles were soaked in diluted bleach for ~24 to 48 h to remove organic materials, and then rinsed and sundried before inspecting for coral spat. All coral spat were counted and identified on each tile using a dissecting microscope (40× magnification). The majority of coral spat recorded were often single corallites <3 mm diameter. At this early stage of development, the morphology of the corallum is not suffi-

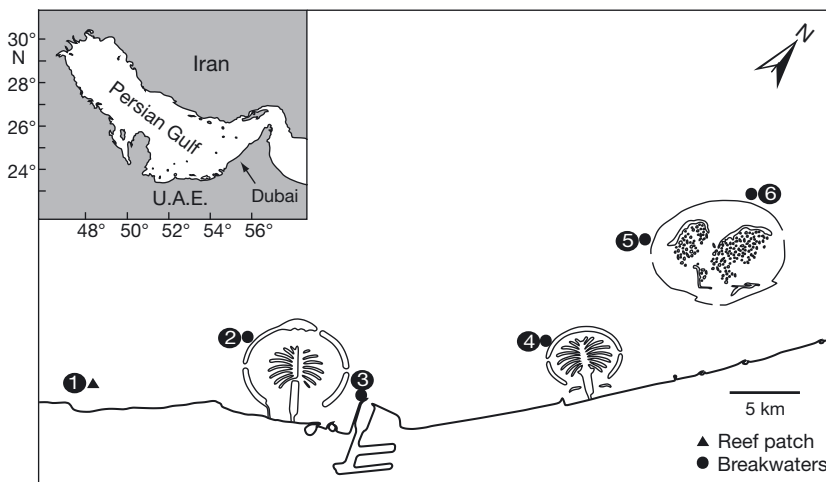


Fig. 1. The coast of Dubai (United Arab Emirates) in the southern Persian Gulf showing the 6 study sites. Sites from west to east: 1 = Jebel Ali Reserve, 2 = Palm Jebel Ali, 3 = Jebel Ali Port, 4 = Palm Jumeirah, 5 = The World West, and 6 = The World East

ciently developed to allow high taxonomic resolution, and only 3 families (Acroporidae, Pocilloporidae, Poritidae) can be reliably distinguished (Babcock et al. 2003). All other coral spat were categorized as 'others'. Coral spat that were too damaged to identify because of overgrowth by other organisms (e.g. barnacles, bryozoans, sponge) or during retrieval were listed as 'unknown'.

### Local coral assemblages

Prior to the deployment of settlement tiles, coral assemblages were surveyed at each site using photo-quadrats. At each site, 6 replicate 30 m long line transects were photographed at 3 m intervals using a 0.25 m<sup>2</sup> quadrat for a total of 66 quadrats per site (or 16.5 m<sup>2</sup> of sampled area). Sampling was standardized to ~5 m depth, the same depth as settlement tiles. Images were analyzed using CPCe version 5 (Kohler & Gill 2006) using 50 randomly distributed points. Scleractinian (hard) corals underlying each point were identified to species. Data from images were then pooled for each transect at each site to provide mean estimates of percent coral cover.

### Seawater temperature

Seawater temperature was recorded at each site using Hobo Tidbit v2 water temperature loggers ( $\pm 0.2^\circ\text{C}$  resolution). At each site, one logger was attached directly to the substrate at approximately the same depth as the settlement tiles. Loggers were set to record hourly, and were retrieved, downloaded and changed each time settlement tiles were replaced (i.e. every 3 mo). All 6 loggers were cross-calibrated prior to each deployment. Initial screening of the temperature data revealed that daily seawater temperatures (mean, high and low) did not vary among sites, therefore temperature records were pooled across all sites and the overall daily mean temperature and range calculated.

### Data analysis

Mean densities of coral spat on each tile were estimated seasonally for each site for both years, and data were  $\log(x + 1)$  transformed prior to analysis. Despite transformation, data were significantly non-normal (Shapiro-Wilks  $W = 0.41$ ,  $p < 0.001$ ). Therefore, to test for overall spatio-temporal variation in

coral settlement, a permutation-based analysis of variance (Anderson & Ter Braak 2003) was used to compare the density of spat among sites, sampling seasons (spring, summer, autumn and winter) and years (2009–2010 and 2010–2011). This procedure is formally equivalent to a standard ANOVA, but the flexibility and robustness of the permutation approach improves the necessity for variables to fulfill standard assumptions, such as normality (Anderson & Ter Braak 2003). Where significant differences were detected ( $p < 0.05$ ), pairwise multiple comparisons were performed using Bonferroni adjusted  $p$ -values to determine which means differed significantly. The density of spat for each family was compared among sites for each season when settlement was observed (summer and autumn) and year using the same procedure (i.e. permutation-based ANOVA), and further investigated using pairwise multiple comparisons. Kendall's coefficient of concordance analysis with correction for tied values was then used to determine whether relative ranks of sites according to mean settlement were consistent among seasons (Zar 2010). The relative abundance of coral cover was then compared among sites, and differences in percent live coral cover and abundance of dominant coral genera, were tested with 1-way ANOVAs. Tukey's post-hoc tests were used to identify significantly different groups. Percent coral cover data were  $\sin^{-1} \sqrt{x}$  transformed prior to analyses. The assumptions of normality and homogeneity of variance were tested through graphical analyses of residuals. Spearman's rank-order correlation was used to analyze the relationship between mean percent coral cover and mean settlement for each family and spat categorized as other.

## RESULTS

### Temporal and spatial coral settlement patterns

A total of 1023 coral spat were observed over 2 yr. The majority of spat (98.8%) were found on the bottom of the tiles, 1.2% on the sides, and no spat on the top. The mean number of spat per tile ranged from 0 (March to May and December to February for all sites in both years) to 8.61 (June to August 2010 at site 4), and the maximum number of spat observed on one tile was 21. The most prominent patterns in total coral settlement were the strong seasonality with peak settlement in the summer ( $3.2 \text{ spat tile}^{-1} \pm 0.21 \text{ SE}$ ) followed by a smaller settlement pulse in the autumn, while no coral spat were observed in the

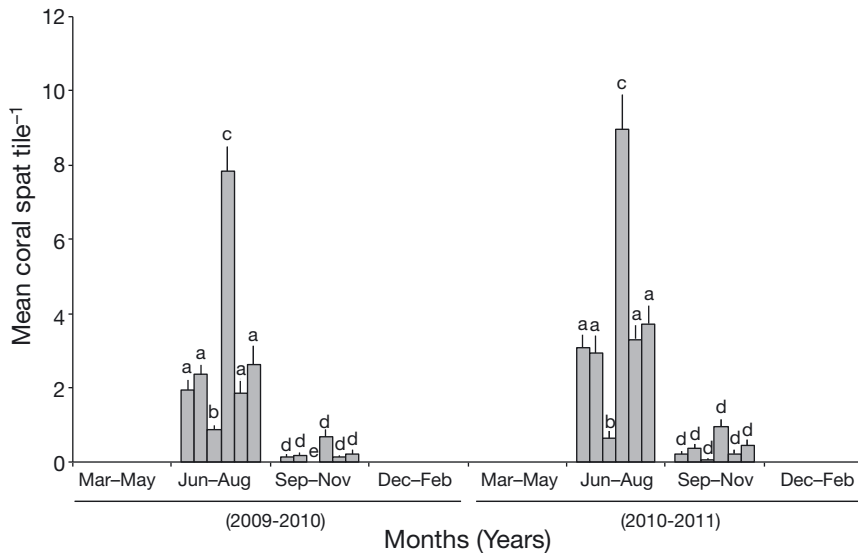


Fig. 2. Overall spatial and temporal variation in coral settlement in Dubai (6 sites arranged from west to east, see Fig. 1). Data are means  $\pm$  SE, and different letters indicate significant differences (Bonferroni adjusted p-values)

winter or spring in either year (Fig. 2). Also striking was the temporal consistency in the rank order among sites in total coral settlement; this despite the dramatic differences in the abundance of spat among seasons and less so between years.

The total abundance of coral spat differed significantly among sites, seasons and years but the spatial patterns were temporally confounded (Table 1). Coral settlement was highest between June and August (summer) at all sites in both years (Bonferroni adjusted p-values,  $p > 0.001$  each, Fig. 2) except site 3 ( $p = 0.306$ ). In addition to differences among seasons, there were also differences in settlement among sites, and these varied seasonally (Fig. 2). Site 4 had the highest settlement of all sites during every

Table 1. Results from permutation-based analysis of variance tests comparing mean spat densities among seasons (spring, summer, autumn, winter) sites (1 to 6) and years (2009–2010 and 2010–2011) using type III sums of squares based on 999 permutations under a reduced model. Values in bold are significant ( $p < 0.05$ )

Source	df	MS	F	p
Season	3	7.67	128.47	<b>0.003</b>
Site	5	0.491	489.89	<b>0.001</b>
Year	1	0.16	210.90	<b>0.001</b>
Season $\times$ Site	15	0.24	309.14	<b>0.001</b>
Season $\times$ Year	5	0.005	77.12	<b>0.001</b>
Year $\times$ Site	3	0.001	1.29	0.298
Site $\times$ Season $\times$ Year	15	0.0006	0.76	0.598
Total	47	0.033		

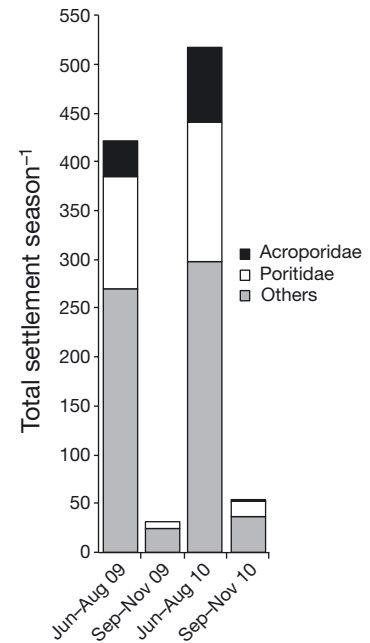


Fig. 3. Total number of coral spat per season and taxonomic composition (pooled across sites) for 2009 and 2010 ( $n = 572$  tiles)

season in which spat were observed, but this was significant only in the summer ( $p < 0.001$ ). The total abundance of coral spat at site 4 (pooled between years) during the summer was 3- to 4-fold higher than spat on sites 1, 2, 5 and 6, and 17-fold higher than site 3. In contrast, site 3 consistently had the lowest settlement of all sites, and this was significant compared with the other sites during the peak settlement periods: summer 2009 and 2010 ( $p < 0.001$ ). All other sites had comparable levels of settlement every season ( $p > 0.05$ , Fig. 2).

The most common coral spat belonged to the taxa categorized as 'others' (61%) followed by the families Poritidae (27%) and Acroporidae (11%). No Pocilloporidae were observed, and damaged coral spat classified as 'unknown' accounted for  $< 1\%$ . Coral spat categorized as 'others' were the most abundant spat in both seasons (summer and autumn) and in both years (i.e. pooled among sites; Fig. 3). The abundance of other spat varied significantly among sites and seasons in both years (Table 2). Other spat were significantly more abundant between June and August than September and November on all sites in both years (Bonferroni adjusted p-values,  $p < 0.005$ , Fig. 4a). Mean settlement of 'others' was highest at sites 4 and 6 in all seasons ( $p < 0.001$ , Fig. 4a). Site 4 had 2.4 to 3.6 times the mean settlement of site 6, and 3.3 to 3.9 times the mean settlement of the next highest site. Site ranks were concordant among all settle-

Table 2. Permutation-based analysis of variance results comparing (a) Others (b) Poritidae and (c) Acroporidae mean spat densities among seasons, sites and years using type III sums of squares based on 999 permutations under a reduced model. Values in bold are significant ( $p < 0.05$ )

Source	df	MS	F	p
<b>(a) Others</b>				
Season	3	4.15	260.52	<b>&lt;0.015</b>
Site	5	0.402	120.81	<b>&lt;0.001</b>
Year	1	0.047	25.91	<b>&lt;0.001</b>
Season × Site	15	0.210	115.28	<b>&lt;0.001</b>
Season × Year	5	0.015	8.77	0.063
Year × Site	3	0.032	1.83	0.161
Site × Season × Year	15	0.013	0.54	0.612
Error	47	0.019		
<b>(b) Poritidae</b>				
Season	3	2.10	248.51	<b>&lt;0.014</b>
Site	5	0.103	51.48	<b>&lt;0.001</b>
Year	1	0.025	26.12	<b>&lt;0.001</b>
Season × Site	15	0.045	47.42	<b>&lt;0.001</b>
Season × Year	5	0.035	2.36	0.070
Year × Site	3	0.006	0.414	0.133
Site × Season × Year	15	0.009	0.256	0.618
Error	47	0.015		
<b>(c) Acroporidae</b>				
Season	3	0.689	34.52	<b>&lt;0.005</b>
Site	5	0.003	14.29	<b>&lt;0.005</b>
Year	1	0.006	1.32	0.285
Season × Site	15	0.004	0.94	0.554
Season × Year	5	0.002	0.46	0.702
Year × Site	3	0.0003	0.005	0.998
Site × Season × Year	15	0.004	0.003	0.956
Error	47			

ment seasons ( $W_c = 0.93$ ,  $(\chi_r^2)_c = 27.2$ ,  $p = 0.001$ ); however, a significant Season × Site interaction indicated variation in the magnitude of differences among sites depending on time of year (Table 2).

Settlement of Poritidae spat also varied significantly among sites and seasons in both years (Table 2). Overall mean Poritidae settlement was highest on site 4 ( $p < 0.005$ ), and second highest at site 6 all seasons (Fig. 4b). Site 4 had 1.6 to 2.2 times the mean settlement of site 6, and 1.85 to 2.5 times the mean settlement of sites 1 to 3 and 5. Site ranks were concordant among all seasons ( $W_c = 0.83$ ,  $(\chi_r^2)_c = 23.1$ ,  $p < 0.01$ ); however, a significant Season × Site interaction indicated variation in the magnitude of differences among sites depending on time of year (Table 2). The family Acroporidae, the least abundant spat, differed significantly among sites and seasons (Table 2). Acroporidae spat were significantly more abundant between June and August than September and November ( $p < 0.005$ , Fig. 4c). Acroporidae settlement was consistently higher at sites 1 and 2 than all other sites in both years ( $p < 0.001$ , Fig. 4c). Site 1 and 2 had between 2.7 and 5.6 times the mean settlement of sites 3, 4 and 6 and almost 13 times the mean settlement of site 5. Site ranks were highly concordant among seasons ( $W_c = 0.67$ ,  $(\chi_r^2)_c = 18.1$ ,  $p < 0.025$ ), and despite changes in rank order of low settlement sites, there was no significant Season × Site interaction (Table 2), indicating that the magnitude of relative differences among sites were consistent.

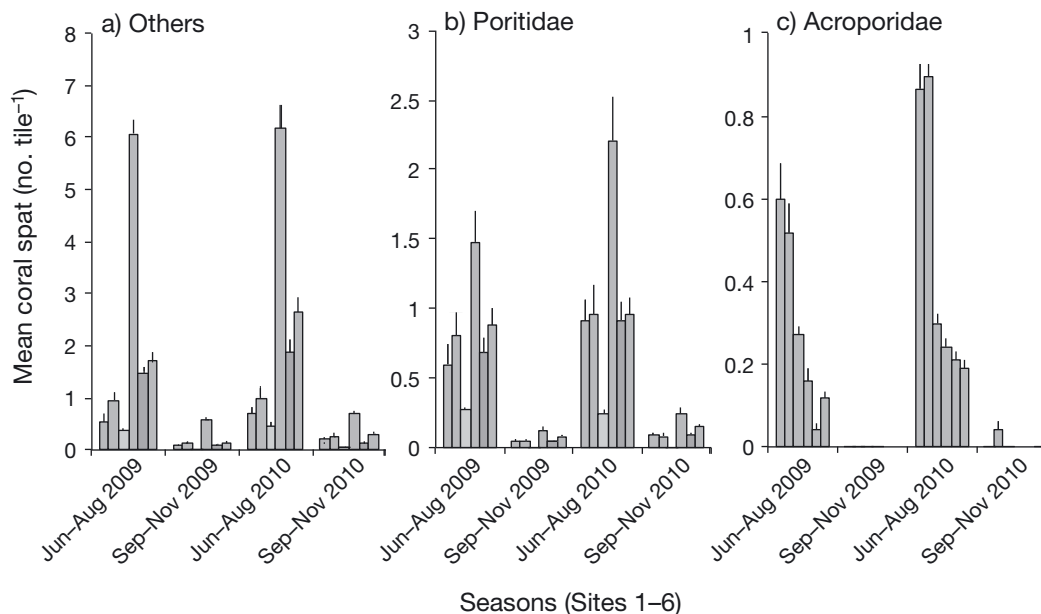


Fig. 4. Mean settlement  $\pm$  SE (20 to 25 tiles site<sup>-1</sup>) of 3 common recruits: (a) Others, (b) Poritidae, (c) Acroporidae for the 6 sites (sites arranged from west to east, see Fig. 1) from June to August and September to November in 2009 and 2010

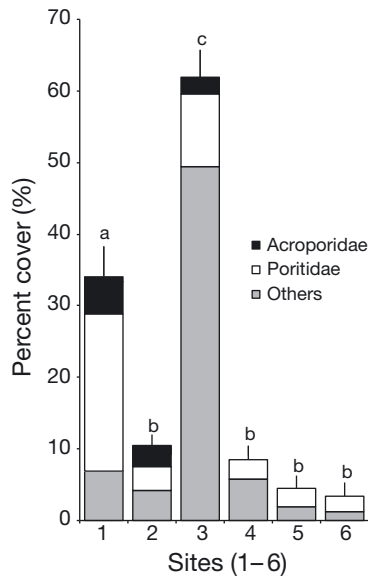


Fig. 5. Percent coral cover at each site (6 sites arranged from west to east, see Fig. 1) broken down by the dominant genera. Data are means  $\pm$  SE, and different letters indicate significant differences (Tukey's test,  $p < 0.05$ )

#### Local coral assemblage structure

Coral cover differed significantly among the sites ( $F = 191.45$ ,  $df = 5, 30$ ,  $p < 0.001$ ), with significantly higher coral cover at sites 1 and 3 than all other sites (Fig. 5). The most common genera were *Porites* ( $35.7 \pm 3.1\%$ ), *Cyphastrea* ( $25.3 \pm 4.6\%$ ), *Platygyra* ( $18.1 \pm 2.8\%$ ), *Acropora* ( $7.9 \pm 1.0\%$ ) and *Favia* ( $9.8 \pm 0.7\%$ ). Collectively, these 5 genera accounted for  $>96\%$  of the total coral cover across all sites, while other genera accounted for  $<3\%$  of total coral cover. Percent cover of the common coral genera differed significantly among all sites: *Porites*,  $F = 53.70$ ,  $df = 5$ ,  $30$ ,  $p < 0.001$ ; *Cyphastrea*,  $F = 167.77$ ,  $df = 5$ ,  $30$ ,  $p < 0.001$ ; *Platygyra*,  $F = 112.59$ ,  $df = 5$ ,  $30$ ,  $p < 0.001$ ; *Acropora*,  $F = 9.52$ ,  $df = 5$ ,  $30$ ,  $p < 0.001$ ; and *Favia*,  $F = 23.65$ ,  $df = 5$ ,  $30$ ,  $p < 0.001$  (Fig. 5). Percent cover of *Porites* was highest on sites 1 ( $21.9 \pm 2.3\%$ ) and 3 ( $10.2 \pm 1.6\%$ ) than the other sites (2, 4 to 6), which all had  $<4\%$  cover. Faviids (including *Cyphastrea*, *Platygyra* and *Favia* spp.) were most abundant on site 3 ( $48.5 \pm 4.6\%$ ) (Fig. 5), while *Acropora* cover was only recorded at sites 1 to 3 (Fig. 5).

Mean density of coral spat and mean percent coral cover at the family level were positively correlated in the family Acroporidae (Spearman's  $R = 0.625$ ,  $p = 0.033$ , Fig. 6a). However, significant correlations were not observed at the family level for either Poritidae (Spearman's  $R = 0.431$ ,  $p = 0.112$ ) or spat identified as 'others' (Spearman's  $R = 0.200$ ,  $p = 0.606$ ) (Fig. 6b,c).

#### Seawater temperatures

Mean annual water temperatures pooled among sites in the southern Gulf showed negligible differences between years:  $28.34^\circ\text{C}$  ( $\pm 0.13$  SE) between March 2009 and 2010 and  $28.51^\circ\text{C}$  ( $\pm 0.18$  SE) between March 2010 and 2011. Mean annual temperature ranges varied considerably in both years:  $16.4^\circ\text{C}$  between March 2009 and 2010 and  $16.9^\circ\text{C}$  between March 2010 and 2011. The mean warmest and mean coldest month in both years were identical, with highest temperatures recorded in August ( $34.9^\circ\text{C}$  in 2009 and  $35.2^\circ\text{C}$  in 2010) and the lowest tempera-

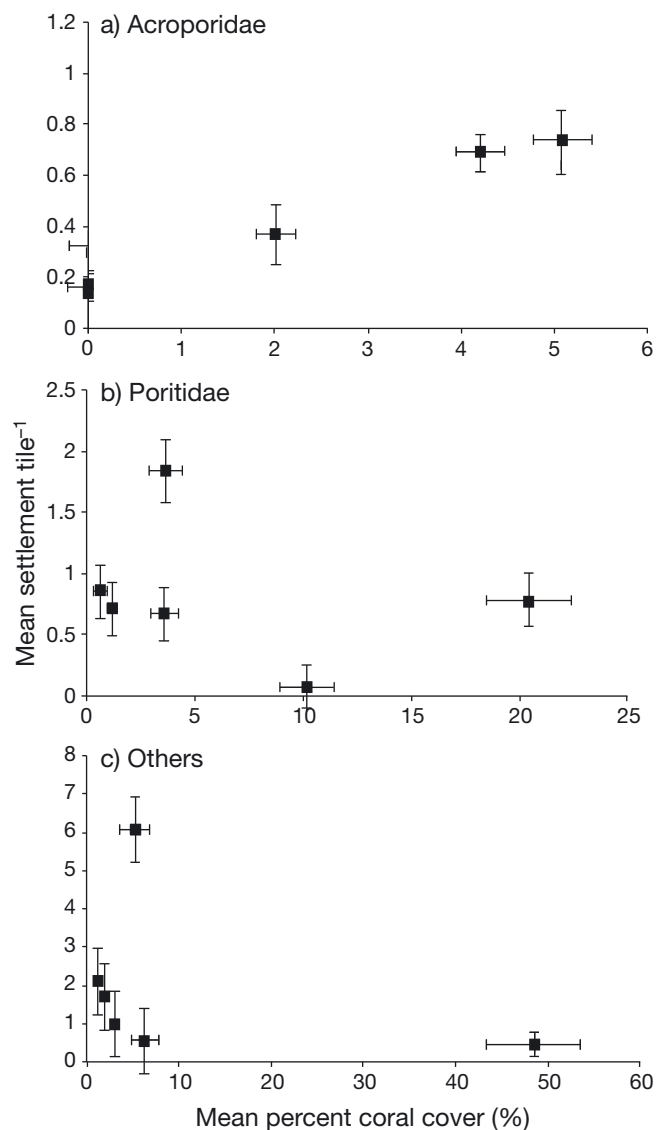


Fig. 6. Relationship between mean adult cover and mean settlement for (a) Acroporidae, (b) Poritidae and (c) Others. Crossed bars represent standard error (SE)

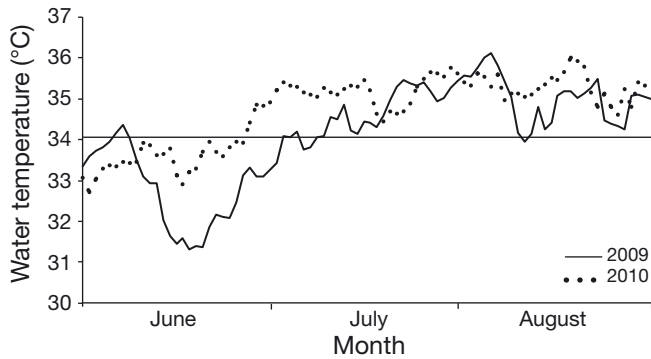


Fig. 7. Mean daily seawater temperatures in Dubai (~5 m depth) during the summer months (June to August) for 2009 and 2010. Black bar indicates mean summer temperature

tures recorded in February (18.5°C in 2010 and 18.3°C in 2011). Summer mean temperatures (i.e. June to August), when the majority of coral spat were observed, were 34.11°C ( $\pm 0.11$  SE) in 2009 and 34.23°C ( $\pm 0.14$ ) in 2010 (Fig. 7). Moreover, temperature loggers recorded temperatures  $\geq 35^\circ\text{C}$  a total of 17 d in 2009, and 23 d in 2010 between July and August.

## DISCUSSION

Coral settlement in Dubai showed a high degree of spatio-temporal variation consistent with patterns reported from other marginal reef environments in the Indo-Pacific (Harriott & Banks 1995, Glassom et al. 2004, Nakamura & Sakai 2010). Overall, rates of coral settlement in Dubai were low ( $\sim 121$  spat  $\text{m}^{-2}$   $\text{yr}^{-1}$ ), but well within the range of values reported from other high-latitude marginal reefs, including the Solitary Islands (132 spat  $\text{m}^{-2}$   $\text{yr}^{-1}$ ; Harriott & Banks 1995) and Taiwan ( $\sim 111$  spat  $\text{m}^{-2}$   $\text{yr}^{-1}$ ; Soong et al. 2003). Coral settlement was highly seasonal with peak settlement in the summer followed by a much smaller settlement pulse in the autumn, while no settlement occurred during spring or winter.

Interestingly, peak settlement occurred when daily-mean temperatures were  $\sim 34^\circ\text{C}$  (June to August), which is above the typical temperatures at which significant increases in larval mortality occur (Edmunds et al. 2001, Bassim & Sammarco 2003, Putnam et al. 2008, Chua et al. 2013). In particular, Baird et al. (2006) and Randall & Szmant (2009) showed that few coral larva can survive at seawater temperatures  $> 32^\circ\text{C}$ , in Japan and the Caribbean, respectively. The fact that coral settlement is occurring at  $34^\circ\text{C}$  indicates that these species have adapted to the extreme environmental conditions in the Gulf.

Highly seasonal patterns of coral settlement are expected because the reproductive output of many coral species is highly seasonal (Baird et al. 2009). Coral species in the southern Gulf (e.g. Acroporidae and Faviidae) also exhibit highly seasonal reproductive patterns (Bauman et al. 2011); however, no coral spat were observed during the peak reproductive period from April to May. Given that comparable coral spawning times have been reported from other locations in the region, including Kuwait (Harrison 1995) and Saudi Arabia (Fadlallah 1996), this was unexpected. Moreover, spawning slicks have previously been observed in April and May along the coast of Abu Dhabi southwest of Dubai (J. Burt pers. comm.). Nonetheless, higher rates of coral settlement outside major spawning events do occur (Babcock 1988, Soong et al. 2003). Babcock (1988), for example, found higher settlement of acroporid species between mid-January and March than in the months following the major spawning period (November/December) on the central Great Barrier Reef (GBR), and suggested that the unusual patterns were caused by strong winds prevailing at the time of spawning that transported larvae off the reef. Likewise, coral larvae in Dubai may have been carried away from reefs due to strong offshore sea breezes generated during the springtime warming of the Arabian Desert (Sheppard et al. 1992, Riegl & Purkis 2012) or from sudden strong wind events known as Shamals. Historical wind records indicate a Shamal wind event (25 to 30 knots) occurred during the April 2009 spawning event (Dubai Municipality: [www.dubai.coast.ae](http://www.dubai.coast.ae)). Short duration Shamal events (24 to 36 h) are considered important wave-generating winds that modify current-strength and flow patterns (Riegl & Purkis 2012).

Given that coral larvae can survive in the water column for periods exceeding 100 d (Graham et al. 2008), and still complete metamorphosis thereafter (Connolly & Baird 2010), coral spat observed from June to August may have originated from corals that spawned in either April or May. Recent research has shown that coral larvae can extend their longevity in the plankton by rapidly reducing their metabolic rates shortly after competency (Graham et al. 2013a). Furthermore, delayed settlement of coral larvae has been shown to have no deleterious effects on post-settlement survival or growth (Graham et al. 2013b). Delayed larval settlement (i.e. the potential to remain in the water column for extended periods of time) is likely to have positive demographic consequences for broadcast-spawning reef-building corals because it increases larval dis-



persal potential, notably enhancing population connectivity (Graham et al. 2013b). Accordingly, it is also possible that the influx of coral spat from June to August originated from coral populations on other reefs, such as the many offshore islands in the Gulf, where corals may spawn at slightly different times compared with those on shallower coastal reefs. Well-developed coral populations on these islands appear well-connected to populations along the UAE coast, based on their position directly within the major current system of the Gulf (Riegl & Purkis 2012). Riegl et al. (2011) suggested that larvae from these populations are likely responsible for the strong regeneration of coral populations in Dubai and Abu Dhabi (Burt et al. 2008, Riegl & Purkis 2009) following recurrent severe bleaching and mortality events in 1996 and 1998.

An alternative explanation for discrepancies between peak timing of settlement, relative to peak spawning (Bauman et al. 2011), may relate to differences in the taxonomy of coral considered in each of these studies. At least some corals in the Gulf may release gametes outside of predicted spawning periods (Baird & Guest 2009, Baird et al. 2009). For example, many *Acropora* species on the GBR spawn up to 2 mo later than previously documented (Baird & Guest 2009, Baird et al. 2009). Clearly, an extended reproductive season is likely to lead to an extended period of coral settlement, at least in some years. Similarly, reports from Dubai (Bauman et al. 2011) and Kuwait (Harrison et al. 1997) found that some species in the Gulf may have extended spawning seasons during late spring and early summer. Bauman et al. (2011) found mature colonies of *Cyphastrea micropthalma* prior to the full moon in June, while colonies of *Platygyra daedalea* were observed spawning in Kuwait after the full moon in June (Harrison et al. 1997). It is therefore likely that a proportion of the coral spat observed from June to August in Dubai were the result of extended reproductive cycles in some species. Clearly, further research on the reproductive biology and larval ecology of coral species in the Gulf is necessary to improve our understanding of the temporal patterns of coral settlement in this area.

Aside from the apparent temporal patterns, the results also showed strong, consistent spatial heterogeneity in coral settlement with marked variation in the abundance of coral spat among the 6 sites. Most interestingly, there were significantly higher numbers of coral spat at site 4 compared with the other sites, and its recurrence among all sampling seasons when spat were observed, suggesting that

this is possibly a product of natural systematic processes rather than chance events (Fig. 2). Sites that receive consistently higher levels of settlement are known as 'recruitment hotspots' (*sensu* Booth et al. 2000), and may be crucial to the persistence of populations (Eagle et al. 2012). Recent studies suggest that both deterministic and stochastic processes may affect settlement variation at these scales (Eagle et al. 2012). For example, Eagle et al. (2012) recently detected 'hotspots' in the lagoon and on the reef slopes at One Tree Island on the southern GBR for different coral families (i.e. Pocilloporidae, Poritidae and Acroporidae). Results indicated that the rank order of settlement among sites at One Tree Island may be highly predictable, even though the magnitude of differences may vary from year to year (Eagle et al. 2012). Although there was congruence among hotspots for different families of coral spat, hotspots were associated with differences in water flow (i.e. hydrodynamics) and the abundance of adult conspecifics. Further work is required to determine the specific mechanisms behind the patterns of settlement observed at site 4, and whether this is an annual reoccurrence.

The composition of coral spat in Dubai differed considerably from those reported on most reefs in the Indo-Pacific (Fisk & Harriott 1990, Baird & Hughes 1997, Hughes et al. 2000) because there were few Acroporidae coral spat and no Pocilloporidae. Most coral assemblages in the Indo-Pacific are dominated by spat from the families Acroporidae, Pocilloporidae or Poritidae (e.g. Hughes et al. 1999, Glassom et al. 2004). These differences are readily explainable by the adult assemblage structure in the southern Gulf, with Faviidae and Poritidae accounting for >89% of the total coral cover. Moreover, the family Pocilloporidae was notably absent throughout this study. Although Pocilloporidae is among the most widespread and ecologically tolerant coral families in the Indo-Pacific (Veron 2000), it is rare throughout much of the Gulf (Sheppard et al. 1992, Riegl 1999, Burt et al. 2008). More important, however, is the loss of the formerly dominant *Acropora* species on these reefs prior to recurrent bleaching events (Riegl 1999, Riegl et al. 2011), which now appears to be affecting the supply of coral spat. Given the increasing incidence of severe bleaching events in the Gulf (Riegl & Purkis 2012), it is unlikely that *Acropora* species will increase in abundance any time soon.

Apart from taxonomic dissimilarities of coral spat on reefs in Dubai and the rest of the Indo-Pacific, there were also marked differences in the composi-

tion of coral spat and the corresponding local abundance of adult corals among individual sites. The results indicated that an apparent positive correlation (*sensu* Caley et al. 1996) exists for Acroporidae at very fine spatial scales (>1 km), but not for Poritidae or other corals. These results require cautious interpretation, however, because we did not measure fecundity simultaneously with rates of settlement (Hughes et al. 2000) or assess the importance of post-settlement processes (Gosselin & Qian 1997). Penin et al. (2010), for example, found a positive relationship between the distribution of adult colonies and juvenile corals (1 to 5 cm diameter) in French Polynesia, but no relationship between adults and newly settled spat (corals  $\leq 3$  mo old); they implicated fish grazing as the source of post-settlement mortality on recruits. Newly settled corals often experience high mortality rates due to overgrowth by macroalgae, competition from other benthic organisms, sedimentation and predation (see review by Ritson-Williams et al. 2009). Given the importance of the early post-settlement period in the life cycle of corals, it is highly likely that these processes are also contributing to the structuring of coral assemblages in the Gulf, and therefore warrants further examination.

In summary, coral settlement rates in the Persian Gulf are low but highly seasonal despite the extreme environmental conditions (i.e. seawater temperatures) and high frequency disturbance events (i.e. bleaching). Importantly, there is clear evidence of ongoing coral settlement. However, the composition of coral spat was highly distinct from other regions in the Indo-Pacific, reflecting the current local condition of the adult assemblages (Riegl & Purkis 2009, Riegl et al. 2011). Furthermore, the current patterns of settlement reinforce previous claims of long-term shifts in community structure away from formerly dominant *Acropora* species towards more robust coral species (Poritidae and Faviidae) that are more resistant to ongoing disturbances (Riegl & Purkis 2009). Although corals in the Persian Gulf have clearly adapted to the extremes experienced, it appears unlikely that they can maintain the current assemblage structure in the face of sustained and ongoing disturbances.

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