Spatio-temporal variability of coral recruitment on shallow reefs in St. John, US Virgin Islands

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ABSTRACT
In this study, coral recruitment was measured on a kilometer-wide scale over two years on shallow (5–6 m depth) fringing reefs in St. John, US Virgin Islands, with the objective of determining the extent to which variation in recruitment was affected by biophysical coupling involving temperature and flow. Coral recruitment was measured using settlement tiles deployed at 10 sites along 10 km of shore. The tiles were first deployed in August 2006, and thereafter replaced every ≈ 6 months to sample from either August to January, or January to August over 2 years. seawater temperature was recorded at the 10 sites using logging thermistors, and flow was quantified using drogues. Overall, corals recruited at a rate equivalent to 76 corals m–2 6 months–1, and were represented mostly by poritids (43% of recruits), agaricids (29%), favids (17%) and sidestraeids (7%). Although the density of recruits differed among sites in a pattern that varied among periods and years, there was a consistent trend for mean density to decline from ≈ 4 corals tile–1 at eastern sites, to ≤ 1 coral tile–1 at western sites. One aspect of seawater temperature – the daily range – differed among sites and was greatest at western compared to eastern sites, and while it was related inversely to recruitment over one of the sampling periods, it was equivocal as a physical process affecting recruitment. Instead, our results are consistent with biophysical coupling involving patch depletion and downstream filtering, whereby patches of coral larvae are delivered to the south shore of St. John and depleted of larvae through settlement as the water progresses westward.

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1. Introduction
For the large number of marine communities dominated by taxa releasing pelagic larvae (Cow and Sponaugle, 2009), considerable effort has been expended to evaluate the extent to which populations are regulated by larval supply and recruitment (Gaines and Roughgarden, 1985; Morgan, 2001; Underwood and Keough, 2001). This effort emerged in the 1980s under the moniker "supply-side ecology" (Lewin, 1987), and the topic is still the subject of review (Cowan and Sponaugle, 2009; Jones et al., 2009). Over much of this period, marine populations were considered demographically "open", with larvae coming from (and going to) a diversity of locations, and only limited reason to expect a relationship between the distribution of adults and recruits (Caley et al., 1996). Over the last 10 years, however, evidence emerged that marine populations can retain pelagic larvae and self-seed, even when the life histories of the component taxa and hydrodynamic conditions suggest that dispersal should be extensive (Cow and Sponaugle, 2009). These findings have prompted a reappraisal of the generality of the open population model, and the new consensus suggests that marine populations are better viewed on a gradient between open and closed with regard to dispersal, recruitment, and dynamics (Cow and Sponaugle, 2009; Jones et al., 2009).

On tropical coral reefs, the recruitment of scleractinians has been measured for decades (Lewis, 1974; Bak and Engel, 1979; Rogers et al., 1984; Connell et al., 1997; Dunstan and Johnson, 1998; Glasson et al., 2004; Adjeroud et al., 2007) with the objective of understanding the processes sustaining coral populations. Settlement tiles have been used in most of these studies – although recruits have been counted directly on natural substrata in a few cases (e.g., Piñaïk et al., 2005; Baird et al., 2006; Vermej and Sandin, 2008; Roth and Knowlton, 2009) – and virtually all have revealed variation at every scale of analysis. The density of coral recruits typically differs among seasons and years (Banks and Harriott, 1996; Harriott, 1999; Dunstan and Johnson, 1998), among settlement tiles placed in a single deployment as well as among sites separated by meters, kilometers or hundreds of kilometers (Fisk and Harriott, 1990; Pleason, 1996; Dunstan and Johnson, 1998; Hughes et al., 1999, 2000; Adjeroud et al., 2007). In contrast to density, the taxonomic composition of recruiting corals is more consistent, at least based on the limited resolution (usually to family) that can be applied to small corals. For instance, coral recruits are consistently dominated by poritids, agaricids, favids, and sidestraeids in the Caribbean (Carlon, 2001; Tougas and Porter, 1992; Smith, 1997; Vermej and Sandin, 2008), and by poritids, pocilloporids, and acroporids in the Pacific (Dunstan and Johnson, 1998; Hughes et al., 1999, 2000; Adjeroud et al., 2007; Edmunds et al., 2010). Family-
level assemblages do, however, change throughout the year in a pattern predictable from the timing of spawning or larval release of individual taxa (Adjeroud et al., 2007).

In light of the spatio-temporal variability in coral recruitment, and uncertainty over the extent to which populations might be open or closed (Caley et al., 1996; Cowan and Sponaugle, 2009), it is not surprising that tests for association between adult corals and their early life-stages have been equivocal. Some studies have reported a significant association (Chiappone and Sullivan, 1996; Vermeij and Sandin, 2008) reminiscent of a stock-recruitment relationship (Shepherd, 1982), but others have found the distributions to be unrelated (Bak and Engel, 1979; Edmunds, 2000). These results require cautious interpretation, however, because the common use of juvenile corals as a proxy for recruits overlooks the importance of post-settlement mortality in modifying the distribution at settlement (Gosselin and Qian, 1997; Hunt and Scheibling, 1997). The importance of post-settlement events in modifying the distribution of corals has recently been underscored by Penin et al. (2010), because their results from Moorea (French Polynesia) revealed a positive association between the distribution of adult (colonies > 5-cm diameter) and juvenile (colonies 1–5 cm diameter) corals, but no relationship between adults and new recruits (corals ≤3 months old); their findings implicated fish predation as a source of post-settlement mortality affecting new recruits.

The demographic role of coral recruitment in population regulation may be modified for some species where the negative demographic consequences arising from the death of large colonies can eclipse the positive effects of recruitment (Edmunds and Elahi, 2007). In this case, recruitment within the range of ecologically relevant densities was unable to halt population decline (Edmunds and Elahi, 2007), and, therefore, recruitment appeared decoupled from the population dynamics of adult corals. Despite the challenges such observations create for the task of elucidating the role of recruitment in coral populations, this undertaking remains important because sexually produced larvae remains the most common means by which coral populations are established on vacant substrata (Done et al., 1991; Dunstan and Johnson, 1998; Vermeij and Sandin, 2008). Describing spatio-temporal variation in coral recruitment, and testing for mechanisms that might drive these patterns are, therefore, important steps in understanding the distribution of corals.

The present study was motivated by the notion that there is still much to learn about coral populations from spatio-temporal variation in coral recruitment. While coral recruitment has been the topic of numerous investigations (cited above), surprisingly few have explored variation over kilometers and years, and where such variation has been addressed, mechanisms driving the patterns have often remained elusive (but see Hughes et al. 1999, 2000; Penin et al., 2010).

In the present study, shallow (5–6 m) fringing reefs along the south shore of St. John, US Virgin Islands, were used to explore the occurrence and causes of spatio-temporal variation in coral recruitment. These reefs provide a good model system in which variation in coral recruitment can be studied, because their ecology is well known, and most are located within a marine protected area (reviewed in Rogers et al. (2008)). Additionally, earlier studies of juvenile corals (≤40-mm diameter) on the same reefs suggested that corals recruited at high densities, but in a pattern that varied among sites separated on a scale of kilometers (Edmunds, 2000); preliminary analyses suggested that seawater temperature and flow differed on a comparable scale (Horst and Edmunds, in press). It was reasonable to hypothesize, therefore, that this biological process (recruitment) might be coupled with these physical phenomena (temperature and flow). Our specific goals were first, to describe spatio-temporal variability in the recruitment of scleractinian corals in St. John, and second, to explore biophysical coupling involving seawater temperature and flow as possible mechanisms to account for this variability.

2. Methods

2.1. Study sites

To test for spatio-temporal variation in coral recruitment and physical processes, 10 sites were selected along 10 km of the south shore of St. John (Fig. 1). These sites were chosen to sample across gradients in exposure to waves and thermal microenvironments, ranging from high flow with offshore temperatures (headlands and their east-facing sides) to low flow with localized warming (within semi-enclosed bays). These gradients were not quantified prior to the study, but their existence was known from years of working in this location (P(J Edmunds personal observations), and by sampling coral recruitment across them, it was possible to explore the influence of two physical processes that have strong effects on pelagic larvae. All sites were within ≈10 m of the shore on fringing reefs at 5–6 m depth, where they sampled habitats characterized by ≈5% cover of scleractinian corals, and ≈50% cover of macroalgae (P(J Edmunds, unpublished data from 2007).

The study began in 2006, and consisted of 4 sampling periods of ≈6 month duration: August 2006 to January 2007, January 2007 to August 2007, August 2007 to January 2008, and January 2008 to August 2008. These periods were chosen to capture seasonal variability in physical and biotic effects, although logistical constraints prevented sampling in synchrony with the astronomic seasons. The January to August sampling was characterized by low (e.g., 26.8 ± 0.1 °C, n = 207 d) but increasing seawater temperatures, whereas August to January was characterized by warm (e.g., 28.4 ± 0.1 °C, n = 173 d) but cooling temperatures (both mean ± SE based on 2008 data from 9-m depth at Yawzi Point (Fig. 1)). The northeasterly trade winds drive the prevailing waves, and therefore the south shore is protected virtually all year; occasional storms and hurricanes that pass to the south of St. John bring large waves to this shore.

2.2. Coral recruitment

Coral recruitment was measured using settlement tiles (15 × 15 × 1 cm) that were deployed in a design modified from the recommendations of Mundy (2000). The modifications affected the mode of attachment, but retained the statistical independence of each tile, the approximate horizontal deployment, and the creation of a cryptic microhabitat beneath the tile. The tiles were unglazed terracotta with a smooth top and a rough underside, and were placed beneath the dock in Great Lameshur Bay for ≈6 months prior to deployment. Each tile was fixed approximately horizontally to the reef using a stainless steel epoxied into dead coral skeletons, and was installed rough side down with a 1–2 cm gap between the tile and the reef to create a cryptic environment favored by settling coral larvae (Rogers et al., 1984; Mundy, 2000). At each site, tiles were clustered haphazardly within an area of ≈5-m radius, with individual tiles ≤0.5 m apart; 10 tiles/site1 were installed in the first year, however this number was increased to 15 tiles/site1 in the second year in order to increase the total number of coral recruits detected on the tiles, and increase the statistical replicates (i.e., tiles) for the site contrast.

Following the first deployment in August 2006, settlement tiles were collected and replaced at approximately 6-month intervals in January and late July/August. Freshly-collected tiles were soaked in dilute bleach to remove living tissue, and then rinsed and air dried before inspecting for coral recruits. Following scoring, the tiles were cleaned of CaCO3 structures in dilute HCl and returned to beneath the reef (Rogers et al., 1984; Mundy, 2000). At each site, tiles were clustered haphazardly within an area of ≈5-m radius, with individual tiles ≤0.5 m apart; 10 tiles/site1 were installed in the first year, however this number was increased to 15 tiles/site1 in the second year in order to increase the total number of coral recruits detected on the tiles, and increase the statistical replicates (i.e., tiles) for the site contrast.

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and taxonomic criteria developed from personal observations, field guides (Veron, 2000), keys (Smith, 1971), and discussions with colleagues (SR Smith and RS Steneck, personal communications to DHG). The most important diagnostic features for identifications were the orders and numbers of septae, the characteristics of the columella, and the development of the thecal wall (if any).

2.3. Seawater temperature

Seawater temperature was recorded using temperature loggers (Hobo WaterTemp Pro V2, ±0.2 °C precision) (Onset Computer Corp., Bourne, MA), with one instrument secured against the substratum in the center of the cluster of tiles at each of the 10 sites (Fig. 1). The loggers recorded temperature every 30 minutes, and were retrieved, downloaded, and replaced at the same time the settlement tiles were exchanged. Prior to deployment, all ten loggers were cross-calibrated by bundling them together under the dock in Great Lameshur Bay and setting them to record temperature every 30 min for 24 h. One of the 10 loggers was selected haphazardly as the reference logger, and the remaining 9 were used with a small correction factor that ensured accuracy relative to the reference logger.

2.4. Seawater flow

To characterize the seawater flow, a section of the shore was chosen based on the marine access that was possible for deployment and recovery of drogues using small boats (~3-m length). This area extended 1.4 km from Cabritte Point to White Point, and served to delineate the area over which the drogues were deployed for short durations during the day. The drogues were based on the design of Austin and Atkinson (2004), and were constructed from PVC pipe with 16 × 28 cm vanes that were suspended from a floating canister (30 cm × 8 cm diameter) with their upper edges ≈ 10 cm beneath the surface. The canister contained a logging GPS (RINO 110, Garmin International Inc.) that recorded position, speed, and direction moved at variable intervals from 30 s to 4 min depending on distance moved. The canister was also marked with a small flag (5 × 5 cm) that assisted in the relocation of the drogues without providing substantial wind drag that might affect their movement. The drogues were released on multiple occasions during the field campaigns, and were allowed to drift freely for 30–120 min with the duration determined in part by how rapidly they moved beyond a range from which they could be retrieved safely using small boats.

Two drogues were available, and were typically deployed in a paired configuration during August 2007, January 2008, and August 2008. The drogues were deployed in three broadly defined locations that were selected to sample areas differing in water motion. One location was south of Cabritte Point and sampled exposed conditions; one in the lee of Cabritte Point and sampled partially protected conditions; and one near the northern shores of the sheltered bays that sampled fully protected conditions. Once deployed, the GPS in each drogue logged position and speed continuously, and these data were downloaded upon drogue recovery. These data (i.e., waypoints) were recorded at either fixed intervals of time or whenever the drogue changed position, whichever occurred sooner, and therefore each deployment generated multiple waypoints that allowed speed and direction to be computed over multiple segments of travel (i.e., “legs”) with each marked at the start and end by unique waypoints. Each deployment generated >25 legs that were analyzed in two ways. First, speed and direction of each drogue were averaged by deployment to create a single measurement of each variable. Second, all the legs for multiple deployments in each of the three locations were analyzed with circular histograms to gain finer resolution in determining the movement of water within each of the three locations. Circular histograms (with a resolution of 20°) together with the mean ± SE of leg directions were calculated and displayed using the software package Oriana 2.02e (Rockware USA, Golden, CO).

2.5. Statistical analyses

A 3-way, Model II ANOVA was used to compare the density of coral recruits (pooled among taxa) over space and time. In this design, sites and periods (August to January, and January to August) were fixed factors, year was a random factor, and individual settlement tiles provided statistical replicates for the density of recruits. The densities of recruits were square-root transformed to restore normality (Sokal and Rohlf, 1995). To test for changes in the relative abundance of coral recruits by family across periods and years, a 3-way contingency table with log-linear analysis was used to compare the number of recruits among taxa (families), periods (August to January versus January to August), and years; a χ² statistic was used to evaluate significance. Due to the small number of siderastreid recruits, this taxon was pooled with
the “other” category to satisfy the statistical requirement of a mean expected cell frequency of 6 (Zar, 2010). To gain insight into the taxon causing the trends detected in the 3-way analysis, the multi-way table was subdivided and analyzed as $2 \times 2 \times 2$, χ²-contingency tables by taxon. Two-way contingency tables were used to test for variation in the relative abundance of recruiting coral taxa among sites. This analysis was completed for each sampling period after pooling among years to increase the observed frequency of each taxon.

An initial screening of the temperature records revealed that the most striking variation involved diurnal warming that differed among site. Additional metrics describing daily seawater temperature (mean, high, and low) varied little among sites and were not analyzed further (and are not displayed here). The daily ranges in temperature were compared with respect to means and SE (based on days as replicates) among sites and years, but were not compared statistically because daily temperature records are serially auto correlated and violate the assumption of independence for both parametric and non-parametric procedures. The autocorrelation was statistically significant ($P<0.05$) out to a time separation of at least 60 days (results not shown) and, therefore, it was not feasible to sub-sample the data at the frequency necessary (>60 d) to ensure independence. Finally, an association between the density of coral recruits and the daily variation in seawater temperature was tested individually for the four sampling periods using sites as replicates and Pearson correlations as the inferential tool.

All statistical procedures were completed using Systat 11.0 running on a Windows platform. The statistical assumptions of ANOVA were tested through graphical analyses of the residuals.

### 3. Results

#### 3.1. Coral recruitment

On average, $1.70 \pm 0.11$ coral recruits tile$^{-1}$ ($\pm$ SE, $n=500$ tiles) were found at each sampling over the two year study, with a total of 846 recruits representing agaricids (29%), poritids (43%), favids (17%), sidereaids (7%), and others (4%); all were on the lower surfaces of the tiles. As the tiles were in place for ~6 months, and all corals recruited to the lower surface, the mean density indicates that the rate of recruitment was ~76 corals m$^{-2}$ 6 months$^{-1}$.

The density of coral recruits was affected significantly by a three-way interaction among sites, periods, and years ($F_{9,460}=2.29$, $p=0.02$) (Table 1), with the interaction driven by differences among sites that varied between years in a pattern that was accentuated between January and August compared to August to January. Additionally, the density of coral recruits differed among sites ($F_{9,9}=8.43$, $p<0.01$) and years ($F_{1,460}=36.85$, $p<0.01$) (Table 1). Between August and January, the highest mean density of recruits was $3.33 \pm 1.35$ corals tile$^{-1}$ at Kiddel Bay over 2007/2008, and the lowest was $0.10 \pm 0.10$ corals tile$^{-1}$, which was recorded at Ditliff Point and also Europa Bay over 2006/2007 (all ± SE, $n=10$–15 tiles) (Fig. 2). Between January and August, the highest mean density of recruits was $3.60 \pm 1.80$ corals tile$^{-1}$ at Kiddel Bay in 2007, and the lowest was $0.10 \pm 0.10$ corals tile$^{-1}$ at Cabritte Point in 2007 (all ± SE, $n=10$ tiles) (Fig. 2). For both periods, there was a trend for the density of coral recruits to decline from east to west, and this trend was repeatable between years (Fig. 2).

Four percent of coral recruits were damaged or unidentifiable and scored as unknown. In all sampling years, poritids were the most common recruits between January and August, when overall (i.e., pooled among sites) they made up 59% of the corals, and agaricids were the most common between August and January, when overall they made up 43% of the recruits. The abundances of favids did not vary noticeably between the sampling years or periods, and they represented 14% and 21% of the recruits between January and August and August and January, respectively. Siderastreids accounted for <7% of the recruits throughout the study, and only one acroporid recruit was encountered (at Cabritte Point between August and January over 2007/2008). Although analyses of percentage composition of the coral recruits by family at each site was made problematic by the small number of recruits found at some of the sites on some of the samplings (e.g., 1 recruit was found at any one site on three occasions through the study), nevertheless, this analysis confirmed the dominance of the recruiting population by poritids and agaricids. Based on the two-year sampling, poritids accounted for 43% to 81% of the recruits at each site between January and August, and between 7% and 69% of the recruits at each site between August and January; agaricids accounted for 7% to 28% of the recruits at each site between January and August, and between 24% and 83% of the recruits at each site between August and January (Fig. 3).

The abundance of recruits by taxon (Poritidae, Agaricidae, Faviidae, and “other”) was dependent on year and period ($\chi^2=144.46, df=9, p<0.010$) with, for example, poritids > 3-fold more abundant than any other taxon between January and August 2008, but only twice as abundant at the next most numerous taxon (Faviidae) between January and August 2007 (Table 2). To gain further insight into which taxon was most influential in driving this pattern, the three-way contingency table was subdivided by taxon and the analysis repeated for $2 \times 2$ (period × year) contingency tables. The abundances of recruiting favids, agaricids, and “other” taxa were affected by period and year of analysis ($\chi^2>2.453, df=1, p<0.039$), but the abundance of poritid recruits were unaffected by year or period ($\chi^2=0.635, df=1, p=0.425$). The taxonomic composition of the recruiting corals did not vary among sites between January and August ($\chi^2=38.319, df=27, p=0.073$), although it did between August and January ($\chi^2=46.01, df=27, p=0.013$), with the differences caused by small departures from expectation at multiple sites rather than a consistent directional gradient from east to west.

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Table 1 Results of a 3-way, mixed model ANOVA testing for differences in density of coral recruits on settlement tiles among periods (fixed factor), sites (fixed factor) and years (random factor). The effect of period was tested over the MS(period × year), the effect of Sites was tested over MS(site), and the effect of period × site was tested over MS(site × period × year); all other effects were tested over MS(error).

3.2. Seawater temperature

There was strong diurnal warming of seawater adjacent to the benthos at all sites throughout the year, with the highest daytime temperature differing as much as 1.6°C from the lowest nighttime temperature. The mean daily range in temperature was similar between the cooling (August to January) and the warming (January to August) portions of the year, as well as among years, although both the high and low extremes of daily variation were recorded between January and August. The largest mean daily range (0.6°C) was recorded at Europa Bay, and the lowest (0.3°C) at Booby Rock. Based on the means and non-overlapping SE values, the daily range in temperature exhibited interactive effects arising from site, period, and year (Fig. 2). For instance, the daily range in temperature was greater at Site 4 than other sites between January and August, but was only slightly larger than at some of the sites between August and January. Similarly, the daily range in temperature was larger at Tekite that at Yawzi Point between August and January of 2007–08, but in the previous year (2006–07), it was similar between these sites. Despite evidence of interactive effects, overall, the among-site variation in the daily range in seawater temperature was...
similar among periods and years, and tended to be small at eastern sites, and large at western sites (Fig. 2).

3.3. Seawater flow

Surface water motion determined from drogues deployed in the winter and summer was slow in the coastal area delineated by White Point and Cabritte Point, with a mean speed of 12±1 cm s\(^{-1}\) (± SE, \(n=15\) deployments each averaging 63 min duration). Flow speed did not vary among the three deployment locations (\(F_{2,12}=0.46, p=0.642\)), with drogues deployed in sheltered localities (i.e., in the lee of headlands) moving at 11±2 cm s\(^{-1}\), those in exposed areas to the south of headlands moving at 14±2 cm s\(^{-1}\), and those near the northern shores of sheltered bays moving at 11±3 m s\(^{-1}\) (all mean±SE, \(n=4\) to 6 deployments averaging 37–121 min duration).

The analysis with circular histograms of drogue movement based on legs of travel (rather than by deployments, as above) revealed more detail regarding the direction of seawater motion. The mean flow direction for all legs of the 15 deployments was 282±3° (\(n=739\) legs), and for each of the three release locations, the mean direction of movement varied between 274±5° (\(n=198\) legs) and 286±5° (\(n=334\); all ± SE) (Fig. 4). These analyses also revealed that the drogues tended to drift north into the bays (with drogue legs recorded in the 0–20° sector), and in the lee of Cabritte Point/Tektite some drogue legs were recorded in the 80–100° sector (Fig. 4).

3.4. Association between recruitment and temperature

The analysis of coral recruitment and daily variation in seawater temperature at the 10 sites along the south coast of St. John revealed an inverse relationship between these variables (Fig. 5); recruitment tended to be higher at sites with more stable thermal environments (i.e., reduced daily variation) towards the east. Although these trends were not significant for recruitment between January and August in 2007 and 2008 (\(r_{b} |0.59|, df=8, p>0.07\), or between August and January of 2007–08 (\(r=−0.45, df=8, p=0.20\), the relation was statistically significant between August and January of 2006–07 (\(r=−0.64, df=8, p=0.05\)).

4. Discussion

The objectives of this study were to evaluate variability in the recruitment of scleractinian corals on the fringing reefs of St. John, and explore the role of biophysical coupling through seawater temperature and flow as causal mechanisms for the patterns observed. The results from 24 months over three years revealed a high degree of spatio-temporal variation in the density and taxonomic composition of recruits, yet there was also evidence of a strong and repeatable gradient of recruitment with high densities in the east and low densities in the west. Aspects of these results are consistent with previous studies of coral recruitment that report spatio-temporal variation at virtually every scale that has been examined (Fisk and Harriott, 1990; Gleason, 1996; Dunstan and Johnson, 1998; Hughes et al., 1999, 2000; Adjeroud et al., 2007), and the variability in the present analysis can easily be reconciled with contemporary theories addressing recruitment in marine taxa with bipartite life cycles (Cowan and Sponaugle, 2009; Jones et al. 2009). However, the westward decline in coral recruitment along the south shore of St. John is unusual, and its recurrence among four sampling intervals suggests that it is a product of systematic processes rather than chance events. Our analyses of temperature and
The rate of coral recruitment in St. John was within the range of values reported for the Caribbean over the last 26 years (i.e., Rogers et al., 1984; Tomascik, 1991; Smith, 1992; Carlzon, 2001). For instance, the grand mean recruitment rate was 76 corals m\(^{-2}\) 6 months\(^{-1}\), whereas Rogers et al. (1984) recorded \(\approx 23\) corals m\(^{-2}\) 3 months\(^{-1}\) at 9-m depth in St. Croix, Tomascik recorded \(\approx 213\) corals m\(^{-2}\) 12 months\(^{-1}\) at 1.4–4 m depth in Barbados. Smith (1992) recorded \(\approx 37\) corals m\(^{-2}\) 2 months\(^{-1}\) at 5–7 m depth in Bermuda, and Carlzon (2001) recorded 133–333 corals m\(^{-2}\) year\(^{-1}\) at 6-m depth on Guana Island (British Virgin Islands). On a broader scale, compilations of studies reporting coral recruitment in the Caribbean and Pacific reveal densities of 2–4590 corals m\(^{-2}\) year\(^{-1}\) (Smith, 1992; Glassom et al., 2004). The recruits detected in the present study serve as the demographic foundation of local coral populations, with recruits that survive contributing to the density of adults. While it was beyond the scope of this study to quantify this critical demographic property (i.e., survivorship of recruits), with densities of 14–22 colonies m\(^{-2}\) for juvenile corals (\(\leq 4\)-cm diameter) on the same reefs (Edmunds, 2004), it is likely that only \(\approx 10\) of the coral recruits survive their first year. Low rates of survivorship are common for invertebrate recruits (Glassell and Qian, 1997), including tropical reef corals (Dunstan and Johnson, 1998; Vermeij and Sandin, 2008) yet, little is known of the factors contributing to their death. Vermeij and Sandin (2008) suggested that microbial pathogens could drive inverse density dependence of survivorship among Siderastrea radians recruits in the Caribbean, and more recently, Penin et al. (2010) implicated the roles of grazing and corallivory by fishes on a Pacific reef as important factors causing high mortality of coral recruits.

In addition to the occurrence of coral recruits at densities similar to those expected from previous studies, the taxa that recruited were broadly the same ones that have dominated surveys of coral recruits and early life history stages on Caribbean reefs for decades. Poritids and agaricids were the most striking recruits that were common in this study as well many others (i.e., Bak and Engel, 1979; Rylaarsdam, 1983; Rogers et al., 1984; Smith, 1992; Carlson, 2001; Edmunds, 2002), although faviids (mostly Favia fragum) (Table 2) have also been conspicuous in surveys for early life stages of corals (Rogers et al., 1984; Smith, 1992; Edmunds, 2000). While the quantification of the corals that settle onto tiles has advantages in providing estimates of recruitment that are more ecologically relevant than, for example, estimates derived from densities of juvenile corals, settlement tiles also have limitations (Harriott and Fisk, 1987; Mundy, 2000; Thomasin et al., 2002). Aside from the unavoidable debate regarding the similarity of recruitment on tiles versus natural surfaces (Mundy, 2000; Norstrom et al., 2007; Nozawa, 2008), which is at least circumvented when tiles within a study are used to compare relative rates of recruitment (sensu Hughes et al., 2000), the necessity of quantifying corals from a single settlement event cannot be rejected when only a coarse taxonomic resolution is applied.

Even though our analysis was based on a coral families, we are confident that most recruits were P. astreoides (yellow morph), P. porites, P. furcata, F. fragum, Agaricia agaricites, A. humilis, S. radians, and S. siderea.; we are also confident that Montastrea annularis did not recruit onto any tiles, and that only one Acropora was found on the tiles throughout the study. These assertions are based on decades of censusing juvenile corals on the same reefs where these taxa are the dominant corals encountered (Edmunds, 2000; 2004), a small number of taxa that are distinct when small (e.g., Acroporidae [Babcock et al., 2003]), and a few cases where recruits grew fast and achieved a size that made identification easier. Based on this conservative estimate of the species assemblage on our tiles, the majority of recruits represented corals with brooding life-history strategies (although S. siderea spawns [Szmant, 1986]), and the variation in familial abundance between

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**Fig. 3.** Bar graphs displaying the percentage contribution of the most abundant families (Poritidae and Agaricidae) of coral recruits to the population of coral recruits on settlement tiles at the 10 sites between January and August (A) and August and January (B); numbering on the abscissa refers to study sites as in Fig. 1. All values are means ± SE, based on \(n = 2\) sampling years, with 373 coral recruits between January to August periods, and 239 between August to January periods.

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**Table 2.** Three-way contingency table displaying the number of coral recruits by taxon on settlement tiles deployed over two periods (August to January and January to August) and over two years. Due to small sample sizes, results were pooled for siderastreids and corals that could not be identified ("others"). The number of corals in each taxon was dependent on the year and season of investigation (log-linear analysis, \(\chi^2 = 144.46, df = 9, p < 0.01\)).

<table>
<thead>
<tr>
<th>Year</th>
<th>Sampling period</th>
<th>Taxon</th>
<th>Portitidae</th>
<th>Faviidae</th>
<th>Agaricidae</th>
<th>Others</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>August 2006–</td>
<td>Portitidae</td>
<td>26</td>
<td>17</td>
<td>25</td>
<td>4</td>
<td>72</td>
</tr>
<tr>
<td></td>
<td>January 2007</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>January 2007–</td>
<td>Portitidae</td>
<td>78</td>
<td>29</td>
<td>24</td>
<td>17</td>
<td>148</td>
</tr>
<tr>
<td></td>
<td>August 2007</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>August 2008</td>
<td>Portitidae</td>
<td>55</td>
<td>60</td>
<td>133</td>
<td>49</td>
<td>297</td>
</tr>
<tr>
<td></td>
<td>January 2008</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>January 2008–</td>
<td>Portitidae</td>
<td>205</td>
<td>36</td>
<td>66</td>
<td>22</td>
<td>329</td>
</tr>
<tr>
<td></td>
<td>August 2008</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td></td>
<td>364</td>
<td>142</td>
<td>248</td>
<td>92</td>
<td>846</td>
</tr>
</tbody>
</table>
periods can be interpreted in terms of the timing of reproduction. Thus, the increased abundance of poritids over January to August probably reflects the release of larvae from *P. astreoides* from December to June (Szmant, 1986; McGuire, 1998); *F. fragum* reproduces year-round (Szmant, 1986) and therefore was found on tiles throughout the year; *A. humilis* releases larvae year-round (van Moorsel, 1983; Raimondi and Fig. 4. Map of St. John showing the three deployment locations for drogues (exposed, fully sheltered, and partially protected, with approximate locations of deployments marked with “X”), together with circular histograms displaying frequency of travel legs (annuli with 20 replicate resolution) by direction (20° resolution) for drogue deployments in the vicinity of Great Lameshur Bay. Solid radius and whiskers indicate the mean direction of travel ± 95% CI as determined by circular statistics (Zar, 2010) for drogue deployments pooled among years and periods.

Fig. 5. Scatterplots showing the density of coral recruits tile⁻¹ and the daily range in seawater temperature among the 10 study sites for August to January (A) and January to August (B), with results pooled by year. The best-fit linear relationship for August-January (2006-07; the only significant correlation) is a model II regression (Sokal and Rohlf, 1995).
Morse, 2000), although A. agaricites releases larvae from May to October (van Moorsel, 1983), which might explain why agaricids were more common over August 2007 to January 2008; and finally, S. radians releases larvae year-round (Soong, 1991; Vermeij, 2005), and should recruit all year, whereas S. siderea spawns from July to September (Szmant, 1986), and therefore might be more common on tiles deployed from August to January.

The dominance of brooding corals among the recruits on the settlement tiles in St. John has implications for evaluating where the larvae might be coming from, and what might be causing the east–west gradient in density of recruits. The brooded larvae of corals are typically released in an advanced stage of development, with Symbiodinium from the parent (Harrison and Wallace, 1990), and are capable of rapid settlement. Indeed, some of the shortest known pelagic larval durations (PLD) for corals – instantaneous-to-minutes have been reported for brooding corals like F. fragum (Lewis, 1974; Carlson and Olson, 1993), S. radians (Vermeij, 2005), and Acropora palifera (Best and Resing, 1987), and larvae of such corals can settle within a few meters of the parent (Best and Resing, 1987; Carlson and Olson, 1993; Vermeij, 2005). However, despite the potential for short PLD and local recruitment, brooded coral larvae also have the potential to remain in the plankton, and can defer settlement, for months (Richmond 1987). While the larvae of broadcast spawning corals are better known for long distance dispersal and lengthy PLDs (conceivably > 1 year) (Graham et al., 2008; Vermeij et al., 2009), pelagic zygotes must develop for several days before they form competent larvae capable of settling (Ball et al., 2002) and, therefore, the shortest dispersal distances for broadcasting corals are longer than those for brooders. In the case of the present study, it is therefore likely that at least some of the recruits of brooding corals on the settlement tiles originated by self-seeding (sensu Caley et al., 1996) acting over several meters. The recruitment of F. fragum and S. radians is most likely to have been affected by such small-scale processes, because both species are common in shallow water along the south coast of St. John where they display aggregated settlement (PJ Edmunds unpublished data), as they do throughout the Caribbean (Carlson and Olson, 1993; Vermeij and Sandin, 2008). The tendency for larvae to settle close to the parent in these (and similar) species in St. John would be accentuated by the slow, near-bottom water flow in this area (i.e., < 8 cm s⁻¹ [Horst and Edmunds, in press]), the slow westerly motion of surface waters (Fig. 4), and eddies and high retention times for seawater within the bays (this study, Horst and Edmunds, in press).

While local recruitment almost certainly contributed to the coral recruits found on our settlement tiles, this mechanism is unlikely to have generated the east–west gradient in density of recruits because the putative parent colonies appeared to be distributed equally over the same gradient. Although the benthic community structure was not quantified in this analysis, in previous work (from 1994/1995) significant differences were detected in community structure at 18 shallow sites over the same spatial scale, although mean coral cover was always low, and ranged between 1% and 13% (Edmunds, 2000). These data confirm anecdotal observations completed during the present study that the coral community was similar at all locations, and importantly, that adult colonies of the most likely recruiting corals (summarized above) were common on the benthos wherever tiles were installed (DH Green and PJ Edmunds, personal observations). The inference that the coral communities in shallow water were similar between Ram Head and Ditleff Point is also consistent with 18 years of time-series analyses at shallow sites between Cabritte Point and White Point, which revealed reefs that are similar in coral cover and the relative abundance of individual coral species (Edmunds, 2002; PJ Edmunds unpublished data). Together, these observations suggest that differential abundance of coral taxa along the south shore of St. John cannot explain the variation in recruitment we detected, although implicit in this conclusion is that the adult colonies were equally fecund at all sites. Unfortunately, it was not feasible in the National Park to test this hypothesis by sampling adult colonies for the presence of brooded larvae, but evidence from Australia demonstrating that the proportion of gravid colonies in a population is a good predictor of local coral recruitment (Hughes et al., 2000) suggests it would be worthwhile to complete a similar analysis in St. John, perhaps through a non-destructive assay for reproductive hormones (Twan et al., 2006).

Assuming localized recruitment and variation in coral community structure cannot account for the differences in coral recruitment along the south shore of St. John, what are the hypotheses that might account for this trend? When this study was conceived, we suspected that temperature might play a role in modulating recruitment, because previous studies along the same shore had implicated temperature as a factor affecting early life stages of corals (Edmunds, 2004, 2006), temperature is well known for its effects on invertebrate larvae (O’Connor et al., 2007), and gross differences in temperature among the study sites were apparent even while snorkeling. While measurements of temperature did reveal differences among study sites, particular for the daily range in temperature, tests of association between temperature and the density of recruits were equivocal. While high densities of recruits tended to occur at sites with relatively stable thermal environments (i.e., low daily ranges) – that is, sites to the east – this effect was only statistically significant between August 2006 and January 2007 (Fig. 5). Given the weakness of this relationship, and the absence in the literature of a mechanistic basis to link thermal variance to recruitment success, we conclude that the apparent thermal association is probably a consequence of other processes. Given the westward seawater flow along the south coast of St. John (Richardson, 2005), and the potential for seawater to warm during the day when it becomes entrained in the shallow semi-enclosed bays to the west of Ram Head, it is likely that the enhanced thermal variability to the west serves as a marker for westward flow and the putative depletion of larvae (described below) as it traverses the fringe reefs along this shore.

Against the context of our results described above, we believe that the pattern of coral recruitment along the south coast of St. John is best described by a patch depletion/downstream filtering hypothesis (Victor, 1984; Gaines et al., 1985; Caselle and Warner, 1996). In this model, pelagic larvae are transported in a cohesive aggregate that sweeps along a shore, and the larval pool is progressively depleted as larvae settle to the benthos as the aggregate is transported. Victor (1984) evoked this hypothesis to account for the settlement of bluehead wrasse (Thalassoma bifasciatum) on multiple patch reefs throughout the San Blas Islands (Republic of Panama), and he used the scale of cohesive settlement to estimate the scale of the larval aggregates at a width of 20–46 km. In another example also involving T. bifasciatum, Caselle and Warner (1996) described a westward reduction in settlement among three sites along the south shore of St. Croix. In one invertebrate system, involving the barnacle Balanus glandula along the California coast, a similar mechanism was detected, but in this case, settlement to the benthos depleted the supply of larvae as the water was transported (Gaines et al., 1985). When applied to the present study, the patch depletion/downstream filtering hypothesis is superimposed on local recruitment effects (described above) and posits that aggregates of coral larvae are swept around Ram Head, and then settle as the water progresses west with greater densities of recruits where the aggregate is better stocked with larvae (i.e., when it first enters the region). Such a mechanism enhancing recruitment is likely to be augmented by eddies that would develop in the lee of the southerly projected headlands – and which occasionally trapped the drogues we deployed – and might deplete the larval aggregates of less common species more rapidly than for the common species. This might explain why poritids and agaricids sometimes made up a larger proportion of the recruits at western, compared to eastern sites (Fig. 3).

Testing the patch depletion/downstream filtering hypothesis for coral recruitment in St. John is likely to be insightful, and such an analysis will require detailed analyses of water motion as well as quantification of the abundance of pelagic larvae. Should this hypothesis
be shown to be correct, the putative importance of the delivery of coral larvae to the south shore of St. John by water flowing around Ram Head has important implications. Critically, it would suggest that these coral populations are demographically more open than closed (Cowman and Sponaugle, 2009; Jones et al., 2009) and potentially are reliant on coral larvae originating from other localities. These localities almost certainly include coral reefs to the east of Ram Head but still in St. John, notable reefs that are both protected and unprotected by MPAs (Rogers et al., 2008), as well as reefs in other countries (i.e., the British Virgin Islands). With only 8 km between St. John (Ram Head) and the nearest up-stream island in the BVI’s (Normal Island), coral larvae could bridge this gap in < 8 h (with a westerly flow of 30 cm s⁻¹ [Richardson, 2005]).

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