A standard unit for monitoring recruitment of fishes to coral reef rubble

Henri Valles a,*, Donald L. Kramer a, Wayne Hunte b

a Department of Biology, McGill University, 1205 Avenue Docteur Penfield, Montreal, Quebec, Canada H3A 1B1
b Department of Biological and Chemical Sciences, University of the West Indies, Cave Hill Campus, Barbados

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Abstract

We developed a benthic standard monitoring unit for recruitment of fishes (SMURF) to sample fishes that settle in coral rubble and tested it on three fringing reefs on the west coast of Barbados, West Indies. These rubble SMURFs are inexpensive to construct and permit newly settled fishes, including cryptic, secretive and small species, to be quickly and fairly completely (>83%) removed by divers without returning the unit to the surface. Over a 3-month period involving 9 collections, 32 units on 3 reefs yielded 948 newly settled fishes belonging to 28 taxa (3.3±0.2 S.E. recruits per sample, n=287) in addition to numerous crustaceans. Most specimens were Sparisoma spp. (Scaridae) (41.8%) and Stegastes partitus (Pomacentridae) (13.6%), with moderate numbers of Scarus spp. (Scaridae) (8.6%), Lythrypnus spp. (Gobiidae) (7.4%), and Pseudogramma gregoryi (Serranidae) (7.2%). Sampling SMURFs at 1-day rather than 11-day intervals yielded approximately twice as many fish, although some taxa were not affected by sampling frequency, indicating taxon-specific differences in post-settlement loss rates. Netting, intended to reduce predation on settlers, did not affect settlement estimates unless algae grew on it, suggesting that the SMURF design minimizes fish predation even in the absence of the netting. Over time, however, the netting resulted in substantial algal growth that was associated with an increase in abundance of Sparisoma spp. and a decrease in the abundance of S. partitus. This suggests that settler estimates are more affected by microhabitat changes from algal growth than by predation. During low settlement periods, SMURFs performed better than light-traps in assessing the daily input of new settlers of two abundant taxa. Eight SMURFs per reef were sufficient to demonstrate differences in settlement rates and temporal correlations in settlement within and among reefs. This study underscores the potential of benthic SMURFs to measure settlement of coral reef fishes at a range of spatio-temporal scales with moderate research cost and effort, and to facilitate the study of the settlement stage of several taxa.

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1. Introduction

Monitoring settlement dynamics of coral reef fishes is a challenging task because newly settled individuals tend to be small, cryptic or hidden (Kaufman et al., 1992), and their arrival is highly variable in time and space (Doherty, 1991), and thus, difficult to predict. Settler counts via underwater surveys can be subject to diver biases (Ebeling and Hixon, 1991) and likely underestimate the effect of potentially important early post-settlement processes such as movement (Frederick, 1997) and predation (Steele and Forrester, 2002), which can distort patterns of relative
abundance established at settlement (Caley et al., 1996). The alternative of measuring the abundance of pelagic larvae as an estimate of settlement, using towed nets and/or light-traps (e.g. Choat et al., 1993) or moored nets (e.g. Doherty et al., 2004), is also problematic. For example, light-traps and towed nets cannot sample continuously and therefore generally fail to capture the patchiness of larval supply (Gaines and Bertness, 1993). Moored nets, which can sample continuously, are subject to biases from changing currents (Anderson et al., 2002).

Studies of benthic invertebrates commonly use units of artificial substrate that collect pelagic larvae near the time of settlement (Witham et al., 1968; references in Moksnes and Wennhage, 2001). These units have the potential to reflect delivery patterns of settling larvae (e.g. Eggleston et al., 1998). Similar techniques have also been used in studies of settlement and early post-settlement dynamics of temperate fishes (Behrens, 1987; Levin, 1994; Silberschneider et al., 2001). Steele et al. (2002) and Ammann (2004) describe the use of units of artificial kelp-like substrate as standard monitoring units for recruitment of fishes (“SMURFs”, Ammann, 2004). SMURFs are particularly useful because they can provide relative estimates of settlement that are undistorted by post-settlement processes while facilitating the collection of settlers with reduced cost and sampling effort.

Studies of recruitment (herein defined as the survival of newly settled fishes until the time of sampling; Keough and Downes, 1982) are relatively common in the coral reef fish literature (reviewed by Doherty, 1991, 2002). However, attempts to estimate settlement before potentially distorting post-settlement processes occur are relatively few and generally obtained through within-day (e.g. Sweatman and St John, 1990; Kingsford, 2001) or daily (e.g. references in Victor, 1991) labor-intensive underwater sampling schemes. Often, these attempts have involved using standardized settlement units of various substrate types (e.g. live coral heads, Sweatman and St John, 1990; coral rubble, Wellington, 1992; anemones, Schmitt and Holbrook, 1996; bricks, Robertson et al., 1988; coil wire, Schroeder, 1987) or natural patch reefs of varying size and composition (e.g. Williams, 1983; Robertson, 1992; Tolimieri, 1995) transplanted or located away from the reefs to minimize uncontrollable post-settlement processes associated with the reef habitat.

In this study, we describe and evaluate a SMURF based on the affinity of settling larvae of several coral reef fish species for coral rubble, a natural component of coral reefs. Unlike previously studied settlement units using rubble, our SMURFs are specifically designed to minimize potentially distorting effects of early post-settlement processes, particularly predation, while allowing for a quick and effective underwater collection of small, hidden and cryptic taxa. Unlike the SMURFs developed by Ammann (2004) and Steele et al. (2002) that were suspended in the water column and deployed at a distance from the reefs, the SMURF described here are designed for deployment directly in the benthic reef habitat in order to maximize the resolution of spatial patterns of settlement. As a consequence, both predators and alternative settling habitat are likely to be abundant in the vicinity of these rubble SMURFs. To assess the potential of these units to reflect natural patterns of settlement, we carried out four studies. First, we assessed the effect of sampling frequency on recruit estimates under the assumption that increased sampling frequency would provide more accurate estimates of settlement because there would be less opportunity for post-settlement processes to operate (Booth, 1991). Second, we focused on the potential importance of predation by fishes and the practicality of attempting to prevent it by using exclosure netting. Third, we examined, for two taxa, how daily patterns of recruit abundance in SMURFs related to those in adjacent quadrats on natural reefs and to larval abundance in the water column as measured by light-traps, a commonly used alternative method. Fourth and finally, we assessed the utility of the SMURFs as replicate units in studies of settlement by comparing long-term trends among different sites.

2. Methods

2.1. Rubble SMURF design and use

Our SMURF consists of a thick layer of rubble held in a mesh-wire basket inside a cylindrical plastic container that holds an open replaceable collecting bag (details in Fig. 1). To prevent access to the rubble matrix by fish predators while still allowing rapid underwater collection, we added a removable circular piece of nylon fish net (9.5 mm square mesh size) tightly fit over the outer perimeter and supported by a dome-shaped wire frame. The day before each study began we removed resident organisms by emptying each SMURF of its rubble and immediately refilling it manually.

Two divers can collect recruits from one SMURF in approximately 1.5 min (3 person-minutes). During collection, one diver deploys an open replacement collecting bag while the other removes the predator-exclusion net, if present, and squirts a clove oil anesthetic solution (1 part clove oil/4 parts 70% isopropanol/9 parts sea water) into the rubble using a spray bottle. Both divers then lift the rubble basket, shake it briefly above the SMURF, and place it on the replacement bag. One diver closes and removes the used bag from the SMURF,
ensuring that it is tightly sealed and properly labeled while the other places the new bag and the rubble basket back inside the SMURF. Finally, the divers scrape off any algae and other material fouling the net and put it back in place. Depending on the specific studies, we sampled the SMURFs either approximately every 10 days (mean: 9.8 days; range: 8–11 days, depending on logistical and sea conditions, hereafter 10-day sampling) or daily.

To assess the effectiveness of collection in clearing the rubble matrix of recruits, we sampled 21 SMURFs using the procedure described above then immediately brought the entire units to shore. The rubble matrices were then thoroughly rinsed, and the remaining organisms collected and counted.

During sorting, we separated the fish and crustaceans from other organisms and debris. We identified the fish specimens considered to have settled between two
consecutive sampling dates using a taxon-specific standard length limit based on available literature and personal observations. Specimens were identified to the lowest taxonomic level possible and preserved in 90% ethanol. Taxonomic authorities for scientific names are in Böhlke and Chaplin (1993). Sorting took approximately 8 person-minutes per sample. Afterwards, the bags were cleaned with a brush and fresh water.

2.2. Study sites and time period

The study was carried out at three sites, at least 2 km apart, along the west coast of Barbados, West Indies (Site 1: 13°8′8″N, 59°38′22″W; Site 2: 13°11′48″N, 59°38′40″W; and Site 3: 13°13′10″N, 59°38′41″W), from June to September 2003. The study was carried out on fringing reefs, in the zone described by Lewis (1960) as the “reef front”. This zone is approximately 250 to 300 m offshore, at a depth of 7 to 12 m. The habitat is a dense, patchy mixture of live coral heads, sponges, sand and rubble, with similar or higher reef-fish density and diversity than shallower zones of the same reefs (H. Valles, unpublished observations).

2.3. Description of the studies

2.3.1. Study 1: The effect of sampling frequency

We compared the number of recruits captured in two sets of adjacent SMURFs. One set was sampled every day for 11 days (daily collection), whereas the other was sampled only at the end of the 11-day period (11-day collection). The study was carried out at Site 1 from June 19 to 29. Section 2.3.5 presents details on the experimental design of this and the other studies. We used a Poisson log-linear fixed effects model with possible over-dispersion (hereafter PLM) to compare recruit abundance between treatments (e.g. Danilowicz et al., 2001). This PLM was fitted using maximum likelihood by the “glm” procedure in R 2.2.1 (http://cran.r-project.org/). We also used a Fisher exact test (Zar, 1999) to examine whether treatments differed in the proportion of SMURFs with recruits. Values are reported as mean±S.E.

2.3.2. Study 2: The effect of predator-exclusion netting

We compared the number of recruits captured in two sets of adjacent SMURFs, one set with predator-exclusion netting, and the other one without it. The SMURFs, located at Site 1, were sampled every 10 days over 9 consecutive time periods, starting on June 19. There was a noticeable increase in algal growth on the rubble and, despite regular scraping, on the netting itself, approximately 20 days after the placement of the netting. The potentially confounding effects of this algal growth led us to compare recruit numbers between netting treatments during the first period, before substantial algal growth, separately from the remaining 8 periods. For the first period, the analysis used a PLM as described for Study 1. For the remaining 8 periods, preliminary analysis using log-linear mixed models with SMURFs as the random factor, to account for repeated measures, indicated that SMURF estimates could be treated as independent measures over time. Thus, for simplicity, we used a fixed-effect PLM with treatment and time as factors. Time was considered fixed given that the sampling periods were temporally adjacent. We also examined whether treatment means were (Spearman rank) correlated over time. A lack of significant interaction in the PLM and a correlation between treatment means over time would suggest a lack of distortion of settlement patterns by predation.

2.3.3. Study 3: Comparison between SMURFs, light-traps, and natural reef surveys

We compared measures of daily settler abundance obtained through sampling of eight SMURFs with those from three nearby light-traps and from surveys on three 36 m² (6×6 m) permanent quadrats (total of 108 m²) of adjacent natural reef habitat. We obtained two sets of short time series involving daily sampling by all three methods (Site 1, June 19–28; Site 2, August 20–28) around the third quarter moon, the lunar period of highest settlement in Barbados (Sponaugle and Cowen, 1996a,b). We focused on a pomacentrid, the bicolor damselshiff, Stegastes partitus, and on unidentified parrotfishes of the genus Sparisoma (hereafter Sparisoma spp., Scaridae), the two most abundant taxa that could be sampled by all three methods. During the series, the methods were implemented daily between 07:00 and 13:00 h, although quadrat surveys were skipped for 1 day to reduce health hazards associated with long bottom time. We used the same light-traps used by Valles et al. (2001), based on the design of Sponaugle and Cowen (1996b). Light-traps sampled at 2 m depth, remained lit for 10–12 h and were retrieved the following morning. Overall, it took approximately 180 person-minutes (with no diving) to use three light-traps (60 person-minutes per trap). This included approximately 30 person-minutes to ready the light-traps, 15 person-minutes to deploy and retrieve them, and 135 person-minutes to process the plankton samples. It took 135 person-minutes of diving bottom time to survey the three quadrats (45 person-minutes per quadrat).

For reef quadrats, we used Kendall’s rank correlation coefficient test to assess whether there was a significant increase in mean recruit abundance over time (Legendre and Legendre, 1998). We compared daily input of settlers,
as assessed by the three methods, using a two-sample Kolmogorov–Smirnov goodness of fit test (K–S test). Specifically, we compared the cumulative distribution of settlers over time between pairs of methods and taxa. P-values were adjusted for multiple pair-wise comparisons within each series using the Holm (1979) procedure for multiple non-independent tests. Daily settler inputs using the SMURFs and light-trap sets were estimated as the total number of recruits and late-stage larvae, respectively, collected daily by each set. We did not collect the recruits during the reef quadrat surveys, so daily settler input to quadrats was estimated as the total number of recruits recorded (over the three quadrats) at one given day minus the total observed the previous day, except for the first day of the series in which we used the total number of recruits observed that day. Negative differences were considered to be due to post-settlement loss and were conservatively truncated to zero.

2.3.4. Study 4: Patterns of settlement among sites under low-frequency sampling

We compared the number of recruits captured over time between sets of SMURFs located at all three sites and sampled within 36 h, every 10 days from June 19 to September 14. We used a PLM as in Study 2, but with sites and time as fixed factors. We treated sites as a fixed factor because we deliberately chose them to encompass a spatial extent of several km. We also used a Kendall’s concordance test (Zar, 1999) to assess whether site means were significantly correlated over time, which, coupled with a lack of significant interaction in the PLM, would suggest that the sites were reflecting the same underlying natural settlement patterns. Because of generally low levels of settlement, we focused on Sparisoma spp., the most abundant taxon, and, as explained in Study 3, expected to see increases in recruit abundance during the third quarter moon periods.

2.3.5. Integrated study design

Although the main studies addressed different questions, Studies 1 and 3 required similar treatments and so did Studies 2 and 4. We therefore carried out the four studies over the same period, with some treatments shared among studies (Fig. 2) and therefore not statistically independent. Because they addressed unrelated hypotheses, we analyzed them separately (Hochberg and Tamhane, 1987; Quinn and Keough, 2002).

At all three sites, we deployed SMURFs in arrays oriented south–north (parallel to shore) to ensure similar sampling depths. We placed the SMURFs on small sand patches within the reef habitat, approximately 9 m apart, at an average depth of 8.7 m (range: 7.7 to 9.8 m).

Fig. 2. Design of the treatment comparisons of the four main studies across the three sites, with some experimental treatments overlapping between studies and two main sampling interval schemes: “Daily”, i.e. every day sampling, and “10 days”, i.e. approximately every 10 days. Study 1 examined the effect of the two sampling frequency schemes on SMURF recruit numbers. Study 2 examined the effect of the presence of a predator-exclusion net on SMURF recruit numbers over 10-day sampling intervals. Study 3 compared daily numbers of recruits on SMURFs with settlement to natural reefs and larva numbers in light-traps. Study 4 compared SMURF recruit numbers among three sites over nine 10-day sampling intervals. Same symbols within columns represent overlapping treatments among studies.

At our main study site, Site 1, we deployed 24 SMURFs in an 8×3 grid on April 28 (Fig. 3). On June 18, we allocated three experimental treatments to sets of 8 SMURFs. The treatments were predator-exclusion netting present with daily sampling (Studies 1 and 3, Fig. 2), netting with sampling every 10 days (Studies 2 and 4; Fig. 2), and netting absent with sampling every 10 days (Study 2; Fig. 2). We assigned treatments in a zigzag fashion across the grid to average out potential spatial effects (Fig. 3).

At Site 2, we deployed two parallel arrays (9 m apart) of 8 SMURFs with netting. We sampled one array every 10 days over the 3-month period (Study 4; Fig. 2). We only used the other array as part of Study 3, in which we sampled the SMURFs daily during a second short time series (9 days; August 20–28). At Site 3, we only deployed one array of SMURFs sampled every 10 days over the 3-month period (Study 4; Fig. 2). At Sites 1 and 2, we placed 3 light-traps approximately 250 m from shore, and at least 50 m from the SMURFs and each other, to ensure that effective light fields did not overlap. The permanent quadrats were approximately 60 m apart at Site 1 and 30 m apart at Site 2, parallel to the SMURF array, at an average depth of 8.9 m (range: 7.5 to 11.2 m) (Fig. 3).

3. Results

3.1. Taxa captured and effectiveness

We captured 948 individuals representing 28 taxa in 287 (every-10-day) SMURF samples (3.3±0.2 recruits per sample — 1 SMURF sample was lost) (Table 1).
Sparisoma spp. (Scaridae) and *S. partitus* (Pomacentridae) dominated the catches (41.8% and 13.6%, respectively). Unidentified *Scarus* parrotfishes (Scaridae) ranked third in abundance (8.6%). Unidentified *Lythrypnus* gobies (Gobiidae, hereafter *Lythrypnus* spp., 7.4%) and *Pseudogramma gregoryi* (7.2%) (Serranidae) ranked fourth and fifth, respectively. At capture, many individuals had not yet fully developed the pigmentation characteristic of post-settlement juveniles. Specimens of a size larger than the taxon-specific size criteria (Table 1) were relatively rare (H. Valles, unpublished data). Although we had intended to target fishes, crustaceans represented the bulk of the catch with 6088 specimens recorded including palaemonids, stenopodids, mysids, majids, and gonodactylids.

The average effectiveness of the collection procedure per SMURF [number removed underwater/(number removed underwater+number removed on shore)] for all fish taxa combined (114 specimens) was 83.6%±5.9 (n=21). Average effectiveness values for the three most abundant taxa, *S. partitus* (20 specimens), *Sparisoma* spp. (32 specimens) and *P. gregoryi* (30 specimens) were 83.9%±9.7, 83.1%±8.5 and 90.6%±6.8, respectively.

### 3.2. Study 1: The effect of sampling frequency

Approximately twice as many taxa and individual recruits were collected after 11 days of daily collections as during the 11-day collection (Table 2). We found a similar pattern in recruit abundance when the data for the three most abundant taxa during that time period, *Sparisoma* spp., *S. partitus* and *P. gregoryi* (combined: 74.4% of the catch), were omitted from the analysis (Table 2). In contrast, we found no significant differences between treatments for these three most abundant taxa, although for *Sparisoma* spp. we collected twice as many recruits during the daily than during the 11-day sampling (Table 2). *Sparisoma* spp. was the only taxon for which the proportion of SMURFs with recruits differed significantly between treatments (Fisher test: *p*=0.025; for others, *p>*0.569), with recruits recorded in all SMURFs during the daily collections, but only in 3 out of 8 SMURFs during the 11-day collection. There were also qualitative differences in the specimens between treatments. Specimens collected during the daily sampling scheme exhibited pigmentation consistent with that of late stage larvae, whereas most specimens collected during the one-time collection had post-settlement juvenile pigmentation.

### 3.3. Study 2: The effect of predator-exclusion netting

Possible predators were diverse and abundant in the vicinity of the SMURFs (H. Valles, unpublished data) and included aulostomids, serranids, muraenids, labrids, ophichthids and synodontids. Based on underwater observations, the netting seemed successful in preventing fish predator access to the SMURF rubble.

During the first period, prior to substantial algal growth, there were no significant differences between SMURFs with and without netting in the number of taxa, total number of recruits, the number of each of the three most abundant taxa (*Sparisoma* spp., *S. partitus* and *P. gregoryi*; Table 2) or the total with the three dominant taxa omitted from the analysis (Table 2). In the last eight time periods, during which there was a noticeable growth of algae on the rubble and netting, again, we found no significant differences between treatments in the number of taxa, total number of recruits, or total recruits without the three dominant taxa (*S. partitus*, *Sparisoma* spp. and *Lythrypnus* spp.; Table 3). Individual examination of the three most abundant taxa showed that captures of *Lythrypnus* spp. were not significantly different between netting treatments (Table 3). In contrast, *Sparisoma* spp. captures were significantly higher...
in the netting treatment whereas _S. partitus_ exhibited the opposite pattern (Table 3). For all variables examined above, there were significant differences among time periods, but no significant interaction between treatment and time, although for _S. partitus_, the interaction term was marginally non-significant (Table 3). We found a

Table 1
The number of recently settled fishes collected on sets of 8 SMURFs, with and without predator-exclusion netting, during a 3-month period (nine consecutive collections at 10-day intervals) at three sites on the west coast of Barbados, West Indies

<table>
<thead>
<tr>
<th>Family</th>
<th>Taxa</th>
<th>Site 1</th>
<th>Site 2</th>
<th>Site 3</th>
<th>Total</th>
<th>S.L. (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apogonidae</td>
<td>Apogon 2.2</td>
<td>0</td>
<td>11</td>
<td>0</td>
<td>1</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td>Apogon maculatus</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Apogon 1.1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Chaeonopsidae</td>
<td>Chaeonopsid sp.</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Chaetodontidae</td>
<td>Chaetodon capistratus</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Cliniidae</td>
<td>Starksia nanodes</td>
<td>2</td>
<td>1</td>
<td>4</td>
<td>3</td>
<td>10</td>
</tr>
<tr>
<td>Gobiesocidae</td>
<td>Arcos rubiginosus</td>
<td>0</td>
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<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Gobiidae</td>
<td>Lythrypnus spp.</td>
<td>32</td>
<td>22</td>
<td>10</td>
<td>7</td>
<td>71</td>
</tr>
<tr>
<td></td>
<td>Coryphopterus glaucoframen</td>
<td>18</td>
<td>11</td>
<td>17</td>
<td>8</td>
<td>54</td>
</tr>
<tr>
<td></td>
<td>Gnatholepis thompsoni</td>
<td>10</td>
<td>26</td>
<td>0</td>
<td>9</td>
<td>45</td>
</tr>
<tr>
<td></td>
<td>Coryphopterus personatus</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Gobiid sp.</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Labridae</td>
<td>Thalassoma bifasciatum</td>
<td>6</td>
<td>1</td>
<td>5</td>
<td>2</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>Halichoeres garnoti</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Muraenidae</td>
<td>Muraenid sp.</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>6</td>
<td>9</td>
</tr>
<tr>
<td>Pomacentridae</td>
<td>Stegastes partitus</td>
<td>39</td>
<td>18</td>
<td>34</td>
<td>38</td>
<td>129</td>
</tr>
<tr>
<td></td>
<td>Stegastes diencaeus</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Stegastes planifrons</td>
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<td>2</td>
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<tr>
<td>Scaridae</td>
<td>Sparisoma spp.</td>
<td>86</td>
<td>139</td>
<td>58</td>
<td>114</td>
<td>397</td>
</tr>
<tr>
<td></td>
<td>Scarus spp.</td>
<td>23</td>
<td>16</td>
<td>5</td>
<td>38</td>
<td>82</td>
</tr>
<tr>
<td>Scorpaenidae</td>
<td>Scorpaenodes caribbaeus</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Scorpaenid sp.</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Serranida</td>
<td>Pseuderograma gregoryi</td>
<td>12</td>
<td>16</td>
<td>14</td>
<td>26</td>
<td>68</td>
</tr>
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<td>5</td>
<td>1</td>
<td>9</td>
<td>15</td>
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<td>Ripticus subbifrenatus</td>
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<td>0</td>
<td>0</td>
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<td>3</td>
</tr>
<tr>
<td></td>
<td>Serranus tigrinus</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Ripticus saponaceus</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Syngnathidae</td>
<td>Cosmocampus elucens</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Tetraodontidae</td>
<td>Canthigaster rostrata</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Unidentified/deteriorated</td>
<td>4</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>Total individuals</td>
<td>242</td>
<td>278</td>
<td>155</td>
<td>273</td>
<td>948</td>
</tr>
<tr>
<td></td>
<td>Total taxa</td>
<td>15</td>
<td>17</td>
<td>13</td>
<td>17</td>
<td>28</td>
</tr>
</tbody>
</table>

Far right column indicates standard length (S.L.) below which specimens were considered to have settled between collection periods.

Table 2
Comparison of the mean number of recruits per SMURF ± standard error captured in a set of 8 SMURFs with netting that were sampled daily over 11 days (daily with net), in a set of 8 nearby SMURFs also with netting that were sampled once at the end of the same time period (11-day with net), and in another set of 8 nearby SMURFs, without netting (11-day without netting), that were sampled once at the end of the same time period

<table>
<thead>
<tr>
<th></th>
<th>Daily with net</th>
<th>11-day with net</th>
<th>11-day no net</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of taxa per SMURF</td>
<td>4 ± 0.6</td>
<td>10.16 (0.007)</td>
<td>1.6 ± 0.3</td>
</tr>
<tr>
<td>Number of recruits per SMURF</td>
<td>6.9 ± 0.8</td>
<td>6.02 (0.028)</td>
<td>2.8 ± 0.8</td>
</tr>
<tr>
<td>Number of recruits excluding the three most abundant taxa</td>
<td>2.5 ± 1.1</td>
<td>5.14 (0.039)</td>
<td>0.3 ± 0.2</td>
</tr>
<tr>
<td>Sparisoma spp.</td>
<td>2.3 ± 0.5</td>
<td>1.57 (0.230)</td>
<td>1.1 ± 0.7</td>
</tr>
<tr>
<td>S. partitus</td>
<td>1.4 ± 0.3</td>
<td>0.23 (0.638)</td>
<td>1.1 ± 0.4</td>
</tr>
<tr>
<td>P. gregoryi</td>
<td>0.8 ± 0.5</td>
<td>0.03 (0.848)</td>
<td>0.9 ± 0.4</td>
</tr>
</tbody>
</table>

_F_ statistics and _p_-values (in brackets) correspond to pair-wise comparisons between adjacent columns using a Poisson log-linear model with possible over-dispersion. Bold font indicates significance at the 0.05 level.
significant positive correlation between treatments over time for all variables examined (Spearman rank test: all $r_s > 0.719$, all $p < 0.045$) except for *S. partitus* recruit abundance (Spearman rank test: $r_s = 0.367$, $p = 0.370$).

3.4. Study 3: Comparison between SMURFs, light-traps, and natural reef surveys

Recruit density on natural reef quadrats increased significantly with time for both taxa during the two series, although for *Sparisoma* spp. during Series 2, significance was only achieved after excluding the final point from the analysis (Kendall’s rank correlation test: for *Sparisoma* spp. in Series 2: $\tau = 0.950$, $N = 7$, $p = 0.004$; for all other cases: $\tau > 0.741$, $N = 8$, $p < 0.012$, Fig. 4). At peak density in Series 1, *S. partitus* recruits (0.35±0.04/m²) were about twice as abundant as *Sparisoma* spp. recruits (0.15±0.04/m²), whereas in Series 2, the relationship was reversed (*S. partitus*: 0.23±0.07/m²; *Sparisoma* spp.: 0.4±0.14/m², Fig. 4).

Light-traps captured no *S. partitus* and only caught *Sparisoma* spp. during Series 2 for a total of 58 specimens to which all three light-traps contributed. In contrast to light traps, SMURFs yielded recruits of both taxa during both series, i.e. 9 *S. partitus* and 18 *Sparisoma* spp. during Series 1 and 11 *S. partitus* and 7 *Sparisoma* spp. during Series 2.

During Series 1, daily settlement patterns did not differ significantly between SMURFs and quadrats for either *S. partitus* (K–S test: $D = 0.217$; adjusted $p = 0.833$) or *Sparisoma* spp. (K–S test: $D = 0.333$; adjusted $p = 0.432$; Fig. 5). Daily settlement patterns did differ significantly, however, between *S. partitus* and *Sparisoma* spp. in the quadrats (K–S test: $D = 0.568$; adjusted $p < 0.001$) and the SMURFs (K–S test: $D = 0.611$; adjusted $p = 0.033$). In this series, *S. partitus* abundance increased gradually over the observation period while *Sparisoma* spp. were very scarce during the first half of the series but increased abruptly in the second half (Figs. 4 and 5). During Series 2, we found no significant differences between SMURFs and quadrats for either taxon, nor between taxa recorded in either SMURFs or quadrats (K–S test: $D > 0.285$; all adjusted $p > 0.5$). There was, for *Sparisoma* spp., a significant difference between light-traps and quadrats (K–S test: $D = 0.647$, adjusted $p < 0.001$), but not between light-traps and SMURFs (K–S test: $D = 0.308$, adjusted $p = 0.792$).

Unlike SMURFs and quadrats, which indicated

### Table 3

<table>
<thead>
<tr>
<th></th>
<th>No net (N=63)</th>
<th>Net (N=64)</th>
<th>Treatment F_{1,111} (p-value)</th>
<th>Time F_{7,111} (p-value)</th>
<th>Treatment x Time F_{7,111} (p-value)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of taxa</td>
<td>2.3±0.2</td>
<td>2.2±0.2</td>
<td>0.52 (0.472)</td>
<td>4.58 (&lt;0.001)</td>
<td>0.41 (0.889)</td>
</tr>
<tr>
<td>Number of recruits per SMURF</td>
<td>3.5±0.3</td>
<td>3.8±0.4</td>
<td>0.50 (0.479)</td>
<td>7.63 (&lt;0.001)</td>
<td>0.90 (0.507)</td>
</tr>
<tr>
<td>Number of recruits per SMURF, excluding three most abundant taxa</td>
<td>1.3±0.2</td>
<td>1.2±0.2</td>
<td>0.03 (0.855)</td>
<td>3.74 (&lt;0.001)</td>
<td>0.76 (0.616)</td>
</tr>
<tr>
<td><em>Sparisoma</em> spp.</td>
<td>1.2±0.2</td>
<td>2±0.3</td>
<td>8.13 (0.005)</td>
<td>7.08 (&lt;0.001)</td>
<td>0.33 (0.936)</td>
</tr>
<tr>
<td><em>S. partitus</em></td>
<td>0.5±0.1</td>
<td>0.1±0.0</td>
<td>20.33(&lt;0.001)</td>
<td>5.99 (&lt;0.001)</td>
<td>1.89 (0.076)</td>
</tr>
<tr>
<td><em>Lythrypnus</em> spp.</td>
<td>0.5±0.1</td>
<td>0.3±0.1</td>
<td>2.71 (0.102)</td>
<td>5.98 (&lt;0.001)</td>
<td>1.43 (0.196)</td>
</tr>
</tbody>
</table>

Values shown in first two columns are overall mean recruit number per SMURF±standard error. Values shown in the next three columns are $F$ statistics with corresponding degrees of freedom and $p$-values (in brackets) of a Poisson log-linear model with possible over-dispersion comparing numbers of recruits between netting treatments over time. One SMURF sample was lost in the no net treatment. Bold font indicates significance at the 0.05 level.
substantial *Sparisoma* spp. settlement from the first day of this series, with moderate increases thereafter, light-trap captures were dominated by a single peak on the fifth night (approximately 68% of total catch; Fig. 5).

3.5. Study 4: Patterns of settlement among sites

There were significant differences among sites in the number of *Sparisoma* spp. captured, with Site 1 and Site 3 exhibiting more recruits than Site 2 (Site 1 = 1.9 ± 0.3 per SMURF sample; Site 2 = 0.8 ± 0.1; Site 3 = 1.6 ± 0.2; PLM: \(df = 2,189; F = 11.08, p < 0.001\)). There were also significant differences among time periods (PLM: \(df = 8,189; F = 5.72, p < 0.001\)). There was, however, no significant interaction between time and site (PLM: \(df = 16,189; F = 1; p = 0.458\)), suggesting that temporal settlement patterns were similar among sites. This was supported by the significant concordance among sites in patterns of mean recruit numbers over the time periods (Kendall’s concordance coefficient test: \(W = 0.688; \chi^2 = 16.52, N = 9; p = 0.035\)). *Sparisoma* spp. exhibited two small settlement peaks at all the three sites (and within two separate sets of SMURFs at Site 1) around the two third quarter moons fully included by the 3-month sampling period (Fig. 6).

4. Discussion

4.1. Catch composition

The catch was dominated by scarids, followed by one pomacentrid, three gobiids and one serranid. In a longer term subsequent study using this SMURF design, but without netting, the taxa mentioned above, plus the labrid *Thalassoma bifasciatum*, were the 8 most abundant taxa collected, indicating that the patterns of taxonomic composition here described are broadly stable over time (H. Valles, unpublished data).

4.2. Comparison with other methods of estimating settlement

The SMURFs described in this study offer several advantages over light-traps, and by extension, over methods that sample pelagic larvae as an estimate of settlement. The use of light-traps and nets implicitly assumes that the pelagic larvae caught are about to settle, but behavioral studies have shown that this assumption is not always warranted (Leis and McCormick, 2002). In contrast, rubble SMURFs sample only larvae that actually settle to the benthos at a specific location. Furthermore, because SMURFs sample continuously, they have the potential to integrate settlement over longer time periods than light-traps or nets, and hence, be more sensitive during a period of low settler abundance such as the one observed during our study. This likely contributes to
explain why in Study 3, SMURFs, but not light-traps, captured settlers of _S. partitus_ and _Sparisoma_ spp. in all series. In temperate reefs, Steele et al. (2002) also found that light-traps caught fewer larvae of a reef fish than benthic rock collectors. Moreover, these SMURFs readily provide a relative measure of settlement rate to natural reef substrata that is not biased by, and does not require information about, local water flow dynamics. This agrees with the concordance observed between SMURF and reef survey estimates during the first daily series of Study 3, where _Sparisoma_ spp. and _S. partitus_ exhibited daily patterns of settlement distinctive enough to be differentiated significantly by both the SMURFs and reef surveys. In contrast, in the second series, the only instance where light-traps captured _Sparisoma_ spp. larvae, we only found a discrepancy between light-traps and reef surveys. Thus, light-traps and methods that measure actual settlement to the benthos are not necessarily concordant at such fine spatio-temporal scales. Studies that have found good correlations between light-trap catches and reef settlement estimates generally involved aggregation of replicate data over larger spatio-temporal scales (e.g. Milicich et al., 1992; Sponaugle and Cowen, 1996a).

Visual reef surveys (e.g. Sale and Douglas, 1981) generally fail to record recruits within the substratum or otherwise out of view (e.g. Robertson et al., 1988) and are likely to underestimate small, immobile or cryptically colored individuals even if they are potentially visible (e.g. Ackerman and Bellwood, 2000). In contrast to these limitations of visual surveys, SMURFs captured consistently over 83% of the specimens present, including those that were small, difficult to see or below the surface.

Coral reef fishes are particularly vulnerable to predation by fishes soon after settlement (Hixon and Webster, 2002), so a problem with reef surveys is that settlement patterns may be rapidly changed by mortality (e.g. Steele and Forrester, 2002) to an unknown extent. In Study 2, the netting was generally effective at excluding fish predators, but the number of recruits was similar with and without netting, provided that algae did not accumulate. When algae did accumulate, and except for _S. partitus_, temporal patterns in recruit relative abundance were still similar between netting treatments, as evidenced by the significant correlations in recruit abundance over time, and the lack of a significant interaction between treatment and time of Study 2. Therefore, the rubble itself seemed to provide an effective refuge against potentially distorting predation by nearby resident fishes, and the net did not appear necessary. This is consistent with other studies showing that microscale physical complexity reduces predation on juvenile fishes (Beukers and Jones, 1997; Nemeth, 1998).

Algal growth on the netting was associated with strong changes in the abundance of _Sparisoma_ spp. and _S. partitus_ recruits, and with a distortion of the underlying settlement pattern of the latter, as indicated by the lack of correlation in _S. partitus_ recruit abundance between netting treatments. Obviously, the SMURF design should ensure that microhabitat characteristics remain relatively constant in time and space, and therefore, removal of the netting to avoid such algal artifacts seems necessary.

While the lack of an effect of netting rules out an effect of fish predation on settler numbers, the results of Study 1 suggest that some combination of mortality, emigration and exclusion as a result of competitive interactions, continues to strongly affect settler numbers within the SMURFs. This is the most plausible explanation for the approximate doubling of the estimated number of recruits, with daily as compared to 11-day sampling of the SMURFs, for the aggregate of all taxa, and that of the less common taxa in Study 1. In contrast, we found no significant effect of sampling frequency for either, _Sparisoma_ spp., _S. partitus_ or _P. gregoryi_, the three most abundant taxa. For _Sparisoma_ spp., however, which doubled in abundance during daily sampling, our test likely lacked power, as suggested by the smaller proportion of SMURFs with _Sparisoma_ spp. recruits observed during the 11-day collection. On temperate reefs, Ammann (2004) also found a species-specific effect of similar sampling intervals on recruit numbers using suspended kelp-like settlement units. He suggested that such differences could be the result of size-dependent negative interactions among settlers. Similarly, exclusion as a result of competitive interactions (Sweatman, 1985; Risk, 1998) as well as predation by small carnivores such as recently settled stomatopods and crabs inside the SMURFs are possible explanations to these taxon-specific differences in recruit abundance between sampling schemes. However, regular removal of crustaceans as well as fishes at each sampling period should have minimized the size and numbers of potential predators and competitors within the rubble. Another possibility is mortality due to insufficient energy reserves for metamorphosis to the juvenile stage (Thorisson, 1994). A fourth possibility is emigration. Some newly settled reef fishes enter the benthos and complete metamorphosis, later moving to different juvenile habitat (e.g. Finn and Kingsford, 1996). Substantial early post-settlement movements have been documented (Frederick, 1997). Two of the species that were unaffected by sampling frequency, _S. partitus_ and _P. gregoryi_, are also species in which older individuals are typically associated with rubble (e.g. Büttner, 1996). Thus, emigration may be an important component of loss. Whatever the source of changes in counts, the removal
sampling process allows optimal sampling intervals for a
given species to be determined much more easily for
SMURFs than for natural reef surveys. On the other hand,
optimal sampling intervals will be dictated by the specific
goals of the research and the taxa of interest. If absolute
measures of settlement are necessary, then Sparisoma spp.
would likely require frequent sampling (e.g. daily),
whereas for S. partitus and P. gregoryi sampling every
10 days could suffice. If, however, only relative measures
of settlement are needed, then the frequency of sampling
could be a compromise between logistic effort, taxa of
interest, and settlement resolution. As such, for Sparisoma
spp., sampling 8 SMURFs every 10 days can still provide
valuable relative measures of settler abundance as
evidenced in Study 4. In this study we observed an in-
crease in Sparisoma spp. recruitment around the third
quarter moon periods and a temporal concordance among
sites located km apart. This suggests that, for this taxon,
all SMURF sets were reflecting the same underlying
temporal variations in natural settlement, despite some
post-settlement loss.

Finally, the cumulative catches for Sparisoma spp. and
S. partitus recruits on SMURFs during the two daily series
of Study 3 were inversely related to their maximum
densities on natural reefs at the two sites. These two sites
differ substantially in benthic substrate composition
associated with the recruit distribution of the two taxa
(H. Valles, unpublished data). Hence, the relationship
between SMURF and reef recruit abundance at a site
likely depends on how much suitable settlement micro-
habitat is available for the settling larvae before reaching
the SMURFs (e.g. Gaines et al., 1985). This warrants
caution when quantitatively comparing SMURF esti-
mates across sites that differ substantially in benthic
composition, and requires further research.

4.3. Cost and sampling effort

These rubble SMURFs are inexpensive and easy to
assemble. SMURFs will generally require SCUBA diving,
however, and they are labor intensive during first de-
ployment, as they require collection and transport of
rubble. Nevertheless, once deployed, sampling eight
SMURFs and processing their samples required the least
amount of time of the methods compared. SMURFs
required a total 112 person-minutes, of which 48 were
diving bottom time, and were followed by surveying three
reef quadrats (108 m²), with 135 person-minutes of bottom
time, and sampling using three light-traps, with 180
person-minutes. Although light-traps do not require
diving, only SMURFs provide useful measures of
settlement under low frequency sampling schemes. Thus,
SMURFs can reduce sampling frequency substantially and
ensure specimen collection with moderate diving bottom
time.

5. Conclusions

We have developed and tested a relatively inexpen-
sive and easy to use method that makes effective use of
limited dive time to sample settling coral reef fishes,
including some cryptic, small and secretive taxa, at the
very earliest stages. These rubble SMURFs can therefore
fill the gap between the abundance of pre-settlement
stages, measured by light-traps and nets, and that of
recently settled fish as documented by visual reef
surveys. This likely also applies to crustaceans, a
group that was in fact much more numerous than fishes.
Finally, these SMURFs have the potential to be modified
to examine species preferring other substrate types or to
study the role of substrate preferences and availability in
settlement processes.

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References

Ackerman, J.L., Bellwood, D.R., 2000. Reef fish assemblages: a re-
206, 227–237.
Ammann, A.J., 2004. SMURFs: standard monitoring units for the
135–154.
Anderson, T.W., Bartels, C.T., Hixon, M.A., Bartels, E., Carr, M.H.,


