



Larval supply to a marine reserve and adjacent fished area in the Soufrière Marine Management Area, St Lucia, West Indies

H. VALLES*‡, S. SPONAUGLE† AND H. A. OXENFORD*

*Natural Resource Management Programme (NRM), University of the West Indies, Cave Hill, P.O. Box 64, Bridgetown, Barbados and †Marine Biology and Fisheries, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149, U.S.A.

A total of 76 reef fish species from 31 families was collected at two coral reef sites, one in a marine reserve and the other in an adjacent fished area of the Soufrière Marine Management Area (SMMA) in St. Lucia. Five families (Scaridae, Pomacentridae, Synodontidae, Apogonidae and Blennidae) dominated the collections at both sites while species of high commercial value were rare. Monthly patterns of larval supply differed among selected species, but overall trends were similar between the two sites for most species. However, despite the geographical proximity of the two sites, the fished area received a consistently higher abundance and diversity of larvae than the marine reserve throughout the study period. Patterns in larval supply generally were reflected in the settlement patterns of *Stegastes partitus*. Results suggest that local-scale variation in hydrodynamic and or biological features is influencing the arrival and hence settlement of larvae at the reef.

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INTRODUCTION

Marine reserves (MRs) that exclude all fishing and other consumptive uses are increasingly being recommended and used for coral reef resource conservation and management (Bohnsack, 1990). They are management tools that require relatively little biological information, are easier to enforce than many, and provide better protection against management failure (Roberts & Hawkins, 1995). Positive effects of MRs on reef fish communities within the boundaries of the reserve have been widely supported (Russ, 1985; Bohnsack, 1990; Roberts & Polunin, 1991; Polunin & Roberts, 1993; Rowley, 1994; Hatcher, 1995; Roberts, 1995a, 1997a; Roberts & Hawkins, 1995; Bohnsack & Ault, 1996; C. M. Roberts, M. Nugues & J. P. Hawkins, unpubl. obs.). These include an increase in the average size of protected individuals, and an increase in the abundance and species diversity of fishes within the MR. Positive effects of MRs on the yield of adjacent reef fisheries are less well documented, but the basic tenet is that MRs will stock fished areas through 'leakage' of adults over MR boundaries into fished areas as abundance in the MR builds up, and through enhanced supply of recruits from the protected breeding stock to fished areas (Bohnsack, 1990).

Several authors have addressed the phenomenon of movement of coral reef fishes across MR boundaries (Alcala & Russ, 1990; Holland *et al.*, 1996; Rakitin

‡Author to whom correspondence should be addressed. Fax: +1 246 424 4204; email: nrm@uwichill.edu.bb

& Kramer, 1996; Appeldoorn, 1997; Corless *et al.*, 1997; Zeller & Russ, 1998; Chapman & Kramer, 1999, 2000; Kramer & Chapman, 1999; Eristhee & Oxenford, 2001). Much less attention has been paid to the contribution and effects of MRs with regard to larval supply and recruitment, although the expected mechanism is well accepted. Increases in average fish size and abundance inside a reserve can be expected to contribute to changes in breeding stock biomass (Roberts & Polunin, 1991). As a consequence of the accumulation of mature adults, as well as the fact that large fish produce exponentially more eggs than smaller fish (Thresher, 1984), egg production is likely to increase. Higher fecundity levels for fishes within MRs may translate into higher recruitment rates both within the reserve and potentially for adjacent fished populations (Bohnsack & Ault, 1996).

Larval supply and recruitment of reef fishes appears to be driven by a combination of predictable factors such as the timing of spawning (Doherty, 1991; Robertson, 1991), the pelagic larval duration (Cowen & Sponaugle, 1997; Sponaugle & Cowen, 1997) and lunar and tidal cues, among others (Shenker *et al.*, 1993; Sponaugle & Cowen, 1996a). Larval supply and recruitment are also affected by stochastic factors such as larval growth and mortality (Cowen *et al.*, 2000); and various oceanographic processes (Richards & Lindeman, 1987; Leis, 1991; Shanks, 1995). The decoupling of the pelagic larval phase from the benthic adult phase and the lack of knowledge of how these processes influence the survival and transport of larvae makes the role of MRs with regard to recruitment production very difficult to assess. The local production of offspring may have little or no direct role in determining local population size because new recruits may be supplied by larvae coming from elsewhere (Koslow *et al.*, 1988; Caley *et al.*, 1996; Roberts, 1997b). However, there is evidence suggesting that in topographically complex areas, typical of coral reefs, many larvae may be retained near the area where they were spawned (Cowen & Castro, 1994; Jones *et al.*, 1999; Swearer *et al.*, 1999; Cowen *et al.*, 2000).

A poorly situated MR might contribute little to the local population since larvae may be carried into the open ocean and lost (J. L. Munro & M. Watson, unpubl. data). Also, reserves whose new recruits come mainly from fished areas may take many years to become established because of poor recruitment, whereas areas receiving high numbers of larvae may be more effective (Roberts, 1997b, 1998; J. L. Munro & M. Watson, unpubl. data).

Patterns of recruitment are also likely to be strongly influenced by ecological processes after and or during settlement, such as predation, competition, behaviour, habitat selection, facilitation, and resource availability (Hixon, 1991; Jones, 1991; Leis, 1991; Cowen & Sponaugle, 1997). Furthermore, spatial differences in fishing pressures can lead to differences in the characteristics of resident fish populations and fish community structure (Russ, 1991; Roberts, 1995b; Bohnsack & Ault, 1996). Hence, it is not unreasonable to suggest that ecological differences between a MR and an unprotected area may also be translated into differences in the settlement and or survival rates of new recruits.

Understanding the importance of the contribution of MRs to larval supply and recruitment both within the reserve and to adjacent reefs is critical for the management and justification for reserves. Correctly sited reserves have the potential to buffer high recruitment variability in sink areas (Bohnsack, 1990),

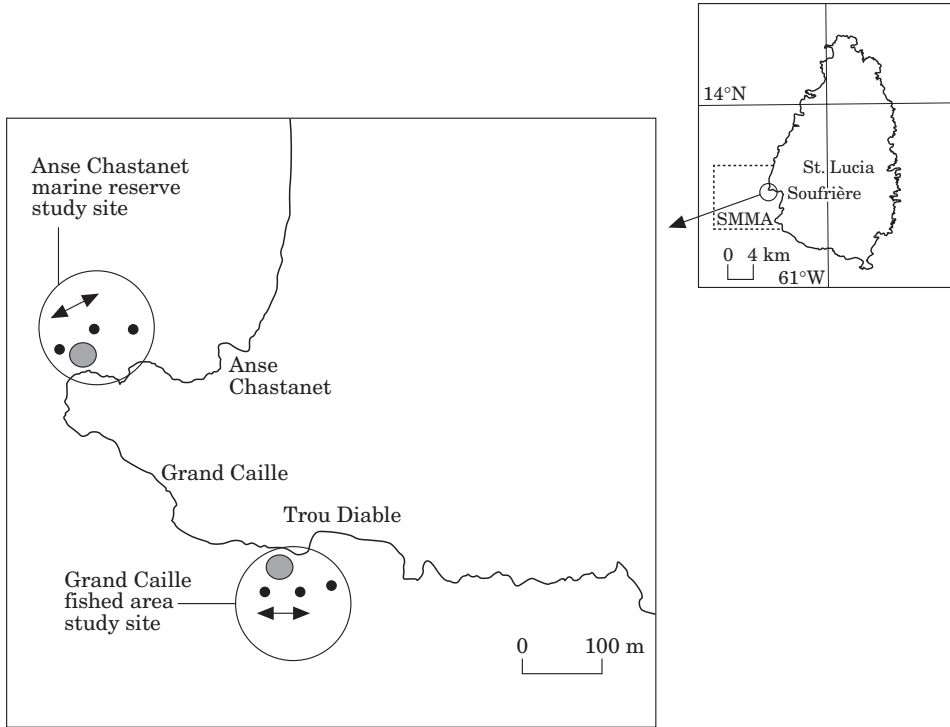


FIG. 1. Map showing the location of the Soufrière Marine Management Area (SMMA) in St. Lucia. Insert shows the location of the light-trap replicates and the sites of the habitat, resident fish and recruit underwater surveys at the Grand Caille (fished area) study site and at the Anse Chastanet (marine reserve) study site within the northern section of the SMMA. ●, Site of habitat, resident fish and recruit surveys; ●, location of replicate traps; →, prevailing current direction.

and to contribute to a faster recovery from the effects of recruitment failure in overfished areas, thereby acting as an insurance against stock collapse in those sink areas (Bohnsack & Ault, 1996).

Several authors have attempted to compare larval supply patterns with subsequent recruitment patterns (Milicich *et al.*, 1992; Meekan *et al.*, 1993; Sponaugle & Cowen, 1996b), but few have done it in the context of a MR (J. L. Munro & M. Watson, unpubl. data). The general objective of this study was to measure patterns of reef fish larval supply to a MR and neighbouring fished area on a Caribbean island (St. Lucia), and to compare patterns of larval supply and subsequent recruitment for a selected species, the common bicolor damselfish *Stegastes partitus* Poey.

MATERIALS AND METHODS

STUDY AREA

The Soufrière Marine Management Area (SMMA), is an 11 km stretch of coastline zoned for multiple uses on the west coast of St. Lucia (Fig. 1). Two study sites were selected on shallow (9 m depth) fringing coral reefs: a protected site within a no-take MR

(Anse Chastanet), which has been protected since August 1995, and an adjacent unprotected site (Grand Caille), which was initially closed to fishing in 1995 but reopened in late 1997 (Fig. 1).

LARVAL SUPPLY

The supply of larvae to the Anse Chastanet and Grand Caille reefs was monitored with the use of light-traps. The light-trap design was adapted from Sponaugle & Cowen (1996a) with a modification to the float mechanism (Valles, 2001). Traps and lights were selected randomly for deployment each night, and the order of deployment was alternated each evening between sites. Traps remained lit for 10–12 h each night. Three replicate light-traps were placed at each site in a roughly East–West direction (*c.* 45 m apart) more or less parallel to shore, about 70 m from shore at Grand Caille and 50 m from shore at Anse Chastanet (Fig. 1). The relative configuration of replicates (including distance to the edge of the reef and among replicates) was maintained at both sites throughout the sampling period by using permanent moorings. The traps were kept at a constant sampling depth of 2 m below the surface.

Larval supply was measured over 62 days at Grand Caille and 61 days at Anse Chastanet spread over a 3-month period (1 October–15 December 1999). When sea conditions allowed, the three replicate traps were deployed at each of the two sites just before sunset and were retrieved at sunrise the following morning. Sampling was interrupted on 2 nights (5 October and 28 November) due to logistical problems. Daily sampling was also interrupted for longer periods due to severe sea conditions associated with the passage of a tropical wave (18–23 October) and Hurricane Lenny (16–25 November at Grand Caille; 16–26 November at Anse Chastanet). Also, leakage due to defects in the light housings (later repaired) resulted in some malfunctions of the lights in October such that the number of replicates varied between sites on 8 nights. Immediately after retrieval, the traps were brought to shore, rinsed and sun-dried. The cod ends were removed with each evening's catch and placed in a refrigerator for sorting (within the next 6 h). If sorting had to be delayed, the samples were frozen. The total catch of fish larvae for each replicate at each site each day was stored separately and preserved in 75% isopropyl alcohol for further examination and identification to the lowest possible taxonomic level.

RECRUIT CENSUS

The bicolor damselfish is a common fish on Caribbean reefs. Relatively site-attached, it settles to coral crevices or sand-rubble areas where new recruits can be easily censused. Newly settled *S. partitus* recruits were censused and collected *c.* every 2 weeks at each of the two sites 17–18 October, 1–2 November, 14–15 November, 29–30 November and 17–18 December 1999. During each census, all recently settled recruits found in 10 randomly placed replicate 5 × 1 m quadrats at each site were counted and allocated into 0.5 mm size classes. At least half of them were also collected for confirmation of size estimate. All counts and collections were made by the same two SCUBA divers, using hand-nets and clove oil as an anaesthetic. Recruits were collected in separate zip-lock bags, and kept cold once at the surface. Once preserved in 75% isopropyl alcohol, recruits were kept in separate vials for later examination. The standard length (L_S) of all the preserved recruits was measured to the nearest 0.5 mm.

ENVIRONMENTAL DATA COLLECTION

Data on habitat characteristics and resident fish abundance were collected following the methods of Sponaugle & Cowen (1996b). No current meters or other equipment suitable for examining physical and chemical water variables were available for this study. Daily qualitative observations of the surface water currents and water clarity were made and additional data were gathered on the prevailing wind direction and state of

tide. However, the results of these observations were eliminated from analysis because sampling proved to be insufficient to adequately test for any site-specific differences in local hydrodynamics.

Habitat surveys

Several habitat variables were quantitatively sampled once (17–18 December) at each site using a standard point-contact method. At each site, ten 5 m long transects were placed randomly and surveyed by the same SCUBA diver. This involved recording the type of substratum and cover type under 20 equidistant points along each transect. The data were used to test for differences between sites in the percentage and diversity of live coral substratum; percentage of igneous rock substratum, dead coral rock, coral rubble, and sand substrata; percentages of turf algae cover, encrusting coralline algae cover, turf algae-sand mixture cover, and sand cover (as a thin layer of sand over a different type of substratum); as well as mean depth and rugosity. The degree of variability (s.d.) in depth among points along each transect was taken as an index of rugosity.

Fish surveys

All fishes (except for small, cryptic species such as gobies, blennies and apogonids) were considered to be resident adults or large juveniles when their L_S was >30 mm. They were visually censused once at each of the two sites (17 and 18 December) to determine whether differences in new recruits were related to differences in resident populations. Two SCUBA divers counted the number of resident fishes within ten randomly placed 5×5 m quadrats at each site. Each diver would swim along one side of the 5 m transect holding (perpendicularly to the transect) a 2.5 m PVC pipe and identifying and counting all fish within the quadrat while the other diver would do the same on the other half.

DATA ANALYSIS

The data sets were stored and handled using MS-Access 97 database and MS-Excel 97 spreadsheets. The Systat 8.0 software package was used for most of the statistical analysis. Some statistical tests were performed manually (i.e. non-parametric Tukey-type multiple range tests, and two-sample tests for homogeneity of variance) following Zar (1984). Prior to analysis, all data sets were tested for normality and homogeneity of variance in order to validate the use of parametric statistical procedures. Data transformations were attempted when non-normality and/or heterogeneity of variance occurred (Zar, 1984). In those cases where the data deviated seriously from the basic conditions necessary for parametric testing, non-parametric statistics were used.

When a replicate light-trap malfunctioned, mean catch was estimated from the remaining two replicates. To facilitate analysis, the two major gaps in the nightly larval supply record were handled by dividing the series into three time-periods of about three weeks each. The first was from 1 to 18 October 1999 (day 274–291), the second from 23 October to 16 November 1999 (day 296–320), and the third from 25 November to 15 December 1999 (day 329–349).

Mean catch rates (number of larvae per light-trap per night) were taken as abundance indices of larval supply ($n=186$ for Grand Caille; $n=183$ for Anse Chastanet). Differences between the two sites in overall abundance, and in abundance during each time-period, were assessed by comparing catch rates using Mann–Whitney tests. Differences among the three time-periods were assessed by comparing catch rates using Kruskal–Wallis tests, followed by non-parametric Tukey-type multiple range tests where appropriate.

A discriminant function analysis (DFA) was performed to identify the most discriminant habitat variables between sites. Square-root transformations, $\sqrt{(x+0.5)}$, were performed on some habitat variables to achieve normality.

The daily supply of larvae (overall and for selected individual species) was compared between sites using Spearman rank correlation tests (Zar, 1984) because of the non-normality of the data sets. These tests were performed for all time-periods combined and for each of the three time periods separately.

Differences in recruit densities at each site across censuses were compared using Kruskal–Wallis tests followed by non-parametric Tukey-type multiple range tests where appropriate. For each census, the comparison of recruit density between sites was examined using Mann–Whitney tests. In order to examine the relationship between mean larval supply and subsequent mean recruit density, the mean daily total catch of larvae over the 2 weeks previous to each of the recruitment censuses was used as the index of larval supply and the mean recruit density observed during each census was used as an index of recruit abundance. These data were compared at each site separately using Spearman rank correlation.

RESULTS

ENVIRONMENTAL VARIABLES

Habitat characteristics and resident fish density and diversity

The DFA was able to correctly classify 100% of the survey transects to their correct sites (squared canonical correlation=92.1%), suggesting that habitat variables were reliable predictors of site membership. The sites differed along a significant dimension that consisted primarily of the amount of igneous rock substratum present (discriminant loading (d.l.)=+0.444) and on the diversity of the living corals (d.l.=+0.39), and to a lesser extent, on the amount of sponge cover (d.l.=+0.159). These three variables were found to be significantly higher at Grand Caille than at Anse Chastanet (Mann–Whitney tests: $U=0$, $U=90.5$, $U=22$ respectively, $n=20$, $P<0.05$). Although Anse Chastanet had a significantly higher reef fish diversity than Grand Caille (two-sample t -test: $t=3.359$, d.f.=18, $P<0.01$) there was no significant difference in overall densities of resident fishes between sites (Mann–Whitney test: $U=65.5$, $n=20$, $P=0.241$).

OVERALL LARVAL SUPPLY

A total of 369 light-traps was deployed over 62 nights during the 3-month sampling period. This resulted in a total catch of 3221 late-stage larval reef fishes, comprising 76 identifiable species or types from 31 families (Table I). An additional 4132 late-stage larvae and 88 262 juveniles in different developmental stages of several pelagic species (but mainly of one clupeid *Harengula clupei* Valenciennes), were also collected and constituted 96.6% of the total catch, but were not considered further. Overall, the most abundant reef fish families were the Scaridae, Pomacentridae, Synodontidae, Apogonidae and Blennidae (Table I). Each was represented by >200 individuals and together these families constituted 79.3% of the total reef fish catch. The most abundant species overall were the stoplight parrotfish *Sparisoma viride* Bonnaterre, the dusky damselfish *Stegastes dorsopunicans* Poey, the sand diver lizardfish *Synodon intermedius* Spix and Agassiz and the bicolor damselfish *Stegastes partitus*.

Spatial patterns

Larval supply to Grand Caille (overall mean catch: 11.6 ± 1.47 s.e. larvae trap⁻¹ night⁻¹) was significantly higher than to Anse Chastanet (overall mean catch rate: 6.33 ± 0.74 larvae trap⁻¹ night⁻¹) (Mann–Whitney test: $U=12396.5$, $n=369$, $P<0.001$). Furthermore, the number of species caught at Grand Caille (overall mean catch: 3.72 ± 0.25 species trap⁻¹ night⁻¹) was also significantly higher than at Anse Chastanet (overall mean catch: 2.81 ± 0.25 species trap⁻¹ night⁻¹) (Mann–Whitney test: $U=13317.5$, $n=369$, $P<0.001$).

TABLE I. Total catch of reef-fish late-stage larvae of all species or types (1 October–15 December 1999) at each site of the two St Lucia sites (for authorities, see Bohlke & Chaplin, 1993). Bold type indicates the 10 most abundant taxa at each site

Family	Species or type	Grand Caille		Anse Chastanet		Overall	
		Total	%	Total	%	Total	%
Lutjanidae	<i>Ocyurus chrysurus</i>	0	0	1	0.09	1	0.03
	<i>Lutjanus mahogani</i>	10	0.47	4	0.36	14	0.43
	<i>Lutjanus jocus</i>	1	0.05	2	0.18	3	0.09
	<i>Lutjanus griseus</i>	7	0.33	8	0.73	15	0.47
	<i>Lutjanus apodus</i>	2	0.09	1	0.09	3	0.09
	Subtotal	20	0.94	16	1.45	36	1.11
Ophichthyidae	Ophichthyidae Type B	1	0.05	0	0	1	0.03
	Ophichthyidae Type A	9	0.42	6	0.54	15	0.47
	Subtotal	10	0.47	6	0.54	16	0.50
Pomacanthidae	<i>Pomacanthus</i> sp.	0	0	2	0.18	2	0.06
Pomacentridae	<i>Stegastes partitus</i>	159	7.50	69	6.26	228	7.08
	<i>Stegastes dorsopunicans</i>	292	13.78	81	7.35	373	11.58
	<i>Stegastes</i> spp.	76	3.59	61	5.54	137	4.25
	<i>Microspathodon chrysurus</i>	36	1.70	7	0.64	43	1.33
	<i>Chromis multilineata</i>	25	1.18	20	1.81	45	1.40
	<i>Abudefduf</i> sp.	2	0.09	0	0	2	0.06
	Subtotal	590	27.84	238	21.60	828	25.70
	Scaridae	<i>Sparisoma viride</i>	636	30.01	338	30.67	974
Scaridae	Scaridae Type A	5	0.24	0	0	5	0.16
	Scaridae Type B	17	0.80	0	0	17	0.53
	Scaridae Type C	2	0.09	3	0.27	5	0.16
	Scaridae Type D	2	0.09	1	0.09	3	0.09
	Scaridae Type F	3	0.14	0	0	3	0.09
	Scaridae Type G	4	0.19	0	0	4	0.12
	Scaridae Type H	4	0.19	2	0.18	6	0.19
	Subtotal	673	31.75	344	31.22	1017	31.58
	Scombridae	<i>Acanthocybium solandri</i>	0	0	2	0.18	2
Scorpaenidae	Scorpaenidae Type B	0	0	1	0.09	1	0.03
	Scorpaenidae Type A	4	0.19	10	0.91	14	0.43
	Scorpaenidae Type D	30	1.42	35	3.18	65	2.02
	Scorpaenidae Type C	1	0.05	0	0	1	0.03
	Scorpaenidae Type E	1	0.05	0	0	1	0.03
	Scorpaenidae Type F	3	0.14	0	0	3	0.09
	Subtotal	39	1.85	46	4.17	85	2.63
Serranidae	<i>Epinephelus cruentatus</i>	3	0.14	18	1.63	21	0.65
	<i>Serranus tigrinus</i>	0	0	2	0.18	2	0.06
	Subtotal	3	0.14	20	1.81	23	0.71
Sphyraenidae	<i>Sphyraena barracuda</i>	9	0.42	8	0.73	17	0.53
Syngnathyidae	<i>Syngnathus</i> sp.	14	0.66	14	1.27	28	0.87
Synodontidae	<i>Synodus intermedius</i>	220	10.38	36	3.27	256	7.95
Tetraodontidae	<i>Canthigaster</i> sp.	3	0.14	5	0.45	8	0.25
Unidentified	Unidentified spp.	4	0.18	0	0	4	0.12
Total		2119	100	1102	100	3221	100

TABLE I. *Continued*

Family	Species or type	Grand Caille		Anse Chastanet		Overall	
		Total	%	Total	%	Total	%
Acanthuridae	<i>Acanthurus bahianus</i>	64	3.02	20	1.81	84	2.61
Apogonidae	Apogonidae sp. 2	0	0	1	0.09	1	0.03
	Apogonidae sp. 3	1	0.05	1	0.09	2	0.06
	Apogonidae sp. 7	2	0.09	0	0	2	0.06
	Apogonidae sp. 6	1	0.05	0	0	1	0.03
	Apogonidae sp. 5	27	1.27	57	5.17	84	2.61
	Apogonidae sp. 4	17	0.80	14	1.27	31	0.96
	Apogonidae sp. 1	60	2.83	69	6.26	129	4.00
	Subtotal	108	5.09	142	12.89	250	7.75
Aulostomidae	<i>Aulostomus maculatus</i>	4	0.19	3	0.27	7	0.22
Balistidae	<i>Monacanthus tockeri</i>	13	0.61	39	3.54	52	1.61
Belonidae	Belonidae sp.	0	0	1	0.09	1	0.03
Blennidae	<i>Ophioblennius atlanticus</i>	95	4.48	19	1.72	114	3.54
	Blennidae Type C	1	0.05	0	0	1	0.03
	Blennidae Type B	8	0.38	15	1.36	23	0.71
	Blennidae Type A	9	0.42	8	0.73	17	0.53
	Blennidae Type J	18	0.85	11	1	29	0.90
	Blennidae Type F	9	0.42	10	0.91	19	0.59
	Blennidae Type G	1	0.05	0	0	1	0.03
	Subtotal	141	6.65	63	5.72	204	6.33
Bothidae	<i>Bothus ocellatus</i>	16	0.76	8	0.73	24	0.75
Carangidae	Carangidae sp.	0	0	1	0.09	1	0.03
Carapidae	Carapidae sp.	51	2.41	23	2.09	74	2.30
Chaetodontidae	<i>Chaetodon</i> sp.	6	0.28	5	0.45	11	0.34
Congridae	Congridae Type A	8	0.38	1	0.09	9	0.28
	Congridae Type B	4	0.19	2	0.18	6	0.19
	Congridae Type C	8	0.38	1	0.09	9	0.28
	Subtotal	20	0.95	4	0.36	24	0.75
Coryphaenidae	<i>Coryphaena hippurus</i>	1	0.05	0	0	1	0.03
Elopidae	Elopidae sp.	18	0.85	4	0.36	22	0.68
Gempylidae	Gempylidae sp.	1	0.05	2	0.18	3	0.09
Gobiesocidae	Gobiesocidae Type A	5	0.24	4	0.36	9	0.28
	Gobiesocidae Type B	25	1.18	19	1.72	44	1.37
	Gobiesocidae Type C	0	0	1	0.09	1	0.03
	Subtotal	30	1.42	24	2.18	54	1.68
Gerreidae	Gerreidae sp.	0	0	1	0.09	1	0.03
Holocentridae	<i>Holocentrus coruscus</i>	2	0.09	6	0.54	8	0.25
Labridae	<i>Thalassoma bifasciatum</i>	6	0.28	5	0.45	11	0.34
	<i>Halichoeres maculipinna</i>	15	0.71	7	0.64	22	0.68
	<i>Halichoeres bivittatus</i>	35	1.65	3	0.27	38	1.18
	<i>Halichoeres</i> spp.	3	0.14	4	0.36	7	0.22
	Subtotal	59	2.78	19	1.72	78	2.42

The relative abundance of the top 10 species varied slightly between the two sites (Table I). Seven of the top 10 species were common to both sites, and two of the same species, *Stegastes viride* and *S. dorsopunicans*, occupied the same ranks (rank 1 and 2, respectively) at both sites. However, as might be expected

based on the observation of overall lower larval supply to Anse Chastanet, the relative catch of the top seven common species differed between the two sites (Pearson's χ^2 test: $\chi^2=88.868$, d.f.=6, $P<0.001$). The lizardfish, *S. intermedius*, accounted for 10.4% (rank 3) of the total catch at Grande Caille but only 3.3% of the total catch at Anse Chastanet. Likewise, the redlip blenny *Ophioblennius atlanticus* Valenciennes, which accounted for 4.5% (rank 5) of the total catch at Grand Caille, did not rank in the top 10 in Anse Chastanet. By contrast, Apogonidae sp. 5 accounted for 5.2% (rank 5) of the catch at Anse Chastanet, but did not rank in the top 10 at Grand Caille (Table I).

Temporal patterns

Larval abundance appears to follow different patterns across days within each of the three time-periods and between sites [Fig. 2(a),(b)]. In time-period I (day 274–291), the larval supply at Grand Caille tended to be rather uniform with small peaks near the new moon and first quarter phases [Fig. 2(a)] whereas at Anse Chastanet, larval abundance was more bimodal, peaking during the third quarter and first quarter lunar phases [Fig. 2(b)]. In time-period II (day 296–320), overall larval abundance was rather low and uniform over both sites, with a gradual increase in larval abundance towards the end of the period at Grand Caille and not Anse Chastanet [Fig. 2(a),(b)]. In time-period III (day 329–349), Grand Caille exhibits a clear unimodal peak in larval abundance around the new moon (day 338), which, again, is less apparent at Anse Chastanet [Fig. 2(a),(b)].

Differences in species diversity (i.e. number of species) between sites and across time-periods are also rather conspicuous and mimic patterns evident in larval abundance [Fig. 2(c),(d)]. During time-period I, species diversity at Grand Caille is unimodal and peaks just before the new moon [Fig. 2(c)]. In contrast, species diversity at Anse Chastanet is bimodal with peaks around the third quarter and first quarter lunar periods [Fig. 2(d)]. During time-period II, at Grand Caille, species diversity tends to increase slightly at the end of the time-period, whereas at Anse Chastanet diversity tends to decrease over time [Fig. 2(d)]. During time-period III, a clear unimodal distribution with a peak around new moon is observed at Grand Caille, but is not as obvious at Anse Chastanet [Fig. 2(d)].

Mean patterns of larval abundance and species diversity differed significantly among the three time-periods at each site (Tables II and III). At Grand Caille, a similar abundance and diversity of larvae was collected during time-periods I and III and this was generally higher than the larval abundance and diversity during time-period II (Table II), although the difference in larval abundance was not statistically significant between time-period III and II (Table III). At Anse Chastanet, although the lowest abundance and diversity of larvae also was collected during period II (Table II), larval abundance and diversity during period II did not differ significantly from period III, and both were significantly lower than period I (Table III). While differences in larval supply and diversity between sites during the first time-period were not significant (Mann–Whitney test: for abundance, $U=1054.5$, $n=102$, $P=0.099$; for diversity, $U=1208$, $n=102$, $P=0.532$), during both time-periods II and III, Grand Caille had significantly higher larval abundance (Mann–Whitney test: for period II, $U=1968.5$, $n=150$,

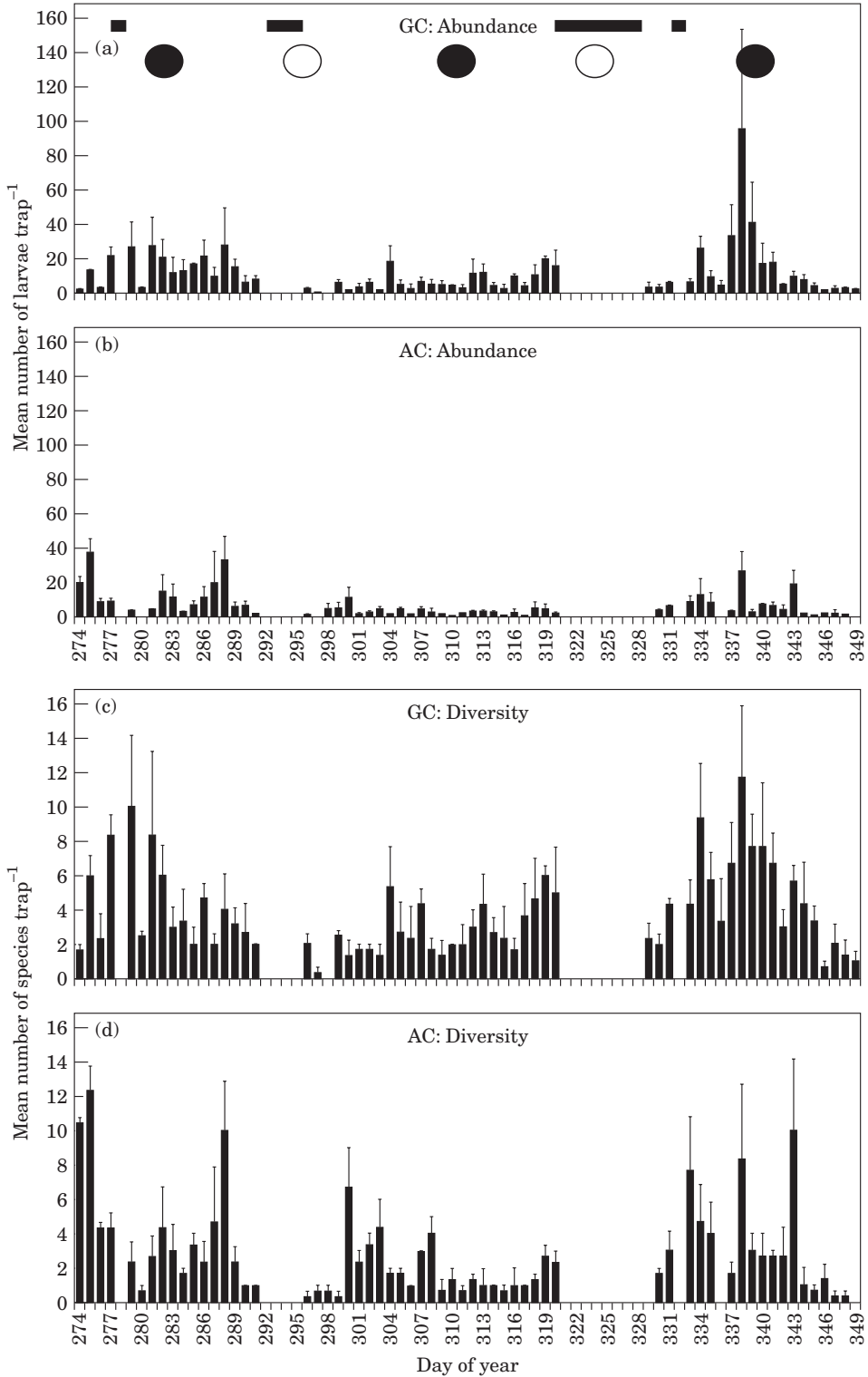


FIG. 2. Mean + s.e. ($n=3$) nightly catch of late-stage larvae per trap over the 3-month sampling period at (a) Grand Caille and (b) Anse Chastanet; and mean + s.e. ($n=3$) nightly diversity (number of species per trap) over the 3-month sampling period at (c) Grand Caille and (d) Anse Chastanet. ●, New moon; ○, full moon; ■, gaps in the time series; GC, Grand Caille; AC, Anse Chastanet.

TABLE II. Mean \pm s.e. nightly catch per trap of reef fish larvae and species for the three time-periods at each of the two sites in St Lucia

Variable	Grand Caille			Anse Chastanet		
	Period I <i>n</i> =51	Period II <i>n</i> =75	Period III <i>n</i> =60	Period I <i>n</i> =51	Period II <i>n</i> =75	Period III <i>n</i> =57
Abundance (larvae trap ⁻¹)	14.64 \pm 2.18	6.67 \pm 0.90	15.20 \pm 3.96	11.51 \pm 2.02	3.00 \pm 0.44	6.10 \pm 1.23
Diversity (species trap ⁻¹)	4.23 \pm 0.53	2.63 \pm 0.28	4.65 \pm 0.52	4.20 \pm 0.56	1.80 \pm 0.21	2.92 \pm 0.51

TABLE III. Kruskal–Wallis and non-parametric multiple comparison test results for number of individuals (abundance) and number of species (diversity) of reef fish larvae caught at each site separately compared among the three time-periods

Variable	Comparison between time-periods	Grand Caille ($n=186$)			Anse Chastanet ($n=183$)				
		H	Q	P	Among-period differences	H	Q	P	Among-period differences
Abundance	I v. II v. III	12.55	—	0.002	Yes	20.136	—	<0.0001	Yes
	I v. II	—	3.49	<0.002	I>II	—	4.48	<0.001	I>II
	I v. III	—	1.45	>0.05	NS	—	2.70	<0.05	I>III
Diversity	II vs. III	—	2.05	>0.05	NS	—	—	>0.05	NS
	I v. II v. III	12.88	—	<0.005	Yes	13.947	—	<0.005	Yes
	I v. II	—	2.61	<0.002	I>II	—	3.71	<0.001	I>II
	I v. III	—	0.54	>0.05	NS	—	2.40	<0.05	I>III
	II v. III	—	3.37	>0.05	III > II	—	—	>0.05	NS

NS, Not significant; statistics: P , probability; H , Kruskal–Wallis statistic; Q , non parametric Tukey-type multiple comparison statistic.

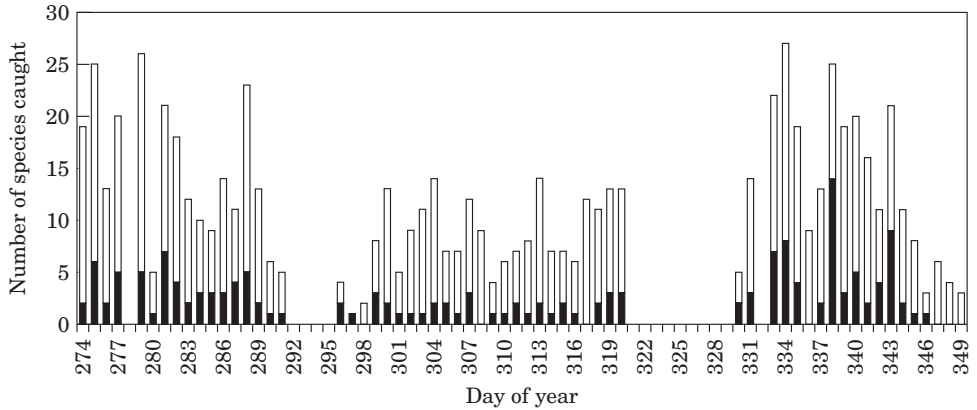


FIG. 3. Total nightly catch of reef fish larval species for both sites combined showing the numbers of species shared (■) and not shared (□) between the sites on a nightly basis.

$P=0.001$; for period III, $U=1168.5$, $n=117$, $P=0.003$), and diversity (Mann–Whitney test: for period II, $U=2262$, $n=150$, $P=0.035$; for period III, $U=1115.5$, $n=117$, $P=0.001$) than Anse Chastanet.

Significant differences in larval abundance and diversity between sites also occurred at a daily level. When each time-period was examined separately, the total number of larvae caught per day was correlated between sites for time-period III (Spearman rank correlation: $r_s=0.634$, $n=19$, $P<0.005$), but not for I or II (Spearman rank correlation: for period I, $r_s=0.123$, $n=17$, $P>0.5$; for period II, $r_s=0.229$, $n=25$, $P>0.2$). Identical patterns were identified with regard to the correlation of total number of species caught daily between both sites: the diversity of larvae collected was significantly correlated between sites only for time-period III (Spearman rank correlation: for period I, $r_s=0.021$, $n=17$, $P>0.5$; for period II, $r_s=0.118$, $n=25$, $P>0.5$; for period III, $r_s=0.7$, $n=19$, $P<0.002$).

Consistent with the observed similarity in patterns between larval abundance and diversity, there was a significant correlation between total number of larvae caught per day and total number of species caught per day at each of the sites (Spearman rank correlation: for Grand Caille, $r_s=0.824$, $n=62$, $P<0.001$; for Anse Chastanet, $r_s=0.811$, $n=61$, $P<0.001$). This suggests that larvae of a variety of species have similar patterns of supply.

As might be expected, as the nightly total number of species caught at both sites increased, the number of species shared by both sites that night also increased (Spearman rank correlation: $r_s=0.79$, $n=61$, $P<0.001$). This pattern is consistent throughout all three time-periods (Spearman rank correlation: for period I, $r_s=0.805$, $n=17$, $P<0.001$; for period II, $r_s=0.449$, $n=25$, $P<0.01$; for period III, $r_s=0.895$, $n=19$, $P<0.001$). Interestingly, on almost all nights, the number of species not shared by the two sites (i.e. number of species found only at Grand Caille or only at Anse Chastanet) was significantly higher than the number of species shared at both sites (Wilcoxon paired-sample test: $Z=6.64$, $n=61$, $P<0.001$; Fig. 3). On a day to day basis, the two sites generally have different larval compositions.

TABLE IV. Results of the comparison between sites of reef fish larval abundance (as mean catch per trap \pm s.e.) of the 10 most abundant species caught for the entire time series (1 October–15 December 1999). Significant differences in bold type

Species	Site		Test result <i>U</i>
	Grand Caille <i>n</i> =186	Anse Chastanet <i>n</i> =183	
<i>Sparisoma viride</i>	3.42 \pm 0.44	1.84 \pm 0.25	14580.5*
<i>Stegastes dorsopunicans</i>	1.56 \pm 0.52	0.45 \pm 0.10	15870
<i>Synodus intermedius</i>	1.19 \pm 0.20	0.21 \pm 0.07	12664**
<i>Stegastes partitus</i>	0.85 \pm 0.34	0.41 \pm 0.12	16161.5
Apogonidae sp. 1	0.32 \pm 0.12	0.40 \pm 0.16	16790
<i>Ophioblennius atlanticus</i>	0.51 \pm 0.23	0.10 \pm 0.04	16109.5
Apogonidae sp. 5	0.14 \pm 0.03	0.33 \pm 0.11	17117.5
<i>Acanthurus bahianus</i>	0.33 \pm 0.12	0.11 \pm 0.04	16025.5*
Carapidae sp.	0.27 \pm 0.06	0.12 \pm 0.03	15832.5*
Scorpaenidae Type D	0.16 \pm 0.04	0.19 \pm 0.06	16713
<i>Chromis multilineata</i>	0.13 \pm 0.11	0.10 \pm 0.03	16858.5

* $P < 0.05$; ** $P < 0.001$.

U, Mann–Whitney statistic; *P*, probability; for authorities, see Bohlke & Chaplin, 1993).

LARVAL SUPPLY OF SELECTED SPECIES

Patterns in larval supply were examined individually for all 10 species with total sample size ≥ 20 individuals at each site (and for *O. atlanticus*, which only had 19 individuals at Anse Chastanet, but was one of the most abundant species overall).

Spatial patterns

Considerably higher numbers of larvae of most of the selected species were caught at Grand Caille than at Anse Chastanet (Table IV), and this pattern was consistent throughout the three time-periods (Wilcoxon paired-sample test for catch during each time-period, $Z = -2.177$, $n = 33$, $P = 0.034$). However, this difference in mean catch abundance between the sites was only significant for four species: *Sparisoma viride*, *Synodus intermedius*, *Acanthurus bahianus* Castelnau, and Carapidae sp. (Table IV), presumably because of the high variation in daily catch rates at each site.

Temporal patterns

Four distinct temporal patterns in larval supply were apparent among the most abundant taxa. Three taxa, *S. viride*, Carapidae sp. and Scorpaenidae Type D exhibited higher abundances of larvae early in the time series, mainly during the first time-period, and relatively lower abundances in the following time-periods [Fig. 4(a)]. Six species, *Stegastes dorsopunicans*, *S. partitus*, *Ophioblennius atlanticus*, *Acanthurus bahianus*, *Chromis multilineata* Guichenot, and *Synodus intermedius* to a lesser extent, showed an opposite pattern, exhibiting lower abundances during the first time-periods and a higher abundance during

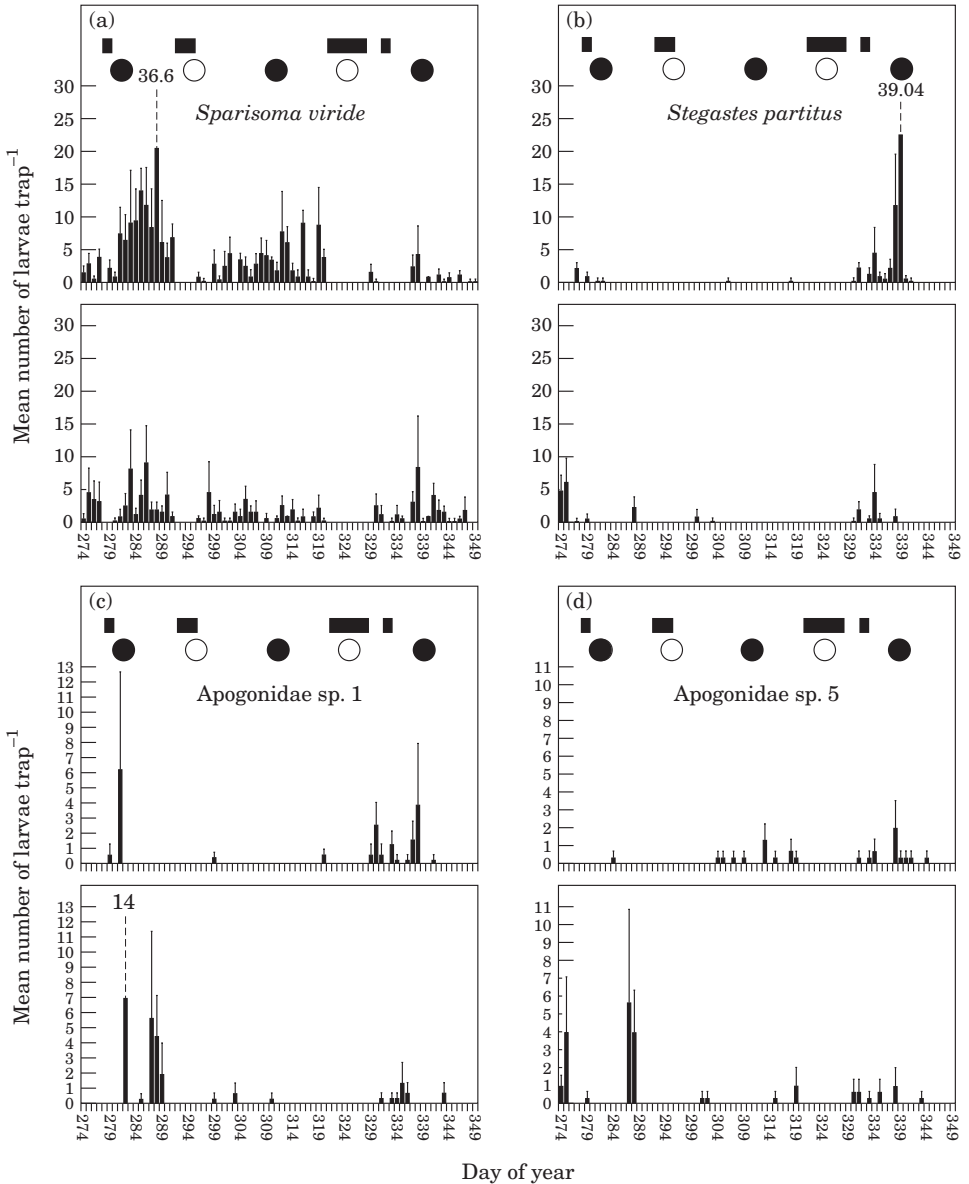


FIG. 4. Mean \pm s.e. ($n=3$) nightly catch per trap of (a) *Sparisoma viride*, (b) *Stegastes partitus*, (c) *Apogonidae* sp. 1, (d) *Apogonidae* sp. 5, over the 3-month (1 October–15 December 1999) sampling period at Grand Caille (upper plots) and Anse Chastanet (lower plots). ●, New moon; ○, full moon, ■, gaps in the time series.

the third time-period [Fig. 4(b)]. One species, *Apogonidae* sp.1, showed high abundance during the first and last time-periods [Fig. 4(c)]. Another species, *Apogonidae* sp. 5, exhibited no relative difference in abundance across time-periods at either site [Fig. 4(d)].

STEGASTES PARTITUS LARVAL SUPPLY AND RECRUITMENT*Larval supply*

The *S. partitus* larval supply time-series [Fig. 4(b)] indicates the appearance of two pulses of larvae. The first one was of low magnitude and occurred during the first week of the time series (1–9 October 1999, day 274–282) with larvae arriving at both sites [Fig. 4(b)]. The mean daily catch per trap during this pulse (for both sites combined) was 1.02 ± 0.35 s.e. larvae per trap, and accounted for 19.2% of all *S. partitus* larvae caught during the 3-month study period. The second pulse of larvae occurred late in the time-series and comprised two peaks. The first peak was of low magnitude and occurred at both sites from 26 November to 2 December, 1999 (day 330–336) [Fig. 4(b)]. The mean daily catch per trap during this peak for both sites combined was 1.55 ± 0.48 larvae per trap and accounted for 25% of all *S. partitus* larvae caught. The second peak was only evident at Grand Caille, occurring from 3 to 7 December, 1999 (day 337–341), and was large, with a mean daily catch per trap of 7.66 ± 2.53 larvae per trap. This accounted for 51.3% of all *S. partitus* larvae caught during the 3-month study period.

For ease of comparison of *S. partitus* larval supply with recruit abundance, the mean total nightly catch over the 2-week period immediately prior to each of the five recruit censuses was used (Fig. 5). Larval supply at Grand Caille varied significantly among census periods (Kruskal–Wallis test: $H=14.396$, $n=62$, $P=0.006$), but only on account of the high numbers observed in mid-December 1999 (Tukey-type multiple range test: for census 5 v. census 2 and census 3, respectively, $q=3.10$ and 2.98 , $P<0.02$ and $P<0.05$; $P>0.05$ in all other cases). However, there were no significant differences in larval supply among census periods at Anse Chastanet (Kruskal–Wallis test: $H=7.967$, $n=61$, $P=0.093$).

When both sites were compared for each 2-week sampling period, *S. partitus* larval supply was only significantly higher at Grand Caille than at Anse Chastanet during the fifth recruit census period (Mann–Whitney test: $U=88$, $n=33$, $P=0.044$) (Fig. 5).

Recruitment

A total of 101 new recruits of *S. partitus* were recorded over the five censuses at both sites. Recruits ranged from 12–19 mm L_S with a mean size of 15.5 ± 0.12 s.e.. Overall mean density was 1.09 recruits 5 m^{-2} of reef habitat.

At both sites, temporal patterns of recruitment followed a similar trend to that of *S. partitus* larval supply, with low numbers of recruits censused during the first four censuses and a peak evident in mid-December (census 5; Fig. 5). However, the trend was not significantly correlated between the two sites (Spearman rank correlation: $r_s=0.7$, $n=5$, $P>0.2$).

As with larval supply, significant differences in recruit abundance over time (i.e. among the five censuses) were apparent at Grand Caille (Kruskal–Wallis test: $H=19.281$, $n=46$, $P=0.001$) with recruit density being significantly higher in the fifth census than in the previous two censuses (Tukey-type multiple range test: $q=3.67$ and 3.82 , respectively, $P<0.005$ and <0.002 , respectively; $P>0.05$ in all other cases). At Anse Chastanet, although a similar trend was exhibited (highest recruit density during the fifth census), there were no significant

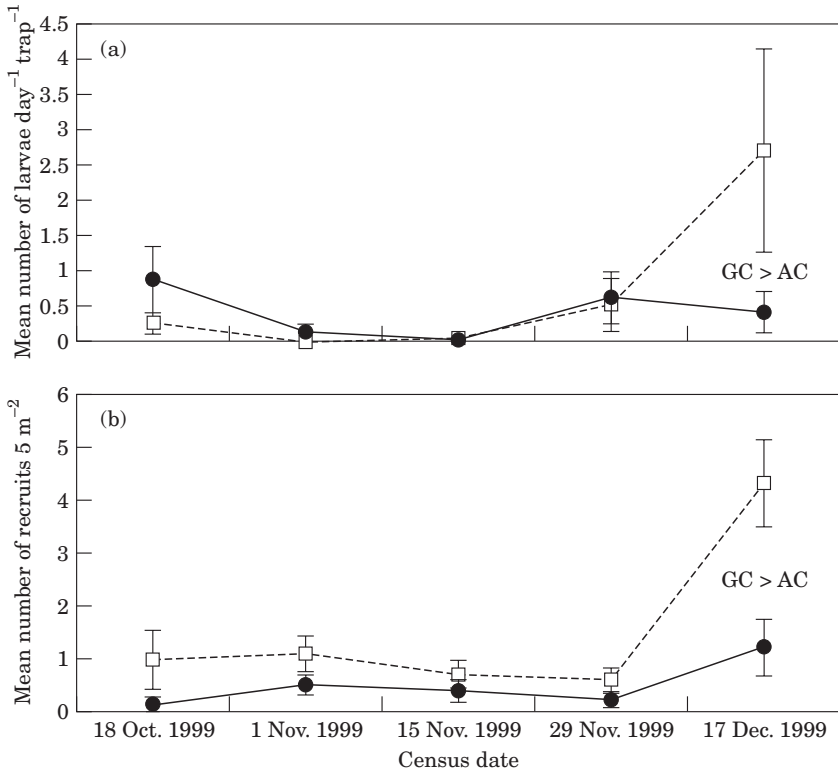


FIG. 5. Comparison between sites of *Stegastes partitus* larval supply (a) and recruit density (b) over the 3-month sampling period at \square , Grand Caille, and \bullet , Anse Chastanet. Larval supply is shown as the mean \pm S.E. nightly catch per trap over the 2-week period prior to recruitment census date. Recruitment is shown as the mean \pm S.E. number of recruits per 5 m² on the day of the census. GC, Grande Caille; AC, Anse Chastanet.

differences in observed mean density of recruits among censuses (Kruskal–Wallis test: $H=4.804$, $n=46$, $P=0.308$), again similar to larval supply.

Recruit densities overall were consistently higher at Grand Caille (overall mean 1.65 ± 0.3 recruits 5 m⁻²) than at Anse Chastanet (overall mean 0.54 ± 0.15 ; Mann–Whitney test: $H=670.5$, $n=92$, $P=0.001$). However, across censuses, this pattern was only statistically significant during the last census (Mann–Whitney test: $U=13$, $n=20$, $P=0.005$) (Fig. 5).

Comparison of recruits with larval supply

Despite similar patterns in recruit density and larval supply throughout the time-series, particularly at Grand Caille (Fig. 5), no significant correlations were detected (Spearman rank correlation: for Grand Caille, $r_s=0.1$, $n=5$, $P>0.5$; for Anse Chastanet, $r_s=-0.6$, $n=5$, $P>0.2$). There appears to be a threshold of larval supply such that only larval pulses of large magnitude are reflected in recruitment.

Comparison of recruits with resident juveniles and adults

Like the overall recruit density for *S. partitus*, the mean density of all resident juveniles and adults of *S. partitus* was significantly higher at Grand Caille (mean

density 27 ± 1.69 s.e. individuals 5 m^{-2}) than at Anse Chastanet (mean density: 17.2 ± 1.65 individuals 5 m^{-2} ; Mann–Whitney test: $U=63.5$, $n=20$, $P<0.003$).

DISCUSSION

LIGHT-TRAPS AND CATCH COMPOSITION

Despite the increasing popularity of using light-traps to examine patterns in the abundance of pre-settlement fishes (Milicich *et al.*, 1992; Meekan *et al.*, 1993; Sponaugle & Cowen, 1996a, b; J. L. Munro & M. Watson, unpubl. data), their use carries an important limitation that only phototaxic larvae will be collected, which may result in a bias in the taxa captured (e.g. labrids, Sponaugle & Cowen, 1996a). Within the Caribbean, among several studies carried out in different areas over various time-periods (Sponaugle & Cowen, 1996a; J. L. Munro & M. Watson, unpubl. data; Wilson, 2002; present study) considerable variation in catch composition is apparent. The composition of the reef fish larvae collected during this study at St. Lucia is similar to some and yet differs from other studies conducted in the Caribbean. At St. Lucia, the catch was dominated by the scarid *Sparisoma viride* and members of the family Pomacentridae, Synodontidae, Apogonidae and Blenniidae. This is generally similar to light-trap catches at Barbados during March–June, which were dominated by blenniids, a scarid (*S. viride*), a pomacentrid (*Stegastes partitus*), an acanthurid (*Acanthurus bahianus*) and a balistid (*Monocanthus tuckeri* Bean) (Sponaugle & Cowen, 1996a). Year-round collections from Tortola, British Virgin Islands (BVI) were dominated primarily by a lutjanid (*Ocyurus chrysurus* Bloch) and a synodontid, and to a lesser extent, by another lutjanid (*Lutjanus synagris* L.) and two pomacentrids (*Stegastes partitus* and *S. leucostictus* Müller and Troschel) (J. L. Munro & M. Watson, unpubl. data). Blennioids and scarids were present but in comparatively low numbers. In Panama, light-traps deployed year-round collected primarily pomacentrids, gerrids, synodontids and lutjanids (Wilson, 2002). All four studies report large numbers of pomacentrids, notably of *S. partitus* and other *Stegastes* spp. However, lutjanids, species of high commercial value, were found in relatively low numbers in St. Lucia (present study) and Barbados (Sponaugle & Cowen, 1996a), compared to the BVI (J. L. Munro & M. Watson, unpubl. data) and Panama (Wilson, 2002). To account for the large numbers of lutjanids found in their catch, J. L. Munro & M. Watson (unpubl. data) suggested the proximity of interconnected nursery grounds for these species and or the concentration of late-stage larvae by water circulation in one of the sampling areas. In the same study, the use of light-traps in a moderately fished area (Tortola, BVI) and a heavily fished area (Discovery Bay, Jamaica), over comparable time-periods, revealed that the abundance of late-stage larvae (and recruits) of exploited fishes was much lower at the heavily fished area. In this area the relative abundance of late-stage larvae was dominated by species with extended larval or post-larval pelagic phases or small species with short pelagic phases that mature before recruitment to the fishery. Species of high commercial value (e.g. snappers and jacks), with relatively short pelagic phases, and which mature after recruitment to the fishery, were relatively more abundant at the moderately fished area (J. L. Munro & M. Watson, unpubl. data). J. L. Munro & M. Watson (unpubl. data) suggest that the heavy exploitation of stocks in the

fished area and its unfavourable geographic location with respect to receiving larvae from elsewhere may account for these differences. In the present study, the relatively low abundance of late-stage larvae of highly valued species may be an indication of a local overexploitation of those species and or of unfavourable pelagic processes resulting in the downstream loss of their larvae. Both Barbados and St. Lucia are upstream islands with few potential upstream sources of larvae once local stocks are depleted. BVI and Panama, however, are downstream, thus depleted stocks potentially could be replenished from upstream sources (Cowen *et al.*, 2000). It is possible that the low numbers of lutjanids at St. Lucia are simply an indication of season-dependent low levels of larval abundance, since evidence from the Caribbean suggests that reef fish spawning activity may peak during the first half of the year (Munro *et al.*, 1973), or of natural interannual variability (Doherty, 1991). However, consistently low numbers of lutjanid larvae at Barbados during the spring months suggest a regional stock problem.

Beyond commercially important species, it is worth noting that light-traps capture large numbers of larvae of species whose settlement stage is cryptic (such as blennioids and scarids), as well as species that remain cryptic throughout their entire life history (such as carapid species). Thus, light-traps are a potentially useful means of monitoring populations of species that would be otherwise very difficult to measure.

TEMPORAL VARIATION IN LARVAL SUPPLY

Temporal patterns in the abundance of larvae have been documented in several studies in the Caribbean. This has been done directly using light-traps (Sponaugle & Cowen, 1996a; J. L. Munro & M. Watson, unpubl. data) and has been (arguably) inferred by examining patterns of recruitment for selected species and performing back-calculations from otolith records (McFarland *et al.*, 1985; Sponaugle & Cowen, 1994, 1997; Robertson *et al.*, 1999). In at least one case, involving a relatively site-attached pomacentrid, patterns of larval supply measured with light-traps agreed well with subsequent patterns of settlement determined by otolith analysis of recruits (Sponaugle & Cowen, 1996b). Most of these studies have revealed the existence of several predictable environmental factors of a periodic nature that seem to influence the larval supply of numerous taxa (Sponaugle & Cowen, 1996a).

In this study, there were relative differences in the temporal pattern of larval supply among the eleven most abundant species with four distinct broad larval abundance patterns. These patterns were consistent within one family (i.e. Pomacentridae) but not within another one (i.e. Apogonidae). In the Caribbean, some confamilial species have been shown to have larvae with contrasting life histories, which could translate into different recruitment patterns (Sponaugle & Cowen, 1994, 1997). There is also evidence that congeners may be differentially affected by pelagic processes (Robertson *et al.*, 1993). Moreover, a particular species may exhibit contrasting temporal patterns of larval supply from one year to another (e.g. *Ophioblennius atlanticus*; Sponaugle & Cowen, 1996a) or between different geographic areas (Sponaugle & Cowen, 1997). Taxa-specific biological factors such as the flexibility in the pelagic larval duration (PLD), larval behaviour, and spawning patterns (Leis, 1991; Cowen & Sponaugle, 1997),

as well as the interaction of various environmental factors or cues (Reyns & Sponaugle, 1999) may account for some of these differences. The interaction of these biological and physical processes results in a series of patterns superimposed with variation at different temporal (e.g. biweekly, monthly) and spatial (e.g. island-wide, microhabitat) scales (Sponaugle & Cowen, 1997). In the present study, similar temporal patterns were observed between larval abundance and diversity for all collected species combined. High synchronicity in larval supply among species appears to be a common occurrence and has been documented in the Caribbean (Victor, 1991; Sponaugle & Cowen, 1996a). As Sponaugle & Cowen (1996a) suggest, despite biological differences among taxa (e.g. variation in PLD, spawning patterns), many taxa respond similarly to certain environmental factors or are subjected to similar oceanographic processes.

DIFFERENCES BETWEEN SITES

Data collected on environmental variables during this study were inconclusive due to inadequacy of sampling protocols (Valles, 2001). There is however well documented evidence of the influence of various environmental factors on larval supply. For example, Sponaugle & Cowen (1996a) suggest that regular patterns of larval supply may be related to the interaction of predictable tidal and lunar signals, but strong externally forced events can be superimposed on these regular patterns (Shenker *et al.*, 1993). For crab post-larvae the timing of settlement may be related to a hierarchy of several environmental cues (day-night and hours of ebbing tides) (Reyns & Sponaugle, 1999). Unfortunately, data of this type were unavailable for the present study.

The two sites (Grand Caille, a fished area, and Anse Chastanet, an MR) shared most of the larval reef fish species caught overall, though in any given night, more larvae were unique to one site than shared. However, despite the geographical proximity of the two sites, the number of larvae supplied to each site varied, with Grand Caille receiving a consistently higher abundance and diversity of larval reef fishes. So, while temporal patterns of larval supply between sites varied considerably on a daily scale, over a broader time frame patterns were consistent between sites, with the MR site consistently receiving a lower abundance and diversity of reef fish larvae. For example, four of the most abundant species (*Sparisoma viride*, *Synodus intermedius*, *Acanthurus bahianus* and Carapidae sp.) were significantly more abundant at the fished area (Grand Caille) than at the MR (Anse Chastanet). Doherty (1991) highlights that, at a spatial scale similar to the one chosen for the present study, temporal variations such as larval pulses are often significantly correlated between sites, however, their magnitude may vary considerably between sites (Doherty, 1987). The distribution of recruits is often better explained if larvae colonize the reefs in small groups (contagious distribution) rather than in independent random settlement events (Doherty, 1981). On the other hand, there is increasing evidence that larval behaviour plays an important role in the spatial distribution of late-stage larvae as well as in temporal and spatial patterns of new recruits (e.g. Leis & Carson-Ewart, 1998). The remarkable larval swimming speeds of some taxa (Leis & Carson-Ewart, 1997; Stobutzki & Bellwood, 1997) stresses the potential importance of active behaviour in determining larval supply and

settlement (Armsworth, 2000). Accordingly, the differences observed in habitat-type between sites (i.e. mainly with regard to rock substratum content, coral diversity, and sponge cover content), may account for some of the observed variation in larval abundance. For many species, habitat characteristics may play an important role in settlement (Eckert, 1985; Levin, 1991; Green, 1992; Carr, 1994; Macpherson & Zika, 1999). Moreover, there is also evidence that settlement of several species may be influenced by the presence of other species (Shulman *et al.*, 1983; Risk, 1998) or other conspecifics (Sweatman, 1983; Booth & Beretta, 1994; Risk, 1998). However, it is unlikely that species with such different ecological characteristics and juvenile habitat preferences such as newly settled scarids (Eckert, 1985; Green, 1992), *Acanthurus bahianus* (Sponaugle & Cowen, 1996b), Carapidae sp. and *Synodus intermedius* (Bohlke & Chaplin, 1993) would have exhibited active preference for the same habitat characteristics found at the fished area (Grand Caille). This suggests that, even though there were similar temporal patterns (at a time-period scale) at both sites, factors other than habitat selection appear to be determining the spatial distribution of most larvae. Perhaps differential larval advection by local scale currents is responsible for either retaining or bringing more larvae to the fished area (Grand Caille) than to the MR (Anse Chastanet), and for causing a low degree of interconnectivity between the two sites. Consistent with this is the observation that on a daily basis, the by-catch of invertebrate plankton in the light-traps also tended to be different in composition and quantity between sites (Valles, unpubl. data). The two sites belong to different sides of a headland and have relatively different nearshore topography, which is likely to result in complex patterns of water movement at the two sites. At an island scale, in Barbados, Sponaugle & Cowen (1996a) found that a central study site along the west coast tended to receive a lower abundance and diversity of larvae than sites at either end of the west coast. They suggested that local differences among the sites in patterns of tidal currents may be the cause. Of interesting relevance to the present study is that the west coast's only MR is situated at the central site. Within a spatial scale <5 km, Booth *et al.* (2000), were able to identify specific areas of high and inter-annually persistent recruitment according to a set of common oceanographic and habitat features. Furthermore, Leis (1991) points out evidence of the existence of small scale (<0.5 km) distributions of reef fish larvae (including blennioids, apogonids and pomacentrids) as a result of intimate interactions between hydrography, reef topography and appropriate larval behaviour.

STEGASTES PARTITUS LARVAL SUPPLY AND RECRUITMENT

Although there is evidence that *S. partitus* settles throughout the year (Robertson *et al.*, 1988), recruitment of this species has been shown to be strongly seasonal, usually peaking in the spring and summer in Panama (April–November; Robertson *et al.*, 1988); May–October in Barbados (Tupper & Hunte, 1994; S. Dorsey & R. Cowen, unpubl. data); and April–October in the USVI (Booth & Beretta, 1994). This could explain the relatively poor numbers of larvae and recruits observed over most of this study (October–December).

Overall, like *S. partitus* larval supply, recruit abundance was greater at Grand Caille than at Anse Chastanet. However a clear temporal and spatial association between larval abundance and recruit density was only apparent during the last

census, when *S. partitus* larval supply and recruit abundance were considerably higher. The sharp increase in recruit numbers during the last census at Grand Caille is in direct response to the large pulse of larvae to that site. This larval pulse was much dampened at Anse Chastanet, where there was no significant increase in recruit density. In Barbados, Sponaugle & Cowen (1996b) found that temporal and spatial patterns of larval supply of *Stegastes partitus*, were well reflected in patterns of new recruits.

The fished area (Grand Caille) also had a significantly higher abundance of older juvenile and adult *S. partitus* than the MR (Anse Chastanet). While it is recognized that this result represents a single snap-shot view of these populations, it is consistent with the present observations of higher rates of *S. partitus* larval supply and recruit density at Grand Caille. The existence of more conspecifics potentially could influence larval supply and settlement. In some cases the presence of conspecifics has been associated with the recruitment of several other *Stegastes* spp (Booth & Beretta, 1994). However, there is no evidence that these factors play an important role in the settlement and distribution of *S. partitus* recruits (Sponaugle & Cowen, 1996b). Hence, it is likely that higher resident conspecific populations are the result, and not the cause, of higher larval supply and settlement to the area.

CONCLUSIONS

This study was conducted over a single autumn period. Clearly, more comprehensive research is needed to examine whether or not temporal and spatial patterns of larval supply observed in this study are maintained over broader temporal scales. Regional differences in taxonomic composition warrant further study and may reflect different gear or sampling protocols, or regional differences in ecological processes or pressures (e.g. the paucity of lutjanid larvae at St Lucia and Barbados may reflect the overfished characteristics of these upstream sites). There is strong evidence of considerable build up of fish biomass at Anse Chastanet since the MR implementation at this site (Roberts, 1997a; C. M. Roberts, M. Nugues & J. P. Hawkins, unpubl. obs.), as well as in other MRs in the region (Roberts, 1995a), without any previous assessment of recruitment supply. Nonetheless, results of this study, demonstrating that a MR site in the SMMA receives a consistently lower abundance and diversity of reef fish larvae than an adjacent fished site, suggests that the local potential for biomass accumulation of overfished species is not being maximized. It is important that MR efficiency be maximized in the Caribbean because regional reef resources are generally overexploited (Rogers, 1985; Mahon, 1993), which is likely to hamper recruitment and or render it more variable (Russ, 1991). Results of this study demonstrate that larval supply and recruitment can vary significantly on small spatial scales, which can influence resource management regimes. Site-specific data on larval supply, where available, should be considered in designing or re-designing particular MRs for maximum efficiencies. A better understanding of the processes involved in population replenishment in marine systems will make MRs a better tool for fisheries management and bio-diversity conservation.

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