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Patterns of lunar settlement and early recruitment in Caribbean reef fishes at Panamá

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Abstract. Lunar patterns of settlement of 15 Caribbean reef fishes were assessed from daily collections of newly arrived fishes from each of two small (A = 63 and B = 28 m^2) patch reefs at Punta de San Blas (Panamá) during two consecutive 2 yr periods (1984, 1985 and 1986, 1987). In 12 species settlement was lunar-cyclic, with a broad peak of activity around the new moon in 11 cases, and at first quarter in 1 species. However, 3 of these "lunar-cyclic" species displayed intermittent semilunar periodicity in settlement, with peaks around the quarter moons. One other species had a semilunar cycle of settlement with peaks at both quarter moons. Two species apparently lacked lunar settlement cycles. In some, but not all, pairs of congeners: (a) monthly variation in settlement intensity was positively correlated, (b) the duration of settlement pulses in the same month consistently differed, and (c) the timing of settlement pulses in the same month often differed (although one species did not consistently arrive before the other). Recruitment of juvenile fish that survived to the end of the lunar cycle in which they settled was monitored monthly, concurrently with settlement, at a number of large sites scattered up to 2 km apart. The levels of variation in the amount of settlement and recruitment each month differed in only 2 of 17 cases, with settlement variation exceeding recruitment variation in only one of these. The intensity of recruitment was positively correlated with the intensity of settlement in 16 of 17 cases. In 15 of those 16 cases, R^2 values for linear regressions of recruitment on settlement exceeded R^2 values for curvilinear regressions that would indicate either increasing or decreasing recruitment success with increasing intensity of settlement. Thus it appears that variation in recruitment can be used to estimate variation in settlement, and that recruitment success may be density-independent.

Introduction

A central idea about the population biology of marine organisms that produce pelagic larvae is that variation in the influx of juveniles at the end of that pelagic phase strongly influences the abundances and spatial distributions of adult populations (e.g. Sissenwine 1984, Connell 1985, Gaines and Roughgarden 1985, Davis 1988, Hughes 1990, Raimondi 1990). This idea permeates the debate about factors that control populations of tropical reef fishes (Talbot et al. 1978, Sale 1980, 1984, Doherty and Williams 1988, 1989, Doherty 1991, Jones 1991).

In population studies of tropical reef fishes, the influx of juveniles into the benthic population is not usually measured immediately after they have settled at the end of their pelagic lives. Intervals between settlement and censuses of the surviving recruits range from a day to a month or more (examples in Booth 1991), with intervals of one to several days being the exception rather than the rule. Early mortality of newly settled reef fishes is typically high (Doherty and Sale 1986, Victor 1986, Sale and Ferrell 1988, Meekan 1989, Sweatman and St. John 1990, Booth 1991). Hence, such mortality has the potential to decouple recruitment from settlement and to strongly influence the sizes and dynamics of benthic populations (Eckert 1987, Shulman and Ogden 1987). While the relationship between settlement and early recruitment has been examined for a number of sessile organisms (Caffey 1985, Connell 1985, McGuiness and Davis 1989, Osman et al. 1989, Raimondi 1990, Hurlbut 1991), there is very little information available for tropical reef fishes (but see Victor 1986 and Meekan 1989).

Both patterns of settlement and the success of early recruitment of reef fishes could be affected by a variety of intra- and interspecific interactions among settlers and between settlers and residents. Such interactions include attraction of settlers by recently settled conspecifics (Shulman 1985), competition among settlers of the same or different species, attraction or repulsion of settlers by subadult and adult residents (e.g. Nolan 1975, Shulman et al. 1983, Jones 1987, Sweatman and St. John 1990) and predator/prey interactions among newly settled fishes (Shulman et al. 1983, Eckert 1987). Since the potential for such interactions will be affected by the order of arrival and abundances of different species of settlers, the

patterning of settlement events on a range of time scales (diel, lunar, and seasonal) may influence recruitment success.

This paper addresses the following questions concerning settlement and recruitment on the lunar time scale: (1) What are the basic lunar patterns of settlement of a suite of species of Caribbean reef fishes that settle into the same small patch of habitat? (2) What are the patterns of intraspecific variation from month to month in the timing and dispersion of settlement over the lunar cycle? (3) How similar are patterns of variation among different species in the intensity of settlement each month, and in the timing and dispersion of settlement over each lunar cycle? (4) Does the amount of recruitment of fish at the end of the lunar cycle during which they settled reflect the amount of settlement that occurred during that lunar cycle and is recruitment density-independent?

Materials and methods

Study area

All samples and data were collected on fringing reefs at Punta de San Blas, on the Caribbean coast of Panamá (map in Robertson 1987).

Study species

Overall lunar patterns of settlement were determined for seven pomacentrids (*Stegastes diencaeus*, *S. dorsopunicans*, *S. leucostictus*, *S. partitus*, *S. planifrons*, *S. variabilis*, and *Abudefduf saxatilis*), three acanthurids (*Acanthurus bahianus*, *A. chirurgus*, and *A. coeruleus*), one labrid (*Thalassoma bifasciatum*), one chaetodontid (*Chaetodon capistratus*), two pomacanthids (*Pomacanthus paru* and *Holacanthus ciliaris*) and one canthigasterid (*Canthigaster rostrata*).

Table 1. Sizes of sampling areas on Caribbean coast of Panamá, where settlement and recruitment were concurrently monitored

Species	Sites
Settlement	
9 species[a]	1984/1985, Reef A – 63 m²
9 species[b]	1986/1987, Reef B – 28 m²
Recruitment (1984–1987)	
5 *Stegastes* spp.	11 sites totalling 2 600 m²
Abudefduf saxatilis	8 sites totalling 14 000 m²
Thalassoma bifasciatum	7 sites totalling 1 900 m²
3 *Acanthurus* spp.	8 sites totalling 14 000 m²

[a] All recruitment species except *T. bifasciatum*
[b] All recruitment species except *A. saxatilis*

Table 2. Sizes of newly settled reef fishes. Data are for fish preserved in 95% ethanol, for both sampling sites combined

Species	Standard length in mm		(*n*)
	Mean (SE)	Range	
Stegastes diencaeus	10.5 (0.18)	8.3–12.5	(38)
Stegastes dorsopunicans	11.5 (0.04)	9.3–14.1	(512)
Stegastes leucostictus	9.3 (0.04)	8.0–12.5	(235)
Stegastes partitus	12.8 (0.05)	10.1–15.1	(425)
Stegastes planifrons	10.5 (0.07)	8.7–11.5	(111)
Stegastes variabilis	10.9 (0.04)	9.0–12.5	(239)
Abudefduf saxatilis	11.0 (0.08)	9.5–14.4	(307)
Acanthurus bahianus	26.9 (0.10)	23–33	(400)
Acanthurus chirurgus	26.9 (0.10)	23–32	(400)
Acanthurus coeruleus	26.7 (0.13)	24–30	(133)
Thalassoma bifasciatum	11.5 (0.05)	10.2–13.7	(200)
Chaetodon capistratus	13.0 (0.14)	11–15	(50)
Pomacanthus paru	9.3 (0.08)	8.5–10.8	(57)
Holacanthus ciliaris	15.4 (0.14)	13.5–16.7	(48)
Canthigaster rostrata	15.5 (0.23)	10.2–23.0	(131)

Settlement

Lunar settlement patterns were determined from daily collections of newly arrived fishes from two small patch reefs (Table 1). Reef A was sampled for 25 lunar cycles, beginning on the full moon of January 1984 and ending in December 1985. Reef B was sampled for 28 lunar cycles, beginning on the full moon of October 1985 and ending in January 1988. Collections were made on 735 of 742 d on Reef A, and on 825 of 828 d on Reef B.

Reefs A and B were about 2.5 km apart. Each was located on the back-reef of a much larger (> 5 ha) reef, in a shallow (≈ 1.0 m deep) bed of seagrass. Reef A was about 25 m from the nearest other reef, while reef B was about 15 m from and in deeper water than the nearest other area of coral. Both reefs were isolated to such a degree that neither could be seen from the nearest other reef by an underwater observer. However, whether their isolation was sufficient to prevent small fish on nearby reefs locating them by olfactory cues (cf. Sweatman 1988) is unclear. Each reef consisted of a low relief patch of coralline rock covered with a scattering of small (up to 30 cm high) growths of live corals, principally *Porites astreoides*. Prior to the beginning of each 2 yr sampling period, all resident individuals of the target species considered here were removed from each study reef. Each reef was sampled at about 14.00 hrs each day by one or, more usually, two collectors who systematically and repeatedly moved back and forth across the reef collecting all individuals of the target species with a hand net and anaesthetic (Quinaldine) administered from a squirt bottle. This procedure was continued for at least 45 min, until no new fish were encountered. Collected fishes were preserved in 95% ethanol. Notes were kept of individuals lost during the collection process. Settlers were the smallest individuals of each species that were encountered. In almost all cases they showed little variation in size (Table 2).

Settlers were removed daily in order to improve the accuracy of settlement estimates by reducing effects of early mortality, of interactions among settlers, and of confusion of settlers that arrived at different times. Residents were removed at the beginning of the sampling period to reduce effects of resident–settler interactions. These removals could have either increased or decreased levels of settlement over natural levels on uncleared habitat.

Recruitment

Recruits of the month were fish that settled during a lunar month and survived until they were censused at the end of that month. Recruitment was monitored in a set of sites that were larger than and situated at least 100 m from either of the settlement reefs. Recruitment censuses were conducted once per lunar month, between first-quarter and full moon. On each occasion a count was made of recruits-of-the-month (individuals that were within a few mm standard length of settlers) in each recruitment site by the same observer, who censused those areas in the same way each time. I censused recruits around full moon because initial observations indicated that settlement was lunar-periodic, with a minimum around full moon. However, if mortality is both high and uniform

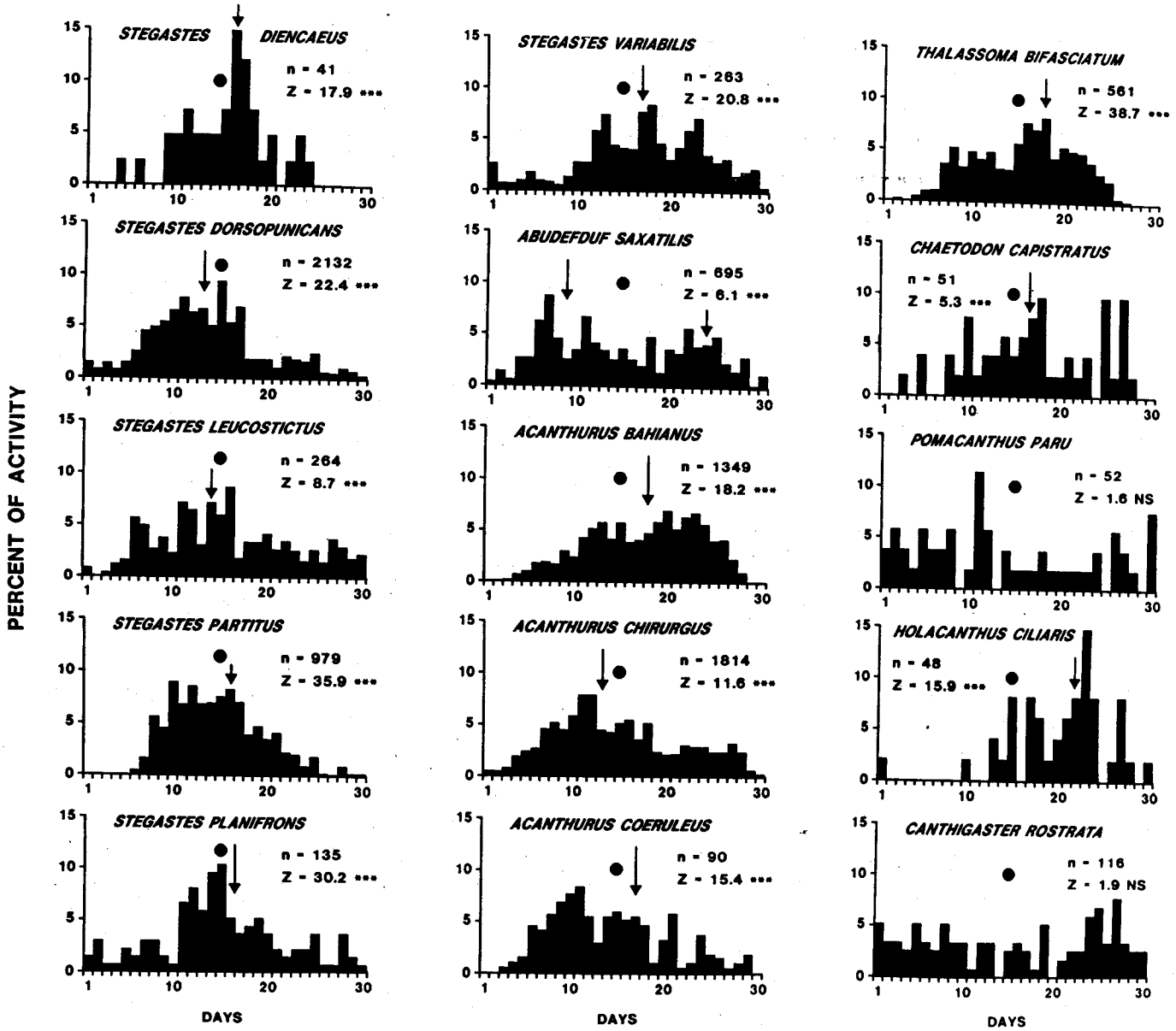

Fig. 1. Lunar patterns of settlement. Percentage of settlers collected on each day of lunar cycle. Data are for all months combined. Patterns for *Stegastes dorsopunicans*, *S. leucostictus*, *S. partitus*, *S. variabilis*, *Thalassoma bifasciatum*, *Acanthurus bahianus* and *A. chirurgus* are averages of those observed on each of two reefs. *Abudefduf saxatilis* was sampled on one reef only. Arrows indicate peaks of activity (the mean angle of each circular distribution, see Batschelet 1981); ●: new moon; Z: Rayleigh statistic (Batschelet 1981); NS: $p>0.05$, ***: $p<0.001$

(but see Victor 1986) throughout the first month of life, equal-sized episodes of settlement that occurred at different intervals during the lunar cycle could produce different levels of "resultant" recruitment. Growth of the study species appears to be sufficiently rapid for an experienced observer to be able to distinguish one month's recruits from the preceding month's recruits. However, slow growth could create some confusion and reduce the accuracy of recruitment estimates.

Data analyses

I tested for the presence of lunar and semilunar cycles in the overall pattern of settlement (data from all months combined) of each species using a Rayleigh test (Batschelet 1981). When less than 100 fish were collected from a reef over the 2 yr sampling period, I combined all data from both reefs when performing these tests. When sample sizes exceeded 100 fish I also tested the data set from each reef separately. In cases in which the Raleigh test indicated nonrandom settlement, I took the date(s) of peak settlement to be the mean vector(s) of the circular distribution (Batschelet 1981).

Sufficient numbers of settlers of ten species were obtained to permit comparisons of monthly variation in their settlement and recruitment. Those species include all of the settlement species (see above) except *Stegastes diencaeus*, *Chaetodon capistratus*, *Pomacanthus paru*, and *Canthigaster rostrata*. I examined the relationship between settlement and early-recruitment in two ways. First, I compared the level of variation in the intensity of settlement per month to the level of variation in the intensity of recruitment per month, using Levene's test for relative variation (Schultz 1985). In this test each of a set of sample variates is transformed relative to

the sample median [i.e., $y=([x-M(x)]/M(x))*100\%$] and a t-test is used to compare the means of the two sets of transformed values (here percent deviation values). Second, I examined the degree of correlation between cumulative settlement from one full moon to the next versus "resultant" recruitment at the end of that period. I tested for a linear relationship in each case by least-squares regression, and used weighted regressions when regression residuals were clearly heteroscedastic (see Neter et al. 1985 and McGuiness and Davis 1989). I used the computer package SYSTAT (Wilkinson 1990) for these analyses. To assess whether recruitment success either decreased or increased with increasing intensity of settlement, I compared R^2 values for linear regressions (density-independence) and curvilinear regressions (density-dependence: $Y=a+b \ln X$; inverse density-dependence: $\ln Y=a+bX$). I assumed that a higher R^2 value for a linear relationship than for either curvilinear relationship indicated that density-independence was more likely than either form of density-dependence.

McGuiness and Davis (1989) discussed problems associated with testing correlations between settlement and recruitment using repeated censuses in the same plot. They pointed out that while settler density is free to vary, recruit density cannot exceed settler density; consequently, the correlation coefficient cannot be meaningfully tested. They suggested that a better test for density-dependence in recruitment in such cases would involve regressions of settler mortality on settler density. In the present analyses, I used regressions of recruit density against settler density, for two reasons. First, since settlement and recruitment were measured at different sites, recruit densities are not constrained in the way described by McGuiness and Davis (1989). Second, I could not estimate mortality without using data on settler density. To do so would include settler density on both sides of a regression equation that examined mortality as a function of density.

Recruitment and settlement were monitored concurrently for a maximum of 4 yr. Even if recruitment were density-independent during that period, density-dependency in recruitment could still be important if settlement and recruitment were unusually low during those 4 yr. To assess this possibility I compared maximum levels of recruitment during the present study period to longer-term recruitment levels.

Other statistical procedures followed Sokal and Rohlf (1981).

Results

Lunar patterns of settlement

Overall patterns

Rayleigh tests indicated that there were nonrandom distributions of settlement over the lunar cycle in 13 of 15 species (Fig. 1). Of these 13 species, 12 had lunar settlement cycles. In 11 of these 12 species the peak of settlement occurred within 3d of the new moon, while the peak occurred at first quarter in the remaining species (*Holacanthus ciliaris*). In one species (*Abudefduf saxatilis*) settlement was semilunar, with two peaks of activity at the quarter moons. There was no evidence of either lunar or semilunar cyclicism in the settlement of *Pomacanthus paru* or *Canthigaster rostrata*.

Intraspecific variability in lunar settlement patterns

Analyses of between-month variation in the lunar timing of settlement of six species are given in Fig. 2. Settlement of *Stegastes dorsopunicans* and *S. partitus* almost invariably occurred in a single pulse each month, and peaks of activity were scattered over the new-moon third of the lunar cycle. There were two distinct pulses of settlement by *S. dorsopunicans* only once in 25 mo, and by *S. partitus* in only one of 19 mo. In both cases there was a major (>80% of the month's activity), "normally" timed pulse and a minor pulse well after the period when settlement peaks normally occurred. In addition, settlement of *S. dorsopunicans* occurred at a low rate (the monthly total was <30% of the maximum monthly total) throughout the lunar cycle, without an obvious peak in 1 month.

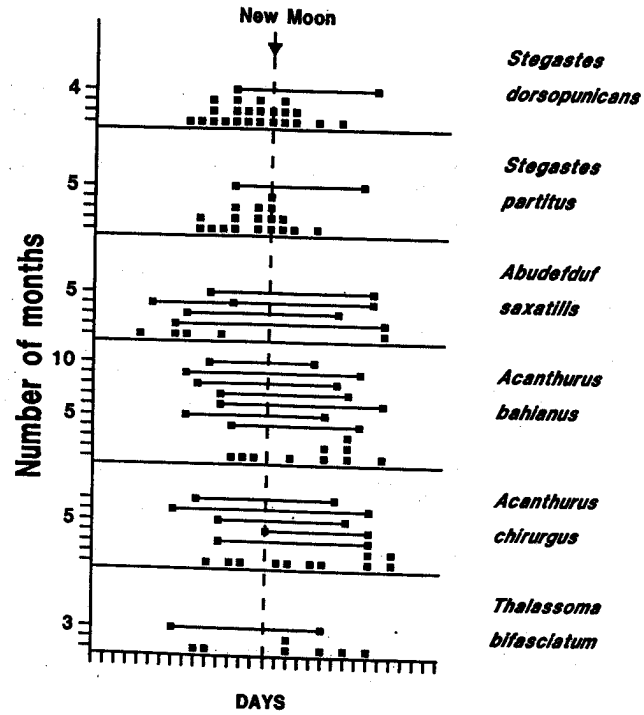

Fig. 2. Variation in lunar timing of settlement pulses. Data points indicate lunar dates of peaks of various pulses; single points are for months in which there was only one pulse of settlement, while lines join peaks of two or more discrete pulses occurring in same month. Data are for months in which at least 20 fish were collected

Although semilunar cyclicism in settlement by *Abudefduf saxatilis* was evident in the consistent timing of peaks of activity around both quarter moons, there were discrete pulses of settlement at both quarter moons in only 3 of 10 mo. In 5 other months there were single pulses of settlement, while there were three pulses in 1 other month. In 1 further month there was low-intensity settlement throughout the lunar cycle without a distinct peak.

Peaks of settlement by *Acanthurus bahianus*, *A. chirurgus* and *Thalassoma bifasciatum* were distributed throughout the new-moon half of the lunar cycle. Settlement by each *Acanthurus* sp. occurred in a single discrete pulse in about two-thirds of the months. In the remaining months there were two pulses of settlement with peaks around the quarter moons. In *Thalassoma bifasciatum* there was a single pulse of settlement in 7 mo, and two pulses around the quarter moons in the remaining month.

Table 3. Correlations between levels of settlement each month by different species on two patch reefs. Sample sizes were, Reef A: $n=25$ for correlations among *Stegastes* spp., $n=19$ for all other correlations; Reef B: $n=28$ in all cases. nd: no data for *S. planifrons* during 1984/1985, nor for *A. saxatilis* during 1986/1987. $*=p<0.05$; in all other cases $p>0.05$; this significance level was adjusted for multiple comparisons using the Bonferroni technique (Rice 1989). When making these adjustments the 1984/1985 and 1986/1987 comparisons were considered as two separate tables

Reef A 1984/1985	Reef B 1986/1987								
	S. dor	*S. leu*	*S. par*	*S. pla*	*S. var*	*A. sax*	*A. bah*	*A. chi*	*A. coe*
Stegastes dorsopunicans (*S. dor*)		0.02	0.87*	0.58*	0.01	nd	0.04	−0.15	0.19
Stegastes leucostictus (*S. leu*)	−0.32		−0.07	0.23	0.44	nd	−0.21	−0.32	−0.12
Stegastes partitus (*S. par*)	0.69*	−0.27		0.38	0.01	nd	0.14	−0.11	0.26
Stegastes planifrons (*S. pla*)	nd	nd	nd		0.40	nd	−0.25	−0.37	−0.04
Stegastes variabilis (*S. var*)	−0.15	0.68*	−0.18	nd		nd	−0.33	−0.35	−0.32
Abudefduf saxatilis (*A. sax*)	0.65	−0.10	0.51	nd	−0.03		nd	nd	nd
Acanthurus bahianus (*A. bah*)	0.07	−0.02	0.54	nd	0.12	0.18		0.76*	0.37
Acanthurus chirurgus (*A. chi*)	0.05	−0.07	0.31	nd	−0.15	0.03	0.21		0.12
Acanthurus coeruleus (*A. coe*)	0.25	−0.09	0.57	nd	−0.07	0.09	0.72*	−0.13	

Table 4. Intensities (no. of fish 100 m^{-2} yr^{-1}) of settlement and recruitment over 4 yr. nd: no data

Species	Settlers				Recruits			
	Reef A		Reef B					
	1984	1985	1986	1987	1984	1985	1986	1987
Stegastes dorsopunicans	1020	970	1950	850	16.8	12.1	19.0	20.0
Stegastes leucostictus	110	110	260	170	3.6	3.3	9.4	9.3
Stegastes partitus	160	220	1630	670	19.9	16.8	23.0	25.0
Stegastes planifrons	10	10	260	180	7.5	9.0	5.3	12.8
Stegastes variabiis	130	60	290	280	3.0	2.1	1.2	2.5
Abudefduf saxatilis	390	760	nd	nd	3.9	6.3	5.1	5.0
Acanthurus bahianus	nd	1270	400	930	9.3	15.5	12.8	24.6
Acanthurus chirurgus	nd	680	730	2550	4.5	8.4	8.7	12.9
Acanthurus coeruleus	nd	30	100	190	3.3	4.8	4.9	5.0
Thalassoma bifasciatum	nd	nd	300	180	nd	nd	13.1	31.7

Interspecific comparison of between-month variation in settlement

Intensity of settlement. Comparisons were made among nine species belonging to three genera in two families (Table 3). Variation in settlement strength was positively correlated within 5 of 36 species-pairs, in one case during both monitoring periods. Each of these 5 cases involved members of the same genus. There were no cases in which settlement variation in one species was negatively related to settlement variation in another.

Timing and dispersion of settlement. One species pair of damselfishes (*Stegastes dorsopunicans*/*S. partitus*) and another of surgeonfishes (*Acanthurus bahianus*/*A. chirurgus*) were compared, using data from months in which at least 20 settlers of each species were collected. There were statistically significant differences between the distributions of settlement by *S. dorsopunicans* and *S. partitus* over the same lunar cycle in 11 of 16 mo (Kuiper's two-sample test, Batschelet 1981), while differences between *A. bahianus* and *A. chirurgus* occurred only infrequently (2 of 13 mo, Kuiper's two-sample test). In both species-pairs there were differences in the timing of activity (10 of 11 mo in *S. dorsopunicans*/*S. partitus* and 2 of 2 mo in *A. bahianus*/*A. chirurgus*). However, settlement of one species did not consistently peak before settlement of the other species in either species-pair (Wilcoxon paired-sample tests, both $p>0.05$). Consistent differences in the duration of settlement pulses occurred only between the two damselfishes: 75% of a month's settlement occurred during (a median of) 10.5 d (range 6 to 16 d) in *S. dorsopunicans* versus 7 d (range 4 to 13 d) in *S. partitus* (Wilcoxon paired-sample test, $n=16$, $T=19$, $p=0.01$).

Relationships between settlement and early recruitment

Intensities of settlement and recruitment

Densities of settlers exceeded densities of recruits by factors of between 10 and 100 in ten species (Table 4). In four species, maximum monthly levels of recruitment recorded during the 4 yr period when both settlement and recruitment were monitored were as high as but did not exceed levels observed during as much as 12 yr. Although

Table 5. Maximum levels of recruitment during 4 yr study period in relation to maximum levels over longer periods. Max. level: maximum level during 4 yr study period as % of maximum level recorded over longer period; % months: percent of months in longer-term observations in which level of recruitment exceeded maximum recorded during 4 yr study period; No. months: number of months in longer-term observations, ending in December 1991

Species	Max. level (%)	% months	No. months
Stegastes dorsopunicans	67	0.7	134
Stegastes leucostictus	100	0	126
Stegastes partitus	68	1.8	114
Stegastes planifrons	64	2.4	126
Stegastes variabilis	100	0	126
Abudefduf saxatilis	75	1.8	114
Acanthurus bahianus	95	0.6	154
Acanthurus chirurgus	100	0	154
Acanthurus coeruleus	100	0	154
Thalassoma bifasciatum	52	1.4	73

Table 6. Relative variation in levels of settlement and recruitment over 4 yr study period. Mean level of variation: mean (SE) % deviation from median value; *t*: *t*-test for equality of means; *: $p<0.05$, NS: $p>0.05$

Species and period	Mean level of variation		(*n*)	*t*
	Settlement	Recruitment		
Stegastes dorsopunicans				
1984/1985	71 (13.4)	79 (11.8)	(25)	0.49 NS
1986/1987	178 (54.4)	104 (25.0)	(28)	1.24 NS
Stegastes leucostictus				
1984/1985	529 (171.2)	365 (117.2)	(25)	0.77 NS
1986/1987	207 (64.3)	157 (52.2)	(28)	0.60 NS
Stegastes partitus				
1984/1985	92 (18.0)	98 (37.6)	(25)	0.14 NS
1986/1987	158 (42.7)	121 (30.8)	(28)	0.71 NS
Stegastes planifrons				
1986/1987	108 (20.8)	137 (36.1)	(28)	0.68 NS
Stegastes variabilis				
1984/1985	174 (45.4)	336 (131.9)	(25)	1.08 NS
1986/1987	143 (27.8)	533 (187.5)	(28)	2.06 *
Abudefduf saxatilis				
1984/1985	243 (75.8)	79 (16.8)	(25)	2.14 *
Acanthurus bahianus				
1984/1985	82 (22.8)	84 (24.6)	(25)	0.04 NS
1986/1987	103 (26.5)	69 (13.6)	(28)	1.11 NS
Acanthurus chirurgus				
1984/1985	50 (8.4)	113 (25.6)	(25)	1.34 NS
1986/1987	289 (86.2)	122 (24.4)	(28)	1.86 NS
Acenthurus coeruleus				
1984/1985	164 (72.2)	185 (74.0)	(25)	0.15 NS
1986/1987	134 (27.8)	100 (22.7)	(28)	0.96 NS
Thalassoma bifasciatum				
1986/1987	160 (29.1)	123 (33.6)	(28)	0.78 NS

Table 7. R^2 values for regressions of recruitment on settlement. Linear regression: $y=a+bx$; curvilinear regressions, negative: $y=a+b\ln x$; positive: $\ln y=(a+bx)$. *t*-test: ***: $p<0.001$, **: $p<0.01$, *: $p<0.05$, NS: $p>0.05$. Weighted least-squares linear regressions were used to accommodate heteroscedasticity in variances (see "Materials and methods – Data analysis") for *S. leucostictus* 1986/1987, *S. partitus* 1986/1987, *S. variabilis* 1986/1987, and *T. bifasciatum* 1986/1987. Data shown in Fig. 3

Species and period	Linear regression	Curvilinear regressions	
		Negative	Positive
Stegastes dorsopunicans			
1984/1985	0.88 ***	0.73 ***	<0.05 NS
1986/1987	0.65 ***	0.53 ***	0.31 **
Stegastes leucostictus			
1984/1985	0.52 ***	0.16 NS	<0.05 NS
1986/1987	0.63 ***	0.10 NS	<0.05 NS
Stegastes partitus			
1984/1985	0.50 ***	0.05 NS	0.38 **
1986/1987	0.59 ***	0.45 ***	<0.05 NS
Stegastes planifrons			
1986/1987	0.18 *	0.24 *	<0.05 NS
Stegastes variabilis			
1984/1985	0.28 **	0.14 NS	<0.05 NS
1986/1987	0.49 ***	0.06 NS	<0.05 NS
Abudefduf saxatilis			
1985/1986	0.23 *	0.12 NS	0.12 NS
Acanthurus bahianus			
1984/1985	0.83 ***	0.55 ***	<0.05 NS
1986/1987	0.08 NS	0.06 NS	<0.05 NS
Acanthurus chirurgus			
1984/1985	0.68 ***	0.49 ***	0.07 NS
1986/1987	0.75 ***	0.25 *	<0.05 NS
Acanthurus coeruleus			
1984/1985	0.94 ***	0.21 NS	<0.05 NS
1986/1987	0.64 ***	0.07 NS	<0.05 NS
Thalassoma bifasciatum			
1986/1987	0.42 ***	0.12 NS	<0.05 NS

higher levels of recruitment were recorded outside the 4 yr study period in the other six species, such events occurred very infrequently (Table 5).

Comparative variation in intensity of settlement and recruitment

There were statistically significant differences between the levels of variation in settlement and recruitment in only 2 of 17 cases (Table 6). In *Stegastes variabilis*, recruitment was more variable than settlement during one sampling period (but not the other), while settlement was more variable than recruitment in *Abudefduf saxatilis* during the single period for which data are available. Considering the 17 samples as an aggregate, the mean levels of variation in settlement and recruitment (Table 6) did not differ in a consistent manner (Wilcoxon paired-sample test, $n=17$, $T=56$, $p>0.20$).

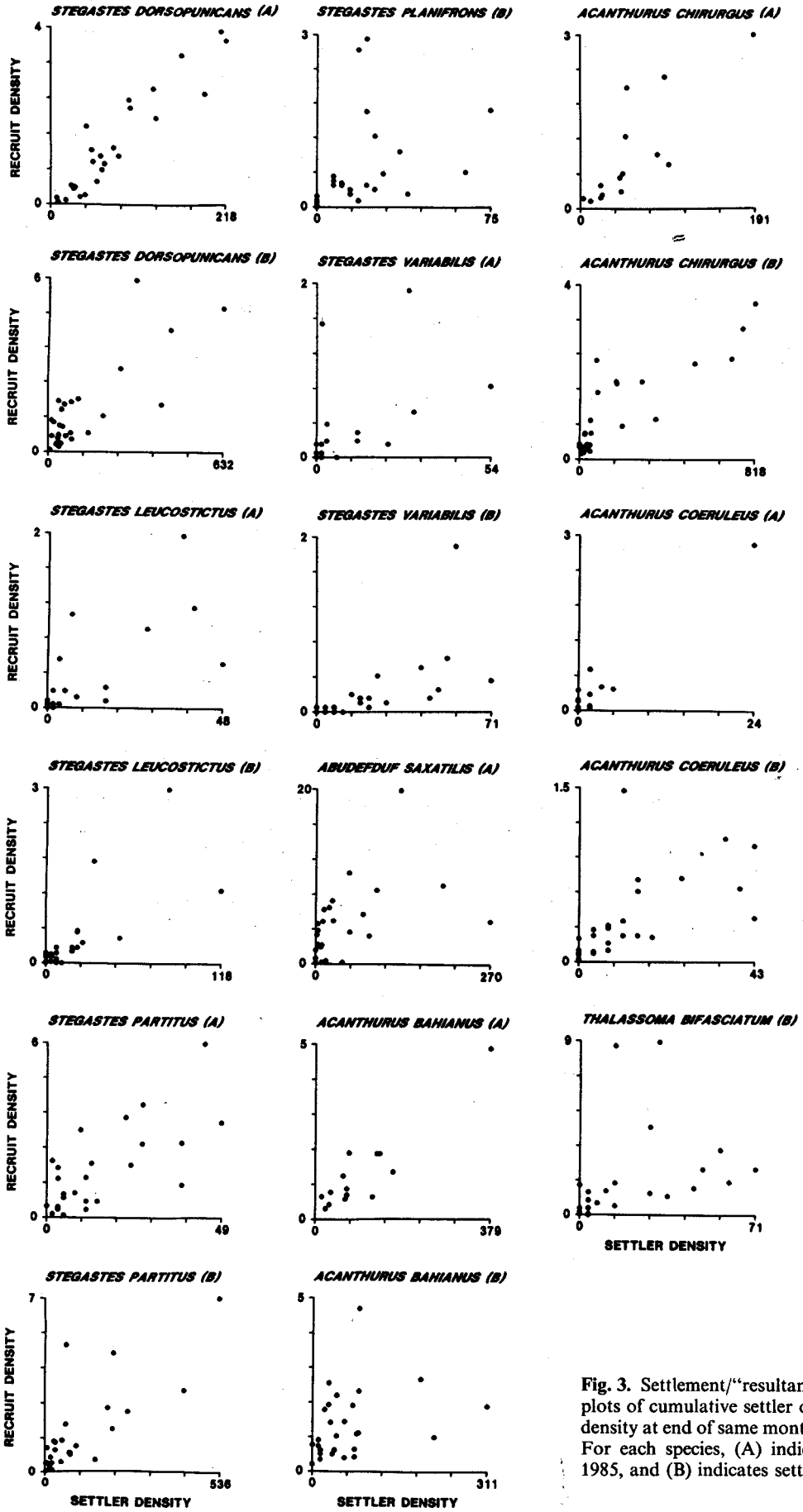

Fig. 3. Settlement/"resultant" recruitment relationships. Scatterplots of cumulative settler density for each lunar month vs recruit density at end of same month. Densities are number of fish/100 m^2. For each species, (A) indicates settlement/recruitment for 1984/1985, and (B) indicates settlement/recruitment for 1986/1987

Serial variation in settlement and "resultant" recruitment

There were statistically significant, positive linear relationships between settlement and "resultant" recruitment in 16 of 17 cases involving 10 species (Table 7). The R^2 value for either curvilinear regression exceeded the R^2 value for the linear regression in only one species, *Stegastes planifrons*, although both values were low. In most cases the R^2 values for the linear regression was substantially greater than that for either curvilinear regression.

Variation in settlement and "resultant" recruitment were tightly linked in only three instances: *Stegastes dorsopunicans* (A), *Acanthurus bahianus* (A), and *A. coeruleus* (A) (Fig. 3). In the latter two cases a single value made a large contribution to the R^2 value. When this outlier was deleted in each case, the linear settlement/recruitment relationship still remained statistically significant. Single outlying points substantially weakened otherwise good relationships in five other cases (Fig. 3 *A. coeruleus* (B), *S. dorsopunicans* (B), *S. leucostictus* (B), *S. partitus* (B), and *S. variabilis* (B)].

There was no relationship between whether or not recruitment was linearly rather than curvilinearly related to settlement (Table 7) and whether or not there was a difference in the levels of variation in the intensity of settlement and recruitment (Table 6).

Discussion

Lunar patterns of settlement

A unimodal cycle with a peak around the new moon was the predominant pattern of settlement (12 of 15 species). However, while there was relatively little variation in the number and timing of peaks of activity each month in two "lunar-cyclic" species (both damselfishes), in three others (*Thalassoma bifasciatum* and two surgeonfishes) settlement was semilunar-cyclic in up to one-third of the months. Victor (1986) obtained similar data for *T. bifasciatum*. The only species with an overall semilunar pattern of settlement (*Abudefduf saxatilis*) also showed considerable between-month variation in the pattern of settlement activity, with a single pulse of activity in half the months, and distinctly semilunar settlement cycles in only about 30% of the months. Thus, a mixture of lunar and semilunar cycles of settlement occurred in 4 of 6 species, with the semilunar peaks of activity timed around the quarter moons. The present study and those of McFarland et al. (1985) and Victor (1986) show that large time-series of data are needed if the complexity of lunar settlement patterns of some species and the conservatism of the patterns of others at the same site are to be fully appreciated.

In two species studied here, there was no evidence of lunar or semilunar cyclicism in settlement. This result should, however, be treated with caution since relatively small numbers of settlers of both species were collected, and there are no data on the consistency in their settlement patterns from month to month. In one of those species (*Canthigaster rostrata*) immigration of recently settled fish onto the settlement reefs may have masked the lunar pattern in its settlement. Immigration of subadults and adults of this species onto the settlement reefs occurred frequently and the range of sizes of individuals classified as settlers varied greatly (Table 2). Nothing suggests that immigration had similar effects on the other apparently acyclic species (*Pomacanthus paru*). All small individuals of all 15 study species that were collected were classified as settlers. Some may have been fish that immigrated into the study reef shortly after they had settled elsewhere. The effect of such immigration on the lunar patterns of settlement as estimated here is unknown.

McFarland et al. (1985) provide the only other long-term series of data for settlement of a Caribbean reef fish at a site other than the present study area. They estimated the settlement of the grunt *Haemulon flavolineatum* at St. Croix, by censusing recently arrived fish at approximately weekly intervals over an 8 mo period, and found a dominant semilunar pattern with peaks at the quarter moons and a minimum around full moon. Shulman et al. (1983), also at St. Croix, found that there was more settlement during the new-moon half of the lunar cycle in two reef fishes, a nonsignificant tendency to the same pattern in three other species, but more settlement during the full-moon half of the cycle in one other species. However, data were collected over less than two lunar cycles in the latter study.

The unimodal lunar cycle of settlement by *Thalassoma bifasciatum* indicated by the present data is very similar to that estimated by Victor (1986) for the same species at the same site. He used a combination of daily censuses (without removals) of newly arrived fish and back-calculation (from analyses of otolith microstructure) of dates of settlement of juveniles collected well after settlement. Victor suggested that *T. bifasciatum* remain hidden in the substratum for ≈ 5 d after settlement, and if the settlement cycle obtained in the present study is adjusted to take into account such delayed appearance, the peak of settlement is still within 3 d of the peak found by Victor. Similar adjustments may be necessary for other settlement cycles shown in Fig. 1. Hunt von Herbing and Hunte (1991) found no statistically significant lunar periodicity for settlement of *T. bifasciatum* at Barbados when, using otolith microstructure, they back-calculated settlement dates of juveniles. They pointed out that the difference in their results and those of Victor (1986) could arise from the action of density-dependent early mortality obscuring the original settlement pattern at Barbados. Densities of *T. bifasciatum* are much higher at Barbados than in Panamá, and there is evidence of density-dependent mortality at the former site (Hunt von Herbing and Hunte 1991), but not at the latter (Victor 1986, and present study).

In summary, most of the Caribbean reef fishes examined exhibit either lunar or semilunar cycles of settlement, or a mixture of both patterns. Peaks of settlement occur around the new and/or quarter moons. Because of the relatively small amounts of data involved, reports of lunar cycles of settlement with peaks at full moon and apparent absences of lunar periodicity are questionable.

It would be premature to compare the lunar patterns of settlement of Caribbean fishes with those of fishes from other geographic regions, since a single species can

show marked concurrent geographic variation in its lunar settlement pattern (Pitcher 1989). Although adequate time-series of data on settlement or early recruitment exist for a number of Western Pacific reef fishes (e.g. Williams and Sale 1981, Williams 1983, Sale 1985, Doherty 1987, Meekan 1989, Pitcher 1989), comprehensive statistical analyses of the extent and patterns of cyclicism have yet to be published.

Similarity in average lunar patterns of settlement among closely related, ecologically similar species (e.g. among the damselfishes and the surgeonfishes in the present study), or among predatory and prey fishes (Shulman et al. 1983, Eckert 1987) should increase the potential for interactions that might affect recruitment success. In such situations the degree of interspecific similarity of monthly variation in the intensity, timing and dispersion of settlement over the lunar cycle will also affect the potential for such interactions. Victor (1986) collected late-stage larvae of reef fishes at a night-light in San Blas, and found that daily variation in the abundance of species was correlated with variation in the abundance of individuals. The present study revealed synchronization of variation in the size, timing and dispersion of monthly settlement pulses among some species, and that both similarities and differences occur among closely related species. However, neither negative correlations in settlement strength nor consistent differences in the order of arrival were observed. Thus, patterns of variation in lunar settlement that could increase the potential for interactions among ecologically similar species were observed, but not patterns that might consistently decrease that potential or place one species at a consistent advantage over another.

Relationships between settlement and early recruitment

Settler and recruit densities

One to two weeks after the monthly peak of settlement, estimated densities or recruits were on the order of 1 to 10% of the densities of settlers. In addition to presumed high mortality immediately after settlement (cf. Victor 1986), several other factors must have contributed to this difference. First, search effort was much more intense on the settlement reefs than in the recruitment plots. Second, while only one habitat type was represented on each small settlement reef, the larger recruitment plots encompassed a variety of habitats in many cases. Differences in the quality of settlement reefs and recruitment plots as habitat for the different species probably affected levels of settlement. Third, daily removals of all recruits and immigrants of many species minimized the potential for interactions between residents and arriving settlers. Consequently, levels of settlement on those reefs may have been inflated in comparison to levels occurring in the unmanipulated recruitment plots (cf. Shulman 1985).

Variation in intensity of settlement and "resultant" recruitment

In almost all cases, monthly variation in the intensity of "resultant" recruitment was linearly related to variation in settlement. However, variation in settlement explained most of the variation in recruitment in only a few cases. This probably reflects effects of both spatial patchiness in settlement and differences in the spatial scales on which settlement and recruitment data were collected. Substantial small-scale spatial patchiness in settlement or recruitment is characteristic of many reef fishes (Williams and Sale 1981, Shulman 1985, Victor 1986). In the present study, each set of data on settlement came from one small plot while data on recruitment represented the combined influx to a series of larger plots scattered over an area of about 1 km^2. Given the differences in the spatial scales on which settlement and recruitment were monitored, it is noteworthy that the amounts of variation in settlement and recruitment differed in only 2 of 17 species, and that settlement variation exceeded recruitment variation in only one species, *Abudefduf saxatilis*. Doherty (1987) noted that pronounced small-scale patchiness in settlement can occur when fish settle in groups. Highly aggregated settlement may well have produced the high levels of variation in settlement by *A. saxatilis*, since its settlers often were encountered in compact schools.

In almost all cases, curvilinear regressions that would indicate either increasing or decreasing success in recruitment with increasing intensity of settlement failed to explain more of the variation in recruitment than did linear regressions. In the single exception, R^2 values for all types of regressions were low. If recruitment were density-dependent one would expect to find that the R^2 value for a curvilinear settlement/recruitment regression exceeded that for a linear regression in cases in which the levels of variation in the intensities of settlement and recruitment differed. Such combinations were not observed. These results indicate that variation in levels of early recruitment can be used to estimate variation in levels of settlement on the same spatial scale and that, on the spatial scale of 1 to 2 km, recruitment generally appears to have been density-independent. While this does not preclude the occurrence of patchily distributed, small-scale density dependence in recruitment, the overall effect of any such density-dependence seems likely to be relatively small.

The present conclusion that recruitment apparently was density-independent must be limited to the range of variation in settlement and recruitment observed between 1984 and 1987. Small changes in mortality rates of juveniles could have large effects on population size (Shulman and Ogden 1987) and infrequent influxes of large numbers of recruits could have long-term effects on the sizes of populations of long-lived species (Warner and Hughes 1989). Levels of recruitment have not risen above the 1984–1987 maxima during much longer sampling periods in four of the study species, and have only infrequently done so in six others. Thus, any nonlinearity in settlement/recruitment relationships due to density effects would occur infrequently.

Victor's (1986) study of *Thalassoma bifasciatum* from one reef in the present study area provides the only published data on the question of density dependence in the *early* recruitment of coral reef fishes. Other studies have considered mortality in older recruits and/or over longer periods of the juvenile stage (Doherty 1982, Eckert 1987,

Jones 1987, 1988, Meekan 1989). Victor's results indicate that mortality of settlers during the first several days after settlement was high but density-independent, and thus are in accordance with the results of the present study. However, due to the nature of Victor's data, we cannot determine how levels of settlement during his study period compare to longer-term levels, and whether early mortality of *T. bifasciatum* is density-dependent at the highest levels of settlement in San Blas. Hunt von Herbing and Hunte (1991) found strong indications of density-dependent juvenile mortality of this species at Barbados, where population densities are much higher than in San Blas.

Using a similar technique to that employed in the present study, Meekan (1989) found no evidence of density-dependence in recruitment of three reef fishes to the northern Great Barrier Reef during the first month of their benthic life. As he pointed out, recruitment was low during the year of his study. Eckert (1987) found increased mortality of fish during the first year of life in years when recruitment was high in some but not all species. She also pointed out that variation in mortality sometimes exceeded and could potentially have greater effects on population size than variation in recruitment (see also Shulman and Ogden 1987).

The present data and those of Victor (1986) and Hunt von Herbing and Hunte (1991) are correlative and pertain to only a few species of reef fishes in a limited range of habitats at two Caribbean localities. Given its potential influence on population dynamics, it is essential to determine patterns in early mortality and to test more precisely the occurrence, intensity and consequences of density-dependence during early recruitment.

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Literature cited

Batschelet, E. (1981). Circular statistics in biology. Academic Press, New York

Booth, D. J. (1991). The effects of sampling frequency on estimates of recruitment of the domino damselfish *Dascyllus albisella* Gill. J. exp. mar. Biol. Ecol. 145: 149–159

Caffey, H. M. (1985). Spatial and temporal variation in settlement and recruitment of intertidal barnacles. Ecol. Monogr. 55: 313–332

Connell, J. H. (1985). The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. J. exp. mar. Biol. Ecol. 93: 11–45

Davis, A. R. (1988). Effects of variation in initial settlement on distribution and abundance of *Podoclavella moluccensis* Sluiter. J. exp. mar. Biol. Ecol. 117: 157–167

Doherty, P. J. (1982). Some effects of density on the juveniles of two species of tropical territorial damselfish. J. exp. mar. Biol. Ecol. 65: 249–261

Doherty, P. J. (1987). The replenishment of populations of coral reef fishes, recruitment surveys, and the problems of variability manifest on multiple scales. Bull. mar. Sci. 41: 411–422

Doherty, P. J. (1991). Spatial and temporal patterns in recruitment. In: Sale, P. F. (ed.) The ecology of fishes on coral reefs. Academic Press, New York, p. 261–293

Doherty, P. J., Sale, P. F. (1986). Predation on juvenile coral reef fishes: an exclusion experiment. Coral Reefs 5: 161–163

Doherty, P. J., Williams, D. McB. (188). The replenishment of coral reef fish populations. Oceanogr. mar. Biol. A. Rev. 26: 487–551

Doherty, P. J., Williams, D. McB. (1989). Are populations of coral reef fishes equilibrial assemblages? The empirical data base. Proc. 6th int. Coral Reef Symp. 1: 131–139 [Choat, J. H. et al. (eds.) Sixth International Coral Reef Symposium Executive Committee, Townsville]

Eckert, G. J. (1987). Estimates of adult and juvenile mortality for labrid fishes at One Tree Reef, Great Barrier Reef. Mar. Biol. 95: 167–171

Gaines, S., Roughgarden J. (1985). Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. Proc. natn. Acad. Sci. U.S.A. 82: 3707–3711

Hughes, T. P. (1990). Recruitment limitation, mortality, and population regulation in open systems: a case study. Ecology 71: 12–20

Hunt von Herbing, I., Hunte I. (1991) Spawning and recruitment of the bluehead wrasse *Thalassoma bifasciatum* in Barbados, West Indies. Mar. Ecol. Prog. Ser. 72: 49–58

Hurlbut, C. J. (1991). The effects of larval abundance, settlement and juvenile mortality on the depth distribution of a colonial ascidian. J. exp. mar. Biol. Ecol. 150: 183–202

Jones, G. P. (1987). Some interactions between residents and recruits in two coral reef fishes. J. exp. mar. Biol. Ecol. 114: 169–182

Jones, G. P. (1988). Experimental evaluation of the effects of habitat structure and competitive interactions on the juveniles of two coral reef fishes. J. exp. mar. Biol. Ecol. 123: 115–126

Jones, G. P. (1991). Postrecruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. In: Sale, P. F. (ed.) The ecology of fishes on coral reefs. Academic Press, New York, p. 294–328

Meekan, M. G. (1989). Settlement and mortality patterns of juvenile reef fishes at Lizard Island Northern Great Barrier Reef. Proc. 6th int. coral Reef Symp. 2: 779–784. [Choat, J. H. et al. (eds.) Sixth International Coral Reef Committee, Townsville]

McFarland, W. N., Brothers, E. B., Ogden, J. C., Shulman, M. J., Bermingham, E. L., Kotchian-Prentiss, N. M. (1985). Recruitment patterns in young french grunts, *Haemulon flavolineatum* (family Haemulidae), at St. Croix, Virgin Islands. Fish. Bull. U.S. 83: 413–426

McGuinness, K. A., Davis, A. R. (1989). Analysis and interpretation of the recruit-settler relationship. J. exp. mar. Biol. Ecol. 134: 197–202

Neter, J., Wasserman, W., Kunter, M. H. (1985). Applied linear statistical models. 2nd ed. Regression, analysis of variance, and experimental design. Irwin, Homewood, Illinois

Nolan, R. S. (1975). The ecology of patch reef fishes. Ph. D. thesis. University of California, San Diego

Osman, R. W., Whitlatch, R. B., Zajac, R. N. (1989). Effects of resident species on recruitment into a community: larval settlement versus post-settlement mortality in the oyster *Crassostrea virginica*. Mar. Ecol. Prog. Ser. 54: 61–73

Pitcher, C. R. (1989). Spatial variation in the temporal pattern of recruitment of a coral reef damselfish. Proc. 6th int. coral reef Symp. 2: 811–816. [Choat, J. H. et al. (eds.) Sixth International Coral Reef Committee, Townsville]

Raimondi, P. (1990). Patterns, mechanisms, consequences of variability in settlement and recruitment of an intertidal barnacle. Ecol. Monogr. 60: 283–309

Rice, W. R. (1989). Analyzing tables of statistical tests. Evolution 43: 223–225

Robertson, D. R. (1987). Responses of two coral reef toadfishes (Batrachoididae) to the demise of their primary prey, the sea urchin *Diadema antillarum*. Copeia 1987: 637–642

Sale, P. F. (1980). The ecology of fishes on coral reefs. Oceanogr. mar. Biol. A. Rev. 18: 367–421

Sale, P. F. (1984). The structure of communities of fish on coral reefs and the merit of a hypothesis-testing manipulative approach to ecology. In: Strong, D. R., Simberloff, D., Abele, L., Thistle, A. B. (eds.) Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, New Jersey, p. 478–490

Sale, P. F. (1985). Patterns of recruitment in coral reef fishes. Proc. 5th int. coral Reef Congr. 5: 391–396. [Gabrié, C. et al. (eds). Antenne Museum-EPHE, Moorea, French Polynesia]

Sale, P. F., Ferrel, D. J. (1988). Early survivorship of juvenile coral reef fishes. Coral Reefs 7: 117–124

Schultz, B. B. (1985). Levene's test for relative variation. Syst. Zool. 34: 449–456

Shulman, M. J. (1985). Variability in recruitment of coral reef fishes. J. exp. mar. Biol. Ecol. 89: 205–219

Shulman, M. J., Ogden, J. C. (1987). What controls tropical reef fish populations: recruitment or benthic mortality? An example in the Caribbean reef fish *Haemulon flavolineatum*. Mar. Ecol. Prog. Ser. 39: 233–242

Shulman, M. J., Ogden, J. C., Ebersole, J. P., McFarland, W. N., Miller, S. L., Wolf, N. E. (1983). Priority effects in the recruitment of juvenile coral reef fishes. Ecology 64: 1508–1513

Sissenwine, M. P. (1984). Why do fish populations vary. In: May, R. M. (ed.) Exploitation of marine communities. Springer-Verlag, Berlin, p. 59–94

Sokal, R. R., Rohlf, F. J. (1981). Biometry. The principles and practice of statistics in biological research. 2nd ed. W. H. Freeman & Co., New York

Sweatman, H. P. A. (1988). Field evidence that settling coral reef fish larvae detect resident fishes using dissolved chemical cues. J. exp. mar. Biol. Ecol. 124: 163–174

Sweatman, H. P. A., St. John, J. (1990). Effects of selective settlement and of aggression by residents on distribution of young recruits of two tropical damselfishes. Mar. Biol. 105: 247–252

Talbot, F. H., Russell, B. C., Anderson, G. R. V. (1978). Coral reef fish communities: unstable, high-diversity systems? Ecol. Monogr. 48: 425–440

Victor, B. C. (1986). Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. Ecol. Monogr. 56: 145–160

Warner, R. R., Hughes, T. P. (1989). The population dynamics of reef fishes. Proc. 6th int. coral Reef Symp. 1: 149–155 [Choat, J. H., et al. (eds.), Sixth International Coral Reef Symposium Executive Committee, Tounsville]

Wilkinson, L. (1990). SYSTAT: The system for statistics. Systat, Inc., Evanston, Illinois

Williams, D. McB. (1983). Daily, monthly and yearly variability in recruitment of a guild of coral reef fishes. Mar. Ecol. Prog. Ser. 10: 231–237

Williams, D.McB., Sale P. F. (1981). Spatial and temporal patterns of recruitment of juvenile coral reef fishes to coral habitats within "One Tree Lagoon", Great Barrier Reef. Mar. Biol. 65: 245–253