

## Spatio-temporal variability in fish recruitment to a coral reef (Moorea, French Polynesia)

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Accepted 15 October 1992

**Abstract.** Spatial and temporal patterns of recruitment of juvenile coral reef fishes were studied on the reefs of the high island of Moorea (Society Archipelago, French Polynesia) during the wet season (October 1988 to April 1989). Two size-classes of fishes (new-recruits and juveniles) were censused by visual counts within 24 quadrats along a transect across the lagoon. Correspondence analysis was used to calculate the hypothetical movements of the two size classes. Spatial variability was far more important than temporal variability; six main spatial communities were revealed, which could result from differences among habitats. Temporal variability in recruitment occurred only at nearshore stations; stations on the outer fringing reef and inner barrier reef displayed stable recruitment patterns.

### Introduction

Most coral reef fishes undergo two distinct phases in their life cycle, a pelagic larval phase followed by a reef-resident phase in the parental habitat (Johannes 1978). Larval recruitment may play a major role in determining the structure and stability of reef-fish populations (Sale 1980; Anderson et al. 1981; Victor 1986). Variability in recruitment has been demonstrated on many different time scales (Doherty and Williams 1988). Generally, there is seasonal variability in recruitment patterns (Yamamoto 1976; Luckhurst and Luckhurst 1977; Molles 1978). Most species peak in summer (Leis and Goldman 1983), while in some species a second less important peak occurs during winter (Walsh 1987; Wyatt 1982). In addition to these seasonal peaks, a correlation between settlement and lunar cycles has been demonstrated (MacFarland et al. 1985; Robertson and Brawn 1988). Most studies also reveal evidence of strong interannual variability in recruitment (Williams 1983; Eckert 1984; Sale et al. 1984).

Variation in recruitment patterns has also been studied over a large range of spatial scales: adjacent reef-patches (Molles 1978; Williams 1980), widely separated sites within a reef zone, reefs separated by several kilometres (Doherty 1983; Sale and Douglas 1984; Sale et al. 1984; Eckert 1984; Victor 1984); and among regions separated by hundreds of kilometres (Doherty and Williams 1988).

We investigated spatio-temporal variability in larval recruitment to the reefs of the high island of Moorea (Society Archipelago, French Polynesia) during the wet season. We examined the following questions:

- Do recruitment patterns at any one time differ between sites, especially between near-shore and seaward locations?
- Do inter-site patterns remain stable throughout the recruitment season?
- Is the main source of variation in recruitment of fish to Moorea spatial or temporal?

### Materials and methods

#### Study location

The high volcanic island of Moorea (149°50'W, 17°30'S) is surrounded by a fringing reef, a narrow channel connecting the lagoon with the open ocean, a barrier reef, and an outer reef that slopes steeply to the ocean bottom (Galzin and Pointier 1985).

#### Sampling

Recruitment was analysed on two different spatial scales. Detailed, small scale observations were made at the Tiahura site. Along a transect from the beach to the open ocean, eight stations were selected based on their geomorphological features (Fig. 1) and their importance with respect to the main reef fish communities (Galzin 1987; Galzin and Legendre 1987). At each station, three 10 × 2 m quadrats were established, each 10 m apart (Fig. 1). Thus, we had three spatially independent measures for eight stations in a transect across the Tiahura lagoon. Within reefs differences in recruitment patterns were examined at 5 sites (including Tiahura), around Moorea island. Each station consisted of three quadrats (10 × 2 m), and was located 150 m from the beach, corresponding to the third

station of the Tiahura transect (Fig. 1). Each quadrat was marked with fixed boundary stones, and visual counts of recruits were made by snorkelling within the quadrats. After each count, fish were removed from the quadrat by a poisoning technique. Recruits were defined as juveniles more than 50% the length of post larvae size. Sampling was done during the wet season, from October 1988 to April 1989, which is the time of maximum abundance in the recruitment of reef fishes at other Pacific sites (Williams and Sale 1981; Leis and Goldman 1983). The five sites around Moorea island were censused once a month for 6 months. Because of a possible correlation between settlement and lunar cycles, censuses were made twice a month for 6 months at the eight stations of the Tiahura transect, during the first and last quarters of the moon. Sampling times 1 and 5 were omitted because of technical problems.

Censuses were carried out between 9:00 am and 3:00 pm to ensure that only diurnal species were sampled. Several families (Moringuidae, Muraenidae, Ophichtidae, Blenniidae, Gobiidae) were deliberately omitted from the study because of difficulties with *in-situ* identification. Furthermore, three species-pairs (*Stegastes nigricans*, *Stegastes albofasciatus*/*Scarus psittacus*, *Scarus sordidus*/*Acanthurus nigrofuscus*, *Ctenochaetus striatus*) could not easily be differentiated during the visual census and were recorded under the first name of each species-pair.

*Numerical analysis*

To determine the main spatial patterns of fish recruitment on the Tiahura transect we first pooled data from all censuses over a 6 month period of the study, omitting counts for the two dominant taxa (*Stegastes nigricans* and *Scarus psittacus*) since these were present in large number in most quadrats. Average group-sorting with 40% similarity was done (Legendre and Legendre 1984) using data from the 24 Tiahura quadrats (8 stations x 3 quadrats). To determine temporal variability in recruitment patterns, similarity matrices (Steinhaus index) were calculated between quadrats on the Tiahura transect for each time period (10 times) for new recruits

only. Sampling time 5 (late December) was omitted from this analysis, since 3 of the 24 quadrats had not been sampled due to logistic problems. Correlations between pairs of similarity matrices (time) were then determined using standardized Mantel tests (Mantel 1967). Principal coordinates were computed for the resulting matrix of Mantel coefficients ("cophenetic correlation coefficients") to obtain an overall picture of variability between sampling times.

The spatio-temporal recruitment patterns were analysed between sites and for the transect scales by using two-way ANOVA with repeated measures (time, sites) (Sokal and Rohlf 1981). A complete two-way ANOVA of all the data could not be used because it requires sites to be sampled in the same detail as the Tiahura site, i.e. a transect, with eight stations comprising three quadrats each across the lagoon. Two two-way ANOVAs were computed according to the two different spatial scales analysed; the first on the five sites around Moorea and the second on the eight stations of the Tiahura transect. At each spatial scale, ANOVAs were calculated for the most abundant species and on total number and species diversity of newly recruited fish. ANOVA results were tested using an F-test for significance, and analysis of the percentage of variance explained by each factor was calculated (Winer 1971). Homogeneity of the variance was tested using the Bartlett's test (Sokal and Rohlf 1981). Because of the homogeneity of the variance observed, the data were not transformed for the ANOVAs.

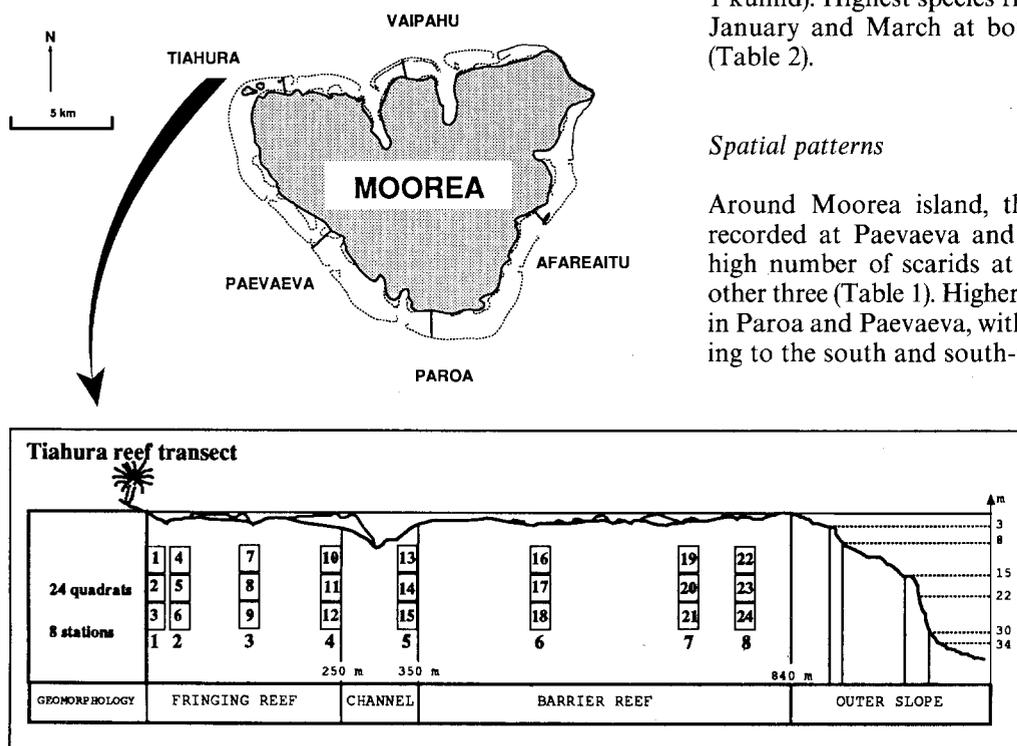
**Results**

*Abundance and species richness of recruits*

Between November 1988 and April 1989, 12,286 newly recruited fish, belonging to 86 taxa, were collected (Table 1). The samples were dominated by a small number of species. Three species constituted 53.3% of all fish collected, and the 25 most common taxa constituted 95.8% of the total. The 25 most common taxa represented 9 families (6 species of labrids, 6 pomacentrids, 4 acanthurids, 3 mugilids, 2 balistids, 1 scarid, 1 chaetodontid, 1 synodontid and 1 kuhlid). Highest species richness was recorded between January and March at both island and transect scales (Table 2).

*Spatial patterns*

Around Moorea island, the highest abundances were recorded at Paevaeva and Tiahura, due mainly to the high number of scarids at these sites compared to the other three (Table 1). Higher species richness was observed in Paroa and Paevaeva, with 28 species each, corresponding to the south and south-west parts of the island.



**Fig. 1.** Map of Moorea Island showing location of the five study sites and profile of Tiahura reef transect, showing position of the 8 sampling stations and the 24 quadrats

**Table 1.** Total abundance of the 25 most common species settling within the five sites around Moorea Island and within the 8 Tiahura transect stations. Species are presented in order of numerical importance. Numbers in parentheses indicate the number of species

Fish taxa	Island scale, site: 1 station × 3 quadrats					Transect Scale, Tiahura transect: 8 stations × 3 quadrats								Total
	Tiahura	Vaihapu	Afareaitu	Paroa	Paevaeva	1	2	3	4	5	6	7	8	
<i>Scarus psittacus</i>	551	106	14	61	655	0	633	888	654	86	368	328	28	3821
<i>Stegastes nigricans</i>	193	67	3	45	261	0	123	307	286	95	114	223	89	1613
<i>Acanthurus triostegus</i>	0	0	23	235	147	587	90	1	0	0	0	0	0	1083
<i>Liza vaigiensis</i>	0	0	0	0	0	875	0	0	0	0	0	0	0	875
<i>Valamugil engeli</i>	0	0	0	0	0	818	0	0	0	0	0	0	0	818
<i>Stethojulis bandanensis</i>	86	7	66	13	33	0	55	124	54	37	121	122	54	686
<i>Thalassoma hardwicki</i>	11	5	6	13	12	0	1	25	121	9	25	85	342	644
<i>Halichoeres trimaculatus</i>	61	6	3	25	31	0	39	114	19	98	61	84	37	517
<i>Dascyllus trimaculatus</i>	0	0	0	0	156	0	0	0	119	0	0	0	0	275
<i>Rhinecanthus aculeatus</i>	0	0	0	79	3	46	82	0	0	0	0	0	0	210
<i>Chaenomugil leuscisus</i>	0	0	0	0	0	206	0	0	0	0	0	0	0	206
<i>Chrysiptera leucopoma</i>	4	2	38	8	0	0	0	4	19	4	8	40	78	201
<i>Kuhlia mugil</i>	0	0	0	0	0	164	0	0	0	0	0	0	0	164
<i>Pomacentrus pavo</i>	0	0	0	0	0	0	17	0	0	107	1	0	0	125
<i>Halichoeres margaritaceus</i>	0	0	15	0	0	0	0	0	0	24	0	2	50	91
<i>Gomphosus varius</i>	0	0	0	1	0	0	0	0	4	0	1	7	46	59
<i>Pseudochelinus hexataenia</i>	0	1	0	0	0	0	0	0	11	9	8	9	16	54
<i>Acanthurus nigrofuscus</i>	0	22	16	1	0	0	8	0	0	1	0	0	2	50
<i>Synodus variegatus</i>	17	0	0	0	0	0	0	17	29	0	0	0	0	46
<i>Chaetodon auriga</i>	0	2	0	14	1	2	24	0	0	0	0	0	0	43
<i>Rhinecanthus rectangulus</i>	0	0	0	36	0	0	6	0	0	0	0	0	0	42
<i>Abudefduf sexfasciatus</i>	0	0	0	14	25	0	0	0	0	0	0	0	0	39
<i>Acanthurus nigricauda</i>	0	0	0	37	0	0	2	0	0	0	0	0	0	39
<i>Naso unicornis</i>	0	28	0	5	0	0	2	0	0	0	0	0	0	35
<i>Dascyllus aruanus</i>	16	0	0	0	0	0	5	21	9	0	0	0	0	35
Others taxa	(4)9	(11)49	(10)22	(13)54	(18)37	(11)77	(20)114	(5)13	(10)23	(10)60	(12)25	(10)28	(10)42	(61)544
Total	948	295	206	641	1361	2775	1201	1514	1348	530	732	928	784	12286
Total number of taxa	12	21	19	28	28	19	34	14	21	20	21	19	20	86

**Table 2.** Temporal variation in the number of recruited fishes of the 25 most common species recorded. The data have been pooled over sites for the island scale and over stations for the reef scale, from the 15th of November 1988 to the 15th of April 1989. Numbers in parentheses indicate the number of species

Fish taxa	Island scale (fish pooled over the 5 sites)					Transect scale (fish pooled over the 8 stations)												Total
	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	Total	2	3	4	6	7	8	9	10	11	12	
<i>Scarus psittacus</i>	147	220	435	260	191	134	1387	207	298	388	345	127	240	161	299	418	204	2687
<i>Stegastes nigricans</i>	81	101	93	80	120	94	569	52	100	125	118	69	124	120	156	135	138	1137
<i>Acanthurus triostegus</i>	74	26	156	50	56	43	405	85	52	24	241	165	1	1	1	53	3	626
<i>Liza vaigiensis</i>	0	0	0	0	0	0	0	122	112	28	10	97	66	59	2	78	189	763
<i>Valamugil engeli</i>	0	0	0	0	0	0	0	234	40	109	160	107	0	7	40	50	31	778
<i>Stethojulis bandanensis</i>	10	36	83	20	37	19	205	47	60	64	76	28	47	35	59	51	40	507
<i>Thalassoma hardwicki</i>	6	6	12	8	10	5	47	21	25	83	83	46	71	65	86	45	58	583
<i>Halichoeres trimaculatus</i>	48	30	17	6	16	9	126	59	81	56	35	16	25	16	30	32	21	371
<i>Dascyllus trimaculatus</i>	4	46	22	29	32	23	156	4	6	3	17	18	16	18	7	12	12	113
<i>Rhinecanthus aculeatus</i>	0	1	8	6	15	52	82	1	6	17	28	20	20	14	9	4	3	122
<i>Chromomugil leuciscus</i>	0	0	0	0	0	0	0	0	30	50	25	0	0	5	50	10	6	176
<i>Chrysiptera leucopoma</i>	12	13	12	3	6	6	52	12	7	8	15	13	7	2	42	18	22	146
<i>Kuhlia mugil</i>	0	0	0	0	0	0	0	40	58	0	1	7	0	0	0	0	0	106
<i>Pomacentrus pavo</i>	0	0	0	0	0	0	0	19	7	7	18	5	0	2	17	19	24	118
<i>Halichoeres margaritaceus</i>	2	3	7	2	1	0	15	4	5	1	9	6	11	5	6	12	12	71
<i>Gomphosus varius</i>	0	1	0	0	0	0	1	3	4	8	5	1	6	12	10	1	4	54
<i>Pseudocheilinus hexataenia</i>	0	0	0	1	0	0	1	2	8	8	3	7	9	3	11	3	4	51
<i>Acanthurus nigrofasciatus</i>	16	1	9	3	5	5	39	6	0	0	1	1	1	2	0	0	0	11
<i>Synodus variegatus</i>	0	17	0	0	0	0	17	0	0	46	0	0	0	0	0	0	0	46
<i>Chaetodon auriga</i>	1	0	8	3	1	4	17	1	1	7	6	5	2	1	1	1	0	25
<i>Rhinecanthus rectangulus</i>	0	0	0	0	2	34	36	0	0	3	0	2	0	0	1	0	0	6
<i>Abudefduf sexfasciatus</i>	14	6	13	3	3	0	39	0	0	0	0	0	0	0	0	0	0	0
<i>Acanthurus migracauda</i>	2	3	3	17	9	3	37	0	0	0	1	0	0	0	1	0	0	2
<i>Naso unicornis</i>	1	1	1	1	25	4	33	0	0	0	0	0	1	0	1	0	0	2
<i>Dascyllus aruanus</i>	1	0	4	2	9	0	16	11	2	0	4	0	4	2	9	1	0	33
Others taxa	(8)10	(4)13	(18)30	(13)33	(17)55	(11)30	(33)171	(13)32	(11)24	(15)32	(21)47	(17)39	(17)38	(18)38	(18)47	(15)39	(16)23	(54)358
Total	419	511	883	494	538	435	3451	961	920	1067	1248	779	689	567	885	982	794	8892
Total number of taxa	23	20	34	30	34	25	53	32	30	34	42	36	34	37	39	33	25	78

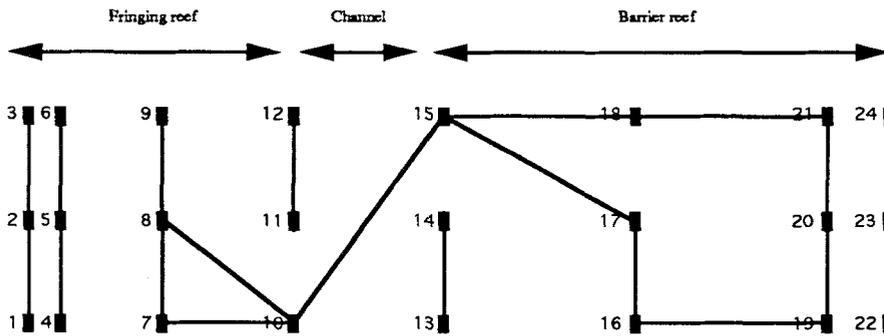


Fig. 2. Average group sorting by cluster analysis of the 24 Tiahura quadrats based on 6 months data for new recruits along the transect. Lines connecting similar quadrats, revealing 6 groups (similarity of 40%)

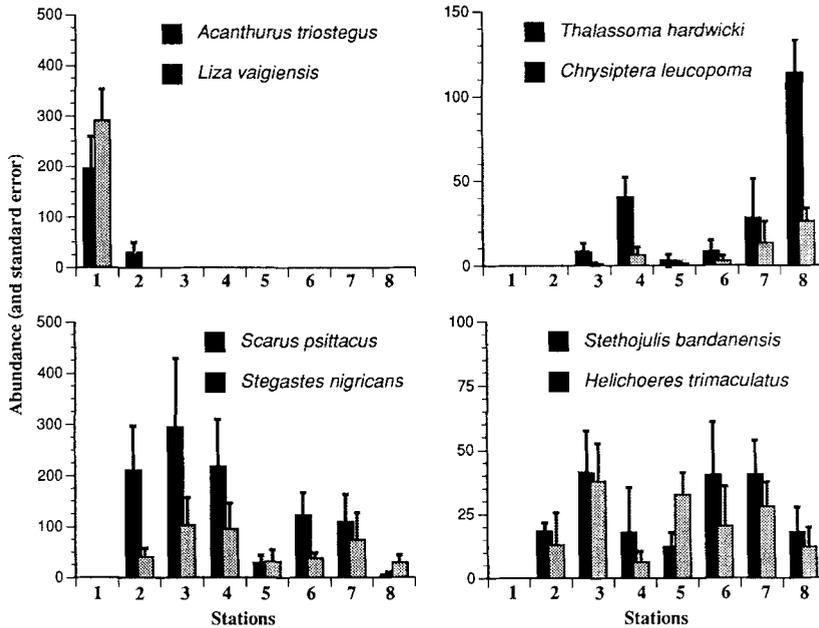


Fig. 3. Mean abundances and standard errors (pooled over November 1988 to April 1989) of eight common species along the eight stations of the Tiahura transect

On the Tiahura transect, abundance and species richness were highest on the fringing reef (stations 1–4). Station 1, located near the beach, showed especially high abundances (2,775 fishes counted during the study) comprising a low number of species, while station 2 located in the narrow reef-channel, displayed very high species richness with 34 species recorded (Table 1).

Using data from the 24 quadrats of the Tiahura transect (the ubiquitous *Stegastes nigricans* and *Scarus psittacus* were omitted), six main spatial communities were identified by cluster analysis along the Tiahura transect (Fig. 2). The following distinct groups were formed:

1. Quadrats 1 to 3 (station 1) are near-shore quadrats, characterised by sandy substratum and shallow water, and mainly occupied by three species: *Liza vaigiensis*, *Valamugil engeli* and *Acanthurus triostegus*.

2. Quadrats 4 to 6 (station 2) are located in a narrow reef-channel connecting the lagoon to the open ocean. High abundance of *Epinephelus merra*, *Chaetodon auriga* and *Chaetodon lunula* were recorded, but some *Myripristis* sp., *Neoniphon sammara* and *Lutjanus kasmira* were also observed in these quadrats (see Table 2).

3. Quadrats 7 to 10 (stations 3, 4), and 15 to 21 (stations 5, 6, 7) are located on the outer fringing reef respectively. Quadrats 7–10 and 15–21 were characterised by shallow water and a substratum consisting mainly of dead coral. Two labrids, *Stethojulis bandanensis* and *Thalassoma hardwicki*, were present in relatively equal proportions in these quadrats.

4. Quadrats 11 and 12 (station 4), located on the outer fringing reef near the reef-channel were characterised by *Dascyllus trimaculatus*.

5. Quadrats 13 and 14 (station 5) also formed a separate group. They were located in the sandy inner barrier reef near the reef-channel.

6. Quadrat 22 to 24 (station 8), on the outer barrier reef, had a low cover of living coral. New recruits of *Thalassoma hardwicki* were present in large numbers.

Analysis of the predominant species along the Tiahura transect showed different patterns of abundance of recruits (Fig. 3). Some species are only found nearshore (*Acanthurus triostegus* and *Liza vaigiensis*), others essentially on the barrier reef near the reef crest (*Thalassoma hardwicki* and *Chrysiptera leucopoma*), and some recruited more equally

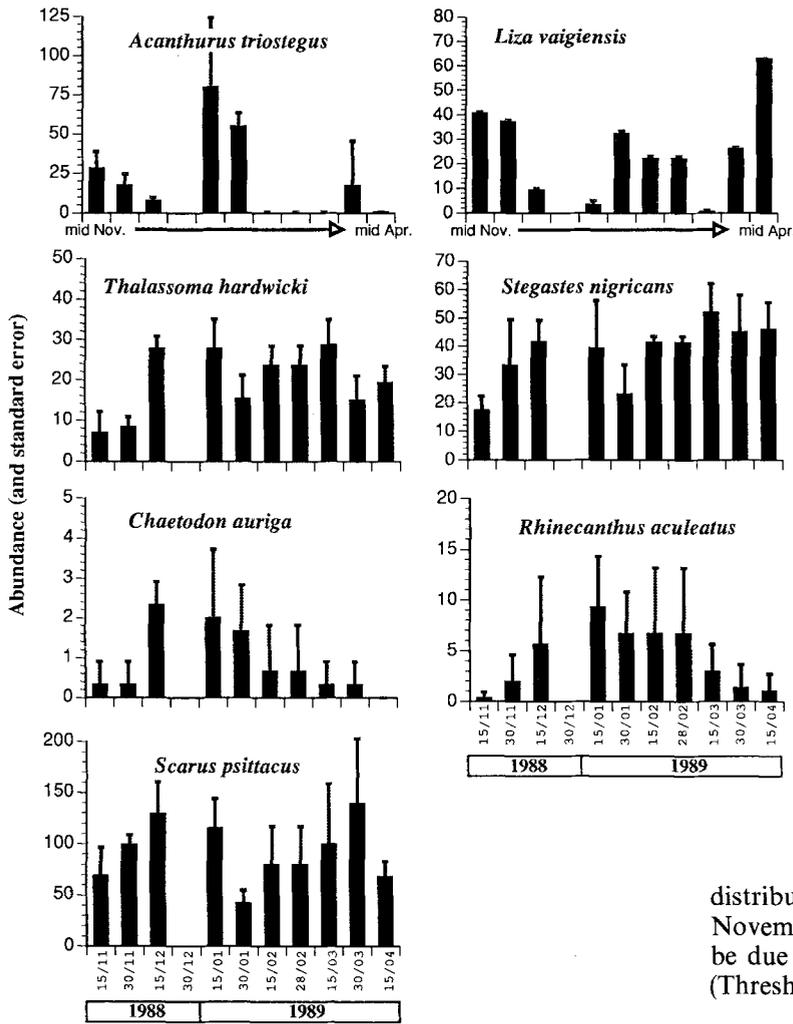


Fig. 4. Mean abundances and standard errors (pooled over the eight stations of the Tiahura transect) of seven common species from November 1988 to April 1989. No census could be recorded on 30/12/1988 because of the weather conditions

distributions showed an increase in recruitment from November to January followed by a decline, which may be due to a short reproductive period for these species (Thresher 1984).

to the fringing and barrier reefs (e.g. scarids, labrids and some pomacentrids).

Temporal patterns

Principal coordinate analysis was used to correlate temporal recruitment patterns for the Tiahura transect. Two cycles were revealed: the first one was from November to January, with clearly separated data points, the second from February to April, with closer data points (i.e., higher Mantel matrix correlations).

We also examined the temporal abundance patterns of dominant species on the Tiahura transect (Fig. 4). There were well-marked pulses for schooling species, with maximum abundances around mid-January for *Acanthurus triostegus* and mid-April for *Liza vaigiensis*. Non-schooling species were abundant year-round with maximum abundances occurring at the beginning of December and in mid-March (e.g. *Thalassoma hardwicki*, *Stegastes nigricans* and *Scarus psittacus*). Two of these taxa (*Stegastes nigricans* and *Scarus psittacus*) consisted of two species combined, which could have obscured any pulse. However, the *Chaetodon auriga* and *Rhinecanthus aculeatus* temporal

Spatio-temporal analysis

Time and location variabilities were examined using two-way ANOVAs (Table 3).

Between the five sites of Moorea (Island scale). Site was a major factor, explaining 40% of the variation in abundance of total recruits and was highly significant on the eight species analysed separately. An exception is *Thalassoma hardwicki*, for which the results suggest that variation in abundance of juveniles cannot be explained by Time, Site or Site  $\times$  Time factors. Site factor explained 21% of variation in recruitment of *Acanthurus triostegus* and 56% of variation for *Stegastes nigricans*. Site is also the major factor which influenced the total number of individuals (40% of the variation explained). This suggests that site is more important than time with respect to recruitment. However, for the species that showed pulses in recruitment, like *Acanthurus triostegus* or *Rhinecanthus aculeatus* (Fig. 4), the Time  $\times$  Site interaction explains a greater proportion of the variance.

Between stations along the Tiahura transect. The same analysis was conducted on the Tiahura transect to test the importance of time versus site at a smaller spatial scale. These results also express the strong influence of site which is highly significant in all analyses. The percentage

**Table 3.** Summary of ANOVA results for comparison of abundances of recently settled fishes between sites around the island and among stations along the Tiahura transect, from November 1988 to April 1989. The variance explained by each component of the model is shown. F-tests have been used to determine the significance of the results

Fish taxa	Five sites around the island Factors in ANOVA				Eight stations along Tiahura transect Factors in ANOVA			
	Time (T)	Site (S)	T × S	Res.	Time (T)	Site (S)	T × S	Res.
Chaetodontidae								
<i>Chaetodon auriga</i>	*	***	**		**	***	***	
	9.6	26.7	16.7	47.0	4.8	32.0	34.9	28.3
Pomacentridae								
<i>Stegastes nigricans</i>	ns	***	*		*	***	ns	
	1.5	55.8	15.7	27.0	6.4	37.8	9.3	46.5
<i>Dascyllus trimaculatus</i>	ns	***	ns		ns	***	ns	
	1.5	25.3	5.9	67.3	1.5	43.7	10.3	44.5
Mugilidae								
<i>Liza vaigiensis</i>	–	–	–	–	*	***	***	
					3.6	51.0	24.9	20.5
<i>Valamugil engeli</i>	–	–	–	–	ns	***	**	
					3.7	33.1	26.0	37.2
Labridae								
<i>Stethojulis bandanensis</i>	***	***	ns		ns	***	ns	
	19.1	21.7	21.2	38.0	3.9	33.6	18.1	44.4
<i>Thalassoma hardwicki</i>	ns	ns	ns		***	***	***	
	4.4	5.2	18.4	72.0	4.7	58.4	22.7	14.2
<i>Halichoeres trimaculatus</i>	***	***	***		***	***	**	
	28.1	26.3	25.3	20.3	13.1	28.9	23.3	34.7
Scaridae								
<i>Scarus psittacus</i>	ns	***	ns		*	***	**	
	8.0	39.9	12.7	39.4	4.4	35.1	24.2	36.3
Acanthuridae								
<i>Acanthurus triostegus</i>	*	***	***		***	***	***	
	9.0	20.8	36.2	34.0	7.3	25.3	48.3	19.1
Balistidae								
<i>Rhinecanthus aculeatus</i>	***	***	***		ns	***	**	
	9.8	21.0	40.4	28.8	4.0	29.1	22.8	44.1
Species richness	***	***	***		*	***	***	
	11.7	25.4	32.7	30.2	5.0	14.9	35.8	44.3
Number of individuals	**	***	**		**	***	***	
	8.2	40.0	22.4	29.4	4.3	36.0	32.9	26.8

ns =  $P > 0.05$ ; \* $P \leq 0.05$ , \*\* $P \leq 0.01$ , \*\*\* $P \leq 0.005$

of variance explained by this factor varied from 25 (*Acanthurus triostegus*) to 58% (*Thalassoma hardwicki*), with 36% for the total number of fish. This analysis confirms the significance of the pattern shown in Fig. 3 associating the recruitment of some species with particular localities.

## Discussion

We found striking differences among sites in abundance of recruits. Cluster analysis (Fig. 2) using 6 month cumulative data on the Tiahura transect revealed 6 spatial groups, corresponding to differences in the relative abundance of new fish recruits. Recruits of some species were present in some quadrats and were absent from others at the same station. These patterns may result from habitat differences (e.g. substratum, water depth, etc.) between the various quadrats in accordance with the environmental-

control hypothesis (Whittaker 1956; Bray and Curtis 1957). Williams and Sale (1981) suggested that most recruits exhibit clear site preferences. We found some species were ubiquitous, while others were restricted in spatial distribution. The schooling juvenile species (*Acanthurus triostegus*, *Kuhlia mugil*, *Liza vaigiensis* and *Valamugil engeli*) were observed exclusively on the fringing reef. The two Mugilidae species occurred only near the beach, while *Scarus psittacus* and *Stegastes nigricans* were present everywhere except near the beach. *Thalassoma hardwicki* was mainly restricted to the outer fringing and barrier reefs.

A comparison of juvenile and adult fish populations at Moorea (Galzin 1990) revealed that most fish settle in sites where fewer adults are present. However, adult–juvenile interactions seem to be species-specific; resident adults may either have no significant effect on rates of recruitment (Williams 1980; Doherty 1983), a positive effect (Sweetman 1983), or a negative effect (Sale 1976; Shulman

et al. 1984) depending on the species. Many processes may be involved in the choice of settlement sites, and new recruits are presumably also influenced by food availability, although this probably affects mainly those species that are highly specialized feeders. *Acanthurus triostegus* ceases to feed during metamorphosis from acronurus larvae (Randall 1961), so that food is presumably not the primary limiting factor for settlement. In contrast, for obligate coral feeders (e.g. Chaetodontidae), "dietary requirements are probably as important as shelter availability for successful recruitment" (Harmelin-Vivien 1989). Indeed, some chaetodontids are extremely selective at settlement, choosing also the time at which they settle (Table 1, 2). Shulman (1985) concluded that "schooling species show clumped, highly variable recruitment which may result from aggregative settlement while non-schooling species show random, less variable recruitment patterns." In our study, recruits near the beach were mainly schooling species (*Acanthurus triostegus*, *Liza vaigiensis*, *Valamugil engeli*), which are able to move over relatively long distances. Along the reef front, recruits (mainly *Thalassoma hardwicki*) were non-schooling species, living in small aggregates (2 to 10 individuals) closer to the bottom. Quadrats at the middle of the transect were mainly occupied by scarids (*Scarus sordidus-psittacus*) which settle in small groups. The greatest variations in abundance of recruitment were found near the beach, as would be expected from Shulman's hypothesis.

Temporal variability of recruitment (abundance and species richness) during summer has been described in several studies (Munro and Williams 1985), and settlement pulses have been demonstrated for Pomacentridae (Williams 1983), Haemulidae (MacFarland et al. 1985) and Labridae (Victor 1983). Sampling, in this study, was from mid-spring to mid-fall in an attempt to include recruits from most resident fish species. Obviously, annual periodicities cannot be detected by means of a 6-month study, but pulses were apparent in many. These may arise through the reproductive potential of the parental stock; through variations in larval abundance; through oceanic physical processes which may affect larval survivorship, growth and dispersal (Richards and Lindeman 1987); and through post-settlement mortality. For example, abundance of new-recruits seemed to be higher around mid-January for *Acanthurus triostegus*. This species was studied by Randall (1961), who found that, in Hawaii, reproduction occurs from June to mid-November. This corresponds with the reproduction from August to February recorded for the same species in French Polynesia, followed by recruitment at the beginning of November after several weeks of pelagic life (Brothers et al. 1983). We observed a decrease in recruitment of *Acanthurus triostegus* from November to December, followed by a second pulse in January. These successive pulses may reflect reproductive periodicity or result from physical oceanic processes. Detailed simultaneous studies on adults, juveniles and the dynamic processes in the water column will be necessary to clarify this.

Our study revealed that 70% of the total number of fish and 65% of the total species richness were recruited to the

fringing reef (Table 1). Comparisons with the adult fish assemblage of the Tiahura transect (Galzin 1987), suggest that variation in mortality between the fringing reef and the barrier reef, or migration from the fringing reef, is consistent with the fringing reef acting as a nursery for the barrier reef. Movement between nursery and adult habitats for fishes in mangrove and seagrass habitats has been described by Parrish (1989) who assumed this would provide improved survival for new recruits. Fringing reefs may also act as nursery sites; the fringing reefs of Moorea island harbour 38% of the potential recruitment stock (Galzin 1990), and our study revealed highest species richness and abundance on the fringing reef along the Tiahura transect.

In conclusion we have shown 1) Spatial variability in fish recruitment between the five sites around the high volcanic island of Moorea was highly significant, 2) Temporal variability during the 6 months of sampling was also significant, although spatial variability (between sites) was far more important than temporal variability (between times), 3) Among stations along the Tiahura transect, spatial variability was far more important than temporal variability, although both were highly significant, 4) Fringing reefs appear to serve as nursery grounds for the barrier reef.

*Acknowledgements.* We thank A. Fagerstrom, J. Leis, V. Jarry, B. Salvat and the two anonymous reviewers who provided critical discussion and comments on the earlier drafts. We thank also Springer Verlag, the editor and C. Hair for the language review. Financial help for this work was received from the Secrétariat d'Etat Chargé de l'Environnement, SRETIE-MERE-7064, Opération N°237-01-87-40027.

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