

Relative importance of recruitment and post-settlement processes in the maintenance of coral assemblages in an insular, fragmented reef system

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ABSTRACT: We compared relationships among distribution patterns of recruits, juveniles and adults of 3 different coral families with distinct life history traits at multiple spatial scales in an insular, fragmented reef system characterized by recurrent disturbances to better understand recruitment and maintenance processes of reef corals. The goal of our study was to detect at what scale most abundance variation occurred, and if this was consistent among life cycle stages and life histories. Results demonstrate a very high spatial variability of recruitment rates at the regional, insular and local hierarchical levels, with some locations displaying much higher recruitment rates than others, in 2 successive seasons. Juvenile and adult abundances were less variable, and most of the variation occurred at a local level for these life cycle stages. Recruit assemblage composition differed from juvenile and adult ones, which were much more similar. Moreover, abundance variation of recruits was unrelated to variation of juveniles and adults, but juvenile abundance was significantly correlated with adult abundance across all levels. These results have important implications for conservation planning, showing that some locations have better recovery abilities, and revealing the paramount importance of events occurring during the first weeks and months after settlement on the distribution of adults at regional, island and local levels, thus confirming the significance of local processes in shaping coral assemblages distribution and maintenance.

KEY WORDS: Scleractinian corals · Recruit · Juvenile · Adult · Spatial scale · Life-cycle · French Polynesia

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INTRODUCTION

Marine assemblages often exhibit strong spatio-temporal variations in their patterns of distribution (Balata et al. 2006). Many processes acting at different life-cycle stages add to this variability, and assessing the relative importance of these processes is essential to understand how populations and assemblages are maintained over time (Caley et al. 1996). This has important implications in ecosystem man-

agement, as strategies incorporating life-history processes are likely to be more successful than those based on abundance patterns alone (Hughes et al. 1999, van Woesik et al. 2011).

Many marine benthic organisms display a bipartite life cycle, with a pelagic dispersive larval phase, followed by a sessile benthic adult stage. For these organisms, spatial heterogeneity of adult distribution and community structure can be influenced by stochastic variations in recruitment rates (Caley et al.

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1996). However, early post-settlement mortality is generally very high (>90% for marine invertebrates; Gosselin & Qian 1997) and can greatly distort patterns established at settlement (Almany & Webster 2006).

Scleractinian corals are the primary framework builders of the reef ecosystem. Thus, understanding how coral populations function is of crucial importance to implementing effective management strategies. For these organisms, the relative contribution of pre-settlement processes such as larval mortality, hydrodynamics and habitat selection by larvae versus post-settlement processes such as competition, predation, facilitation and disturbances on distribution and size of adult populations is still unclear (Edmunds et al. 2010), despite numerous studies over the last decades (Bak & Engel 1979, Rylaarsdam 1983, Connell et al. 1997, Hughes et al. 1999, Quinn & Kojis 2010). The contribution of larval supply to the structure of adult communities is evident in some situations (Raimondi & Morse 2000, Baird et al. 2003), while post-settlement events and differential rates of post-settlement survivorship appear to have a stronger effect on other reef systems (Baird & Hughes 2000, Vermeij 2006).

Scleractinian corals are a challenge for population dynamic studies, because they are exceedingly small in size at settlement compared to their adult form, and have a long life span. For practical reasons, most studies of coral recruitment focus either on recruits (i.e. sexually immature corals aged <1 yr, usually sampled using artificial substrate for later microscopic examination) or juveniles (sexually immature colonies visible on the substratum, i.e. aged at least 1 yr; Penin et al. 2010). Consequently, the relative importance of events occurring during the first weeks versus the first months or even years of the benthic life remains largely unknown. These 2 life stages are, however, very different. Sizes can vary by factor 10 over the course of a year (i.e. 1 mm at settlement versus 1 cm after 1 yr) and many processes, such as mortality, are size-dependent in corals (Brock 1979, Vermeij 2006, van Woosik et al. 2011). Scleractinian corals exhibit a broad range of life history traits, such as reproduction strategies, growth capacities or competitive abilities, which each modify maintenance processes which further contributes to their assemblage-level complexity.

In French Polynesia, the only available information on recruitment and post-settlement processes derived from studies conducted on Moorea Island (Gleason 1996, Adjeroud et al. 2007a, Penin et al. 2007, 2010, Edmunds et al. 2010). In particular, Penin et al. (2010) demonstrated the paramount importance of early

post-settlement events in shaping adult distributions around this island and highlighted the links existing between these life history traits and population maintenance processes. In this system, Pocilloporidae tend to settle in disproportionate abundance compared to other families, but then most likely show higher rates of early post-settlement mortality. This may be linked to the fact that *Pocillopora* is an opportunistic genus, capable of high recruitment, but presenting high turnover and mortality (Tomascik et al. 1996, Adjeroud et al. 2007b). On the contrary, for the Poritidae, higher abundance of recruits appeared to lead directly to higher abundance of juveniles and adults. This relates to their high resistance to harsh conditions and catastrophic events (Wittenberg & Hunte 1992, Adjeroud et al. 2009), which results in lower post-settlement mortality. For Acroporidae, the preponderance of recruitment or early stage mortality in population maintenance was unclear, which can be, to some extent, the result of asexual reproduction (Smith & Hughes 1999, Lirman 2000).

Nevertheless, processes influencing spatial distribution of corals occur at different scales. Indeed, larvae can disperse over several hundreds of kilometers (van Oppen et al. 2008, Rudorff et al. 2009), whereas processes like habitat selection, competition or predation occur at a much smaller scale (Brock 1979, Baird & Hughes 2000, Penin et al. 2010). As a consequence, the relative importance of pre- and post-settlement events may appear to be very different depending on the scale considered (Wiens 1989). Some studies aiming at understanding the implications of spatial scales on maintenance processes have been conducted on the Australian Great Barrier Reef or on the Mesoamerican Barrier Reef System, which are continua of reefs under terrestrial influence (Hughes et al. 1999, Ruiz-Zarate & Arias-Gonzales 2004). However, no information is available on the influence of scale on these processes in oceanic fragmented systems like French Polynesian islands.

In this context, the goal of our study is to investigate relationships among patterns of distribution of coral recruits, juveniles and adults of different families with variable life histories at multiple spatial scales, to better understand the relative importance of recruitment versus early post-settlement processes on spatial structure, and complement the information available for the island of Moorea (Adjeroud et al. 2007a, Penin et al. 2007, Penin et al. 2010). To identify the spatial scale at which most variability in recruits, juvenile and adult distributions occurs, patterns of variation have been assessed for each of these life cycle stages at 3 hierarchical level: (1) the regional

level, among islands of the Society archipelago, (2) the island level, among locations within an island and (3) the local level, among habitats within a location.

MATERIALS AND METHODS

Study sites

A hierarchical sampling design was used to encompass 3 hierarchical levels (Murdoch & Aronson 1999; Fig. 1). (1) The regional level includes the 3 islands

Moorea, Tahiti and Raiatea (Society archipelago, French Polynesia). They are all high volcanic islands surrounded by a reef belt separating the lagoon from the ocean. Polynesian islands are characterized by steep environmental gradients (mainly hydrodynamic, terrestrial versus oceanic influences, and depth). In turn, these gradients induce a high spatial variability in coral reef community patterns of distribution (Galzin & Legendre 1987, Cadoret et al. 1995, Adjeroud 1997). Tahiti is the biggest island of the archipelago, with 1042 km² of land, whereas Raiatea

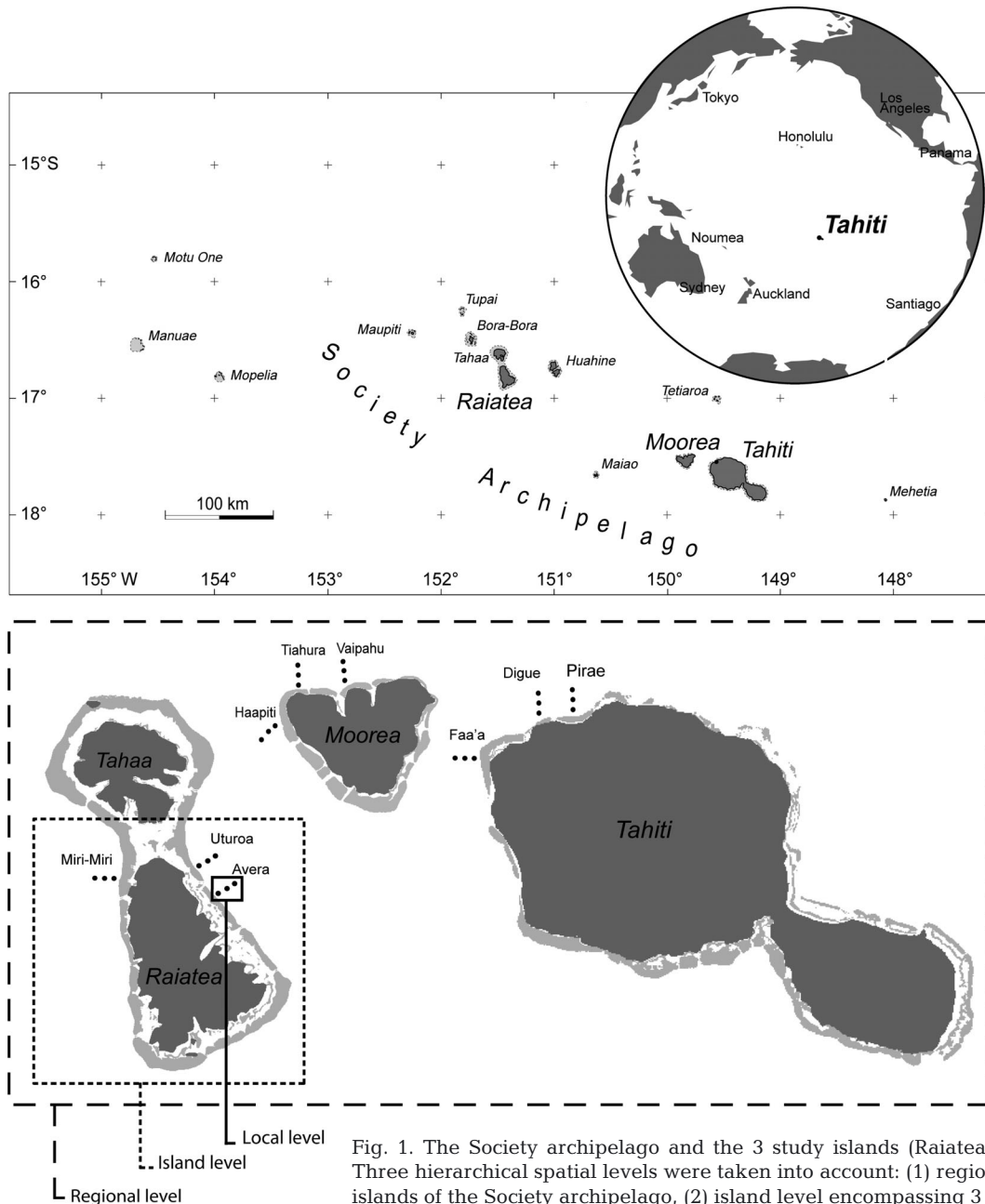


Fig. 1. The Society archipelago and the 3 study islands (Raiatea, Moorea and Tahiti). Three hierarchical spatial levels were taken into account: (1) regional level comprising 3 islands of the Society archipelago, (2) island level encompassing 3 locations within an island and (3) the local level comprising 3 stations within a location (6 m, 12 m and 18 m)

and Moorea are smaller in size (170 and 134 km², respectively). Tahiti and Moorea are only ~20 km apart, whereas Raiatea is ~190 km away from Moorea and 215 km away from Tahiti. (2) The island level incorporates 3 different locations for each island, all located on the outer reef slope. Locations were selected depending on their exposure to the dominant swells, which influences coral recruitment processes (Edmunds et al. 2010). For each island, 1 location is exposed to southern and southwestern swells, which are the most frequent and the highest in magnitude (Laurent et al. 2004) and the 2 other stations are exposed to northern swells, which are only dominant during the austral summer (November to March). Western locations are Haapiti in Moorea, Faa'a in Tahiti and Miri Miri in Raiatea. Northern locations are Tiahura and Vaipahu in Moorea, and Digue and Pirae in Tahiti. In Raiatea, there is no outer slope off the northern coast, because of the direct proximity of another island, Tahaa. Only a 5 km wide lagoon separates these 2 islands (Fig. 1). As a consequence, 2 locations were located on the east coast of Raiatea: Uturoa and Avera. The orientation of the island of Raiatea protects these sites from southern and southwestern swells, whereas they are exposed to northern swells. Locations within an island are 3 to 8 km apart from each other. (3) The local level, among stations within a location, encompasses 3 habitats characterized by different depths: 6 m, 12 m and 18 m, on the outer reef slope. All stations were located on top of spurs in the spur and groove zone, and chosen to represent similar living coral cover (35–50%). Within a location, stations were 50 to 100 m apart. All the stations being located on the outer reef slope, they receive very low stress from land based anthropogenic activities, which are limited due to the low population density observed on the islands of Society archipelago. GPS coordinates of the 12 m stations under WGS 84 standard are: Haapiti: 149° 55' 583 W, 17° 30' 587 S; Tiahura: 149° 54' 68 W, 17° 28' 987 S; Vaipahu: 149° 51' 135 W, 17° 28' 795 S; Miri-Miri: 151° 30' 280 W, 16° 44' 288 S; Avera: 151° 24' 408 W, 16° 45' 481 S; Uturoa: 151° 25' 467 W, 16° 43' 941 S; Faa'a: 149° 37' 775 W, 17° 34' 731 S; Digue: 149° 33' 751 W, 17° 31' 099 S; Pirae: 149° 31' 977 W, 17° 30' 907 S.

Spatial patterns of recruit, juvenile and adult abundance

In the present study, recruit, juvenile and adult life cycle stages were defined by size, following Penin et

al. (2010). Colonies were considered as recruits when their maximum diameter was <1 cm, as juveniles when their maximum diameter ranged from 1 to 5 cm and as adults when it was >5 cm. For each of the 6 major genera (*Pocillopora*, *Acropora*, *Porites*, *Pavona*, *Montastrea* and *Montipora*), colonies of <5 cm maximum diameter are non-reproductive (Harrison & Wallace 1990). Two size classes of adults were distinguished: small adults had a maximum diameter of <10 cm, and large adults had a maximum diameter of >10 cm. The different studied taxa represent variable size structures in Society archipelago, and, thus, certain taxa, like Poritidae, can reach sizes that other taxa, like Pocilloporidae, cannot (Adjeroud et al. 2007b). However, colonies which do not exceed 10 cm in diameter can be considered small for all the families, and we, therefore, decided to keep the same size classes for all taxa. Artificial substrata were used to sample recruits, whereas juveniles and adults were sampled directly on the natural substrata.

Recruits were sampled using 11 × 11 × 1 cm unglazed terracotta tiles. At each station, 3 PVC racks carrying 6 tiles were attached flush with the substratum with polyamide strings. Racks within a station were located between 2 and 5 m apart. Tiles were attached to the rack using a central bolt and a wing nut. A hexagonal nut and 2 washers here sandwiched between the rack and the tile, to maintain a gap between the underside of the tiles (where the majority of recruits are found) and the rack. For each tile, 2 drops of silicone sealant were deposited on the rack to act as a shock absorber (Fig. 2).

Contrary to other locations in the Indo-Pacific, synchronous mass spawning is not observed in French Polynesia (Carroll et al. 2006). Recruitment occurs throughout the year, with an important peak between September and March (>80% of total recruitment; Adjeroud et al. 2007a). To cover this recruitment period, 2 successive batches of tiles were immersed: 1 from September to December (Sept–Dec season), and 1 from December to March (Dec–Mar season). All the tiles were replaced within the same week, from November 30 to December 7, 2004. Two successive batches immersed for 3 months were preferred to one immersed for 6 months, in order to limit the influence of post-settlement mortality on final abundance of recruits (Gosselin & Qian 1997, Penin et al. 2010, Penin et al. 2011).

In the laboratory, coral recruits were identified using a dissecting microscope after the tiles had been bleached and sun-dried. All surfaces of the tiles were analyzed (top, bottom and edges), and no tiles were missing at the end of the experiment. At this stage of

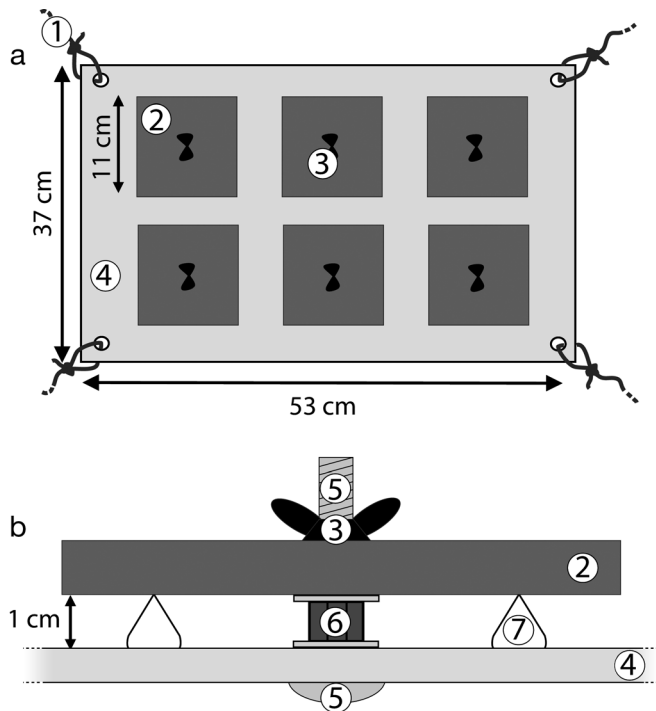


Fig. 2. Settlement device. (a) Top view and (b) cross section. 1: rope attaching the rack to the substrate, 2: settlement tile, 3: wing nut, 4: PVC rack, 5: central bolt, 6: hexagonal nut and washers, 7: drop of silicone sealant

development, the micro-architecture of the corallum is not sufficiently developed to allow high taxonomic resolution, and so recruits were categorized to each of the 3 major families (Acroporidae, Pocilloporidae and Poritidae) or to an 'other families' category (Babcock et al. 2003, Adjeroud et al. 2007a).

Spatial variability of recruitment rates was explored using a 3 factor nested ANOVA (island, location and depth). Since the purpose of these analyses was to assess spatial variability of recruitment rates, and not seasonal variation, abundances measured over the 2 sampling periods were added, thus reflecting an annual recruitment rate. As the 6 tiles of a rack could not be considered as independent replicates, each rack was used as a sampling unit. Data were $\log(x + 1)$ transformed to satisfy ANOVA assumptions (normality and homoscedasticity).

Juvenile and adult corals were sampled on natural reef substrates along 3 replicate 10×1 m belt-transects at each station. Transects were parallel to the depth contour, and separated by 2 to 5 m. All juvenile and adult colonies at least partially encompassed in the belt transects were counted, identified to the genus level and assigned to a size class. Special attention was paid to find juvenile colonies located in cryptic habitats like crevices or overhangs.

Abundance was preferred to percent cover as a metric to document spatial patterns of adults, since the objective of the study was to compare spatial variability of recruits, juvenile and adults. In most cases, 1 recruit is growing into 1 juvenile, and ultimately 1 adult colony. As a consequence, percent cover, which is highly dependent on the size of colonies, appeared to be less relevant than abundance in the context of this study.

Spatial variability of juvenile and adult abundance was assessed with a 3 factor nested ANOVA (island, location and depth). Data were square root transformed to meet ANOVA assumptions (normality and homoscedasticity).

Relationship among recruit, juvenile and adult spatial patterns

Spearman non-parametric correlations were used to determine the relationship among recruit, juvenile and adult abundances. Considering differences in sampling, correlation between recruits and juveniles and recruits and adults were performed using the station as a sampling unit ($n = 27$ at the regional level), whereas correlations between juvenile and adult abundances were calculated using each transect as a sampling unit ($n = 81$ at the regional level), to improve statistical power.

RESULTS

Recruitment patterns

An average of 16.26 recruits tile^{-1} were counted at the 27 study stations over the recruitment period (Sept-Mar), that is 568.54 recruits m^{-2} . Most of the observed recruits belonged to the Pocilloporidae family (67.1% of the recruit assemblage), followed by Acroporidae (22.9%) and Poritidae (9.8%). Recruits of other families were less abundant, representing only 0.2% of the total assemblage (Fig. 3). A strong seasonal variability was observed, with 4 times as many recruits in the Dec-Mar season (12.84 recruits tile^{-1}) compared to the Sept-Dec season (3.42 recruits tile^{-1}). Nevertheless, the Acroporidae displayed a temporal pattern different from Pocilloporids and Poritids, with more recruits during the Sept-Dec season (75.9%) than during the Dec-Mar season.

A strong spatial variability was observed for recruit abundance, especially at the regional and island levels. At the regional level, recruit abundance showed

a 5-fold variation among the 3 islands (Table 1; ANOVA, $p < 0.0001$; Table 2). Recruit abundance was much higher in Raiatea (31.58 recruits $\text{tile}^{-1} \text{yr}^{-1}$) than in Tahiti (10.54 recruits $\text{tile}^{-1} \text{yr}^{-1}$) and Moorea (6.00 recruits $\text{tile}^{-1} \text{yr}^{-1}$). These differences were observed for each of the 3 major families.

At the island level, the level of variability differed among the 3 islands. Recruit abundance displayed a 2-fold variation among locations around Moorea, a 6-fold variation around Tahiti and an 8-fold variation around Raiatea. In particular, Miri Miri (Raiatea western location) had about 10 times more recruits than the average over the 8 other locations. The 3 major families all presented the highest recruitment rates at the same stations, despite asynchronous recruitment peaks between Acroporidae on one hand and Pocilloporidae and Poritidae, on the other hand. No clear among-locations pattern was identified; whereas the highest recruit abundances were observed at locations facing the influence of southern and southwestern swells in Tahiti and Raiatea, the opposite was true in Moorea (Fig. 4).

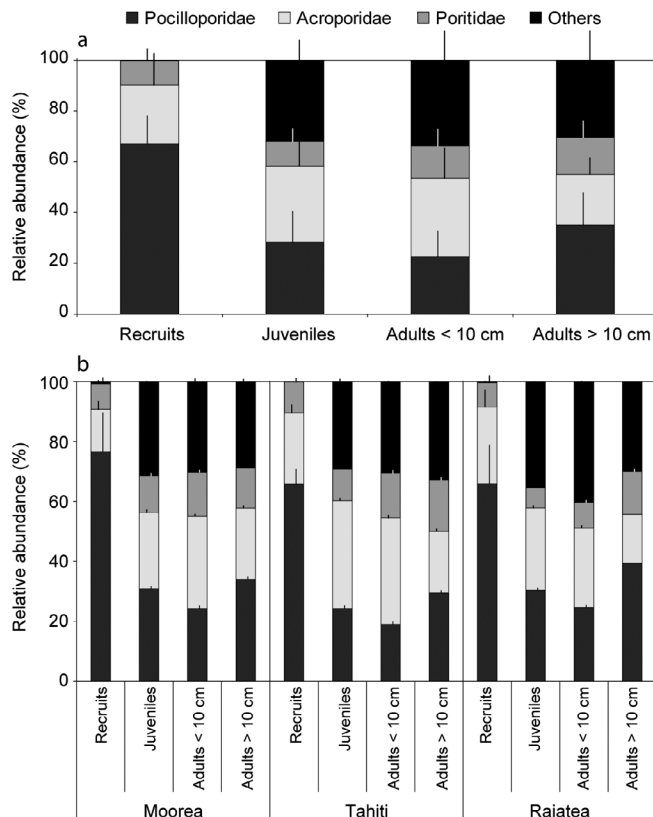


Fig. 3. Relative abundance (means + SD) of coral families for recruits, juveniles (i.e. $1 \text{ cm} \leq \text{max. diameter} \leq 5 \text{ cm}$), small adults ($5 \text{ cm} < \text{max. diameter} \leq 10 \text{ cm}$) and large adults (max. diameter $> 10 \text{ cm}$). (a) For all stations pooled. (b) At each of the 3 studied islands (Moorea, Raiatea and Tahiti)

At the local level, recruit abundance varied as a function of depth, but differently among families, islands and locations (Table 2; Fig. 4). No consistent bathymetric pattern could be highlighted, despite high variability. The ratio between maximum and minimum recruit abundance among stations within a location varied between 1.39 at Tiahura and 6.26 at Digue.

Juvenile and adult abundance patterns

A mean of 6.4 juveniles and 22.4 adults m^{-2} was observed at the study stations. We observed 18 genera, among which the most abundant, both as adults and juveniles, were *Pocillopora* (respectively 32.4 and 28.4% of the total assemblage), *Acropora* (16.5 and 27.0%), *Porites* (14.4 and 9.7%), *Pavona* (7.2 and

Table 1. Number of recruits tile^{-1} (mean \pm SD) at each of the 27 stations for the 3 main coral families

Location	Depth (m)	Acroporidae	Pocilloporidae	Poritidae
Moorea				
Haapiti	6	0.28 ± 0.10	1.22 ± 0.42	0.17 ± 0.17
	12	0.56 ± 0.35	2.94 ± 2.75	0.56 ± 0.51
	18	0.78 ± 0.48	3.22 ± 3.56	0.33 ± 0.29
Tiahura	6	0.89 ± 0.63	4.22 ± 2.75	0.22 ± 0.10
	12	1.39 ± 0.84	5.33 ± 3.77	0.61 ± 0.54
	18	0.44 ± 0.10	5.22 ± 0.54	1.00 ± 0.17
Vaipahu	6	0.78 ± 0.19	4.00 ± 2.29	0.44 ± 0.42
	12	1.50 ± 0.73	8.89 ± 4.07	0.94 ± 0.48
	18	0.50 ± 0.33	3.72 ± 1.27	0.11 ± 0.10
Raiatea				
Miri-Miri	6	40.11 ± 8.56	29.22 ± 11.55	4.56 ± 3.60
	12	8.72 ± 3.31	74.72 ± 31.08	16.94 ± 5.42
	18	1.83 ± 0.60	40.06 ± 21.97	4.06 ± 5.29
Uturoa	6	4.00 ± 1.80	5.28 ± 2.66	0.61 ± 0.79
	12	2.39 ± 0.84	7.83 ± 4.10	1.17 ± 0.67
	18	0.78 ± 0.63	3.89 ± 2.31	0.50 ± 0.44
Avera	6	6.17 ± 2.83	7.00 ± 0.87	0.22 ± 0.25
	12	1.39 ± 0.35	4.44 ± 0.51	0.44 ± 0.19
	18	1.06 ± 0.25	11.06 ± 7.59	0.56 ± 0.25
Tahiti				
Faa'a	6	4.56 ± 0.67	18.00 ± 7.94	2.67 ± 1.76
	12	8.72 ± 1.25	17.78 ± 6.02	2.72 ± 1.78
	18	1.22 ± 0.96	6.00 ± 5.92	1.28 ± 2.07
Digue	6	4.44 ± 1.25	6.78 ± 5.45	0.17 ± 0.29
	12	0.61 ± 0.10	2.39 ± 0.79	0.11 ± 0.10
	18	0.33 ± 0.00	1.39 ± 0.77	0.00 ± 0.00
Pirae	6	1.56 ± 0.51	3.50 ± 0.60	0.33 ± 0.17
	12	0.67 ± 0.33	2.56 ± 0.25	0.17 ± 0.17
	18	0.50 ± 0.60	0.89 ± 0.35	0.00 ± 0.00

Table 2. Three factor nested ANOVA (Island, Location and Depth) on the abundance of recruits, juveniles and adults of different size classes. Transformations: recruit abundance $\log(x + 1)$, juvenile and adult abundance square root. Significant p-values (<0.05) indicated in **bold**

	df	All Taxa		Acroporidae		Pocilloporidae		Poritidae	
		F	p	F	p	F	p	F	p
Recruits									
Island	2	42.53	<0.0001	64.17	<0.0001	26.66	<0.0001	15.14	<0.0001
Location (Island)	8	24.40	<0.0001	18.49	<0.0001	17.14	<0.0001	15.18	<0.0001
Depth (Island \times Location)	18	3.41	<0.0001	10.89	<0.0001	1.77	0.055	2.00	0.026
	df	All Taxa		Acropora		Pocillopora		Porites	
		F	p	F	p	F	p	F	p
Juveniles									
Island	2	8.90	<0.0001	32.68	<0.0001	8.90	<0.0001	2.54	0.088
Location (Island)	8	10.53	<0.0001	19.74	<0.0001	8.26	<0.0001	1.16	0.339
Depth (Island \times Location)	18	6.05	<0.0001	5.12	<0.0001	5.62	<0.0001	3.59	<0.0001
Adults (all sizes)									
Island	2	47.76	<0.0001	9.47	<0.0001	69.37	<0.0001	4.99	0.010
Location (Island)	8	37.40	<0.0001	29.96	<0.0001	13.33	<0.0001	13.15	<0.0001
Depth (Island \times Location)	18	8.02	<0.0001	14.05	<0.0001	8.10	<0.0001	12.39	<0.0001
Adults < 10 cm									
Island	2	1.03	0.362	3.336	0.043	4.208	0.020	4.581	0.015
Location (Island)	8	20.84	<0.0001	9.629	<0.0001	8.707	<0.0001	2.816	0.019
Depth (Island \times Location)	18	4.91	<0.0001	6.607	<0.0001	2.599	0.004	3.109	0.001
Adults > 10 cm									
Island	2	60.88	<0.0001	20.45	<0.0001	65.19	<0.0001	14.74	<0.0001
Location (Island)	8	31.83	<0.0001	23.95	<0.0001	9.40	<0.0001	13.01	<0.0001
Depth (Island \times Location)	18	8.09	<0.0001	11.44	<0.0001	8.42	<0.0001	11.79	<0.0001

5.8%), *Montastrea* (6.8 and 10.9%), *Fungia* (6.4 and 5.7%), *Leptastrea* (5.3 and 0.9%), *Montipora* (5.4 and 2.9%) and *Psammocora* (1.3 and 6.3%). The other genera together represented $<5\%$ of the assemblage (*Leptoseris*, *Acanthastrea*, *Herpolitha*, *Sandalolitha*, *Favia*, *Cyphastrea*, *Astreopora*, *Lobophyllia* and *Gardineroseris*).

Adult (2 size classes pooled) and juvenile total abundances (all taxa pooled) were variable at several spatial levels (ANOVA, $p < 0.001$; Table 2), but the differences observed were much lower than those detected for recruit abundance (Fig. 5). At the regional level, juvenile abundances were between 1.23 and 1.25 times lower at Moorea (5.5 juveniles m^{-2}) than at Raiatea (6.8 juveniles m^{-2}) and Tahiti (6.9 juveniles m^{-2}). Adults at Tahiti (26.0 adults m^{-2}) were 1.25 times more abundant than at Moorea (21.9 adults m^{-2}) and 1.34 times more abundant than at Raiatea (19.4 adults m^{-2}).

At the island level, abundance of adults was lower at the western locations than at the other locations in Moorea and Tahiti (Student-Newman-Keuls test [SNK], $p < 0.05$). The opposite pattern was observed at Raiatea, the western location (Miri-Miri) had the highest abundance (SNK, $p < 0.05$). The ratio between maximum and minimum adult abundance among locations was 1.64 at Moorea, 1.84 at Raiatea

and 1.32 at Tahiti. In Moorea, juvenile abundance was lower at Haapiti (western location) than at Tia-hura and Vaipahu (SNK, $p < 0.05$). In Raiatea, the opposite pattern was observed again, with a higher juvenile abundance at the western location (Miri-Miri) than at the other locations. In Tahiti, juvenile abundance was not significantly variable among sites (SNK, $p > 0.05$). The ratio between maximum and minimum juvenile abundance among locations was 1.63 at Moorea, 2.12 at Raiatea and 1.20 at Tahiti.

At the local level, no consistent bathymetric pattern was observed in the abundance of juveniles and adults. Mean juvenile abundance tended to increase with depth, but this trend was not observed at all locations, some like Haapiti even showed the opposite pattern (Table 2; Fig. 5). The ratio between maximum and minimum juvenile abundance among stations within a location varied between 1.04 at Digue and 3.20 at Haapiti. Mean adult abundance was maximal at intermediate depth, but again, the bathymetric pattern varied among locations. For example, it increased with increasing depth at Vaipahu, Faa'a or Digue, but showed the opposite trend at Uturoa (Table 2; Fig. 5). The ratio between maximum and minimum adult abundance among stations within a location varied between 1.10 at Faa'a and 3.02 at Avera.

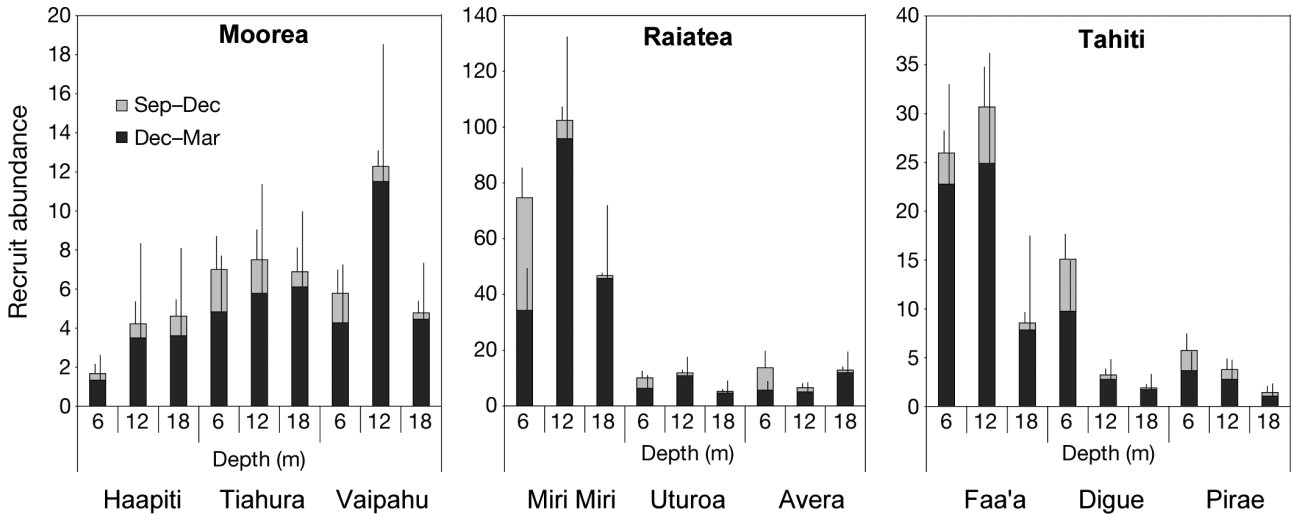


Fig. 4. Recruit abundance (mean + SD) per tile (11 × 11 × 1 cm) at the 27 stations corresponding to 3 depths (6 m, 12 m and 18 m) and 3 locations at each of the 3 islands (Moorea, Raiatea and Tahiti), during the September to December (Sep–Dec) and December to March (Dec–Mar) seasons. Scales are different among islands

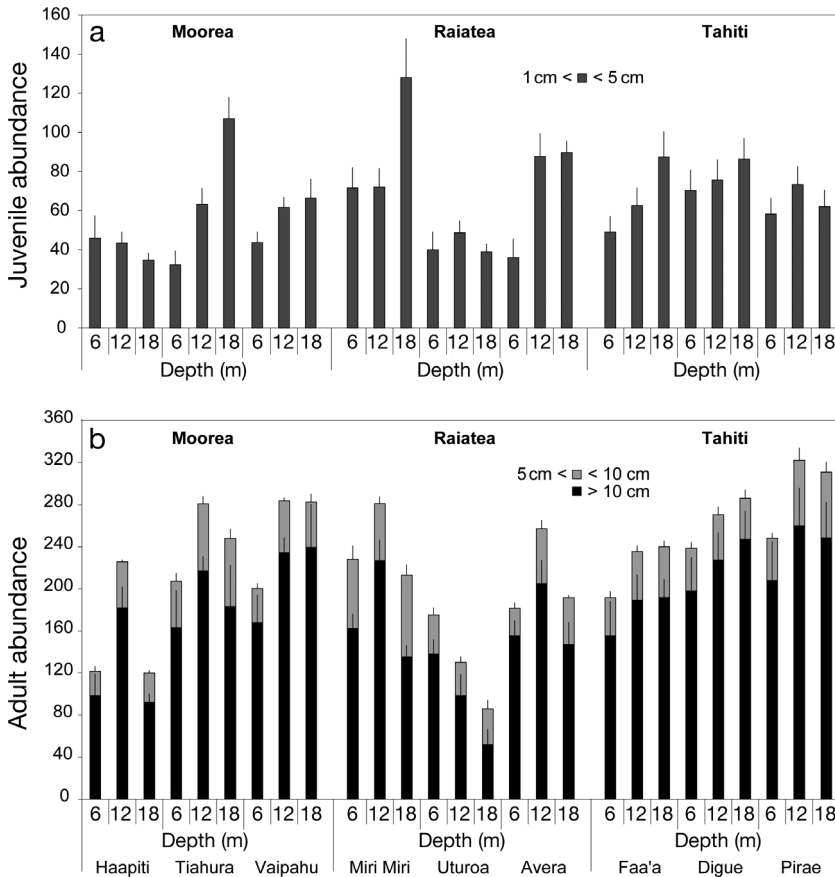


Fig. 5. Juvenile (a) and adult (b) abundance per 10 m² transect (mean + SD) at the 27 stations corresponding to 3 depths (6 m, 12 m and 18 m) and 3 locations at each of the 3 islands (Moorea, Raiatea and Tahiti). Small adults (5 cm < max. diameter < 10 cm) in grey and large adults (max. diameter > 10 cm) in black

Relationship among recruit, juvenile and adult assemblages

Assemblages of recruits, juveniles and adults were all dominated by Pocilloporidae (only represented by the genus *Pocillopora* in the Society archipelago). Acroporidae (genera *Acropora*, *Montipora* and *Astreopora*) and Poritidae (genus *Porites*) both represented a high proportion of these assemblages as well. Nevertheless, relative abundances of these families varied greatly between recruits and the other stages (Fig. 3). Recruit assemblage was notably characterized by a higher proportion of pocilloporids.

When considering the whole assemblage, abundance of recruits in the study stations was not correlated with abundance of juveniles or adults at the regional level ($n = 27, p > 0.05$, Table 3). The stations where the abundance of recruits was the highest were not the stations where juvenile and adult abundance was the greatest. On the contrary, abundance of juveniles in transects was positively and significantly correlated with abundance of adults, whatever size class considered ($n = 81, p < 0.05$, Table 3). At the island level, abundance of recruits was not

Table 3. Spearman correlations among abundance of recruits (R), juveniles (J), small adults (A < 10 cm), large adults (A > 10 cm) and all adults (A) at the regional level and at the island level for Moorea, Raiatea and Tahiti. Significant p-values (<0.05) indicated in **bold**

	Regional level				Moorea				Raiatea				Tahiti			
	R		J		R		J		R		J		R		J	
	r _s	p	r _s	p	r _s	p	r _s	p	r _s	p	r _s	p	r _s	p	r _s	p
All taxa																
J	0.185	0.3456			0.383	0.2783			0.317	0.3704			-0.300	0.3961		
A <10	0.260	0.1846	0.649	<0.0001	0.817	0.0209	0.596	0.0024	0.517	0.1439	0.824	<0.0001	-0.300	0.3961	0.349	0.0755
A >10	-0.260	0.1847	0.445	<0.0001	0.567	0.1090	0.628	0.0014	0.517	0.1439	0.419	0.0327	-0.867	0.0142	0.243	0.2156
A	-0.184	0.3479	0.561	<0.0001	0.667	0.0593	0.715	0.0003	0.617	0.0811	0.599	0.0022	-0.883	0.0125	0.314	0.1096
Pocilloporidae																
J	-0.031	0.8738			-0.192	0.5862			0.717	0.0427			0.150	0.6714		
A <10	0.129	0.5108	0.504	<0.0001	-0.051	0.8856	0.496	0.0115	0.586	0.0976	0.758	0.0001	0.250	0.4795	-0.221	0.2596
A >10	-0.113	0.5636	0.195	0.0818	0.167	0.6374	-0.181	0.5614	0.383	0.2783	0.019	0.9242	0.283	0.4229	0.013	0.9463
A	-0.129	0.5113	0.246	0.0279	0.000	>0.9999	-0.028	0.8883	0.383	0.2783	0.120	0.5407	0.150	0.6714	-0.025	0.8979
Acroporidae																
J	0.105	0.5914			0.059	0.8684			0.075	0.8313			-0.477	0.1773		
A <10	0.278	0.1558	0.460	<0.0001	0.435	0.2184	0.472	0.0160	0.655	0.0637	0.506	0.0099	0.008	0.9810	0.417	0.0334
A >10	-0.441	0.6591	0.312	0.0052	0.510	0.1488	0.455	0.0204	0.617	0.0811	0.546	0.0053	-0.870	0.0138	0.299	0.1270
A	0.101	0.6060	0.438	<0.0001	0.586	0.0976	0.544	0.0055	0.733	0.0381	0.587	0.0028	-0.767	0.0301	0.430	0.0283
Poritidae																
J	0.216	0.2701			0.728	0.0395			0.000	>0.9999			-0.203	0.5651		
A <10	0.371	0.0584	0.459	<0.0001	0.795	0.0245	0.483	0.0138	0.383	0.2783	0.342	0.0809	-0.397	0.2619	0.477	0.0150
A >10	0.296	0.1310	0.176	0.1145	0.283	0.4229	0.208	0.2897	0.583	0.0990	0.212	0.2786	0.172	0.6261	0.231	0.2397
A	0.338	0.0845	0.287	0.0104	0.427	0.2274	0.321	0.1014	0.583	0.0990	0.295	0.1321	0.197	0.5765	0.278	0.1571

correlated with abundance of juveniles or adults on any of the islands studied (n = 9, p > 0.05, Table 3). On the contrary, juvenile abundance was correlated with abundance of adults on Moorea and Raiatea.

At the regional level, recruit abundance of the Pocilloporidae in the 27 stations was not correlated with abundance of juveniles or adults. Abundance of juveniles was significantly correlated with that of adults, but was not significant at the bigger size-class. At the island level, recruit abundance was significantly correlated with the abundance of juveniles in Raiatea, but not on the other islands, and not correlated with adult abundance on any island. Juvenile abundance was correlated with small adult abundance in Moorea and Raiatea, but not in Tahiti. It was not correlated with large adult abundance at any of the islands (Table 3).

For the Acroporidae, recruit abundance was not correlated with juvenile or adult abundance at the regional level. Conversely, juvenile abundance was correlated with abundance of adults at each size class. At the island level, recruit abundance was not correlated with adult abundance at any of the study islands, but it was correlated with adult abundance at Raiatea and Tahiti. Juvenile abundance was correlated with adult abundance at each of the 3 islands considered (Table 3).

For the Poritidae, at the regional level, abundance of recruits was not correlated with abundance of

juveniles or adults, whereas juvenile and adult abundance patterns were correlated. These relationships were the same at the island level for each of the 3 islands, except juvenile abundance was not correlated with the one of large adults in Raiatea and Tahiti (Table 3).

DISCUSSION

Recruitment patterns

Recruit assemblages of the outer reef slopes of Moorea, Raiatea and Tahiti were characterized by a very high proportion of Pocilloporids (65.4%), followed by Acroporidae (22.3%) and Poritidae (9.5%), which is consistent with previous findings on the outer slopes of Moorea Island (Gleason 1996, Adjeroud et al. 2007a, Penin et al. 2007, Penin et al. 2010). Relative abundance of families other than Acroporidae, Pocilloporidae and Poritidae was particularly low on the tiles (2.6%). However, this is probably due, to some extent, to the use of artificial substrate. Whereas relative abundances of Pocilloporidae, Acroporidae and Poritidae on the tiles were representative of those observed on natural substrates, other families appeared to be under-represented (Penin et al. 2010).

Recruit abundance displayed high spatial variability at all spatial scales. At the regional level, recruit-

ment was 5 times higher at Raiatea than at Moorea, and nearly twice as high at Tahiti than at Moorea. Variations at the island level were the highest. In particular, Raiatea's western location (Miri-Miri) displayed recruit abundance nearly 10× higher than at Avera and Uturoa. A similar pattern was observed at Tahiti, albeit to a lesser extent; abundance at the western location (Faa'a) was 5 times higher than at the others (Digue and Pirae). In Moorea, variations were smaller and showed an opposite trend regarding exposure to swells, with the northern locations (Tiahura and Vaipahu) displaying twice as many recruits per tile than the western location (Haapiti). Lower abundance of recruits on the most exposed site has previously been observed at Moorea, and is hypothesized to be a consequence of low residence times and high flushing rates resulting from high swells (Adjeroud et al. 2007a). This does not seem to be a general pattern in the Society archipelago, and, therefore, this hypothesis needs to be revisited.

Interestingly, variations of recruit abundance at the regional and island levels were very similar among the 3 main families, despite seasonal differences among coral families. This inter-site variation may be due to differences in larval flow in relation to local current patterns (Edmunds et al. 2010), variable larval settlement and/or immediate post-settlement mortality, which can be the result of different local conditions (Ritson-Williams et al. 2009). Factors responsible for this variation are most likely to be consistent in time, at least at the seasonal scale. Such consistent variations in recruitment rates over time among locations were already observed around Moorea Island during longer-term studies (3 or 5 yr, respectively; Adjeroud et al. 2007a, Penin et al. 2010).

Results of the present study, together with previous findings (Adjeroud et al. 2007a, Penin et al. 2010), show that in this region, some locations routinely display significantly higher recruitment rates than others, for each of the 3 major coral families. Regardless of the reasons for this phenomenon, documenting this spatial variability and its consistency in time and among families is of particular interest. Recruitment is one of the prerequisites for population and assemblage recovery after disturbances (Hughes & Tanner 2000, Elmhirst et al. 2009). As such, this process is extremely important in systems under recurrent disturbances regime, like French Polynesia (Adjeroud et al. 2005). Locations exhibiting higher recruitment rates are likely to present higher recovery capacities, enhancing community resilience to disturbances (Nystrom et al. 2000, Bellwood et al. 2004). This has implications for conservation planning; determining which

locations display higher recruitment rates would help in predicting where recovery capacity may be the highest after a catastrophic event. With the predicted increase in frequency and intensity of disturbances linked with anthropogenic pollutions and global climate change (Wilkinson 2004), conservation measures do not only need to take into account coral cover and abundance, but also the capacity of coral assemblages to recover from these perturbations (Hughes et al. 1999). As a consequence, spatial differences in recruitment rates should be one of the parameters to consider when setting up conservation measures (Hughes et al. 1999).

At the local level, depth variation patterns were not consistent among locations or islands, despite high variability. Bathymetric variations in recruit abundance can be the result of variable larval input, settlement rates and/or early post settlement mortality (Mundy & Babcock 1998, Norström et al. 2007, Penin et al. 2010). These processes are influenced by many factors. Some of them, like light conditions, display consistent gradients with depth, but others like predation pressure or recent disturbances may present different depth patterns among locations, thus leading to differences in bathymetric patterns of recruit abundance (Wittenberg & Hunte 1992, Maida et al. 1994).

Juvenile and adult assemblage patterns

A mean of 6.4 juveniles m^{-2} was observed at study stations of Moorea, Raiatea and Tahiti. This is comparable to values obtained in New Caledonia, higher than values generally observed in Florida or on the Mesoamerican Barrier Reef System, but much lower than in the Virgin Islands (Edmunds 2000, Ruiz-Zarate & Arias-Gonzales 2004, Adjeroud et al. 2010). Mean adult abundance in Society archipelago is similar to what is generally observed on the outer slopes of the Great Barrier Reef (reviewed by Hughes et al. 2002) or in New Caledonia (Adjeroud et al. 2010), and higher than in the Ryukyu archipelago in Japan (Adjeroud 2006).

Like recruits, juveniles and adults exhibited spatial variability on several spatial scales, as it is generally observed in coral reefs (Edmunds 2000, Ruiz-Zarate & Arias-Gonzales 2004). Nevertheless, the magnitude of abundance variation was much lower for juveniles and adults than for recruits, and most of the variation occurred at the local level. At the regional level, recruit abundance showed a 5-fold variation among the 3 islands, whereas juvenile and adult

abundance displayed a much milder 25% and 34% variation among islands, respectively. At the island level, no consistent pattern was observed in regard to swell exposure. While the most exposed site had the lowest abundance of juveniles and adults in Moorea, it was the opposite in Raiatea, and it differed among life cycle stages in Tahiti (adult abundance being lower at the most exposed location and juvenile abundance displaying no significant among location variations). This demonstrates that swell exposure is only one of many factors influencing spatial distribution of corals in French Polynesia (Adjéroud 1997). History of disturbances is most likely another important aspect. In Raiatea, the most sheltered sites (Uturoa and Avera) are also the ones that were the most impacted by cyclones Osea and Martin in 1997. Following these cyclones, the coral cover dropped drastically (Adjéroud et al. 2005). These sites were probably still recovering at the time of our survey, which explains the lower abundance of juveniles and adults compared with the western site (Miri-Miri). Similar to recruit abundance, adult and juvenile abundances did not display any consistent depth pattern of variation at a local level, despite high variability. This underlines the hypothesis that factors influencing distribution of juveniles and adults are not homogeneously distributed with depth at all locations and islands.

The high spatial variability observed in the distribution of recruits, juveniles and adults is probably related to the strong environmental gradients characterizing high islands of the Society archipelago (Galzin & Legendre 1987, Cadoret et al. 1995, Adjéroud 1997). Moorea, Tahiti and Raiatea all display narrow reef systems that compact, over small distances, the natural gradients in environmental conditions. Three major types of gradients have been observed in Polynesian Islands: a land-ocean gradient, a depth gradient and a gradient along the bays (Adjéroud & Salvat 1996, Adjéroud 1997). These strong gradients at a small spatial scale are one of the distinctive characteristics of French Polynesian reefs, in comparison with continental reef systems such as the Great Barrier Reef, where gradients are observed on larger spatial scales (>100 km; Done 1982).

Relative importance of recruitment versus post-settlement processes on assemblage distribution

Around the 3 islands studied, recruit, juvenile and adult coral assemblages were dominated by 3 families: pocilloporids, acroporids and poritids. Neverthe-

less, relative abundances of these families varied greatly between recruits and the other stages (juveniles and adults), which were very similar. Pocilloporids displayed a much higher proportion of recruit assemblages than juvenile or adult assemblages. In contrast, acroporids were less dominant at the recruit stage assemblage than at juvenile or adult stages. Poritids displayed more similar proportions in the 3 assemblages. This is consistent with previous studies conducted around Moorea Island, and underlines discrepancies among families in terms of maintenance processes, that are most likely linked with differences in life history traits (Adjéroud et al. 2007a, Edmunds et al. 2010, Penin et al. 2010).

Moreover, spatial patterns of recruit distribution did not match those of juveniles and adults, whatever the scale considered. The island with the highest recruitment rate showed the lowest adult abundance, and recruit abundance was not correlated with abundance of juveniles and adults among locations or stations. On the contrary, juvenile and adult patterns were much more similar, regardless of the scale considered. This suggests important spatial and taxonomic differences in early-stage mortality, and underlines the major importance of early post-settlement events (i.e. those occurring during the first weeks or months after settlement) on shaping assemblage distribution at the scale of Society archipelago. Reciprocally, the similarities between juvenile and adult assemblages distribution indicates that patterns of spatial variability of juvenile mortality are probably similar to those of adult mortality. The families Acroporidae and Poritidae followed these general trends, with recruit abundances generally not correlated with those of juveniles and adults, and juvenile and adult abundances usually correlated on all spatial scales. Pocilloporidae displayed slightly different among-stages relationships, with fewer correlations between juvenile and adult abundances than the other taxa. These taxonomic differences are likely to be related to different life history traits and juvenile mortality rates (Adjéroud et al. 2007a, Penin et al. 2007, Penin et al. 2010).

These results complement those obtained around Moorea in a longer term study (Penin et al. 2010), and show that the lack of consistency between recruit patterns of distribution and juvenile and adult patterns of distribution not only occur at the island level (i.e. among locations and depths of an island), but also at the regional level (i.e. among different islands of the archipelago). This underlines the predominance of early post-settlement processes, such as predation, competition or sedimentation, which

happen at a local scale on the reef (Gilmour 2002, Birrell et al. 2005, Wilson & Harrison 2005, Christiansen et al. 2009) compared with pre-settlement processes such as larval dispersion and supply, occurring at much larger spatial scales (Sammarco 1994, Vermeij et al. 2006, van Oppen et al. 2008). This has implications in terms of conservation as it emphasizes the importance of local conditions faced by young corals, such as water quality or predation and competition pressures in coral recruitment success and assemblage maintenance (Fabricius et al. 2005, Mumby et al. 2007, Arnold et al. 2010). These local conditions can be improved by conservation measures regarding land use or fishing practices (see for example Mumby et al. 2006, Mumby & Harborne 2010, Shenton et al. 2010).

To conclude, results of the present study highlight the high variability of recruitment patterns at several spatial scales. However, spatial patterns of distribution among islands and locations were highly consistent among taxa and between seasons. This can have important implications in terms of conservation planning, showing that some locations display better abilities to recover after mass disturbances. This is critical in the actual context of recurrent disturbances faced by coral reefs. Results also reveal the paramount importance of events occurring during the first weeks and months after settlement in the distribution of adults at regional, island and local levels, thus confirming the significance of local processes in shaping coral assemblages distribution and maintenance.

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