Vol. 692: 67–79, 2022
https://doi.org/10.3354/meps14073

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published June 30

Extremely high but localized pulses of coral recruitment in the southwestern lagoon of New Caledonia and implications for conservation

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ABSTRACT: Recruitment processes largely drive spatial distributions, dynamics, and recovery potential of marine communities. Determining scales of variation in recruitment rates and composition can help in understanding population replenishment mechanisms, while identifying recruitment hotspots is crucial for improving conservation strategies, particularly for threatened marine ecosystems such as coral reefs. We examined the spatial and interannual variability (2012–2014) of coral recruitment at multiple scales within and among reef habitats (14 stations) in the southwestern lagoon of New Caledonia. Recruit assemblages were characterized by high recruitment rates compared to other regions (overall mean of 34.9 recruits per 11 × 11 × 1 cm settlement tile, corresponding to 1220.9 recruits m^{-2}) and strong dominance of Acroporidae. We found a marked spatial heterogeneity among habitats but also exceptionally high interannual variation (100-fold), with extreme recruitment peaks (up to 13 572.8 recruits m^{-2}, with a maximum of 811 recruits on a single tile) recorded in 2014 at some fringing and mid-shelf reefs, the highest records ever reported to date. These encouraging results contrast with other reefs where recent declines in coral recruitment rates have been documented with major concerns for their resilience capacities. However, the marked spatio-temporal variability of coral recruitment complicates conservation strategies, as it makes it difficult to identify 'recruitment hotspots' as priority sites to protect for their potential capacity to boost the replenishment of local populations.

KEY WORDS: Coral reefs · Scleractinian corals · Recruitment · Population dynamics · Spatio-temporal variability · New Caledonia

1. INTRODUCTION

Recruitment is a critical process governing the distribution and dynamics of marine communities (Caley et al. 1996, Cowen et al. 2000, Hixon et al. 2002, Richmond et al. 2018). The regulation of scleractinian coral populations, the major reef-building taxa and key components to the exceptional biodiversity of coral reef ecosystems, is largely determined by early recruitment patterns and post-settlement events (Connell et al. 1997, Hughes et al. 1999, 2000, Ritson-Williams et al. 2009, Adjeroud et al. 2017). Larval supply, settlement and metamorphosis, and subsequent coral survival and growth also have a marked influence on recovery trajectories following mass mortality events (Hughes & Tanner 2000, Gilmour et al. 2013, Lukoschek et al. 2013, Mumby et al. 2016, Adjeroud et al. 2018a),

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with relative contributions that vary with species life strategies and reef environments (Doropoulos et al. 2015, Edmunds 2018, Kayal et al. 2018, Gouezo et al. 2019, 2020). In fact, coral recruitment is a key indicator of reef community resilience capacities (McClanahan et al. 2012, Adjeroud et al. 2017, Hughes et al. 2019, Guerrini et al. 2020). Improving our knowledge of coral recruitment processes has become critically important as large-scale perturbations and local stressors increasingly threaten the economic, cultural, social, and aesthetical goods and services coral reefs provide to ~850 million people from more than 100 countries (Bellwood et al. 2004, Hoegh-Guldberg & Bruno 2010, Kittinger et al. 2012, Hughes et al. 2017, Woodhead et al. 2019). In this context of 'coral-reef crisis', integrating empirical knowledge on coral recruitment processes into management strategies is essential for successful conservation of coral reef ecosystems (Mumby & Steneck 2008, McClanahan et al. 2012, Hughes et al. 2019, Edmunds & Riegl 2020).

Since the 1980s, patterns of coral recruitment have been documented for many coral reefs worldwide (reviewed in Adjeroud et al. 2017). One of the main characteristics of coral recruitment is its variability across spatial scales, from large geographic scales of regions and oceanic basins to local scales within and among reef habitats and sites (Hughes et al. 2002, Adjeroud et al. 2007, Sola et al. 2015, Davidson et al. 2019, Jouval et al. 2019). This high heterogeneity is largely related to the variety of biophysical processes that may influence the biology of coral recruits and which vary in frequency, intensity, and spatial scale, as well as to the contrasting life history traits observed among coral taxa (Ritson-Williams et al. 2009, Kayal et al. 2015, Richmond et al. 2018, Gouezo et al. 2020, Thomson et al. 2021). For example, physical factors such as hydrodynamics and wave exposure, sedimentation, substrate characteristics, and water quality largely influence the composition and abundance of coral recruit assemblages at local scales (Ritson-Williams et al. 2009, Edmunds et al. 2010, Edmunds 2022). The preference of larvae for some wavelengths of light, substrate color, and sound has also been demonstrated (Vermeij et al. 2009, Mason et al. 2011). Biotic interactions such as predation, allelopathy, and competition with algae may affect coral recruitment and adult distribution through space pre-emption, overgrowth, and chemical cues (Kuffner et al. 2006, Dixson et al. 2014). In addition, variation in recruitment at local scales may also be driven by larval preferences and selective mortality (Mundy & Babcock 1998, Baird et al. 2003, Doropoulos et al. 2020, Shlesinger & Loya 2021). In some regions, studies have identified sites that receive consistently high levels of recruitment, also known as 'recruitment hotspots' (Fisk & Harriott 1990, Glassom et al. 2004, Eagle et al. 2012, Bauman et al. 2014, Edmunds 2021a). The temporal variability of coral recruitment has also been widely documented (reviewed in Adjeroud et al. 2017). Seasonal variability of coral recruitment appears to be mainly related to the reproductive and spawning strategies of coral assemblages, with one reproductive cycle per year for most broadcast spawning species and possible multiple events for brooders (Harrison & Wallace 1990, Baird et al. 2009, Richmond et al. 2018). Interannual changes in climatic and oceanographic conditions can affect fecundity, pre-settlement mortality, dispersal, and early post-settlement events (Harrison & Wallace 1990, Shlesinger & Loya 2019, Edmunds 2021a), with major impacts from large-scale perturbations such as thermally induced coral bleaching events or cyclones (Mumby 1999, Mallela & Crabbe 2009, Lukoschek et al. 2013, Doropoulos et al. 2014, Hughes et al. 2019). This interannual variability in fecundity, settlement rates, and post-settlement events therefore results in 'good' and 'bad' recruitment years, which may have important implications for the regulation of adult populations (Hughes 1990, 1996, Connell et al. 1997, Hughes et al. 2000, Edmunds 2017). Thus, for marine invertebrates with a bipartite life cycle, adult population abundances are the result of 10 yr variation averages in larval production and post-settlement mortality, although sporadic episodes of extremely high recruitment may also be major drivers of population dynamics (Warner & Chesson 1985, Witman et al. 2003, Sams & Keough 2012, Bethoney et al. 2016).

Patterns of coral recruitment are, however, increasingly altered by global environmental changes, threatening the resilience capacities of coral reefs (Hughes et al. 2019, Price et al. 2019, Edmunds & Riegl 2020, Guerrini et al. 2020). A recent synthesis has pointed out the global decline in coral recruitment since 1974, with decreasing rates in equatorial reefs but increasing densities at sub-tropical latitudes reflecting a poleward expansion in coral reef distribution (Price et al. 2019). Declining recruitment rates may also be associated with shifts in recruit assemblage compositions, as recently recorded on the Australian Great Barrier Reef (GBR) following thermally induced coral bleaching events (Hughes et al. 2019). In fact, these bleaching events have mainly affected broadcast-spawning *Acropora* species, whose tabular, corymbose, and digitate growth forms

are characterized by high rates of larval recruitment ('superrecruiters'; Roff 2021).

In this context of increasing concerns about the capacity of recruitment to replenish adult coral populations, we examined the spatial and interannual variability (2011–2014) of coral recruitment at various scales (from cm to 10s of km) within and among various reef habitats in the southwestern lagoon of New Caledonia, from fringing reefs situated within bays to oceanic outer-reef slopes. The main goal of this study was to document the level and variability of coral recruitment, identify potential sites with higher recruitment rates, and assess if such 'recruitment hotspots' could be proposed as priority conservation sites. Implications of our results for broader coral reef conservation are also discussed.

2. MATERIALS AND METHODS

2.1. Study area

This study was conducted between October 2011 and February 2014 in the southwestern portion of the main island ('Grande Terre') of New Caledonia (Fig. 1). The southwestern lagoon is large (~10–30 km separates the coast and the outer reef slope) and contains diverse reef habitats (fringing, mid-shelf, barrier, and outer-slope reefs) characterized by contrasting environmental conditions (Adjeroud et al. 2010, 2019). Terrigenous influence is mainly restricted to fringing reefs, particularly those within bays with long water residence times, whereas mid-shelf, barrier, and outer-slope reefs are mostly under oceanic influences (Jacquet et al. 2006). New Caledonian reefs are exposed to some localized anthropogenic impacts, primarily associated with human concentration at the main city of Nouméa and extensive nickel mining for over a century. However, compared to other Pacific reefs, such as the GBR or the French Polynesian islands, large-scale natural disturbances are relatively rare in New Caledonia, and no widespread mass mortality of corals has been recently recorded (Wantiez 2008, Adjeroud et al. 2019). Instead, coral mortalities caused by disturbances have been acute in time and space, such as following cyclone Erica in 2003 (Wantiez et al. 2006, Guillemot et al. 2010), ephemeral increases in the abundance of the coral-killing seastar *Acanthaster* spp. in 2012–2013 (Adjeroud et al. 2018b, Dumas et al. 2020), and the 2016 bleaching event (<10% coral mortality; Payri et al. 2018, 2019, Bollati et al. 2020).

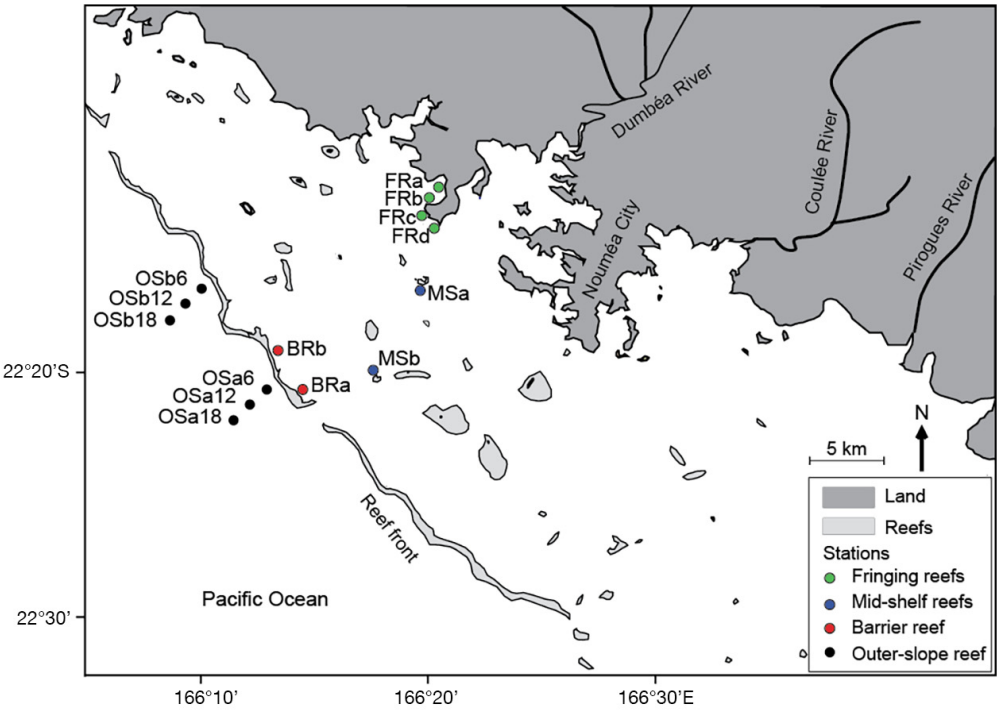

Fig. 1. Location of the 14 stations in the southwestern lagoon of the main island ('Grande Terre') of New Caledonia where coral recruitment was monitored. Stations encompassed the 4 major reef habitats: fringing reefs (FR), mid-shelf reefs (MS), barrier reefs (BR), and outer-slope reefs (OS). See Section 2.2 for station codes

2.2. Sampling strategy and data analysis

To study the spatio-temporal variability of coral recruitment, 14 stations were selected on the 4 major reef habitats that compose the cross-shelf gradient in the southwestern lagoon (Fig. 1, Table S1 in the Supplement at www.int-res.com/articles/suppl/m692p067_supp.pdf). Station codes are abbreviated as follows: the first 2 letters indicate the reef habitats (FR for fringing, MS for mid-shelf, BR for barrier, OS for outer-slope), the different stations within each habitat are coded 'a' to 'd', and the associated number represents the depth (6, 12, and 18 m) for reef slope stations (Fig. 1). Four stations were established on fringing reefs (Stns FRa and FRb within Maa Bay, and Stns FRc and FRd at its exit), 2 stations on mid-shelf reefs (Stns MSa and MSb, 10–15 km from Nouméa), 2 on the barrier reef (Stns BRa and BRb, 21–22 km from Nouméa), and 6 stations (Stns OSa6, OSa12, OSa18, OSb6, OSb12, OSb18) at each of the 2 outer-slope reef sites (Dumbéa and Uitoé, 23–26 km from Nouméa). On fringing, mid-shelf, and barrier reefs, stations were placed between 2 and 6 m depth, whereas on the outer-slope reefs, stations were distributed at 6, 12, and 18 m depth. Among the 14 stations surveyed in this study, 6 (Stns FRa, FRb, MSa, MSb, BRa, BRb) were also studied for adult coral assemblages in 2006–2008, including data on generic richness, abundance, and cover (Table S2).

At each station, 20 unglazed terracotta tiles (11 × 11 × 1 cm) were directly attached to the substratum following the method described by Mundy (2000). Tiles were immersed for 5 mo (October to late February), over a 3 yr period (2011–2012, 2012–2013, 2013–2014; hereafter referred to as the 2012, 2013, and 2014 recruitment events, respectively). At the end of the immersion periods, the tiles were retrieved, bleached, and sun-dried to expose the skeleton of coral recruits for identification under a dissecting microscope. At this stage of development, the micro-architecture of the corallum is not sufficiently developed to allow high-resolution identification, and only 3 families (Acroporidae, Pocilloporidae, Poritidae) of coral recruits can be reliably distinguished (Babcock et al. 2003). All other coral families were compiled into a category named 'other' recruits (Fig. S1). We also used a category 'broken' that comprised all spats that were too damaged to be identified with certainty. This category represented less than 1.2% of the overall recruits and was not specifically analyzed hereafter, but was considered in the overall recruitment counts (all categories pooled).

Normality and homoscedasticity of the data were examined using Shapiro-Wilk and Bartlett tests, respectively. Since the data were heteroskedastic and over-dispersed, generalized linear mixed-models (GLMM) for negative-binomial distributed data (log-link) were performed, using the 'glmmPQL' function from the 'MASS' package to test for spatial and temporal variability of recruit abundance for all taxa combined and for each of the dominant coral family categories: Acroporidae, Pocilloporidae, Poritidae, and others. Separate sets of GLMMs were used to assess recruitment variability at the scale of reef habitats (interaction year × habitat) while accounting for the random effects of observations performed at different stations (station as a random factor), and at the scale of stations (interaction year × station) while accounting for random effects of different habitats (habitat as a random factor). Tukey's HSD post hoc tests were performed using the 'lsmeans' function to identify pairwise differences among significant groups. Differences in proportions of recruits among the 3 surfaces of the settlement tiles (lower, upper, and sides) were assessed by the non-parametric chi-squared test. All analyses were performed using R version 3.1.0 (R Development Core Team 2014).

3. RESULTS

3.1. General recruitment characteristics

Over the 3 yr of the study, an overall mean ± SD (all recruit categories, stations and years combined) of 34.9 ± 35.4 coral recruits per tile (1220.9 recruits m^{-2}) was recorded. Means of 15.7 ± 3.2 and 12.1 ± 6.2 recruits per tile (550.7 and 423.1 recruits m^{-2}, respectively) were recorded in 2012 and 2013, respectively, whereas 2014 was characterized by a higher mean recruitment rate of 76.9 ± 56.5 recruits per tile (2689.1 recruits m^{-2}).

Coral recruits were largely dominated by Acroporidae (10.4 ± 5.1, 8.6 ± 6.6, and 71.1 ± 40.7 recruits per tile, representing 67.2, 70.8, and 93.1% of the recruits in 2012, 2013, and 2014, respectively; Fig. 2), followed by Pocilloporidae (4.4 ± 2.4, 2.6 ± 2.2, and 4.1 ± 4.2 recruits per tile, representing 28.2, 21.5, and 5.4%, in 2012, 2013, and 2014, respectively). Acroporid recruits were dominant at all stations except one of the 6 m depth stations on the outer slope (Stn OSa6), where pocilloporids were slightly more abundant. Poritidae (0.5 ± 0.4, 0.7 ± 0.8, and 0.5 ± 0.6 recruits per tile, representing 3.4, 5.9, and 0.7%, in 2012, 2013, and 2014, respectively) and 'other'

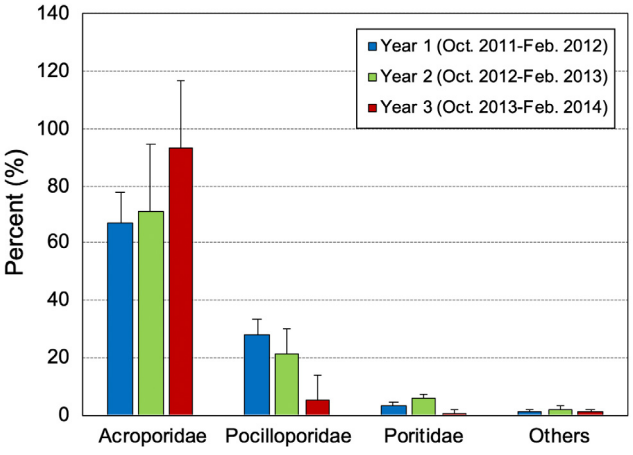

Fig. 2. Relative proportion (%) of the 4 dominant coral recruit categories (all stations and habitats pooled) for the 3 years of this study. Errors bars: +SD

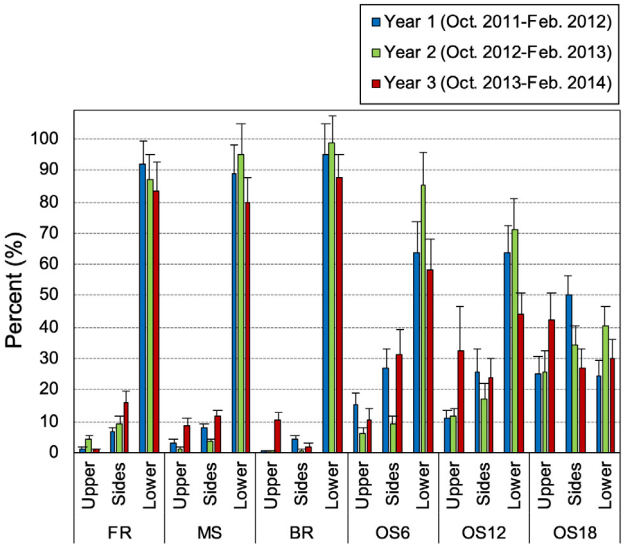

Fig. 3. Relative proportion (%) of coral recruits (all categories pooled) on the different surfaces of the settlement tiles (upper, sides, and lower) at the 4 major reef habitats (FR: fringing reefs; MS: mid-shelf reefs; BR: barrier reefs; OS: outer-slope reefs), and the 3 depth zones on the outer-slope (6, 12, and 18 m). Errors bars: +SD

recruits (0.2 ± 0.2, 0.2 ± 0.2, and 0.7 ± 0.6 recruits per tile, representing 1.3, 1.7, and 0.9%, in 2012, 2013, and 2014, respectively) were characterized by lower abundances over the study period (Fig. 2).

3.2. Settlement preferences

The proportion of recruits recorded on the different surfaces of the settlement tiles was variable among stations and years (chi-squared tests, all $p < 0.0001$; Fig. 3, Table S3). At fringing, mid-shelf, and barrier reef stations, where water depth was 2–6 m, the vast majority of recruits were recorded on the lower surfaces of the tiles (FR: 84.4%, MS: 83.9%, BR: 94.2%), compared to the sides (FR: 14.5%, MS: 9.5%, BR: 2.1%) and the upper surfaces (FR: 1.0%, MS: 6.5%, BR: 3.6%). In contrast, the proportion of recruits among tile surfaces differed at the outer-slope reef stations, with increasing abundances on sides (23–44%) and upper surfaces (8–28%) with increasing depth. Indeed, a higher proportion of recruits were still recorded on the lower surfaces at 6 and 12 m depth stations (66.7 and 61.9%, respectively), whereas at 18 m depth, most recruits were found on sides (43.7%), compared to lower (28.7%) and upper (27.6%) surfaces (Fig. 3).

3.3. Spatio-temporal and taxonomic variability

Significant spatio-temporal variability in recruitment rates was recorded, both for all recruit categories combined as well as individually per category (Tables S4, S7, S10, S13 & S16). In 2012, no significant difference in overall recruitment rates (all categories combined) was recorded among the 4 reef habitats (Tukey's HSD tests, all $p > 0.05$; Table S5); values were relatively similar among the 14 stations, except Stn Bra, which was distinguished by a lower recruit density (Fig. 4, Table S6). Densities of Acroporidae recruits were higher on fringing reefs compared to mid-shelf reefs (Tukey's HSD test, $p = 0.0330$), with no other significant differences detected among habitats (Fig. 5, Table S8). Within habitats, no significant

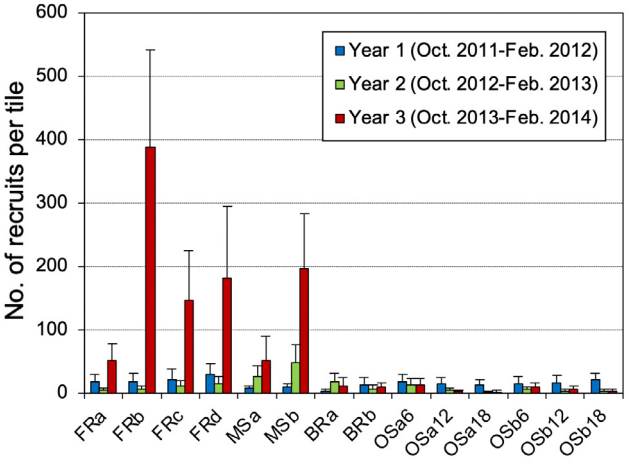

Fig. 4. Spatio-temporal variation in overall coral recruitment rates (all categories pooled) among the 14 stations established on the 4 major reef habitats. See Section 2.2 for station codes. Errors bars: +SD

differences in recruitment rates of Acroporidae were found among fringing reef or mid-shelf stations, whereas significant differences were recorded among barrier reef and among outer-slope stations (Tukey's HSD tests, all $p < 0.05$), with lower densities found at Stn OSa6 compared to Stn OSb18 (Table S9). For Pocilloporidae, Poritidae, and 'other' recruits, no significant differences in recruitment rates were recorded between the 4 habitats in 2012 (Tukey's HSD tests, all $p > 0.05$; Tables S11, S14 & S17). The abundance of Pocilloporidae recruits was not significantly different between mid-shelf reef stations or between barrier reef stations, whereas within-habitat differences were found at fringing reefs and outer-slope stations (Tukey's HSD tests, all $p < 0.05$; Table S12). Poritidae and 'other' recruits were characterized by low but variable densities at the scale of the station (i.e. among the 20 replicate settlement tiles), and no significant difference was recorded among stations within habitats (Tukey's HSD tests, all $p > 0.05$; Tables S15 & S18), except for Poritidae on the outer reef slope, where a decreasing trend with depth was observed at Stn OSa during the 3 yr, and an increasing trend at Stn OSb was seen in 2012 (Tukey's HSD tests, all $p < 0.05$; Fig. 5, Table S15).

In 2013, substantial variations in overall recruitment rates were observed among habitats for all categories (Tukey's HSD tests, all $p < 0.05$; Tables S5, S8, S14 & S17), except for Pocilloporidae (Tukey's HSD tests, all $p > 0.1$; Table S11). Significant differences were also recorded between stations within the same habitat, except at mid-shelf reefs, where relatively high recruit densities were recorded at both stations, notably for Acroporidae and Pocilloporidae (Fig. 5, Tables S6, S9 & S10). For Poritidae and 'other' recruits, no significant variations in densities were observed among stations within each habitat, except on the outer reef slope where a higher value was recorded at Stn OSa6 (Tukey's HSD tests, all $p < 0.05$; Tables S15 & S18).

In 2014, spatial variability among reef habitats was more pronounced for all coral recruit categories except Poritidae (Tables S5, S8, S11, S14 & S17), with particularly elevated densities at fringing and mid-shelf reefs (Fig. 4), notably at Stn FRb where the highest values were recorded: a mean of 388.1 ± 76.0 recruits per tile (all categories combined), corresponding to 13 572.8 recruits m^{-2}, with a record of 811 recruits on a single tile (Fig. S2). Marked variability was also found among stations within the same habi-

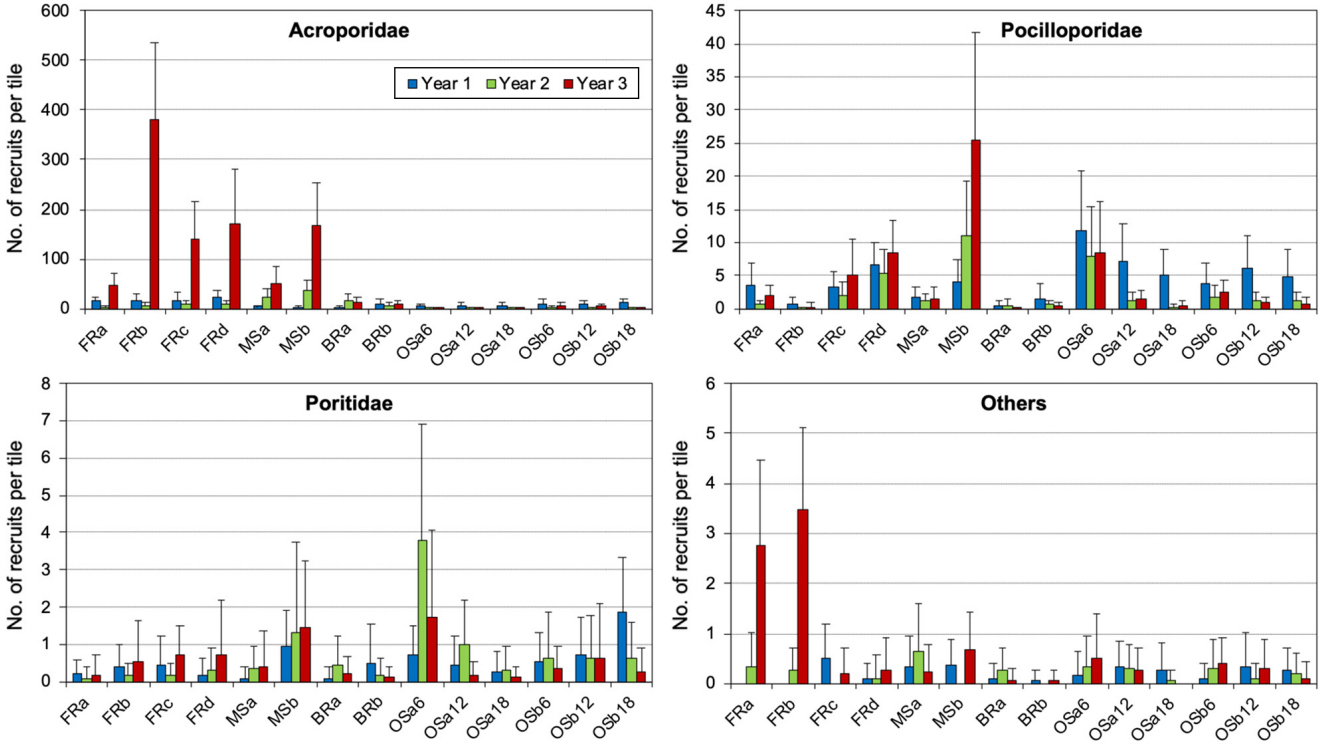

Fig. 5. Spatio-temporal variation in recruitment rates of the 4 dominant coral categories (Acroporidae, Pocilloporidae, Poritidae, and 'others' recruits) among the 14 stations established on the 4 major reef habitats. See Section 2.2 for station codes. Errors bars: +SD

tats (Tukey's HSD tests, all $p < 0.05$; Tables S6, S9, S12, S15 & S18), except at the barrier reef, where similar densities were found between the 2 stations. The high recruitment rate in 2014 was predominantly driven by Acroporidae, with higher densities on fringing and mid-shelf reefs (47.0–381.3 recruits per tile) compared to other habitats (0.9–11.4 recruits per tile; Fig. 5; Tukey's HSD tests, all $p < 0.05$; Table S8). Pocilloporidae recruits were also highly variable within and among habitats with, as in 2013, highest values recorded at Stn MSb and, to a lesser degree, at Stns FRc, FRd, and OSa6 (Table S12). Poritidae and 'other' recruits were characterized by low densities, with no significant differences between stations of the same habitat, except among reef slope stations for Poritidae and among fringing reef stations for 'other' recruits, with highest densities recorded at Stns FRa and FRb (Tukey's HSD tests, all $p < 0.05$; Tables S15 & S18).

Significant interannual variability in overall coral recruitment (all categories combined) was recorded for fringing, mid-shelf, and outer-slope habitats (Tukey's HSD tests, all $p < 0.05$; Table S19), whereas recruit densities were relatively consistent over the 3 yr at the barrier reef (Fig. 4). At fringing and mid-shelf reefs, recruit densities were significantly lower in 2012 and 2013 compared to 2014, when peak values were recorded (51.8–388.1 recruits per tile), with lowest values observed in 2013 for fringing reefs (4.2–14.3 recruits per tile) and in 2012 for mid-shelf reefs (7.5 and 9.3 recruits per tile). For the outer-slope reefs, 2012 was characterized by higher recruitment rates compared to 2013 and 2014, the latter 2 yr showing no significant difference, except at some stations located at 12 and 18 m depth, where a slight increase was recorded in 2014 (Tukey's HSD tests, all $p < 0.05$; Table S20). For Acroporidae, significant interannual variability in recruitment rates was found for all habitats except at the barrier reef and at the outer-slope stations between 2013 and 2014 (Tukey's HSD tests, all $p < 0.05$; Table S21) and for all stations except Stn BRb, where densities were consistent over the 3 yr (Table S22). For Pocilloporidae, significant interannual variability was recorded at all habitats (Tukey's HSD tests, all $p < 0.05$), except at mid-shelf reefs (Table S23). Recruitment rates of Acroporidae showed a significant interannual variation at all stations (Tukey's HSD tests, all $p < 0.05$), except at Stns BRb and OSa6 (Table S24). Compared to other categories, the interannual variability among habitats and stations was less pronounced for Poritidae and 'other' recruits (Tables S25–S28).

4. DISCUSSION

4.1. A world record in coral recruitment rates

The overall mean coral recruitment rate of 34.9 recruits per tile recorded in our study, corresponding to 1220.9 recruits m^{-2}, was quite high compared to most Western Pacific reefs such as the GBR (Table 1), a region known for its high recruitment rates (Price et al. 2019), with up to 4590 recruits m^{-2} reported in 1995–1997 (Hughes et al. 1999) before recent declines (Hughes et al. 2019). Furthermore, the peak mean values of 388.1 recruits per tile we recorded at some stations in 2014, corresponding to 13 572.8 recruits m^{-2}, are to our knowledge the highest records to date, representing about 4 times the upper rates reported in other regions (Table 1). The high recruitment rates recorded in the southwestern lagoon of New Caledonia clearly contrast with those in other coral reef regions and at most subtropical reefs where <150 recruits m^{-2} are typically found (Table 1). Furthermore, the maximum recruitment rate of 811 recruits we recorded on a single tile demonstrates the ability of coral larvae to settle and survive long enough to metamorphose into a polyp and initiate calcification at a very high density on a small (11 × 11 × 1 cm) substrate.

4.2. Taxonomic composition of coral recruit assemblages

Coral recruit assemblages in the southwestern lagoon of New Caledonia were characterized by the large dominance of Acroporidae (67–93%), which is similar to patterns found at most coral reefs in the Western Pacific (Table 1) such as Fiji and the GBR, where Acroporidae reach up to 85% (Hughes et al. 2000, 2002, Kojis & Quinn 2001, Davidson et al. 2019), although a decline in acroporids has recently been recorded on the GBR (Hughes et al. 2019). Pocilloporidae recruits were also relatively abundant (5–28%), whereas Poritidae and other coral families represented smaller proportions of recruits (1–6 and 1–2%, respectively). The taxonomic composition recorded at New Caledonia and most Western Pacific reefs clearly contrasts with that found in the central Pacific, subtropical reefs, and the south-western Indian Ocean (Table 1), where recruit assemblages are generally dominated by Pocilloporidae (typically >60%), and where Acroporidae contributions

Table 1. General characteristics of coral recruitment patterns in various coral reefs of the Pacific and Indian oceans. Only contemporary studies (published since 2000) using a similar sampling protocol (ceramic or terracotta tiles directly attached to the substratum) were selected. Average: recruitment rate averaged among sites and years of survey; Range: minimal and maximal values recorded during the survey; NA: data not available; GBR: Great Barrier Reef. The present study is highlighted in **bold**

Location	Survey period	Recruitment rates (m^{-2}) Average	Range	Dominant categories (listed in descending order)	Reference
Pacific Ocean					
Singapore	2011–2013	55	0–2791	Pocilloporidae (84%)	Bauman et al. (2015)
Indonesia (southeastern Sulawesi)	2008–2009	149	35–209	Other families (41–62%), Acroporidae (12–20%), Pocilloporidae (10–21%)	Salinas-de-Leon et al. (2013)
Japan (Amakusa)	2001–2003	2	0–2	Recruitment rates too low to determine	Nozawa et al. (2006)
Australia (GBR)	1995–1997	4590	NA	Acroporidae (80%)	Hughes et al. (2000)
Australia (GBR)	2016–2017[a]	405	NA	Pocilloporidae, Acroporidae,	Hughes et al. (2019)
Australia (Lord Howe)	2011–2012	230	150–1154	Pocilloporidae (44%), Acroporidae (30%), Poritidae (19%)	Cameron & Harrison (2016)
New Caledonia	**2012–2014**	**1220**	**423–13572**	**Acroporidae (77%), Pocilloporidae (4%)**	**Present study**
French Polynesia (Moorea)	2000–2003	40	0–1223	Pocilloporidae (60%), Poritidae (19%), Acroporidae (11%)	Adjeroud et al. (2007)
Indian Ocean					
Mozambique	2012–2013	1130	15–2232	Acroporidae (80%)	Sola et al. (2015)
Reunion	2015–2017	86	20–154	Pocilloporidae (86%)	Jouval et al. (2019)
Rodrigues	2015–2017	4	2–40	Poritidae (80%) in 2015–2016, Acroporidae (69%) in 2016–2017	Jouval et al. (2019)
Seychelles	2012	595	82–2167	Acroporidae, Pocilloporidae, Poritidae	Chong-Seng et al. (2014)
Northeastern Arabian Peninsula	2012–2013	NA	0–82	NA	Bento et al. (2017)
Southern Gulf — Dubai	2009–2011	121	0–331	Other families (61%), Poritidae (27%), Acroporidae (11%)	Bauman et al. (2014)
Australia (Dampier Archipelago)	2015–2017	600	2–2730	Acroporidae	Thomson et al. (2021)

[a]This survey was conducted following a severe bleaching event

are reduced (typically <15%) even if adult acroporid colonies may be locally abundant (Adjeroud et al. 2007, 2018a, Ho & Dai 2014, Jouval et al. 2019). In addition to latitude, which is known to influence the composition of recruit assemblages (Hughes et al. 2002), the dominance of Acroporidae recruits in New Caledonia may also be explained by the high diversity and densities of adult colonies and the absence of large-scale mass-mortality of adult acroporid brood stock, such as the one recently recorded on the GBR (Hughes et al. 2019). Indeed, Pichon (2007) identified 58 *Acropora* spp. among the 310 coral species recorded in New Caledonia, while Adjeroud et al. (2019) estimated ~20–100 colonies of *Acropora* spp. per 10 m^2 at most reef habitats of the southwestern lagoon.

4.3. Spatio-temporal variability

As documented for a variety of coral reefs worldwide (Hughes et al. 2002, Adjeroud et al. 2007, Davidson et al. 2019, Jouval et al. 2019, Thomson et al. 2021), our results underline the strong spatial heterogeneity in recruitment rates at various scales, complementing the marked variability reported for the older coral life stages of juveniles and adults prevailing in the southwestern lagoon of New Caledonia (Adjeroud et al. 2010, 2019). At the small scale of individual recruitment tiles, at most stations, we found a higher proportion of recruits occupying the lower surface and sides of tiles compared to upper surfaces, where high grazing levels by herbivorous fish likely result in higher post-settlement mortality

(Penin et al. 2010). The higher proportion of recruits that we recorded on sides and upper surfaces at greater depth on the outer-reef slope is consistent with findings from other coral reefs and may be attributable to reduced light intensity on lower sides making this microhabitat less suitable for coral recruits (Mundy & Babcock 2000, Baird et al. 2003, Nozawa et al. 2011, Chui & Ang 2017, Doropoulos et al. 2020). Our results also underline the patchy distribution of coral recruitment at the station scale (i.e. among recruitment tiles, as shown by the high standard deviations recorded at all stations), which may reflect the small-scale variation in delivery of larvae by currents along with biotic interactions on the substrate such as chemical attractants and predation, competition, and other inhibitory effects (e.g. allelopathy) of resident benthic organisms such as hard and soft corals, sponges, ascidians, and algae (Birrell et al. 2008, Ritson-Williams et al. 2009, Dixson et al. 2014, Richmond et al. 2018, Whitman et al. 2020).

At the reef scale, marked spatial heterogeneity was recorded within and among major coral reef habitats. However, spatial patterns among stations were not conserved through time (i.e. peak recruit abundances were observed at different sites among years), which prevents the identification of persistent coral recruitment hotspots as can be found in some other coral reefs (Edmunds 2021b). Overall, higher recruit abundances were observed at some fringing and mid-shelf reefs, whereas recruitment rates were generally lower at barrier and outer-slope reefs. On the outer slope, recruit abundances were, on average, lower at 12 and 18 m compared to 6 m depth. Such reef scale and depth variation in recruitment patterns may result from differential larval delivery and settlement preferences, or early post-settlement mortality caused by variation in physical conditions (sedimentation, hydrodynamics, light) as well as different forms of biotic interaction (Mundy & Babcock 1998, Birrell et al. 2008, Penin et al. 2010, Gouezo et al. 2020, Whitman et al. 2020, Koester et al. 2021, Shlesinger & Loya 2021, Thomson et al. 2021).

Our results highlight particularly strong interannual variability in recruitment rates, with an extreme peak of Acroporidae in 2014 at some fringing and mid-shelf reef stations (>100 and up to 381.3 mean recruits per tile for this category). Surprisingly, such a peak in Acroporidae was not reported on the outer-reef slope, which, on the contrary, had very low recruitment rates recorded during the study period, though diversity, abundance, and cover of adult colonies of *Acropora* are quite high on this habitat (authors' pers. obs.). In contrast, the outer-reef slope was the habitat where the recorded Pocilloporidae recruitment rates were highest during the first year of the survey (2012). These findings highlight the contrasting spatial patterns and dynamics of recruitment processes that exist among coral taxa and habitats at the reef scale. Marked temporal variability in coral recruitment has been widely documented in many reefs around the world (Soong et al. 2003, Adjeroud et al. 2017, Hughes et al. 2000, 2019, Thomson et al. 2021), but the level of the interannual variation recorded here, with up to 100-fold differences in recruitment rates among neighboring stations and consecutive years, stands out as exceptional. Indeed, such extremely high recruitment events have only rarely been recorded in marine ecosystems, with the only recent reports being sea scallops in the Mid-Atlantic (Bethoney et al. 2016), damselfish in Western Australia (Pearce et al. 2016), and *Mytilus edulis* in the Gulf of Maine (Witman et al. 2003). Although identifying factors influencing recruitment variability was not within the scope of this study, we hypothesize that the recruitment peaks at some fringing reefs may be linked to changes in local hydrodynamic patterns. Indeed, differences in coastal water surface flows can generate recruitment variation by determining whether drifting larvae complete their development near a favorable habitat (Gaines & Bertness 1992, Golbuu et al. 2012, Oprandi et al. 2019, Thomson et al. 2021). In our case, we hypothesize that lower circulation in the southwestern lagoon, linked to periods of weak south-easterly trade-winds and occasional west breezes during the stormy wet season, favors larval retention near the coast, particularly within areas of high residence time such as the Maa Bay (Jacquet et al. 2006, Ouillon et al. 2010, Cuif et al. 2014), where the coral recruitment records were found. In contrast, the lower recruitment rates that we recorded on the outer-reef slope, most notably for Acroporidae, may be linked to higher exposure to wave and swell actions and the oceanic surface currents that characterize this habitat (Ouillon et al. 2010), which may reduce the settlement of coral larvae of numerous coral species, as suggested for other coral reefs worldwide (Hata et al. 2017, Koester et al. 2021). Obviously, other hypotheses could be proposed to explain the recruitment peak of Acroporidae in 2014, such as a sporadic year of higher fecundity and lower pre- and/or post-settlement mortality. Such alternative mechanisms, which could not be examined in New Caledonia due to a lack of adequate data, should be explored if we are to improve our knowledge of underlying processes that control the spatio-temporal variability in coral re-

cruitment. However, self-recruitment processes occurring at the habitat scale seem an inadequate explanation, as the highest adult *Acropora* abundances were recorded on the barrier reef (Table S2), where recruitment of Acroporidae was the lowest. This finding contrasts with several previous surveys that demonstrated a positive relationship between recruitment and cover of adult colonies at the habitat scale (Hughes et al. 2000, Kayal et al. 2015, Edmunds 2022).

4.4. Implications for conservation strategies

The high rates of coral recruitment reported in this study are encouraging compared to many reefs where recruitment appears insufficient to replenish coral assemblages (Chui & Ang 2017, Guerrini et al. 2020), particularly as recruitment declines and coral composition shifts were recorded following recurrent bleaching events even at the nearby GBR (Hughes et al. 2019, Price et al. 2019). The unique attributes of coral recruitment in New Caledonia, together with the high diversity and abundance of corals (Pichon 2007, Adjeroud et al. 2019), bring hope for the resilience potential of this UNESCO World Heritage site, provided that no significant changes in the occurrences of large-scale disturbances or local stressors to the reefs occur in the future.

The marked variability in coral recruitment reported here emphasizes the need for large-scale and long-term studies to determine temporal trends, identify the frequency of sporadic peak events, and examine their implications for the resilience of adult assemblages (Kayal et al. 2018, Hughes et al. 2019, Edmunds 2021b, Thomson et al. 2021). Identifying the major biological and environmental factors underlying this variability is also essential to improve knowledge on drivers of coral recruitment, enable predictions of such extreme events, and assess implications for reef conservation (Mumby & Steneck 2008). The results of this study suggest a continued need for adaptable management based on empirical data. The strong spatio-temporal variability in coral recruitment demonstrated here, with recruitment peaks reported at different habitats and years depending on coral taxa, together with those of juvenile and adult assemblages (Adjeroud et al. 2019), highlights the difficulty in identifying specific reefs as both recruitment hotspots and adult sanctuaries to prioritize protection. Thus, the conservation strategy to define reef areas that may act as larval 'sources' for other 'sink' reefs (Fontoura et al. 2022) seems difficult to achieve for certain coral reef systems, including the southwestern lagoon of New Caledonia. Rather, our findings suggest that conservation measures should integrate large scales encompassing the different reef habitat types, with sufficiently large coverage to capture these localized pulses of high recruitment. However, as spatial prioritization at large scales may be inefficient in heterogeneous landscapes, and because resources allocated to conservation are often limited, such broad-scale marine protected areas are difficult to implement (Nolan et al. 2021). Overall, despite the consensus on recruitment being a key factor to include in conservation strategies, its spatial and temporal heterogeneity make it difficult to incorporate into conservation actions for ecosystems as complex as coral reefs (Mumby & Steneck 2008, McClanahan et al. 2012, Adjeroud et al. 2017).

Acknowledgements. The authors thank the staff of IRD Nouméa for their field support. We also gratefully acknowledge critical comments made by Erwan Sola, Jane Ballard, and 3 anonymous reviewers. This research was supported by grants from the GOPS (Grand Observatoire de l'environnement et de la biodiversité terrestre et marine du Pacifique Sud) and from IRD. This paper is also a contribution to the SCORE-REEF group funded by the Centre de Synthèse et d'Analyse sur la Biodiversité (CESAB) of the Fondation pour la Recherche sur la Biodiversité (FRB) and the Agence Française pour la Biodiversité (AFB).

LITERATURE CITED

Adjeroud M, Penin L, Carroll A (2007) Spatio-temporal heterogeneity in coral recruitment around Moorea, French Polynesia: implications for population maintenance. J Exp Mar Biol Ecol 341:204–218

Adjeroud M, Fernandez JM, Carroll AG, Harrison PL, Penin L (2010) Spatial patterns and recruitment processes of coral assemblages among contrasting environmental conditions in the southwestern lagoon of New Caledonia. Mar Pollut Bull 61:375–386

Adjeroud M, Kayal M, Penin L (2017) The importance of recruitment processes in the dynamics and resilience of reef coral assemblages. In: Rossi S, Bramanti L, Gori A, Orejas C (eds) Marine animal forests. Springer, Cham, p 549–569

Adjeroud M, Kayal M, Iborra-Cantonnet C, Vercelloni J and others (2018a) Recovery of coral assemblages despite acute and recurrent disturbances on a South Central Pacific reef. Sci Rep 8:9680

Adjeroud M, Kayal M, Peignon C, Juncker M, Mills SC, Beldade R, Dumas P (2018b) Ephemeral and localized outbreaks of the coral predator *Acanthaster* cf. *solaris* in the southwestern lagoon of New Caledonia. Zool Stud 57:e4

Adjeroud M, Poisson E, Peignon C, Penin L, Kayal M (2019) Spatial patterns and short-term changes of coral assemblages along a cross-shelf gradient in the southwestern lagoon of New Caledonia. Diversity (Basel) 11:21

Babcock RC, Baird AH, Piromvaragorn S, Thomson DP, Willis BL (2003) Identification of scleractinian coral recruits from Indo-Pacific reefs. Zool Stud 42:211–226
Baird AH, Babcock RC, Mundy CP (2003) Habitat selection by larvae influences the depth distribution of six common coral species. Mar Ecol Prog Ser 252:289–293
Baird AH, Guest JR, Willis BL (2009) Systematic and biogeographical patterns in the reproductive biology of scleractinian corals. Annu Rev Ecol Evol Syst 40:551–571
Bauman AG, Baird AH, Burt JA, Pratchett MS, Feary DA (2014) Patterns of coral settlement in an extreme environment: the southern Persian Gulf (Dubai, United Arab Emirates). Mar Ecol Prog Ser 499:115–126
Bauman AG, Guest JR, Dunshea G, Low J, Todd PA, Steinberg PD (2015) Coral settlement on a highly disturbed equatorial reef system. PLOS ONE 10:e0127874
Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. Nature 429:827–833
Bento R, Feary DA, Hoey AS, Burt JA (2017) Settlement patterns of corals and other benthos on reefs with divergent environments and disturbances histories around the Northeastern Arabian Peninsula. Front Mar Sci 4:305
Bethoney ND, Asci S, Stokesbury KDE (2016) Implications of extremely high recruitment events into the US sea scallop fishery. Mar Ecol Prog Ser 547:137–147
Birrell CL, McCook LJ, Willis BL, Diaz-Pulido GA (2008) Effects of benthic algae on the replenishment of corals and the implications for the resilience of coral reefs. Oceanogr Mar Biol Annu Rev 46:25–63
Bollati E, D'Angelo C, Alderdice R, Pratchett M, Ziegler M, Wiedenmann J (2020) Optical feedback loop involving dinoflagellate symbiont and scleractinian host drives colorful coral bleaching. Curr Biol 30:2433–2445
Caley MJ, Carr MH, Hixon MA, Hughes TP, Jones GP, Menge BA (1996) Recruitment and the local dynamics of open marine populations. Annu Rev Ecol Syst 27:477–500
Cameron KA, Harrison PL (2016) Patterns of scleractinian coral recruitment at Lord Howe Island, an isolated subtropical reef off eastern Australia. Coral Reefs 35: 555–564
Chong-Seng KM, Graham NAJ, Pratchett MS (2014) Bottlenecks to coral recovery in the Seychelles. Coral Reefs 33: 449–461
Chui APY, Ang P Jr (2017) Recruitment failure of scleractinian corals in a subtropical marginal environment: three-year monitoring in a Hong Kong marine park. Mar Pollut Bull 124:668–677
Connell JH, Hughes TP, Wallace CC (1997) A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecol Monogr 67:461–488
Cowen RK, Lwiza KMM, Sponaugle S, Paris CB, Olson DB (2000) Connectivity of marine populations: Open or closed? Science 287:857–859
Cuif M, Kaplan DM, Lefèvre J, Faure VM and others (2014) Wind-induced variability in larval retention in a coral reef system: a biophysical modelling study in the South-West Lagoon of New Caledonia. Prog Oceanogr 122: 105–115
Davidson J, Thompson A, Logan M, Schaffelke B (2019) High spatio-temporal variability in Acroporidae settlement to inshore reefs of the Great Barrier Reef. PLOS ONE 14:e0209771
Dixson DL, Abrego D, Hay ME (2014) Chemically mediated behavior of recruiting corals and fishes: a tipping point that may limit reef recovery. Science 345:892–897
Doropoulos C, Roff G, Zupan M, Nestor V, Isechal AL, Mumby PJ (2014) Reef-scale failure of coral settlement following typhoon disturbance and macroalgal bloom in Palau, Western Pacific. Coral Reefs 33:613–623
Doropoulos C, Ward S, Roff G, Gonzales-Rivero M, Mumby PJ (2015) Linking demographic processes of juvenile corals to benthic recovery trajectories in two common reef habitats. PLOS ONE 10:e0128535
Doropoulos C, Thomson DP, Trapon M, Cresswell AK, Turner JA, Babcock RC (2020) Depth gradients drive changes in early successional community composition and associated coral larvae settlement interactions. Mar Biol 167:59
Dumas P, Fiat S, Durbano A, Peignon P and others (2020) Citizen science, a promising tool for detecting and monitoring outbreaks of the crown-of-thorns starfish *Acanthaster* spp. Sci Rep 10:291
Eagle JV, Baird AH, Jones GP, Kingsford MJ (2012) Recruitment hotspots: consistent spatial patterns in the relative abundance of coral recruits at One Tree Island, Australia. Galaxea 14:5–22
Edmunds PJ (2017) Unusually high coral recruitment during the 2016 El Niño in Mo'orea, French Polynesia. PLOS ONE 12:e0185167
Edmunds PJ (2018) Implications of high rates of sexual recruitment in driving rapid reef recovery in Mo'orea, French Polynesia. Sci Rep 8:16615
Edmunds PJ (2021a) Spatiotemporal variation in coral recruitment and its association with seawater temperature. Limnol Oceanogr 66:1394–1408
Edmunds PJ (2021b) Recruitment hotspots and bottlenecks mediate the distribution of corals on a Caribbean reef. Biol Lett 17:20210149
Edmunds PJ (2022) Finding signals in the noise of coral recruitment. Coral Reefs 41:81–93
Edmunds PJ, Riegl B (2020) Urgent need for coral demography in a world where corals are disappearing. Mar Ecol Prog Ser 635:233–242
Edmunds PJ, Leichter JJ, Adjeroud M (2010) Landscape-scale variation in coral recruitment in Moorea, French Polynesia. Mar Ecol Prog Ser 414:75–89
Fisk DA, Harriott VJ (1990) Spatial and temporal variation in coral recruitment on the Great Barrier Reef: implications for dispersal hypotheses. Mar Biol 107:485–490
Fontoura L, D'Agata S, Gamoyo M, Barneche DR and others (2022) Protecting connectivity promotes successful biodiversity and fisheries conservation. Science 375:336–340
Gaines SD, Bertness MD (1992) Dispersal of juveniles and variable recruitment in sessile marine species. Nature 360:579–580
Gilmour JP, Smith LD, Heyward AJ, Baird AH, Pratchett MS (2013) Recovery of an isolated coral reef system following severe disturbance. Science 340:69–71
Glassom D, Zakai D, Chadwick-Furman NE (2004) Coral recruitment: a spatio-temporal analysis along the coastline of Eilat, northern Red Sea. Mar Biol 144:641–651
Golbuu Y, Wolanski E, Idechong JW, Victor S and others (2012) Predicting coral recruitment in Palau's complex reef Archipelago. PLOS ONE 7:e50998
Gouezo M, Golbuu Y, Fabricius K, Olsudong D and others (2019) Drivers of recovery and reassembly of coral reef communities. Proc R Soc B 286:20182908
Gouezo M, Olsudong D, Fabricius K, Harrison P, Golbuu Y, Doropoulos C (2020) Relative roles of biological and physical processes influencing coral recruitment during the

lag phase of reef community recovery. Sci Rep 10:2471
Guerrini G, Yerushalmy M, Shefy D, Shasha N, Rinkevich R (2020) Apparent recruitment failure for the vast majority of coral species at Eilat, Red Sea. Coral Reefs 39: 1715–1726
Guillemot N, Chabanet P, Le Pape O (2010) Cyclone effects on coral reef habitats in New Caledonia (South Pacific). Coral Reefs 29:445–453
Harrison PL, Wallace CC (1990) Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky Z (ed) Ecosystems of the world, Vol 25: Coral reefs. Elsevier, Amsterdam, p 133–207
Hata T, Madin JS, Cumbo VR, Denny M and others (2017) Coral larvae are poor swimmers and require fine-scale reef structure to settle. Sci Rep 7:2249
Hixon MA, Pacala SW, Sandin SA (2002) Population regulation: historical context and contemporary challenges of open vs. closed systems. Ecology 83:1490–1508
Ho MJ, Dai CF (2014) Coral recruitment of a subtropical coral community at Yenliao Bay, northern Taiwan. Zool Stud 53:5
Hoegh-Guldberg O, Bruno JF (2010) The impact of climate change on the world's marine ecosystems. Science 328: 1523–1528
Hughes TP (1990) Recruitment limitation, mortality, and population regulation in open systems: a case study. Ecology 71:12–20
Hughes TP (1996) Demographic approaches to community dynamics: a coral reef example. Ecology 77:2256–2260
Hughes TP, Tanner JE (2000) Recruitment failure, life histories, and long-term decline of Caribbean corals. Ecology 81:2250–2263
Hughes TP, Baird AH, Dinsdale EA, Moltschaniwskyj NA, Pratchett MS, Tanner JE, Willis BL (1999) Patterns of recruitment and abundance of corals along the Great Barrier Reef. Nature 397:59–63
Hughes TP, Baird AH, Dinsdale EA, Moltschaniwskyj NA, Pratchett MS, Tanner JE, Willis BL (2000) Supply-side ecology works both ways: the link between benthic adults, fecundity, and larval recruits. Ecology 81: 2241–2249
Hughes TP, Baird AH, Dinsdale EA, Harriott VJ and others (2002) Detecting regional variation using meta-analysis and large-scale sampling: latitudinal patterns in recruitment. Ecology 83:436–451
Hughes TP, Kerry JT, Alvarez-Noriega M, Alvarez-Romero JG and others (2017) Global warming and recurrent mass bleaching of corals. Nature 543:373–377
Hughes TP, Kerry JT, Baird AH, Connolly SR and others (2019) Global warming impairs stock-recruitment dynamics of corals. Nature 568:387–390
Jacquet S, Delesalle B, Torréton JP, Blanchot J (2006) Response of phytoplankton communities to increased anthropogenic influences (southwestern lagoon, New Caledonia). Mar Ecol Prog Ser 320:65–78
Jouval F, Latreille AC, Bureau S, Adjeroud M, Penin L (2019) Multiscale variability in coral recruitment in the Mascarene Islands: from centimetric to geographical scale. PLOS ONE 14:e0214163
Kayal M, Vercelloni J, Wand MP, Adjeroud M (2015) Searching for the best bet in life-strategy: a quantitative approach to individual performance and population dynamics in reef-building corals. Ecol Complex 23:73–84
Kayal M, Lenihan HS, Brooks AJ, Holbrook SJ, Schmitt RJ, Kendall BE (2018) Predicting coral community recovery using multi-species population dynamics models. Ecol Lett 21:1790–1799
Kittinger JN, Finkbeiner EM, Glazier EW, Crowder LB (2012) Human dimensions of coral reef social–ecological systems. Ecol Soc 17:17
Koester A, Ford AK, Ferse SC, Migani V, Bunbury N, Sanchez C, Wild C (2021) First insights into coral recruit and juvenile abundances at remote Aldabra Atoll, Seychelles. PLOS ONE 16:e0260516
Kojis BL, Quinn NJ (2001) The importance of regional differences in hard coral recruitment rates for determining the need for coral restoration. Bull Mar Sci 69:967–974
Kuffner IB, Walters LJ, Becerro MA, Paul VJ, Ritson-Williams R, Beach KS (2006) Inhibition of coral recruitment by macroalgae and cyanobacteria. Mar Ecol Prog Ser 323:107–117
Lukoschek V, Cross P, Torda G, Zimmerman R, Willis BL (2013) The importance of coral larval recruitment for the recovery of reefs impacted by cyclone Yasi in the Central Great Barrier Reef. PLOS ONE 8:e65363
Mallela J, Crabbe MJC (2009) Hurricanes and coral bleaching linked to climate changes in coral recruitment in Tobago. Mar Environ Res 68:158–162
Mason B, Beard M, Miller MW (2011) Coral larvae settle at a higher frequency on red surfaces. Coral Reefs 30: 667–676
McClanahan TR, Donner SD, Maynard JA, MacNeil MA and others (2012) Prioritizing key resilience indicators to support coral reef management in a changing climate. PLOS ONE 7:e42884
Mumby PJ (1999) Bleaching and hurricane disturbances to populations of coral recruits in Belize. Mar Ecol Prog Ser 190:27–35
Mumby PJ, Steneck RS (2008) Coral reef management and conservation in light of rapidly evolving ecological paradigms. Trends Ecol Evol 23:555–563
Mumby PJ, Steneck RS, Adjeroud M, Arnold SN (2016) High resilience masks underlying sensitivity to algal phase shifts of Pacific coral reefs. Oikos 125:644–655
Mundy CN (2000) An appraisal of methods used in coral recruitment studies. Coral Reefs 19:124–131
Mundy CN, Babcock RC (1998) Role of light intensity and spectral quality in coral settlement: implications for depth-dependent settlement? J Exp Mar Biol Ecol 223: 235–255
Mundy C, Babcock R (2000) Are vertical distribution patterns of scleractinian corals maintained by pre- or post-settlement processes? A case study of three contrasting species. Mar Ecol Prog Ser 198:109–119
Nolan MKB, Kim CJS, Hoegh-Guldberg O, Beger M (2021) The benefits of heterogeneity in spatial prioritisation within coral reef environments. Biol Conserv 258:109155
Nozawa Y, Tokeshi M, Nojima S (2006) Reproduction and recruitment of scleractinian corals in a high-latitude coral community, Amakusa, southwestern Japan. Mar Biol 149:1047–1058
Nozawa Y, Tanaka K, Reimer JD (2011) Reconsideration of the surface structure of settlement plates used in coral recruitment studies. Zool Stud 50:53–60
Oprandi A, Montefalcone M, Morri C, Benelli F, Bianchi CN (2019) Water circulation, and not ocean acidification, affects coral recruitment and survival at shallow hydrothermal vents. Estuar Coast Shelf Sci 217:158–164
Ouillon S, Douillet P, Lefebvre JP, Le Gendre R and others (2010) Circulation and suspended sediment transport in

a coral reef lagoon: the south-west lagoon of New Caledonia. Mar Pollut Bull 61:269–296
Payri C, Benzoni F, André LV, Houlbrèque F (2018) The 2016 coral bleaching event. In: Payri CE (ed) New Caledonia: world of corals. IRD Editions/Solaris, Marseille/Nouméa, p 161–166
Payri CE, Allain V, Aucan J, David C and others (2019) New Caledonia. In: Sheppard C (ed) World seas: an environmental evaluation, 2nd edn, Vol 2: The Indian Ocean to the Pacific. Springer, New York, NY, p 593–618
Pearce A, Hutchins B, Hoschke A, Fearns P (2016) Record high damselfish recruitment at Rottnest Island, Western Australia, and the potential for climate-induced range extension. Reg Stud Mar Sci 8:77–88
Penin L, Michonneau F, Baird AH, Connolly SR, Pratchett MS, Kayal M, Adjeroud M (2010) Early post-settlement mortality and the structure of coral assemblages. Mar Ecol Prog Ser 408:55–64
Pichon M (2007) Scleractinia of New Caledonia: check list of reef dwelling species. In: Payri C, Richer de Forges B (eds) Compendium of marine species from New Caledonia. Documents Scientifiques et Techniques II7, 2nd edn. IRD Editions, Nouméa, p 149–157
Price NN, Muko S, Legendre L, Steneck R and others (2019) Global biogeography of coral recruitment: tropical decline and subtropical increase. Mar Ecol Prog Ser 621:1–17
R Development Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
Richmond RH, Tisthammer KH, Spies NP (2018) The effects of anthropogenic stressors on reproduction and recruitment of corals and reef organisms. Front Mar Sci 5:226
Ritson-Williams R, Arnold SZ, Fogarty ND, Steneck RS, Vermeij MJA, Paul VJ (2009) New perspectives on ecological mechanisms affecting coral recruitment on reefs. Smithson Contrib Mar Sci 38:437–457
Roff G (2021) Evolutionary history drives biogeographic patterns of coral reef resilience. Bioscience 71:26–39
Salinas-de-Leon P, Dryden C, Smith DJ, Bell JJ (2013) Temporal and spatial variability in coral recruitment on two Indonesian coral reefs: consistently lower recruitment to a degraded reef. Mar Biol 160:97–105
Sams MA, Keough MJ (2012) Effects of pulse versus steady recruitment on sessile marine communities. Oecologia 170:209–219
Shlesinger T, Loya Y (2019) Breakdown in spawning synchrony: a silent threat to coral persistence. Science 365: 1002–1007
Shlesinger T, Loya Y (2021) Depth-dependent parental effects create invisible barriers to coral dispersal. Commun Biol 4:202
Sola E, Marques da Silva I, Glassom D (2015) Spatio-temporal patterns of coral recruitment at Vamizi Island, Quirimbas Archipelago, Mozambique. Afr J Mar Sci 37:557–565
Soong K, Chen M, Chen C, Dai C, Fan T, Li J, Fan H (2003) Spatial and temporal variation of coral recruitment in Taiwan. Coral Reefs 22:224–228
Thomson DP, Babcock RC, Evans RD, Feng M and others (2021) Coral larval recruitment in north-western Australia predicted by regional and local conditions. Mar Environ Res 168:105318
Vermeij MJA, Smith JE, Smith CM, Vega Thurber R, Sandin SA (2009) Survival and settlement success of coral planulae: independent and synergistic effects of macroalgae and microbes. Oecologia 159:325–336
Wantiez L (2008) Les récifs coralliens de Nouvelle-Calédonie en 2006: état des lieux et réseau de suivi. Rev Ecol Terre Vie 63:117–132
Wantiez L, Chateau O, Le Mouellic S (2006) Initial and mid-term impacts of cyclone Erica on coral reef fish communities and habitat in the South Lagoon Marine Park of New Caledonia. J Mar Biol Assoc UK 86:1229–1236
Warner RR, Chesson PL (1985) Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. Am Nat 125:769–787
Whitman TN, Negri AP, Bourne DG, Randall CJ (2020) Settlement of larvae from four families of corals in response to a crustose coralline alga and its biochemical morphogens. Sci Rep 10:16397
Witman JD, Genovese SJ, Bruno JF, McLaughlin JW, Pavlin BI (2003) Massive prey recruitment and the control of rocky subtidal communities on large spatial scales. Ecol Monogr 73:441
Woodhead AJ, Hicks CC, Norström AV, Williams GJ, Graham NAJ (2019) Coral reef ecosystem services in the Anthropocene. Funct Ecol 33:1023–1034

Editorial responsibility: Peter Edmunds, Northridge, California, USA
Reviewed by: 3 anonymous referees

Submitted: November 9, 2021
Accepted: May 2, 2022
Proofs received from author(s): June 24, 2022