FEATURE ARTICLE

Global biogeography of coral recruitment: tropical decline and subtropical increase

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ABSTRACT: Despite widespread climate-driven reductions of coral cover on tropical reefs, little attention has been paid to the possibility that changes in the geographic distribution of coral recruitment could facilitate beneficial responses to the changing climate through latitudinal range shifts. To address this possibility, we compiled a global database of normalized densities of coral recruits on settlement tiles (corals m^{-2}) deployed from 1974 to 2012, and used the data therein to test for latitudinal range shifts in the distribution of coral recruits. In total, 92 studies provided 1253 records of coral recruitment, with 77 % originating from settlement tiles immersed for 3–24 mo, herein defined as long-immersion tiles (LITs); the limited temporal and geographic coverage of data from short-immersion tiles (SITs; deployed for <3 mo) made them less suitable for the present purpose. The results from LITs show declines in coral recruitment, on a global scale (i.e. 82 % from 1974 to 2012) and throughout the tropics (85 % reduction at <20° latitude), and increases in the sub-tropics (78 % increase at >20° latitude). These trends indicate that a global decline in coral recruitment has occurred since 1974, and the persistent reduction in the densities of recruits in equatorial latitudes, coupled with increased densities in sub-tropical latitudes, suggests that coral recruitment may be shifting poleward.
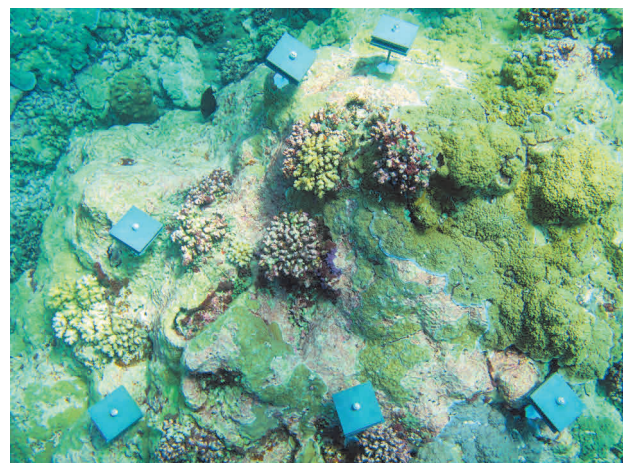
Coral settlement plates that are used to systematically enumerate the number of baby corals arriving on a reef in Palmyra Atoll National Wildlife Refuge.

Photo: Nichole Price

KEY WORDS: Coral settlement · Poleward range shift · Range extension · Equatorial retraction · Retrospective analyses · Global warming

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1. INTRODUCTION

Organismal thermal tolerance drives biogeographic variation in the distribution of plants and animals on land and in the sea (Somero 2002, 2005), and as the Earth is warming through climate change, these distributions are changing (Parmesan & Yohe 2003, Pinsky et al. 2013). Range shifts are one example of such changes, and they occur through persistent extensions of organismal range concomitant with contractions within historical range limits. In marine systems, range shifts typically are detected through the arrival of novel organisms to previously unoccupied areas, and declines in their physiological performance within the original distribution boundaries (Bates et al. 2014). Latitudinal or elevational range shifts have allowed many mobile terrestrial and marine organisms to escape increasing temperatures associated with global warming (Sorte et al. 2010, Chen et al. 2011, Beaugrand 2015), but for sessile marine organisms such as corals and sponges, temperature-mediated changes in distribution are more difficult to detect. These difficulties arise from the lag in time between the dispersion of larval stages and the time necessary for them to grow to adults, and the high likelihood that temporal trends in distribution are expressed over regional scales (i.e. 200–4000 km; sensu Mittelbach et al. 2001, Wernberg et al. 2011) instead of the local scale on which most research operates.

Tropical coral reefs are subject to a wide variety of disturbances of natural and anthropogenic origin, but one of the most immediate threats is seawater warming, which can drive high coral mortality through bleaching (e.g. Glynn 1993, Lesser 2004, 2011, Gilmour et al. 2013, Hughes et al. 2017, 2018). Decades ago, coral populations usually recovered from episodic catastrophic events (Connell 1997, Connell et al. 1997, Pearson 1981), but recently, it has become clear that coral communities on many reefs appear to have lost the capacity to recover following mass mortality events (Hughes et al. 2018). For reefs that do recover from major disturbances, a critical factor supporting recovery is the capacity for high coral recruitment supported by larvae produced through sexual reproduction (Bramanti & Edmunds 2016, Mumby et al. 2016). Sexually-produced larvae are also the only means by which corals can re-establish where adult populations have been driven to local extirpation, or perhaps become established in novel biogeographic locations where historically they have not existed (i.e. range extensions; Ritson-Williams et al. 2009). Potential examples of such range extensions include the appearance of juvenile colonies of *Acropora* corals along the eastern coast of Florida (Precht & Aronson 2004) and the appearance of colonies representing several coral species along the eastern coast of Japan (Yamano et al. 2011). While an extensive poleward range shift of tropical corals is likely to be limited by the underwater availability of light, particularly during winter months (Muir et al. 2015), even a modest latitudinal range shift could provide an ecologically meaningful refuge against adverse conditions likely to occur in tropical seas (van Hooidonk et al. 2014).

Assuming a poleward shift of the latitudinal range of physical environmental conditions favouring coral settlement and growth, early signs of range shifts in the distribution of tropical corals could be revealed by at least 2 trends. First, the fecundity of corals in tropical regions would likely be depressed as the adult colonies decline in abundance, which ultimately would result in 'recruitment failure' (sensu Hughes & Tanner 2000). Second, viable coral recruits would begin to appear poleward of historical range limits in tropical regions (i.e. a 'range shift', sensu Sunday et al. 2015). These 2 possibilities are of central importance to understanding the response of coral communities to climate change, but testing for evidence supporting these possibilities requires information on coral recruitment extending over large spatio-temporal scales. To date, such analyses have not been conducted for scleractinian corals.

The objective of the present analysis was to exploit available data to test the hypotheses that the abundance of coral recruits has (1) changed over time, and (2) extended poleward relative to historic distributions. Achieving this objective was made difficult by the high variability in the number of coral recruits observed at almost every scale of investigation (Fisk & Harriott 1990, Gleason 1996, Dunstan & Johnson 1998), and a loose definition in historical studies of the size of a coral that constitutes a 'recruit'. We sought to overcome these difficulties by using as much of the data available in published and unpublished sources as possible, and by rigorously defining recruits as follows: corals that are a few-months-to-a-year old and quantified using settlement tiles (Mundy 2000, Ritson-Williams et al. 2009).

2. METHODS

2.1. General overview

Using data compiled from studies in which coral settlement tiles had been immersed for similar durations in shallow reef habitats, we first tested for

geographic patterns of temporal variations in recruitment. This test required consideration of the immersion time of tiles, which allows studies to be categorized as using short-immersion tiles (SITs, underwater for <3 mo) or long immersion tiles (LITs, underwater for 3–24 mo). SITs were not widely used by the research community until synchronized mass spawning of corals was described in the early 1980s (Harrison et al. 1984). Thereafter, SITs were used extensively to focus on the short period when spawning corals release their gametes; LITs have remained common sampling tools in many locations, particularly the tropical Atlantic. Many corals in the tropical Atlantic are brooders that release larvae over protracted periods (Richmond & Hunter 1990), and LITs are thus well suited for detecting the coral recruitment signal in this region. We therefore included a systematic comparison of results obtained from SITs and LITs deployed at varying times and locations between 1974 and 2012. Second, we tested for variation in the density of coral recruitment from 1974 to 2012 as a function of latitude for shallow-water scleractinian corals.

Coral recruitment over the last 40 yr has mostly been quantified using settlement tiles (Ritson-Williams et al. 2009). Following a period of immersion, the numbers of coral recruits (typically ≤1 cm diameter) settled on the tiles are counted under magnification, and are usually reported as density (i.e. number of recruits per area or tile) for each deployment. We define immersion time as the time the tiles could be accumulating corals at the study site, after any preconditioning period, if reported. Mean recruit density by site is used in the present study (number of recruits m^{-2}), where site refers to the location (typically an area covering ~100s of m^2 of reef) in which tiles were deployed. Our analyses are based on densities of recruits as described in the original studies, but they are normalized to 1 m^2 based on proportional scaling of the area of each tile in order to create a measure of recruitment density expressed on a common scale to facilitate a global synthesis. Inherent in this approach is the assumption that recruits are uniformly distributed across the surfaces of individual tiles, which probably is violated by edge effects whereby recruits tend to be close to tile edges rather than close to the center. The bias introduced by this effect will depend on the size of the tile and the orientation of the tile, but with small tiles, it is likely to result in an overestimate of densities when scaled to meter-squared areas.

Results were compiled from peer-reviewed literature (n = 98 studies) that were identified through searches on the Web of Science and Google Scholar, and from 24 unpublished studies supplied by the present authors and professional referrals. This process provided data from 185 sites scattered between 31.5°S and 32.8° N, and included 1253 records of coral recruitment (Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m621p001_suppl1.xls; Fig. S1 in Supplement 2 at www.int-res.com/articles/suppl/m621p001_supp2.pdf). These studies are not intended to provide an exhaustive summary of pertinent research, but they were instead intended to provide a large data set, from an extensive biogeographic range of locations, that was suitable for a statistically rigorous test of our central hypothesis. Because the compiled studies resolved coral recruits with varying (and inconsistent) taxonomic resolution, recruitment was analysed with the coarsest taxonomic resolution (i.e. pooled among taxa as Scleractinia). For similar reasons, tiles in the global analysis were not distinguished by deployment orientation on the bottom, tile texture, or processing method, but the analysis was restricted to tiles deployed in water <30 m depth on fringing reefs, barrier reefs, or in lagoons. Although 6% of the records did not report depth of tile deployments, the remaining records (n = 1176 records) described tile deployment by depth, with 74% at <10 m depth, 21% at 10–20 m depth, and 4% at >20 m depth. Only the latter 4% could have had meaningful influence on recruitment patterns as a function of depth.

Settlement tiles in the compiled studies varied in size and material, but ~75% (n = 906 records) were either 0.01 m^2 (10 × 10 cm) or 0.025 m^2 (15 × 15 cm) in area, <10% (n = 129 records) were >0.045 m^2 in area, and the largest (n = 15 records) were 1.5 m^2 in area; the aforementioned areas represent a single side of the tile. Most tiles were made of unglazed terracotta or other ceramic (72%), roughened plastic (either polyvinyl chloride or acrylic, 14%), or calcium carbonate rock (6%). Tile material influences the density of coral recruits recorded upon them (Harriott & Fisk 1987), as can the treatment of tiles after collection. A common practice in settlement tile studies is to rinse freshly collected tiles in fresh water, bleach them in a dilute solution of domestic bleach, and dry them before viewing under a microscope to reduce the likelihood that recruits are obscured. In some studies tiles are scored alive and then returned to seawater (i.e. immersion is repeated) for longitudinal survival studies, or in some cases freshly collected tiles are fixed (e.g. in formalin) for further analyses. The majority of tiles in our database were processed either following bleaching and drying or following fixation (n = 838 records, 67.7%) while only 15% (n = 189 records)

were scored 'live'. For the remaining 229 records (18.2%), no post-processing methods are described, but given the ubiquity of the bleaching and drying practice, it is likely this approach was taken.

A principal component analysis with depth, tile size and type (i.e. material from which they are made), post-processing method, duration of deployment, and latitude as loading variables showed no statistically significant covariance among explanatory variables ($r \leq 0.5$). The first and second principal components accounted for only 32 and 21% of the total variance, respectively (Fig. S2), indicating that variation in recruit density on these settlement tiles was not consistently 'explained' by any one of the variables describing how the tiles were deployed and processed.

Wherever possible, densities of recruits on the tiles were normalized to all surfaces exposed to the seawater and censused (i.e. potentially top + bottom + sides), unless tiles were directly attached to the seafloor, or the study reported values for one side of the tile alone. Where methods were insufficiently described to evaluate how the tile areas were determined, it was assumed for normalization purposes that the settlement area on the tiles was reported as the combined area of all surfaces.

To evaluate the role of geography in determining the density of recruits, locations of tile deployments were categorized within the Marine Ecoregions of the World (MEOW) framework (Spalding et al. 2007), which is based on biotic and abiotic features (e.g. endemism, seawater temperature, salinity) defining regional boundaries stratified by depth (<30 m depth) and distance apart (Table S2 in Supplement 2). Adapting this framework, 'Ocean basins' represent the largest spatial units (~1 000 000s of km²; Indo-Pacific versus Western Atlantic), 'Realms' represent subdivisions of ocean basins that are located in coastal areas (~100 000s km²), 'Provinces' represent subdivisions of realms (~10 000s of km²), 'Precincts' represent subdivisions of provinces that meet a suite of tile deployment criteria (~100s of km², and were applied only to a small subset of site locations), and 'Sites' are areas of 100s of m² where researchers deployed settlement tiles. For this study, we defined 2 ocean basins and 22 biogeographic provinces. Frequency distributions of the studies (number of studies × number of visits) across provinces were used to investigate inequalities in deployments of settlement tiles throughout the global sampling area (Figs. 1 & S1). To normalize sampling effort to reef area available for coral recruitment, the number of studies and visits (or records) was also divided by the aggregate area of coral reef benthos in each ocean basin (in units of

1000 km²), using spatial estimates from Spalding et al. (2007).

To explore limitations in estimates of recruitment using SITs and LITs, and to test for spatio-temporal trends in coral recruitment, we employed unweighted Generalized Additive Models (GAMs) with penalized regression splines (estimated by restricted maximum likelihood; Wood 2006) that assumed a Tweedie distribution (and exponential dispersion model; Arcuti et al. 2013). Densities of organisms on settlement tiles typically are zero-inflated (i.e. the probability of getting null values is higher than expected under a normal distribution), and generalized linear models using Poisson or negative binomial link functions are over-dispersed. The Tweedie distribution model, with a linear exponential parameter and a dispersion parameter (Arcuti et al. 2013), addressed the over-dispersion issue of zero-inflated data. Tweedie distributions with an index parameter (P) having a value defined by $1 \leq P \leq 2$ (i.e. compound Poisson–gamma distributions) are best suited to model zero-inflated data (Arcuti et al. 2013), and in the present study were fitted using maximum likelihood estimates in the R package 'Tweedie' (Dunn & Smyth 2005, 2008, Dunn 2017). GAMs were used to allow for unknown smoothing functions of observed explanatory variables in the linear predictor (i.e. geographic region or immersion time). Selections of predictors and their inclusion in the final model were based on the total deviance explained in coral recruitment as evaluated by the Akaike information criterion (AIC) (Akaike 1974) and the Bayesian information criterion (BIC) (Schwarz 1978). To determine if trends over time represented significant increases or decreases in recruitment, 95% confidence intervals were calculated for the predicted fits of the smoothing term.

2.2. Comparison of SITs and LITs

We tested for limitations in the data arising from immersion time (i.e. SITs, n = 279; versus LITs, n = 974), and this analysis included a contrast of geographic locations of tile deployment (which varied greatly across the compiled data). Analyses were conducted by first summarizing the data using descriptive statistics to compare results obtained from SITs with those from LITs. To examine the influence of immersion time on coral recruit density more explicitly, a GAM was used to describe the relationship between immersion time (the smoothing factor) and recruit density on tiles for all compiled data (n = 1253). To further define the relationship between recruit density and immer-
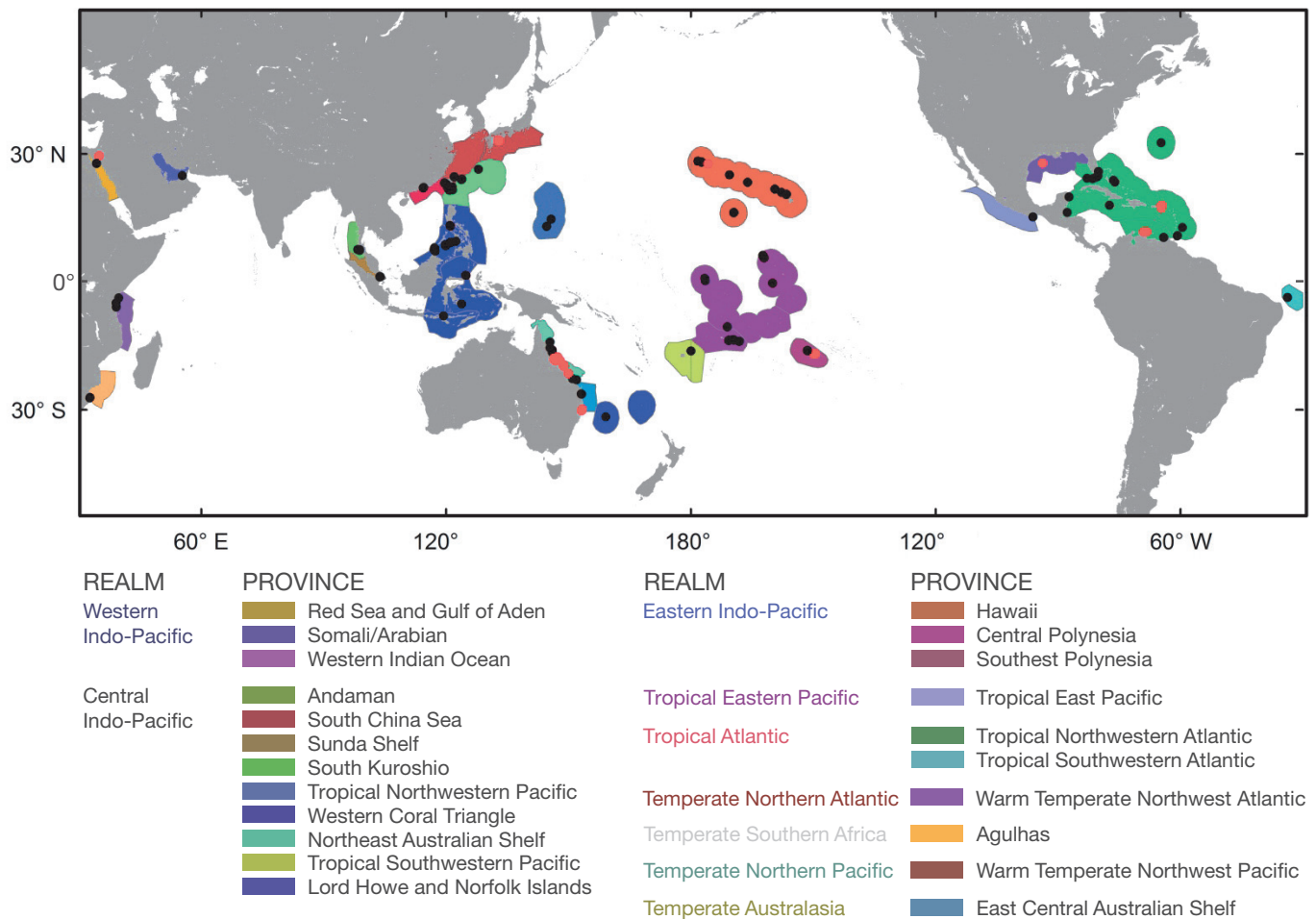
REALM

Western Indo-Pacific

Central Indo-Pacific

Eastern Indo-Pacific

Tropical Eastern Pacific

Tropical Atlantic

Temperate Northern Atlantic

Temperate Southern Africa

Temperate Northern Pacific

Temperate Australasia

PROVINCE

Red Sea and Gulf of Aden
Somali/Arabian
Western Indian Ocean

Andaman
South China Sea
Sunda Shelf
South Kuroshio
Tropical Northwestern Pacific
Western Coral Triangle
Northeast Australian Shelf
Tropical Southwestern Pacific
Lord Howe and Norfolk Islands

Hawaii
Central Polynesia
Southest Polynesia
Tropical East Pacific
Tropical Northwestern Atlantic
Tropical Southwestern Atlantic
Warm Temperate Northwest Atlantic
Agulhas
Warm Temperate Northwest Pacific
East Central Australian Shelf

Fig. 1. Coral recruitment study sites (n = 185). Shaded shapes of various colors (see key) indicate Marine Ecosystems of the World (MEOW) marine provinces (Table S2 in Supplement 2). Within the colored shaded shapes, red dots identify the 12 locations (clusters of sites <0.25° apart where long-immersion tiles were deployed over at least 4 yr) used for analyses of changes in recruitment over time; black dots identify all other study sites. See also Fig. S1 in Supplement 2; raw data in Table S1 in Supplement 1

sion time, we selected a subset of studies meeting more restrictive criteria: only studies in which both SITs and LITs were deployed at the same sites using the same methods (tile material, orientation, depth, habitat, deployment date, etc.) were included. These strict criteria were met by 26 sites, distributed across 5 of the 9 geographic realms, and 10 of the 22 geographic provinces. Least squares linear regressions between mean recruit densities (y) and immersion time (x) for SITs and LITs were calculated, with each datum representing mean coral recruit density by site for SITs (mean ± SE immersion time of 2.2 ± 0.1 mo) and LITs (mean immersion time of 4.5 ± 0.3 mo). We considered using the linear relationships between recruit density and immersion times for SITs and LITs to standardize recruit densities by immersion time for the entire database, enabling inclusion of all records in subsequent analyses. This possibility was rejected

because the difference in immersion time between SITs and LITs for this subset of data was ~2.3 mo, making it unclear whether this relationship remained linear for larger differences in immersion time.

2.3. Temporal changes in densities of coral recruits

We addressed the central hypothesis of this study independently for the tropical Atlantic and Indo-Pacific. GAMs were used in which recruit density was a function of categorical linear predictors that included immersion time (i.e. SITs versus LITs) and Ocean basin (Indo-Pacific versus Western Atlantic). 'Year' was included in the full model as the continuous smoothing term, but was determined separately for SITs and LITs; all possible nested model combinations are listed in Table S3 in Supplement 2.

Many sites were sampled only once or infrequently, which created the possibility that stochastic spatio-temporal variation in recruitment, or under-representation of a province within a realm, could mask temporal trends in recruit density, or generate spurious results within an ocean basin. To address these limitations, we analyzed temporal trends in coral recruitment within select biogeographic areas ('precincts'), and using a subset of results from LITs meeting the following criteria. As it was uncommon for sites to be consistently sampled for many years, temporal variations were examined using 'precincts' as statistical replicates (Table S2). Precincts were defined as areas of reef bounded by ± 0.25° latitude/longitude (i.e. ~28 × 28 km) within a province, where tiles had been repeatedly deployed using consistent methodologies to support analyses of temporal trends (i.e. ≥10 yr). To be considered in this analysis, a precinct had to include ≥1 site with at least 4 independent tile deployments at different times; the site needed to have been sampled in at least 4 separate years. In cases when the same researcher(s) had conducted the sequential studies, methodology was typically consistent among deployments. While different precincts might have been sampled with tiles made of different materials, or deployed at varying depths or for dissimilar immersion times, the trends within each precinct were not influenced by these factors and thus trends across precincts could be compared directly.

We used GAMs to examine temporal variation in recruitment within 12 precincts, which represented 497 records spanning ~60° latitude from 32.8° N (Shikoku, Japan) to 30.2° S (Solitary Islands, Australia). In these GAMs, 'precinct' was designated as a linear predictor dependent on 'year' as a smoothing factor (model structure was determined a priori). We took the annual smoothing term estimates for each precinct as the best estimates of the rate of change in coral recruitment over time. The linear trend in estimates of this term over the study period provided the mean annual change in recruitment within each precinct.

2.4. Latitudinal changes in coral recruitment

We used 2 approaches to determine biogeographic trends among precincts in the temporal trends for coral recruitment. Firstly, we used parametric simple least squares regressions in which absolute latitude was the continuous predictor, and the annual trends for coral recruitment from the smoothing coefficients in the GAMs (Table S4 in Supplement 2) were the response variable. We used this regression analysis to test for relationships between latitude and changes in recruitment over time (across precincts). The distribution of the smoothing term estimates from GAMs was tested for normality using q-q plots and Shapiro-Wilks test prior to parametric analysis. Because not all locations were evenly sampled (e.g. n = 5 for Bonaire, versus n = 212 in Eilat and Egypt; Table S4), the regression model was weighted by sample size. Secondly, we conducted a contingency table analysis (Fisher's exact test) to further elucidate consistency in spatial patterns — particularly in positive and negative trends — across precincts at binned latitudes.

To determine temporal trends in global coral recruitment (not just within and across precincts) with latitude, the density of coral recruits on LITs (n = 965 records) was compared among latitudes using GAMs. Firstly, we divided all LIT records of coral recruitment into 2 latitudinal bins describing the location of the sites at which the tiles had been deployed: (1) 20° N to 20° S, and (2) 20° to 35° N and S. The 20° latitude (N and S) was the median latitude (mean = 19.6°) of all studies in which LITs had been used, and the bins approximated tropical and subtropical regions, respectively. While the Tropics of Cancer and Capricorn (23.0°) are standard biological boundaries between tropical and subtropical regions, binning the available data above and below 23° latitude would have resulted in an uneven distribution of the binned data over space and time. The 20° latitude criterion was data-driven and resulted in the 2 latitudinal zones yielding studies spanning similar periods (i.e. 1970s to 2012; Fig. 2A) with similar replication (n = 511 for <20°, and n = 454 for ≥20°). Secondly, we applied GAMs to recruitment densities using penalized regression splines and Tweedie distributions to test for latitudinal variation over time. 'Year' was included in the full model as the smoothing term, and 'ocean basin' and 'latitude' (<20° or ≥20°) were the linear predictors, with the smoothing factor estimated separately for each 'latitude' category (Table S5 in Supplement 2). Mean coral recruit densities on LITs in the 1980s to the 2000s above and below 20° latitude were compared using t-tests.

3. RESULTS

3.1. Comparison of coral recruitment on SITs and LITs

Studies of coral recruitment using settlement tiles have increased in frequency over the past 4 decades (Fig. S1). The coral recruitment studies compiled in

the present analysis were distributed among 22 marine provinces (Fig. 1), with most data from the Indo-Pacific (76% of studies, n = 98, and 88% of records, n = 1253 total records; Fig. S1C), but the proportion of reef area sampled (i.e. number of studies and number of records per 1000 km^2 of reef) was greater in the Western Atlantic (1.04 studies and 6.33 records per 1000 km^2) than the Indo-Pacific (0.04 studies and 2.03 records per 1000 km^2).

The mean immersion time of all the tiles (pooled among all studies) was 7.0 ± 0.2 mo (n = 1253), with some SITs immersed for as little as 2 wk, and some LITs for as much as 2 yr; the majority (77%) was immersed for ≥3 mo (i.e. they were LITs). Of the SITs, 49% (n = 136 out of 279) were immersed for 2 mo, and the mean immersion time was 1.9 ± 0.03 mo. Of the LITs, 16% (n = 153 out of 974) were immersed for 12 mo, and the mean immersion time was 8.5 ± 0.2 mo. LITs were deployed as early as 1974 and became common by 1980, and therefore provide the longest and most consistent record of ocean-wide coral recruitment (Fig. S3 in Supplement 2). SITs were first used in 1981, but did not become common (i.e. ≥5 studies yr^{-1}) until 1995 (Fig. S3).

The density of coral recruits declined non-linearly as a function of immersion time (Fig. 2, Table S3). Overall, recruitment was lower on LITs versus SITs (Figs. 2 & S2), although tiles with very short immersion times (~2 wk) have low recruit densities (Fig. 2B). However, there were also very few records of extremely short immersion times (for ~2 wk, n = 6), as reflected in the hashes along the x-axis of Fig. 2B. While the declining trend of recruit density against immersion time was not constant, it was consistently

negative (Fig. 2B). Where SITs and LITs were deployed concurrently with similar methodology, the density of recruits was positively correlated between methods (r = 0.96, df = 19, p < 0.001), and was ~67% lower on LITs than on SITs (Fig. 2C).
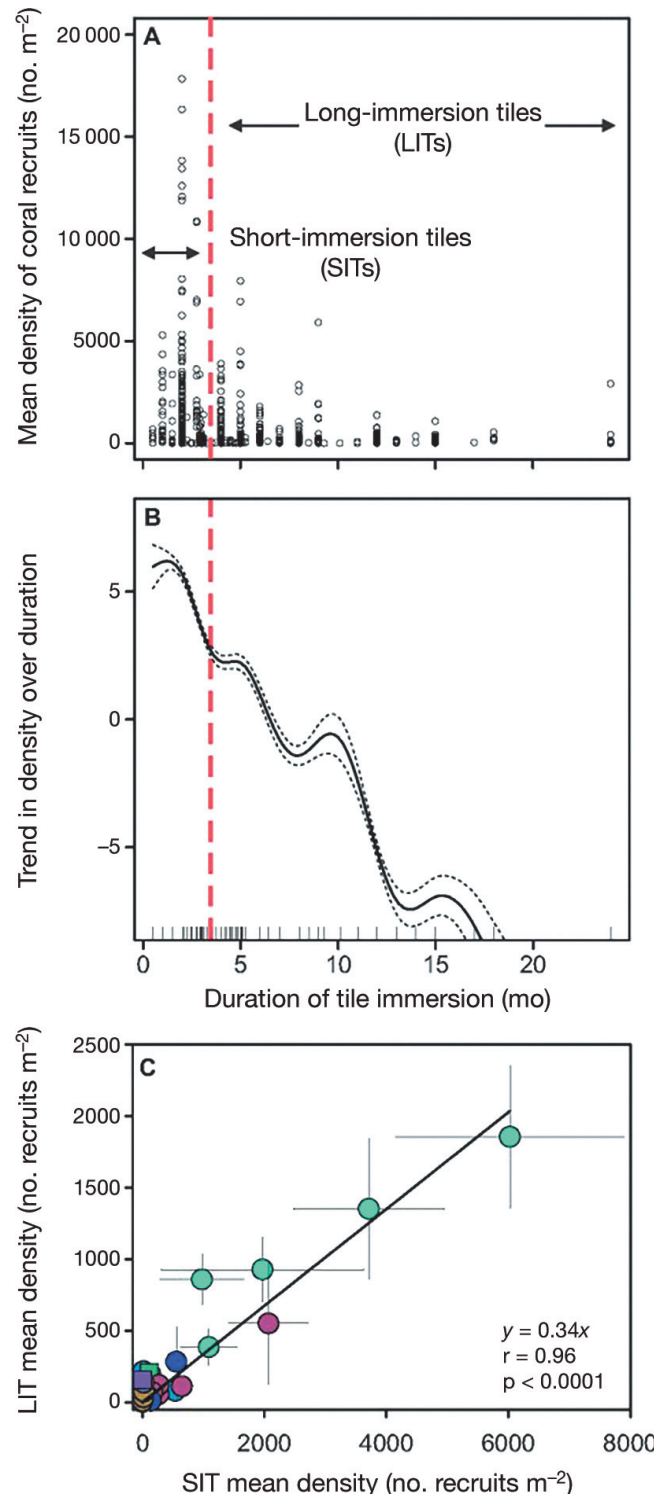

Fig. 2. Effects of tile immersion duration (SITs and LITs) on the density of coral recruits, and relationship between methodological approaches. (A) Recruit density (n = 1253) as a function of the duration of tile immersion. Dashed red lines (A,B): 3-mo cut-off for SITs versus LITs, based upon GAM analysis and sample size. (B) Results from GAM analysis indicating inflection points in the trend of decreasing coral density on tiles as a function of tile immersion duration. Black tick marks along x-axis: actual tile immersion durations. The y-values represent change in density over time: values >0 represent the rate of increase in the average numbers of recruits appearing on tiles from one year to the next; values <0 represent the mean rate of decrease. Approximate significance of smoothed duration term: edf = 8.81, residual df = 8.988, F = 718.6, p < 0.001; 20.4% deviance explained. (C) Results (means ± SE) from targeted correlation analysis of SITs vs. LITs at sites where the same methods were used in the same years (n = 26 sites); symbols color coded as in Fig. 1, by MEOW provinces (Table S2 in Supplement 2)

3.2. Temporal changes in densities of coral recruits

The GAM selected using AIC and BIC indicated that the best fit was for the full model with immersion time and ocean basin as interacting linear factors, and the smoothing term estimated separately for each immersion category (Table S3). For SITs, temporal trends in recruitment could not be reliably assessed in the western North Atlantic due to the small number of recruits on tiles, and the small number of tiles deployed. Temporal trends in recruitment from SITs in the Indo-Pacific were not consistent over time (Fig. 3A). Overall, few investigations used SITs (n = 26 studies, in 11 countries), and the deployments covered only a few provinces and represented 7 of the 9 realms (i.e. there were no SITs from the temperate Southern Africa or tropical Atlantic). Thus, the few studies using SITs could not support robust tests of temporal variation in the early stages (<3 mo) of recruitment, as shown by the wide confidence intervals for the fits of recruit density against year prior to 1990 (Fig. 3A,C,E). After 1990, there was no consistent temporal trend in the density of coral recruits based on SITs (Fig. 3A,C,E).

Based on LITs, there has been an overall global decline in recruitment spanning 3 decades, equivalent to a reduction of 2–3 coral recruits m^{-2} yr^{-1} (Fig. 3F). This decline resulted in an 82% reduction in global mean density of coral recruits from 785 ± 61 recruits m^{-2} on average in the 1980s to 137 ± 4 recruits m^{-2} on average in the 2000s. The rate of decline of coral recruitment on LITs significantly differed between ocean basins and decades (Table S3). Between 1980 and 1990, densities of coral recruits increased consistently each year in the Indo-Pacific (positive partial residuals significantly greater than zero, Fig. 3B), but stayed relatively constant in the western North Atlantic (partial residuals not different from zero, Fig. 3D). By the late 1990s, the density of coral recruits was declining globally, but particularly steeply in the Indo-Pacific (Fig. 3B), and had not recovered by 2012 (Figs. 3F & S2). The decline was about 3-fold greater between 2005 and 2010 in the Indo-Pacific (Fig. 3B) compared to the western North Atlantic (Fig. 3D).

3.3. Latitudinal changes in coral recruitment

Across all geographic precincts, the mean annual rate of change in coral recruitment (determined by fitting a linear trend to the smoothing terms and weighted by sample size within a precinct) ranged from -0.364 ± 0.14 corals m^{-2} yr^{-1} to $+0.578 \pm 0.116$ corals m^{-2} yr^{-1} within the precincts of Curaçao (12° N) and Shikoku (33° N), respectively (Table S4). These rates of change correspond to a significant decline in density of 14.6 coral recruits m^{-2} over 40 yr (Curaçao), and to a significant increase of 23.1 recruits m^{-2} (Shikoku) at the most equatorial and poleward precincts, respectively. The rates of change in density of coral recruits within precincts varied over time and differed across the 12 precincts and across and within 8 provinces (Tables S4 & S5). For example, within the northeast Australian Shelf province, the mean rate of change in coral recruitment predicted by the GAM ranged from -0.122 ± 0.034 corals m^{-2} yr^{-1} to $+0.174 \pm 0.001$ corals m^{-2} yr^{-1} in the Wet Tropics (17° S) and the Mackay-Whitsunday (20° S) precincts, respectively (Fig. 4; Table S4).

The trends for variation in coral recruitment over several decades changed from a negative to a positive slope at ~20° latitude (Fig. 4). The density of coral recruits on LITs increased with distance from the equator, north or south ($r^2 = 0.82$, $F_{1,11} = 45.70$, p < 0.001, $y = 0.36x - 7.42$ where y = density of recruits, and x = distance from equator), and was similar in the Indo-Pacific and Western Atlantic Ocean basins (Fig. 4A). Parameter estimates for the linear relationship could not be generated for the Western Atlantic could due to small sample size (n = 4 precincts, 2 realms, and 2 provinces; see Table S4), but the relationship followed the same trend across latitudes as observed in the Indo-Pacific. The parameter estimates of the least square regression were statistically indistinguishable for the full dataset or for the Indo-Pacific alone (slope = 0.36 ± 0.05 and 0.33 ± 0.07 corals m^{-2} $decade^{-1}$ [degree latitude]$^{-1}$). The largest data sets available for precincts offering the most influence to the regression also covered the longer periods of study — Eilat (1974–2004; n = 212) at high latitudes and Tahiti (1990–2014; n = 100) nearer the equator (Fig. 4B).

Recruit densities on tiles generally decreased over time at low latitudes towards the equator, but increased at high latitudes north or south, and these patterns were similar in the Indo-Pacific and Western Atlantic (Fig. 5). Among the 12 precincts, mean annual recruitment significantly declined in 4 of 6 locations at <20° latitude, and significantly increased at 5 of the 6 other locations at >20° latitude (Table S4); for those precincts where trends were not significantly different from zero, the trend remained upheld. The sign of the temporal change in mean annual recruitment was dependent on latitude (contingency table analysis; Fisher's exact test, p = 0.002).
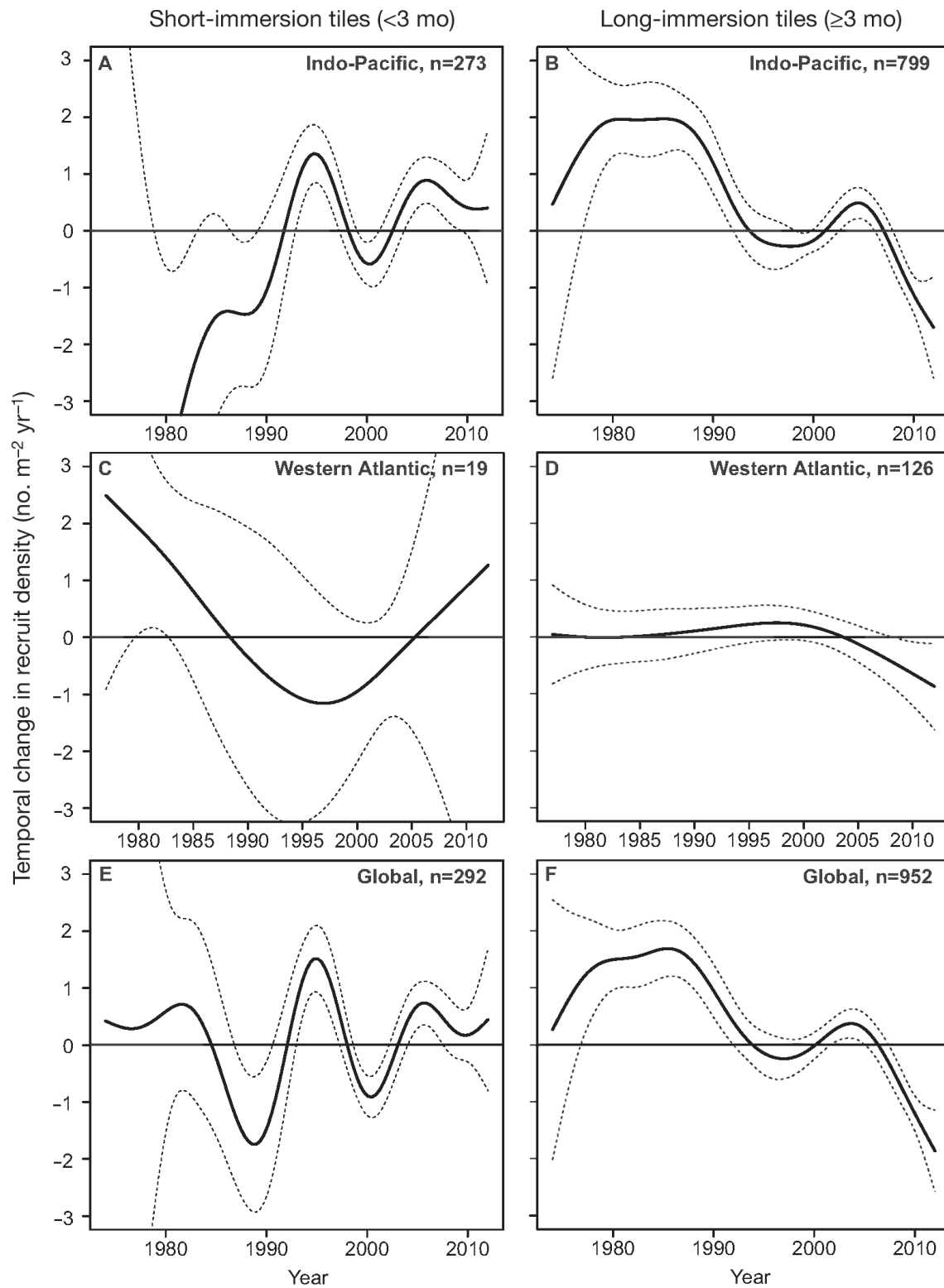
Fig. 3. Results of GAM analyses supporting temporal trends in coral densities for SITs and LITs. The *y*-values represent change in density over time: values >0 represent the rate of increase in the average numbers of recruits appearing on tiles from one year to the next; values <0 represent the mean rate of decrease. (A,B) Indo-Pacific Ocean. (C,D) Western Atlantic Ocean. (E,F) Global Ocean. Data presented are year-to-year changes in recruit densities (solid black lines); dashed lines are the 95% confidence intervals (results in Table S3 in Supplement 2)
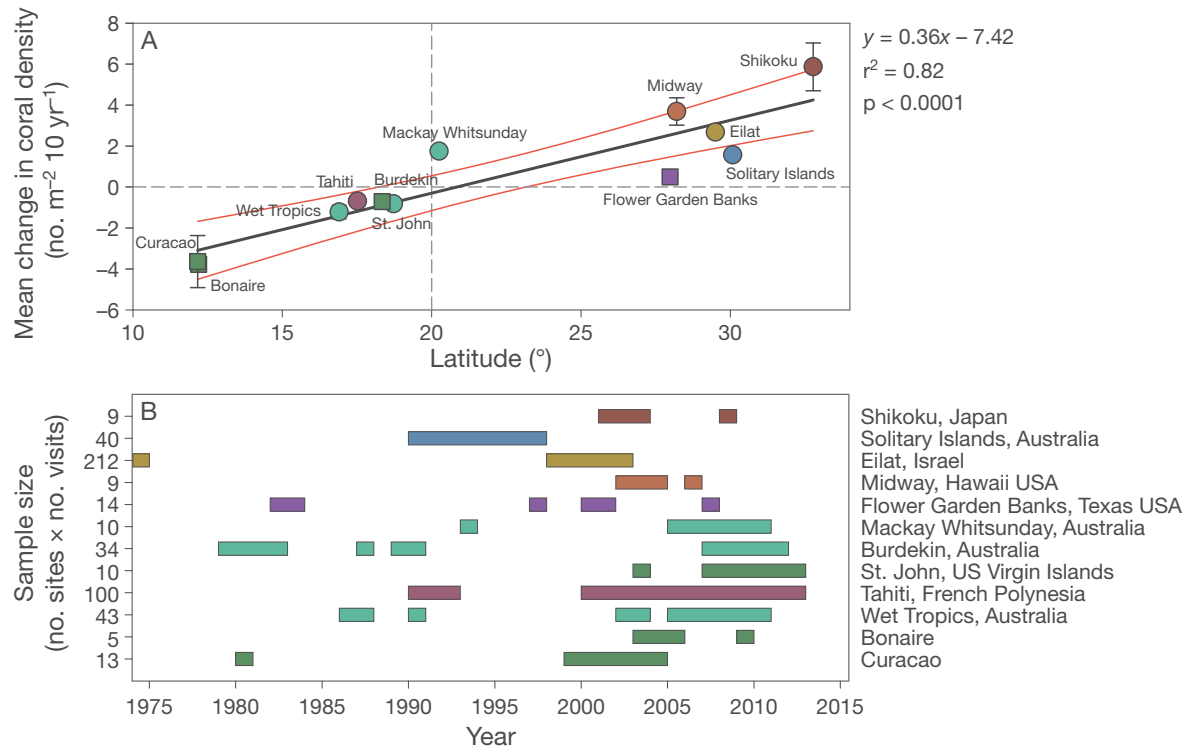
Fig. 4. Trends of recruit density on LITs deployed at locations visited more than once. (A) Annual mean (±SE) rates of change in coral recruitment (corresponding to the slope estimates from GAM in Table S4 in Supplement 2; negative values: annual decline; positive values: annual increase) as a function of the absolute latitude (i.e. north or south) at frequently revisited locations in the Indo-Pacific and Western Atlantic (results in Table S4). Black line: least-square linear regression; red lines: 95% confidence intervals on the regression; symbol shape: ocean basin (circles: Indo-Pacific; squares; Western Atlantic); symbol color: MEOW provinces (as in Fig. S1). Dashed lines: bins used for contingency table analysis (above and below 20° latitude and positive versus negative change in coral density over time). (B) Gantt chart of timing and sample size (primary y-axis) for repeat tile deployments at revisited locations (secondary y-axis) from 1974 to 2012
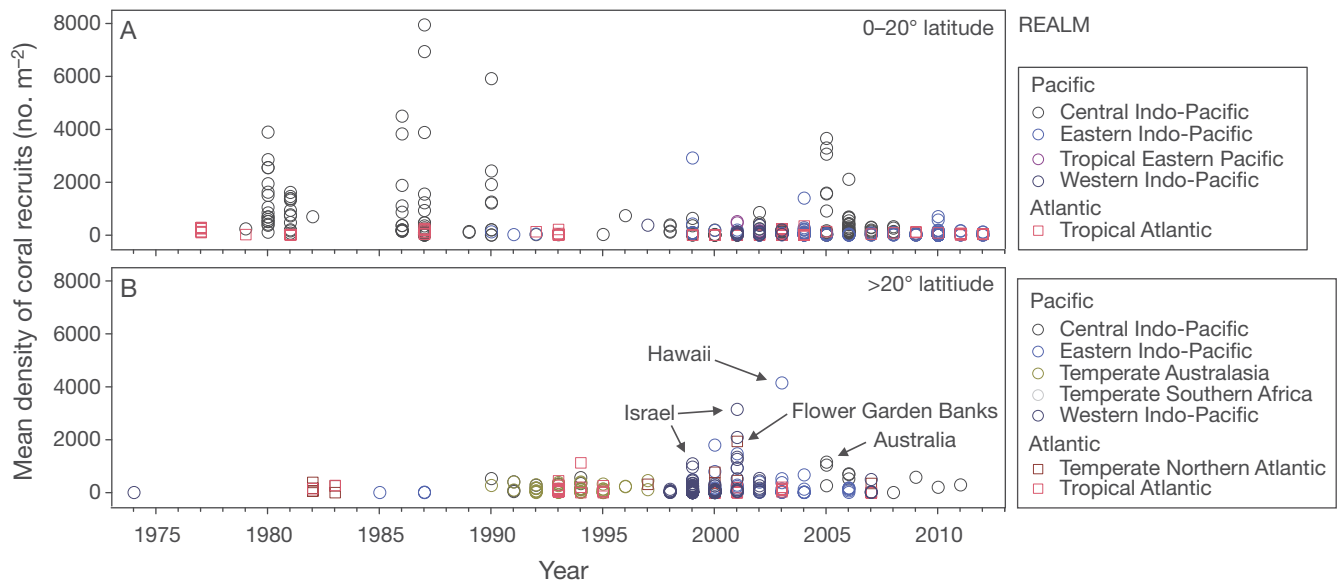

Fig. 5. Mean density of coral recruits on LITs as a function of year of deployment from 1974 to 2012, for 2 latitudinal zones. (A) Tropical (<20° latitude, north or south). (B) Subtropical (>20° latitude, north or south). Symbols color-coded by MEOW realms

Temporal trends in coral recruitment using both precinct analyses and the entire database significantly depended upon latitude (Tables S4 & S5), but were independent of ocean basin (Tables S4 & S5). At <20° latitude, high densities of recruits (>1000 corals m^{-2}) at any study site were routinely found in the central and eastern Indo-Pacific Ocean prior to the 1980s, but subsequently these densities became rare (Fig. 5A). In contrast, high-density recruitment events increased in frequency at higher latitudes in the same realms (Fig. 5B), and at 20−35° latitude, such events did not appear until after 2000 (Fig. 5B). Even then, the greatest densities of recruits recorded at >20° latitude

were only half the highest densities recorded at <20° latitude prior to 1990 (i.e. ~3000 vs. ~6000 corals m^{-2}, respectively). But relatively high densities of coral recruits were recorded in 4 realms >20° latitude (Central, Eastern, and Western Indo-Pacific, Temperate North Atlantic) after 2000 (Fig. 5B).

From the entire database, densities of recruits in the tropics (<20° latitude, north or south) significantly decreased after the mid-1980s (Fig. 6A,C), with mean (± SE) densities decreasing 85% from 757 ± 26 corals m^{-2} to 115 ± 4 corals m^{-2} in the 1970s−1980s and the 2000s, respectively (mean ± SE, n = 511, t = 4.71, p < 0.0001). Around 2000, densities of recruits on LITs in
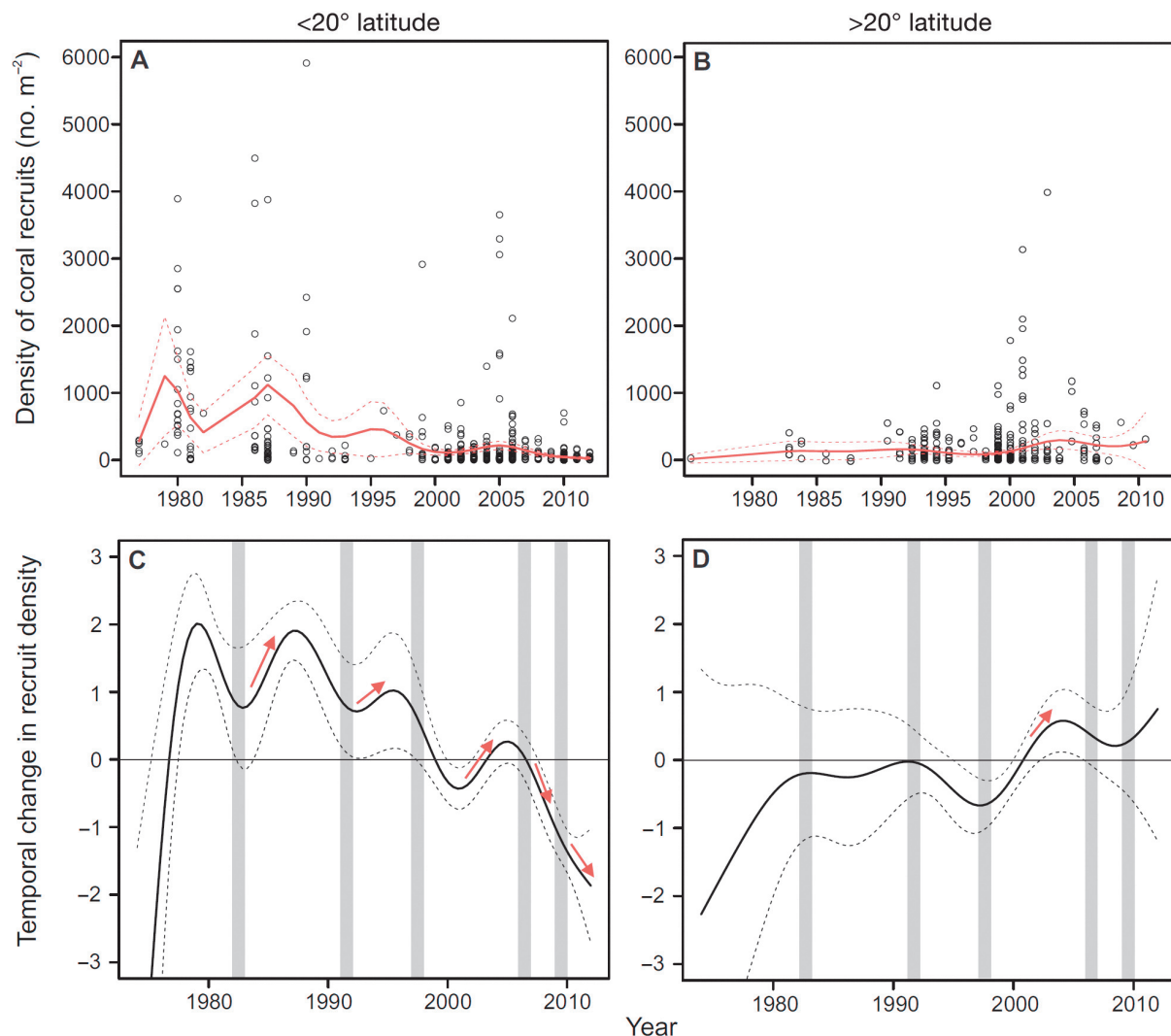

Fig. 6. Density of coral recruits on LITs at latitudes <20° and >20° (north and south) as a function of sampling year. (A,B) Observations (n = 511 and 454, respectively, shown as open circles; darker appearing symbols are caused by stacking of points), and predictions of GAM analyses of global trends (solid lines), showing a long-term decrease at <20° and increase at >20°. (C,D) Model smoothing curves of temporal changes (solid lines, GAM analyses). The y-values represent the change in density over time: values >0 represent the rate of increase in the average numbers of recruits appearing on tiles from one year to the next; values <0 represent the mean rate of decrease. Red arrows: significant change in rate. Vertical shading: El Niño years. All panels: dashed lines are 95% confidence intervals; results in Table S5 in Supplement 2

equatorial regions were significantly lower than ex-pected based on the negative partial residuals and respective confidence intervals (Fig. 6C). Episodes of decline in recruit densities were followed by increases in recruit densities in the tropics in ~1983, 1991 and 1998, whereas the declines that occurred more recently in 2007 were not (Fig. 6C). Although densities of recruits near the equator temporarily increased in the late 1980s and mid 1990s (Fig. 6A), they did not recover to historic mean high values (i.e. 827 ± 83 corals m^{-2} in the 1980s), and by the late 2000s densities were again declining (Fig. 6C). Sharp declines in coral recruitment in the tropics in 1983, 1998, and 2010 roughly corresponded with El Niño events (Fig. 6C). In contrast to the tropics, mean densities of coral recruits in subtropical regions (20–35° latitude) significantly increased over time (Fig. 6B,D) nearly doubling from 137 ± 3 corals m^{-2} in the 1970s–1980s, to 244 ± 5 corals m^{-2} in the 2000s (n = 462, t = 2.48, p = 0.014). The change in densities of recruits between 20° and 35° latitude was negligible over time, at least until ~2004, when the density of recruits significantly increased (based on confidence intervals not containing zero, Fig. 6B,D).

4. DISCUSSION

Settlement tiles are one of the oldest experimental techniques employed by coral ecologists (e.g. Mackie 1976, Birkeland 1977), but despite their long history of use, there has been little attempt to integrate results across multiple decades to test for long-term geographic trends (but see Smith 1992, Glassom et al. 2004). This is surprising, since putative changes in coral recruitment, particularly over regional scales, is a parsimonious hypothesis (Hughes & Tanner 2000) to account for the persistent global declines in coral cover that have taken place over the last decades (Gardner et al. 2003, Bruno & Selig 2007, Jackson et al. 2014). Additionally, this standardized methodology for assaying densities of coral recruits represents a statistically precise, but potentially inaccurate (i.e. settlement tiles provide relative estimates) source of evidence when observing the earliest stages of range shifts in marine species (Bates et al. 2014).

4.1. Changes in coral recruitment from 1974 to 2012

To estimate spatial and temporal patterns in the recruitment of corals to reef ecosystems, we compiled

results from studies in which settlement tiles had been deployed in varying configurations from as early as 1974. This analysis showed differences in results according to approaches (i.e. SITs versus LITs). There were more coral recruits on tiles deployed specifically to capture selected recruitment events (i.e. SITs) than on tiles deployed for longer periods (i.e. LITs), although the results from both methods are strongly related (Fig. 2C). The mortality of coral recruits during the first few months of settlement typically is very high (Vermeij 2006, Vermeij & Sandin 2008), and therefore densities of coral recruits on SITs are higher than those integrated naturally into adult populations over ecologically significant time scales. LITs, typically selected by investigators (Harrison et al. 1984, Hughes et al. 1999), allow researchers to capture the cumulative recruitment in corals that utilize different reproductive strategies, including those that spawn, usually annually ('spawners'), and corals that release offspring throughout a lengthy portion of the year ('brooders'). Some shallow coral reefs now are dominated by brooding corals (Edmunds 2018), as occurs throughout the tropical Western Atlantic. Considering regionally-specific trends in representation of life history strategy paired with the availability of robust and balanced global coral recruit density datasets, values of LITs are better suited for the objective of the present study. Hence, the tests for latitudinal variations in coral recruitment at the core of the present study provided the most unequivocal answer when using LITs (Figs. 3–6, Tables S2–S4). Results from LITs provided strong evidence of a global decline in coral recruitment since 1974, with a progressive decline with time at absolute latitudes <20°, and >20° (Figs. 4 & 5).

Our data show that pantropical coral recruitment declined rapidly (mean decline of 82%) from the 1980s to the 2000s, but more in the Indo-Pacific than the Western Atlantic (Fig. 3). Moreover, the decrease in recruitment at <20° latitude in the 2 oceans during the same time span (mean decrease of 85%; Fig. 4) is consistent with long-term reductions in coral cover that have occurred in equatorial and tropical waters since the 1980s (Gardner et al. 2003, De'ath et al. 2012, Jackson et al. 2014). Conversely, some regions in the subtropics have been experiencing increases in total live coral cover (Precht & Aronson 2004, Schleyer et al. 2008); likewise, there are subtropical regions where coral recruitment has either not changed or even slightly increased each decade from 1976 to 2012 (Fig. 4; example precincts: Flower Garden Banks, Solitary Islands, Mackay Whitsunday, Eilat, Midway, and Shikoku). At >20° latitudes in both

oceans, the density of coral recruits has increased from the 1980s to the 2000s (mean increase of 78 %). For example, after the 1990s, relatively high densities of coral recruits (~1000 to 3000 m^{-2} in 1994 and 1999, respectively) have been recorded on LITs at the Flower Garden Banks (Northern Gulf of Mexico, 28° N) and in Hawaii (Hawaii, 22° N), and after 2000, on reefs in Australia (Southern Great Barrier Reef, 20° S) and Egypt (Northern Red Sea, 28° N) (Fig. 5). Together, these latitude-dependent patterns in density of coral recruits are striking when the results are pooled among studies and locations (Fig. 6). The temporal trends in recruitment density are consistent with a hypothesized latitudinal shift in the distribution of reef-building corals, i.e. poleward extensions and equatorial contractions, as has been described for acroporids in Florida (Vargas-Ángel et al. 2003, Precht & Aronson 2004), Japan (Yamano et al. 2011), and Australia (Greenstein & Pandolfi 2008, Baird et al. 2012, Hughes et al. 2012). Unfortunately, taxonomic identification of coral recruits beyond the family level rarely is feasible, and it is therefore impossible to assess whether the same genera of recruits (e.g. *Acropora*) and adults are appearing in greater densities at higher compared to lower latitudes. Nevertheless, latitudinal gradients in total coral recruitment described herein over the last 4 decades provide a compelling case for climate-change mediated latitudinal shifts in the distribution of members of the coral assemblage (Parmesan & Yohe 2003, Pinsky et al. 2013).

4.2. Mechanisms of latitudinal trends: supply, connectivity, and survival

The temporal trend for changing densities of coral recruits that differ between latitudinal bins likely reflected the effects of multiple causal agents. The leading mechanisms, however, involve the supply and successful settlement of coral larvae, both of which are the proximal causes of the recruits detected on settlement tiles. In tropical regions (<20° latitude), larval supply might have declined as coral cover was lost following episodic mass coral mortality (Bruno & Selig 2007, Jackson et al. 2014), and/or as coral 'health' or performance was compromised (Hartmann et al. 2018). The latter effect would have been enhanced by non-lethal conditions that increasingly are impeding coral success in tropical waters (van Hooidonk et al. 2014).

In sub-tropical regions (>20° latitude), the supply of coral larvae might have increased if changes in environmental conditions enhanced coral fecundity.

As an example, eutrophication can reduce fecundity (Ward & Harrison 2000) and, presumably, a reversal of nutrient enrichment in otherwise oligotrophic waters would allow for greater fecundity. It is generally accepted that animals have a thermal optimum for most physiological processes, including reproduction. Particularly for reefs that existed previously on the lower end of thermal optimum spectrum for corals (e.g. subtropical reefs), any warming would represent a move towards an ideal temperature for reproduction. At Heron Island in Australia (23° S), the peak reproductive period for pocilloporid corals is limited to the relatively warmer summer months (Tanner 1996). This period could be lengthened under regional tropicalization, a phenomenon being reported elsewhere at high-latitude coral reefs (Kuffner et al. 2015). Increases in coral abundance in subtropical regions could also increase larval supply (Precht & Aronson 2004).

In tropical waters, the reproductive success of coral populations on degraded reefs is likely low (Gilmour et al. 2013, Hartmann et al. 2018), thereby decreasing their ability to support self-seeding of the natal reef, and increasing the reliance on distantly-sourced larvae to support coral recruitment. However, climate change-induced seawater warming probably will reduce larval connectivity between populations by accelerating larval development and thus shortening the duration of the pelagic larval stage (O'Connor et al. 2007, Hoegh-Guldberg & Bruno 2010), which would reduce the capacity to support recruitment through distantly-sourced larvae. Smaller dispersal kernels for coral larvae would lead to greater local larval retention (Cowen & Sponaugle 2009, Figueiredo et al. 2014), and might favour local extinctions (Hughes et al. 2005). It is unclear if smaller dispersal kernels in the tropics might also limit larval supply from these source populations to subtropical regions otherwise incapable of self-seeding (Wood et al. 2014), thus potentially altering the likelihood of range extensions and limiting density of recruits at higher latitudes.

Factors contributing to adult coral mortality, such as coral bleaching, increased macroalgal abundance, and disease (Rasher & Hay 2010, Hughes et al. 2017), will probably reduce survivorship of coral recruits (Steneck et al. 2014), thereby impeding the ability of affected reefs to recover from disturbances. The relative contribution of the presence or absence of these stressors to the survivorship of coral recruits in subtropical regions cannot be determined using the data compiled in the present study. Hence, we could not distinguish the processes that limited coral recruit-

ment in tropical regions from those that favored recruitment in the subtropics, particularly whether their effects were concentrated on larval supply, dispersal, settlement, or post-settlement success.

4.3. Biogeographical patterns in coral recruitment and global ocean warming

Combining the latitudinal distribution of coral recruits across time at select locations (Fig. 6) with the decadal trends in densities of corals on recruitment tiles at the global scale (Figs. 2 & 3) suggests a long-term contraction of coral recruitment at tropical latitudes accompanied by a poleward expansion to the sub-tropics during recent decades. Sub-tropical environments are classically considered 'marginal' for reef-building corals (Couce et al. 2013), and therefore increased recruitment in these waters implies that conditions have become more favourable for coral recruitment in recent decades. The most parsimonious explanation for the 2 patterns shown in our global dataset involves negative effects of acutely rising sea surface temperatures (especially during El Niño events; Fig. 6C) in tropical latitudes that have probably exceeded the thermal tolerance of the most stenothermal reef corals (Fitt et al. 2001, Howells et al. 2013), and positive effects of warming in the sub-tropics that are likely to have approached (or exceeded) the thermal optima for coral fitness and survival.

The data presented here are too sparse for a detailed exploration of the relationship between seawater thermal anomaly events and coral recruit densities, which can be complex, spatially variable, and confounded by boundary currents. However, there was a possible association between the timing of the empirical decline in density of coral recruits in the tropics and El Niño events in 1983, 1998, and 2010 (Fig. 6C). The effects of seawater warming on the success of coral recruits are likely to be exacerbated during such events (Wolter & Timlin 2011, Hughes et al. 2017), perhaps explaining the observed association between coral recruitment and some El Niño events (Fig. 6). In subtropical waters, the observed inflections in temporal trends of densities of coral recruits did not correspond with El Niño events (Fig. 6D), suggesting that coral recruitment at these latitudes is less sensitive to short-term changes in temperature than in the tropics, or that these events did not dramatically alter the thermal optima or surpass thermal thresholds for corals in marginal habitats. More detailed analyses of regional climatology and thermo-geography are required to link episodic ther-

mal events with drastic recruitment failure in the tropics of particular coral species.

Seawater warming in the tropics is predicted to exceed the capacity for physiological tolerance or adaptation of reef corals within the next 20 to 50 yr (Donner et al. 2005, Couce et al. 2013, Freeman et al. 2013, Mora et al. 2013). However, the effects of global warming on corals could perhaps be detected earlier than would be possible through local thermal extirpation, if analyses were broadened to consider the early life history stages such as recruits. The long-term trends in changing recruitment reported here suggest that reef corals may be already reducing some of the negative effects of rising seawater temperature in the tropics by shifting their latitudinal range poleward, as reported elsewhere for other marine and terrestrial species (Sorte et al. 2010, Pinsky et al. 2013, Bates et al. 2014). The latitudinal displacement of coral recruitment reported here matches bioclimatic envelope models (sensu Couce et al. 2013) that predict the most suitable habitat for corals will be >20° latitude within a few years and corresponds to the poleward-flowing warm boundary currents in major ocean basins (e.g. Kuroshio, Gulf Stream, and Eastern Australian Currents, and through the Suez Canal; Vergés et al. 2014). Paleontological records confirm that global range-shifts in coral distributions, or even extinctions, have been associated with climatic events in the past 10 000–60 000 yr (Precht & Aronson 2004, Greenstein & Pandolfi 2008, Kiessling et al. 2012).

4.4. Suitability of subtropical habitats as refuges for coral recruitment

Corals will also be impacted by the combined environmental stresses created by warming seawater and ocean acidification (Albright et al. 2010, Doney et al. 2012). Because marine environments at higher latitudes are characterized by higher benthic algal biomass, lower seawater pH, lower light intensities over winter, and a reduced ability to support coral calcification (i.e. they have a lower aragonite saturation state) than the tropics (Guinotte et al. 2003, Muir et al. 2015), regions of favoured coral recruitment in the 2 hemispheres may be sandwiched between tropical and subtropical regions with conditions that are unfavorable to their fitness. At low tropical latitudes, coral recruitment will likely be impeded by rising seawater temperatures, but at higher latitudes, coral recruitment is likely to be limited by reduced aragonite saturation state, competition with macroalgae, and low winter light intensities, as predicted for coral

reefs around Japan (Yara et al. 2012). Also, direct anthropogenic impacts on the marine environment (e.g. from large coastal cities and industrial areas) may potentially be stronger at mid than low latitudes. Thus, the future persistence of coral-dominated reefs may depend on the suitability of marginal habitats that would remain capable of hosting 'refugee recruits' in a narrow zone of suitability between unfavourable conditions poleward and equatorially.

The focus of the present analysis on the potential effects of temperature on coral recruitment should not detract attention from the wide set of conditions that affect the settlement of coral larvae and their subsequent post-settlement success (Ritson-Williams et al. 2009, Gleason & Hofmann 2011). Indeed, coral larvae have evolved a complex suite of behaviours involving responses to multiple cues that result in settlement to microhabitats characterized by specific chemicals, microbial consortia, light intensities, and surface rugosity (Raimondi & Morse 2000, Negri et al. 2001, Gleason & Hofmann 2011). Once metamorphosed, corals face ecological challenges to their success including competition for space, either by exploitative means (for space or light) or direct interference (allelopathy), abrasion from adjacent benthic organisms, grazing by fishes and sea urchins, and securing nutrients and energy to ensure their survival (Harrison & Wallace 1990, Ritson-Williams et al. 2009, Gleason & Hofmann 2011, Harrison 2011). Critically, on present-day and future reefs, the importance of the aforementioned biotic factors in determining where and when tropical coral recruits appear and persist to adult stages, may be overshadowed by the abiotic limitations placed on coral recruitment by rising seawater temperature and ocean acidification (Gilmour et al. 2013, Fabricius et al. 2017). Our study suggests the multi-decadal history of coral recruitment already captures biogeographic dynamics that are consistent with on-going patterns of global warming. The future of 'tropical' coral reefs may lie in relatively narrow zones poleward of tropical waters.

Dedication. We dedicate this paper to the memory of Dr. Ruth Gates whose enthusiasm for all things coral reef, inclusion and support for early career scientists, and commitment to solution-oriented science was instrumental in generating this paper.

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