Coral Reefs (2021) 40:1463–1471
https://doi.org/10.1007/s00338-021-02169-9

REPORT

Latitudinal variation in growth and survival of juvenile corals in the West and South Pacific

Yoko Nozawa[1] · **Ronald D. Villanueva**[2] · **Munasik Munasik**[3] · **Kakaskasen Andreas Roeroe**[4] · **Takuma Mezaki**[5] · **Takashi Kawai**[6] · **James Guest**[7] · **Seiji Arakaki**[8] · **Go Suzuki**[9] · **Jean J. B. Tanangonan**[10] · **Put O. Ang**[11] · **Peter J. Edmunds**[12]

Received: 11 March 2021 / Accepted: 9 August 2021 / Published online: 18 August 2021

Abstract Reef-building corals are found across > 30° of latitude from tropical to temperate regions, where they occupy habitats greatly differing in seawater temperature and light regimes. It remains largely unknown, however, how the demography of corals differs across this gradient of environmental conditions. Variation in coral growth is especially important to coral populations, because aspects of coral demography are dependent on colony size, with both fecundity and survivorship increasing with larger colonies. Here we tested for latitudinal variation in annual growth rate and survival of juvenile corals, using 11 study locations extending from 17° S to 33° N in the West and South Pacific. Regression analyses revealed a significant decline in annual growth rates with increasing latitude, whereas no significant latitudinal pattern was detected in annual survival. Seawater temperature showed a significant and positive association with annual growth rates. Growth rates varied among the four common genera, allowing them to be ranked *Acropora* > *Pocillopora* > *Porites* > *Dipsastraea*. *Acropora* and *Pocillopora* showed more variation in growth rates across latitudes than *Porites* and *Dipsastraea*. Although the present data have limitations with regard to difference in depths, survey periods, and replication among locations, they provide evidence that a higher capacity for growth of individual colonies may facilitate population growth, and hence population recovery following disturbances, at lower latitudes. These trends are likely to be best developed in *Acropora* and *Pocillopora*, which have high rates of colony growth.

Keywords Growth · Survival · Juvenile corals · Latitudinal variation · Seawater temperature · Recovery

---

Topic Editor Morgan S. Pratchett

Ronald D. Villanueva: Deceased

✉ Yoko Nozawa
nozaway@gate.sinica.edu.tw

[1] Biodiversity Research Center, Academia Sinica, Taibei, Taiwan

[2] Marine Science Institute, University of the Philippines, Diliman, Quezon, Philippines

[3] Department of Marine Science, Faculty of Fisheries and Marine Science, Diponegoro University, Semarang, Indonesia

[4] Faculty of Fisheries and Marine Sciences, Sam Ratulangi University, Manado, Indonesia

[5] Kuroshio Biological Research Foundation, Kochi, Japan

[6] Tokyo Kyuei Co., Ltd., Saitama, Japan

[7] School of Natural and Environmental Sciences, Newcastle University, Newcastle NE17RU, UK

[8] Amakusa Marine Biological Laboratory, Kyushu University, Kumamoto, Japan

[9] Yaeyama Station, Fisheries Technology Research Institute, Ishigaki, Okinawa, Japan

[10] Department of Environmental Management, Faculty of Agriculture, Kindai University, Nara, Japan

[11] Institute of Space and Earth Information Science, The Chinese University of Hong Kong, Hong Kong SAR, China

[12] Department of Biology, California State University, Northridge, CA 91302-8303, USA

Introduction

Many reef-building corals are found in habitats characterized by a wide range of environmental conditions (e.g., temperature and irradiance) from the tropics to temperate regions across > 30° of latitude (Veron 1995). While the influence of these environmental conditions on coral biology has been a topic of research for decades (Coles and Jokiel 1977; Jokiel and Coles 1977; Kleypas et al. 1999), it is not well understood how the performance of different coral taxa varies across a wide latitudinal gradient. For reef corals, growth rates are especially important with respect to fitness because fecundity and survivorship are largely size-dependent in corals (Hughes et al. 1992).

Most knowledge of latitudinal variation in the growth of corals comes from massive *Porites* spp. (Lough and Barnes 2000; Pratchett et al. 2015; Lough et al. 2016) (but see Anderson et al. 2017). Analyses of growth bands in massive *Porites* spp. across latitudinal gradient of up to 16° have revealed higher growth rates at lower latitudes, which is consistent with latitudinal variation in seawater temperature (Lough and Barnes 2000; Lough et al. 2016). A limitation of using skeletal growth bands to evaluate variation in coral growth is that the method can only reliably be applied to massive corals like *Porites* and *Orbicella* (Pratchett et al. 2015). Therefore, for many non-massive coral taxa (i.e., branching, tabular, and encrusting forms), analyses of latitudinal variation in growth are mostly informed by syntheses and meta-analyses of studies that have measured the growth rates of coral at different latitudes (Pratchett et al. 2015; but see Anderson et al. 2017). While such analyses have aided in understanding of general latitudinal patterns of variation in coral growth (Pratchett et al. 2015), the usefulness of historical studies for this purpose is limited by variation in methodology among studies.

Among a range of environmental conditions that vary with latitudes, seawater temperature, photosynthetic photon flux density (PPFD), and aragonite saturation state have been considered to be the most important factors affecting the growth of corals (Pratchett et al. 2015; Lough et al. 2016; Anderson et al. 2017). Seawater temperature influences coral metabolism (Coles and Jokiel 1977), affecting calcification and, therefore, coral growth (Jokiel and Coles 1977; Allemand et al. 2011); PPFD influences photosynthetic activity of symbiotic algae, affecting the supply of metabolic energy for calcification (Allemand et al. 2011), and aragonite saturation state influences the capacity of corals to deposit aragonite in their skeletons (Kleypas et al. 1999). Previous studies that have addressed the role of these conditions in affecting coral growth have suggested that seawater temperature is the primary driver of growth over a latitudinal gradient in massive and branching corals (Weber and White 1974; Lough and Barnes 2000; Lough et al. 2016; Anderson et al. 2017).

Compared to growth, there is almost no information available regarding the latitudinal variation in other key demographic variables of coral, such as fecundity and survival. If coral growth varies among latitudes, it is likely that coral fecundity and survival might also have similar latitudinal variation driven by differences in growth rate, given that these traits are associated with colony size (Hughes et al. 1992). The aforementioned processes support demographic mechanisms that could generate latitudinal variation in the rate at which coral populations grow, and hence their potential to recover following disturbances. Despite the strong ecological implications of this fundamental mechanisms, which ultimately will affect the biogeography, evolution, and conservation of coral communities at different latitudes, only limited information is available on latitudinal growth variation in corals (Pratchett et al. 2015; Lough et al. 2016; Anderson et al. 2017).

In this study, we tested for latitudinal variation in annual growth rate and annual survival of juvenile corals at 11 locations across a wide latitudinal range (17° S–33° N) mostly in 2012–2013, throughout the West and South Pacific. The study focused on four scleractinian genera that are common on shallow reefs throughout this region: *Acropora*, *Pocillopora*, *Porites*, and *Dipsastraea*. Annual average seawater temperature and annual average PPFD were examined as environmental correlates of variation in growth rates among latitudes. The study focused on juvenile corals (i.e., 1–5 cm^2 or 1–2.5 cm diameter) because they have high relative growth rates (Hughes and Connell 1987; Borgstein et al. 2020) and usually have simple encrusting or mounding morphologies that are tractable to measurement.

Materials and methods

Coral surveys

Data on annual growth rates and survival of juvenile corals were obtained from shallow reefs [ca. 5-m depth, except for Moorea (10-m depth)] in 11 locations extending from 17° S to 33° N in the West and South Pacific (Fig. 1, Supplementary Table S1). Corals in eight locations were surveyed for the present study with annual sampling from 2012–2013. In Amakusa (Japan), Hong Kong (China), and Moorea (French Polynesia), results were obtained from existing long-term monitoring studies that employed methods comparable to those employed herein (Nozawa et al. 2008; Tam and Ang 2008; Edmunds et al. 2018).

Annual growth rates and survival of juvenile corals were assessed using permanently marked quadrats in which individual corals could be tracked over time. For the eight locations surveyed in 2012–2013, up to 30 permanent quadrats (50 × 50 cm) were established within a 50 × 50 m area of reef at each of 1–3 adjacent sites at each location (Supplementary Table S1). When the study began, quadrats were haphazardly placed on hard substrata where juvenile corals (< 5 cm diameter) were located and were permanently marked (Fig. 1C). Using digital cameras with underwater housing (Canon PowerShot G12 or G16; 10 and 12.1 megapixels, respectively), each permanent quadrat and individual juvenile corals were photographed in planar view, and each image included a scale. This procedure was repeated in the second year.

Individual juvenile corals in the quadrats were evaluated for size (planar tissue area) and status (i.e., alive vs dead) using the photographs, and the corals were identified to genus based on polyp morphology and color (Veron 2000; Budd et al. 2012). It was not possible to identify most of the corals to species, as this requires detailed examination of corallite morphology from skeletons or genetic analyses. Small coral fragments created by fission of colonies, which typically occur as a group of conspecific colonies sharing the same color and morphology, were excluded. Planar tissue area of juvenile corals was measured from photographs by outlining them using ImageJ software (Schindelin et al. 2015). Annual growth rates of juvenile corals (cm^2 $year^{-1}$) were calculated by subtracting the initial size in the first year from the size in the second year. Because the time between initial and second surveys varied from 344 to 490 d among the locations (Supplementary Table S1), the annual growth rate was proportionately standardized to 365 d, by dividing the growth rate by the survey interval (d) and then multiplying by 365. Annual survival of juvenile corals was determined by the presence/absence of the same individuals on the photographs of permanent quadrat between the first and the second year. In

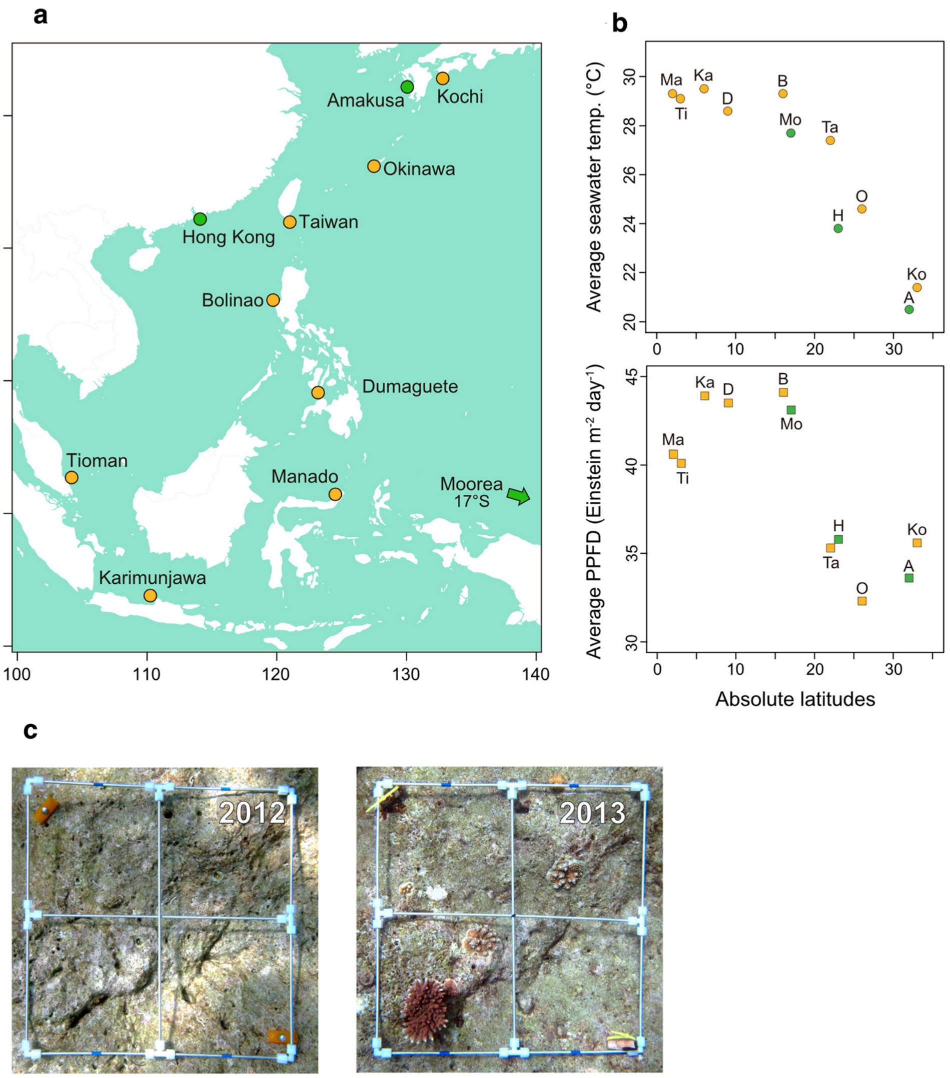

Fig. 1 **A** 11 study locations in the West and South Pacific used in the present study. Data at Amakusa, Hong Kong, and Moorea were obtained from comparative monitoring studies (green marks). Data at the other locations were collected in this study in 2012–2013 (orange marks). **B** Annual average seawater temperatures and annual average photosynthetic photon flux density (PPFD) at the study locations (color marks corresponding to the location groups) are also provided. For details, refer to Supplementary Figure S1 and S2. **C** A photographic pair image of a permanent quadrat (50 cm × 50 cm) used for data collection at Karimunjawa, Indonesia in 2012–2013. In the images, the permanent quadrat was marked with two orange tubes at the opposite corners of the quadrat (upper left and lower right)

Amakusa and Hong Kong, the same methods were used for the measurement of annual growth rate and annual survival. In Moorea, because coral size was recorded as the average of two major diameters perpendicular to one another (Edmunds et al. 2018), annual growth of juvenile corals was estimated from geometrically calculated planar areas assuming they were circular in shape. Survivorship was not measured in Moorea. As the growth and survival of corals is typically size-dependent (Hughes and Connell 1987; Hughes et al. 1992), we focused on measuring the growth rates and survival of juvenile corals in a narrow range of initial sizes [i.e., 1–5 cm^2 (1–2.5 cm diameter)], and the initial size of individual juvenile coral was used as a covariate (control variable) in statistical analyses.

Environmental data

Seawater temperature (°C) was obtained from loggers (accuracy of $< \pm 0.53$ °C: HOBO Pendant Temperature/Light Data Logger 64 K or HOBO Water Temperature Pro V2; Onset Computer Corporation, Bourne, MA, USA) that recorded at intervals of 0.5 or 1 h at each site. PPFD (Einstein m^{-2} d^{-1}) was obtained for each site using remote sensing data obtained from NOAA (http://coastwatch.pfeg.noaa.gov/erddap/index.html) to provide monthly averaged surface PPFD from Aqua MODIS satellite at 4-km resolution. For GPS coordinates and monitoring durations of each survey site, refer to Supplementary Table S1. For seawater temperature and PPFD, we initially considered four descriptive statistics: annual cumulative of daily or monthly average, annual maximum, annual minimum, and annual average (after Lough et al. 2016). However, as these metrics were collinear (Pearson's correlation coefficients, mostly $r > 0.7$; Supplementary Fig. S1 and S2) only the annual average values were used in the analyses. Seawater temperature and PPFD were averaged among individual study sites at which corals were surveyed in the 8 locations censused over 2012–2013, or over all years of monitoring period for the three locations from the comparable studies (Supplementary Table S1).

Statistical analysis

We conducted regression analyses using generalized linear mixed models (GLMMs) to test associations between the annual growth rate or the annual survival of juvenile corals and latitudes. For the GLMM for the annual growth rate, a gamma distribution with a log link function was chosen, and growth rates (response variable) were upwardly adjusted with a constant of + 5 to remove negative values (the minimum value of − 5 cm^2 $year^{-1}$) in the gamma distribution. For the GLMM for the annual survival, data on survival of individuals were used as a response variable with a binomial distribution and a logit link function. For both GLMMs, absolute values of latitude at the study locations and the four coral genera were considered as two fixed factors. The interaction term of genus × latitude was included in both models to examine variation among genera in the effect of latitude on the annual growth rate or the annual survival. The initial size of juvenile coral was included as a control factor (covariate). Study locations, each including 1–3 adjacent sites (Supplementary Table S1), were incorporated as random factors, with the sites nested within the locations. Following the analyses with data pooled among genera, genus-level analyses were completed using a subset of data for each genus to test the association between annual growth rate or annual survival and latitudes; the GLMMs was identical to that used for annual growth rate or annual survival for the pooled data, without the fixed factor, genus and the interaction term genus × latitude. For all the models, collinearity of fixed factors was examined using the variance inflation factor (< 2.5) and Pearson's correlation coefficient ($r < 0.09$). Model validation was completed using visual assessment of residual plots. Because of the significant association of growth with latitudes, the annual growth rate of corals was examined for associations with seawater temperature and PPFD. The two environmental factors were examined separately due to the collinearity between them (Pearson's correlation coefficient, $r = 0.71$) (Dormann et al. 2013). We used the same GLMM for the annual growth rate, in which latitude was replaced with either annual average seawater temperature or annual average PPFD. The analysis of deviance based on the Wald Chi-squared test was used to test for significance ($p < 0.05$) of latitude in the models. Post hoc pairwise comparisons for the factors, genus (four levels) and the interaction of genus × latitude were performed using Tukey tests. All analyses were performed in R v.3.5.3. (R Core Team 2019); with the glmer function of package lme4 v.1.1–21; the vif and Anova functions of package car v.3.0–2; the emmeans function of package emmeans v. 1.4.3.01; the ggpredict function of package ggeffects v.4.1–4; and the chart.Correlation function of package PerformanceAnalytics v.2.0.4.

Results

We analyzed 870 juvenile corals for annual growth rates, and 1106 for annual survival (Supplementary Table S2, S3, S4). Median and maximum of annual growth rates (cm^2 $year^{-1}$) recorded at each location were summarized for each genus in Table 1. Median growth rates ranged from 3.1–15.0 cm^2 yr^{-1} for *Acropora*, 1.0–14.2 cm^2 yr^{-1} for *Pocillopora*, − 0.1–5.3 cm^2 yr^{-1} for *Porites*, and 0.4–2.5 cm^2 yr^{-1} for *Dipsastraea*. The GLMM indicated a significant negative association between annual growth rates and latitude ($\chi^2 = 28.6$; $p < 0.001$) (Table 2). In the genus-level analysis, the significant negative association was also detected in *Acropora* ($\chi^2 = 7.3$, $p = 0.007$), *Pocillopora* ($\chi^2 = 26.5$, $p < 0.001$), and *Dipsastraea* ($\chi^2 = 11.8$, $p < 0.001$), expect for *Porites* ($\chi^2 = 3.7$, $p = 0.054$). Growth rate differed among genera ($\chi^2 = 156.4$, $p < 0.001$) (Table 2), with post hoc analyses revealing a hierarchy of declining growth (Fig. 2): *Acropora* > *Pocillopora* > *Porites* > *Dipsastraea* (pairwise comparisons by the Tukey test: *Porites* vs. *Dipsastraea*, $p = 0.008$; all others contrasts, $p < 0.001$). The degree of change in annual growth rates as a function of latitudes (i.e., the slope of regression line) varied among genera ($\chi^2 = 22.5$, $p < 0.001$) (Table 2), and pairwise comparisons of slopes by the Tukey test divided them into two groups: *Acropora* and *Pocillopora* > *Porites* and *Dipsastraea* (*Acropora* vs. *Pocillopora*, $p = 0.95$; *Porites* vs. *Dipsastraea*, $p = 0.95$; all other contrasts, $p < 0.006$) (Fig. 2). The GLMMs also revealed a significant and positive association of annual growth rates with annual average seawater temperature ($\chi^2 = 7.3$, $p = 0.007$), but not with annual average PPFD ($\chi^2 = 3.2$, $p = 0.075$) (Table 2).

The range of annual survival rates among the locations was 53–82% for *Acropora*, 39–93% for *Pocillopora*, 53–93% for *Porites* and 72–100% for *Dipsastraea* (Table 3). In contrast to the growth rate, the analysis of annual survival using the GLMM did not show a significant association with latitude ($\chi^2 = 1.4$, $p = 0.24$) (Table 4). The GLMM for the genus-level analysis also did not show any significant association between them for *Acropora* ($\chi^2 = 3.8$, $p = 0.052$), *Pocillopora* ($\chi^2 = 3.7$, $p = 0.055$), *Porites* ($\chi^2 = 1.7$, $p = 0.20$), and *Dipsastraea* ($\chi^2 = 2.7$, $p = 0.10$). However, annual survival varied among genera ($\chi^2 = 21.3$, $p < 0.001$) (Table 4), and pairwise comparisons showed significant differences in *Dipsastraea* > *Acropora* ($p < 0.001$) and *Dipsastraea* > *Porites* ($p = 0.003$) (Fig. 3). The extent to which annual survival varied as a function of latitude (i.e., the regression slope) also varied among genera ($\chi^2 = 13.8$, $p = 0.003$) (Table 4), and pairwise comparisons showed a significant difference between *Acropora* and *Pocillopora* ($p = 0.002$; all other contrasts, $p > 0.08$).

Table 2 Analysis of deviance table using type II Wald Chi-squared tests for the three generalized linear mixed models (a–c) estimated for annual growth rates of juvenile corals

Fixed factor	χ^2	Df	Pr (> χ^2)
(*a*)			
Latitude	28.6	1	< 0.001
Genus	156.4	3	< 0.001
Size	59.9	1	< 0.001
Latitude × Genus	22.5	3	< 0.001
(*b*)			
Temperature	7.3	1	0.007
Genus	127.0	3	< 0.001
Size	56.2	1	< 0.001
Temperature × Genus	8.2	3	0.042
(*c*)			
PPFD	3.2	1	0.075
Genus	126.0	3	< 0.001
Size	58.6	1	< 0.001
PPFD × Genus	12.3	3	0.007

Table 1 Annual growth rates (cm^2 $year^{-1}$) of juvenile corals (initial size; 1–5 cm^2) recorded at 11 study locations in the West and South Pacific. Median (bold) and maximum values of annual growth rate and sample size in parentheses are shown. Blank cells denote no, or sparse data (i.e., $n < 5$ individuals)

Latitude	Location	*Acropora*	*Pocillopora*	*Porites*	*Dipsastraea*
Annual growth rate (cm^2 $year^{-1}$)					
2° N	Manado			**3.3**, 8.9 (30)	**2.5**, 8.2 (35)
3° N	Tioman	**10.7**, 138.2 (9)	**13.5**, 24.6 (6)		
6° S	Karimunjawa	**15.0**, 125.7 (60)	**10.3**, 54.2 (11)		
9° N	Dumaguete			**1.2**, 22.5 (17)	**2.5**, 5.4 (9)
16° N	Bolinao		**14.2**, 23.3 (6)	**1.6**, 10.4 (45)	**1.3**, 11.9 (39)
17° S	Moorea	**3.1**, 4.8 (9)	**5.0**, 17.1 (29)	**2.3**, 19.1 (56)	
22° N	Taiwan	**4.4**, 33.5 (14)	**3.2**, 22.9 (92)	**2.1**, 20.0 (101)	**2.0**, 10.0 (23)
23° N	Hong Kong			**5.3**, 20.2 (15)	**1.6**, 7.3 (31)
26° N	Okinawa	**6.7**, 16.0 (25)	**4.4**, 14.0 (14)	**1.1**, 7.3 (43)	**1.4**, 4.5 (22)
32° N	Amakusa	**5.8**, 21.7 (18)	**1.0**, 3.4 (13)	**1.8**, 7.9 (23)	**1.2**, 3.5 (13)
33° N	Kochi		**3.2**, 10.8 (15)	− **0.1**, 3.0 (15)	**0.4**, 5.4 (17)
Range of median		***3.1–15.0***	***1.0–14.2***	− ***0.1–5.3***	***0.4–2.5***

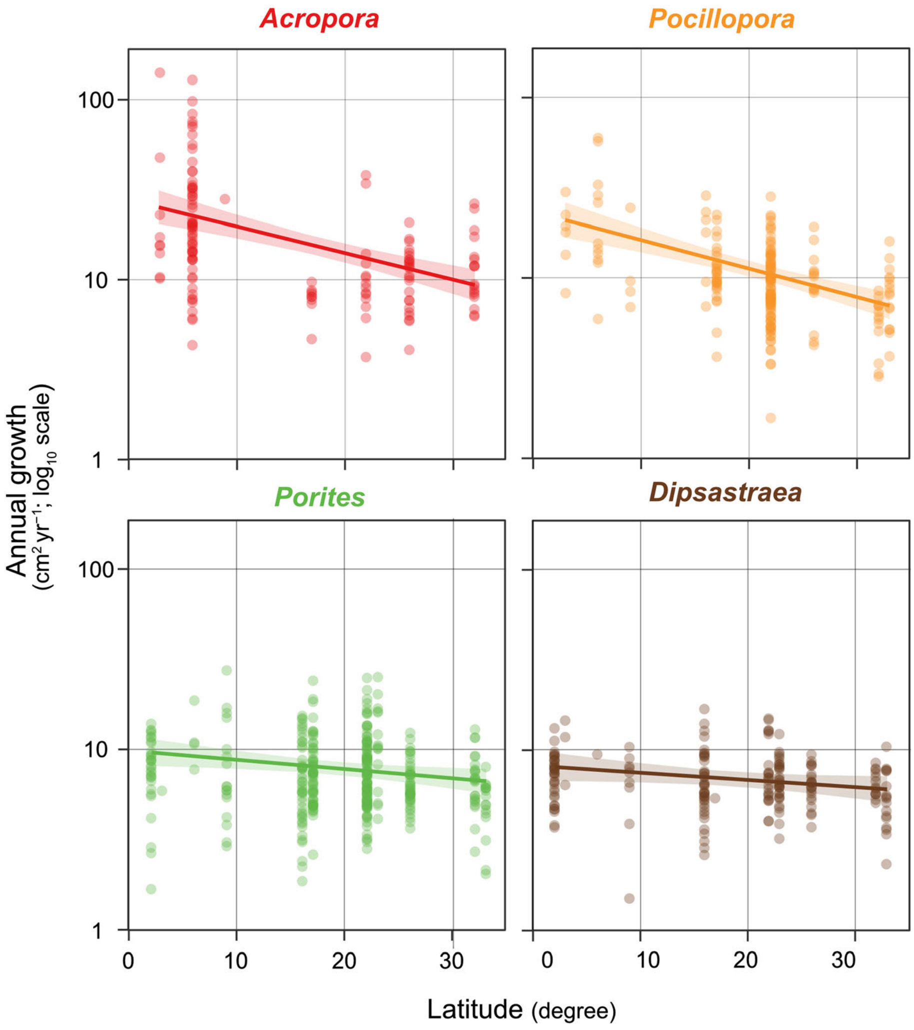

Fig. 2 Variation in annual growth rates (cm^2 year^{-1}) of juvenile corals at the 11 locations across latitudes in the West and South Pacific. Generalized linear mixed models were used for the estimation, based on a variable of growth value + 5. The estimated exponential regression line, 95% confidence intervals, and data of growth + 5 (dots) are shown for the four common coral genera separately. Absolute latitudes are used in the x-axis. For details of sample number and actual data analyzed, refer to Supplementary Table S2 and S3, respectively

Table 3 Annual survival rates (%) of juvenile corals (initial size; 1–5 cm^2) recorded at 11 study locations in the West and South Pacific. The samples number is shown in parentheses. Blank cells denote no, or sparse data (i.e., $n < 5$ individuals)

Latitude	Location	*Acropora*	*Pocillopora*	*Porites*	*Dipsastraea*
Annual survival rate (%)					
2° N	Manado			58 (52)	73 (48)
3° N	Tioman	60 (15)	43 (14)		
6° S	Karimunjawa	69 (87)	69 (16)	67 (6)	
9° N	Dumaguete		44 (9)	53 (32)	90 (10)
16° N	Bolinao		39 (18)	69 (65)	78 (50)
17° S	Moorea				
22° N	Taiwan	82 (17)	82 (112)	71 (142)	72 (32)
23° N	Hong Kong			93 (29)	97 (32)
26° N	Okinawa	56 (45)	88 (16)	84 (51)	85 (26)
32° N	Amakusa	53 (34)	93 (14)	72 (32)	100 (13)
33° N	Kochi		63 (24)	54 (28)	86 (18)
Range		53–82	39–93	53–93	72–100

Discussion

The present study demonstrates that the annual growth rate of juvenile corals on shallow coral reefs differs over 31° of absolute latitude in the West and South Pacific. The regression models and empirical data indicate a consistent pattern of faster growth rates at lower latitudes in juvenile corals of the four coral genera examined. The fast-growing genera, *Acropora* and *Pocillopora*, exhibited greater variation in growth across latitudes than the slow-growing genera, *Porites* and *Dipsastraea*. Higher growth rates at low latitudes reported in the present study align with previous studies, notably those obtained through analyses of growth bands in massive corals, mostly *Porites* spp. (Lough and Barnes 2000; Pratchett et al. 2015; Lough et al. 2016) and analyses of linear extension in branching corals such as *Acropora muricata*, *Pocillopora damicornis*, and *Isopora palifera* (Anderson et al. 2017).

Table 4 Analysis of deviance table using type II Wald Chi-squared tests for the generalized linear mixed model for annual survival of juvenile corals

Fixed factor	χ^2	Df	Pr (> χ^2)
Latitude	1.4	1	0.24
Genus	21.3	3	< 0.001
Size	7.9	1	0.005
Latitude × Genus	13.8	3	0.003

Seawater temperature and PPFD have often been considered as primary environmental factors influencing latitudinal variation in coral growth (Kleypas et al. 1999; Pratchett et al. 2015). However, the strong correlation among these environmental factors often makes it difficult to separate the magnitude of their relative influences on the latitudinal growth pattern of corals (Lough et al. 2016; this study). In the present study, we observed a significant and positive association of seawater temperature with the latitudinal growth variation. This agrees with previous studies that indicate a predominant influence of seawater temperature on latitudinal coral growth variations (Grigg 1982; Lough and Barnes 2000; Lough et al. 2016; Anderson et al. 2017), in situ measurement of seasonal calcification (Courtney et al. 2017), decadal growth trends (Cooper et al. 2012), and the global distribution pattern of coral reefs (Couce et al. 2012, 2013; Jones et al. 2019). This could be because seawater temperature directly influences both the

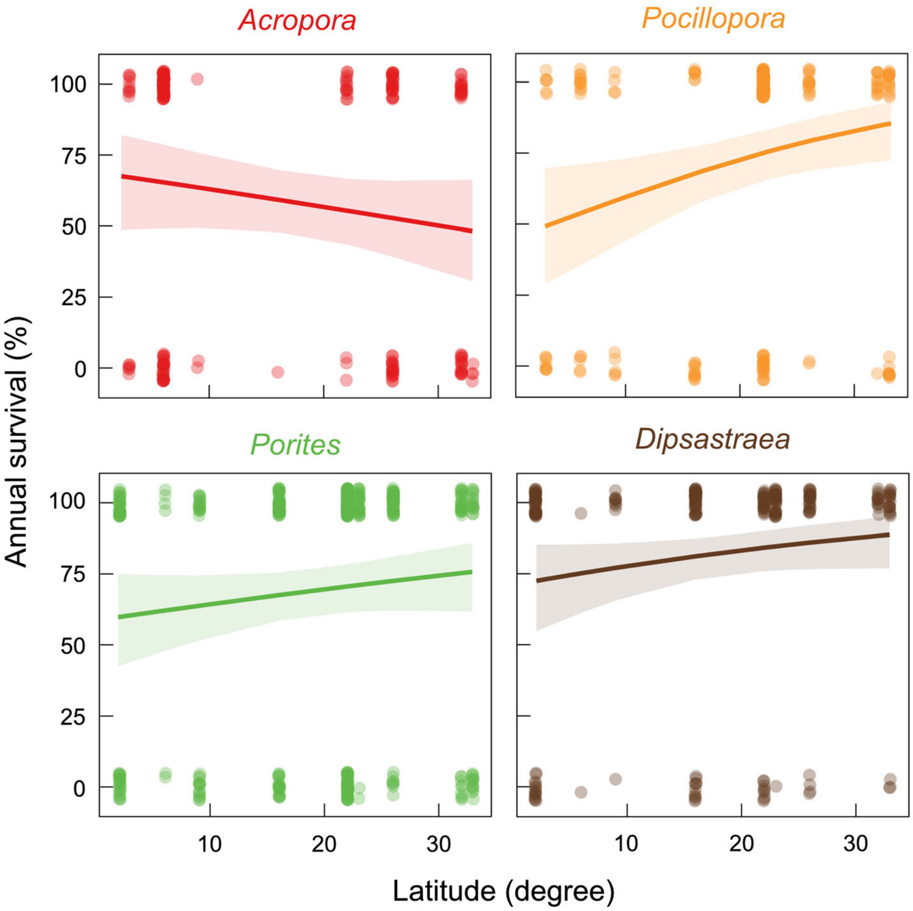

Fig. 3 Variation in annual survival rates (%) of juvenile corals at the 11 locations across latitudes in the West Pacific. A generalized linear mixed model was used to estimate the logistic regression line and 95% confidence intervals. Results are shown for the four common coral genera separately, with binomial survival data (top dots = alive, bottom dots = dead) used for the estimation. Absolute latitudes are used in the x-axis. For details of sample number and actual data analyzed, refer to Supplementary Table S2 and S4, respectively

metabolism of corals (Jurriaans and Hoogenboom 2019) and photosynthesis of Symbiodiniaceaen symbiotic algae (Oakley et al. 2014). In contrast, PPFD influences only the photosynthesis of Symbiodiniaceaen symbiotic algae (autotrophic nutrition), and not heterotrophic feeding of coral that can account for up to 66% of carbon incorporated into coral skeletons (Goreau et al. 1971; Houlbrèque and Ferrier-Pagès 2009).

Contrary to the latitudinal variation in growth rates, we did not find a significant association with latitude in the annual survival of juvenile corals over the same gradient for all taxa combined and for each genus. This was unexpected given the positive effect of increasing colony size on coral survival (Hughes and Connell 1987; Hughes et al. 1992; Nozawa et al. 2008; Madin et al. 2020), even within the more restrictive size range of small colonies (i.e., < 100 cm^2) (Vermeij 2006; Vermeij and Sandin 2008). There are several possible explanations for the absence of a latitudinal effect on survivorship as shown in the present results. The most likely explanation is that survivorship is colony size-dependent, but this effect is hidden by strong local-scale stressors that kill juvenile corals regardless of size. If mortality effects were concentrated at the initial period of the present study when juvenile corals were small across latitudes (i.e., mortality was strong size-dependent: Vermeij 2006; Vermeij and Sandin 2008), no latitudinal survival pattern would occur. If local-scale stressors have stronger effects on survival than colony size, then an effect of latitude on survival might have been obscured. Previous studies demonstrated the positive effect of colony size on survival of juvenile corals at a single location under the same local stressors (Vermeij 2006; Vermeij and Sandin 2008). To our knowledge, no studies have examined the extent of positive colony size dependency on coral survival against stressors of various types and magnitudes across multiple locations. Therefore, we infer that mortality probably had a stronger effect over the early study period, and/or local-scale stressors varying in types and magnitude could possibly counteract the effects of colony size on the annual survival of corals in the present study.

Given colony size dependency in coral demography (Hughes et al. 1992), latitudinal variation in growth rates creates a mechanism by which population growth could be affected. As most corals are colonial, and their fecundity is a function of polyp fecundity and the number of polyps (Hall and Hughes 1996), fast growth enhances coral fecundity through increasing number of polyps (Hughes et al. 1992; Hall and Hughes 1996; Sakai 1998). Fast growth could also accelerate the survival probability of corals by shortening time to attain a larger body size at which survivorship is elevated (Hughes et al. 1992). Therefore, higher growth may result in higher fecundity and higher survival, enhancing population growth at lower latitudes. Faster rates of population growth could result in a higher potential for coral populations to recover following disturbances. Given taxonomic variation in the latitudinal growth pattern, fast-growing genera such as *Acropora* and *Pocillopora* could have a greater advantage at lower latitudes. This hypothesis, involving cascading effects of latitudinal growth variation on development and recovery of coral population, could have important implications not only in biogeography and evolution, but also conservation and management of corals in the face of unprecedented disturbance.

While the aforementioned mechanism could support a latitudinal gradient of population development and recovery throughout the tropical Pacific Ocean, the ongoing effects of ocean warming are increasing thermal stress on coral reefs at lower latitudes (Couce et al. 2013; Jones et al. 2019), which is likely to offset the capacity of coral growth to mediate latitudinal variation in the growth of coral populations. Further research is needed to examine how ongoing climate change (notably rising seawater temperature and the implications for coral bleaching) will affect latitudinal variation in coral growth and its consequences for coral population growth. Further testing of the present hypothesis is warranted given the limitations of our study, in which we only recorded growth over a single year and augmented our empirical data with results drawn from existing studies. Comprehensive demographic studies (i.e., focusing on the full size range of colonies) that can quantify vital rates (growth, survival, fecundity) at multiple latitudes are likely to be effective to testing the central hypothesis of the present study.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00338-021-02169-9.

Acknowledgements We appreciate volunteers, students, and assistants for data collection. Y.N. especially thank H.-S. Hsieh and C.-H. Liu for data measurement, and V. Denis for his comments on the manuscript. Comments from two anonymous reviewers improve our manuscript greatly. The study was funded by the thematic research grant of Academia Sinica (23-2g) and an internal research grant of Biodiversity Research Center, Academia Sinica to Y.N. The Okinawa survey was partly supported by the Japan Society for the Promotion of Science through NEXT Program #GR083. Temperature data for the Okinawa site were provided by the coral reef survey of Monitoring Sites 1000 Project, operated by the Ministry of the Environment, Japan. Temperature data for Moorea were provided by the Moorea Coral Reef LTER, funded by the US National Science Foundation (OCE-0417412).

Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

References

Allemand D, Tambutté É, Zoccola D, Tambutté S (2011) Coral calcification, cells to reefs. Coral reefs: an ecosystem in transition. Springer, Dordrecht, Netherlands, pp 119–150

Anderson KD, Cantin NE, Heron SF, Pisapia C, Pratchett MS (2017) Variation in growth rates of branching corals along Australia's Great Barrier Reef. Sci Rep 7:1–13

Borgstein N, Beltrán DM, Prada C (2020) Variable growth across species and life stages in Caribbean reef octocorals. Front Mar Sci 7:483

Budd AF, Fukami H, Smith ND, Knowlton N (2012) Taxonomic classification of the reef coral family Mussidae (Cnidaria: Anthozoa: Scleractinia). Zool J Linn Soc 166:465–529

Coles S, Jokiel P (1977) Effects of temperature on photosynthesis and respiration in hermatypic corals. Mar Biol 43:209–216

Cooper TF, O'Leary RA, Lough JM (2012) Growth of Western Australian corals in the anthropocene. Science 335:593–596

Couce E, Ridgwell A, Hendy EJ (2012) Environmental controls on the global distribution of shallow-water coral reefs. J Biogeogr 39:1508–1523

Couce E, Ridgwell A, Hendy EJ (2013) Future habitat suitability for coral reef ecosystems under global warming and ocean acidification. Glob Change Biol 19:3592–3606

Courtney TA, Lebrato M, Bates NR, Collins A, de Putron SJ, Garley R, Johnson R, Molinero J-C, Noyes TJ, Sabine CL (2017) Environmental controls on modern scleractinian coral and reef-scale calcification. Sci Adv 3:e1701356

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46

Edmunds PJ, Nelson HR, Bramanti L (2018) Density-dependence mediates coral assemblage structure. Ecology 99:2605–2613

Goreau TF, Goreau NI, Yonge C (1971) Reef corals: autotrophs or heterotrophs? Biol Bull 141:247–260

Grigg RW (1982) Darwin Point: a threshold for atoll formation. Coral Reefs 1:29–34

Hall V, Hughes TP (1996) Reproductive strategies of modular organisms: comparative studies of reef-building corals. Ecology 77:950–963

Houlbrèque F, Ferrier-Pagès C (2009) Heterotrophy in tropical scleractinian corals. Biol Rev 84:1–17

Hughes TP, Ayre D, Connell JH (1992) The evolutionary ecology of corals. Trends Ecol Evol 7:292–295

Hughes TP, Connell JH (1987) Population dynamics based on size or age? A reef-coral analysis. American Naturalist:818–829

Jokiel PL, Coles SL (1977) Effects of temperature on the mortality and growth of Hawaiian reef corals. Mar Biol 43:201–208

Jones LA, Mannion PD, Farnsworth A, Valdes PJ, Kelland S-J, Allison PA (2019) Coupling of palaeontological and neontological reef coral data improves forecasts of biodiversity responses under global climatic change. R Soc Open Sci 6:182111

Jurriaans S, Hoogenboom M (2019) Thermal performance of scleractinian corals along a latitudinal gradient on the Great Barrier Reef. Philos Trans R Soc B 374:20180546

Kleypas JA, McManus JW, Menez LA (1999) Environmental limits to coral reef development: where do we draw the line? Am Zool 39:146–159

Lough J, Barnes D (2000) Environmental controls on growth of the massive coral *Porites*. J Exp Mar Biol Ecol 245:225–243

Lough J, Cantin N, Benthuysen J, Cooper T (2016) Environmental drivers of growth in massive *Porites* corals over 16 degrees of latitude along Australia's northwest shelf. Limnol Oceanogr 61:648–700

Madin JS, Baird AH, Baskett ML, Connolly SR, Dornelas MA (2020) Partitioning colony size variation into growth and partial mortality. Biol Let 16:20190727

Nozawa Y, Tokeshi M, Nojima S (2008) Structure and dynamics of a high-latitude scleractinian coral community in Amakusa, southwestern Japan. Mar Ecol Prog Ser 358:151–160

Oakley CA, Schmidt GW, Hopkinson BM (2014) Thermal responses of Symbiodinium photosynthetic carbon assimilation. Coral Reefs 33:501–512

Pratchett MS, Anderson KD, Hoogenboom MO, Widman E, Baird AH, Pandolfi JM, Edmunds PJ, Lough JM (2015) Spatial, temporal and taxonomic variation in coral growth—implications for the structure and function of coral reef ecosystems. Oceanogr Mar Biol Annu Rev 53:215–295

R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Sakai K (1998) Effect of colony size, polyp size, and budding mode on egg production in a colonial coral. Biol Bull 195:319–325

Schindelin J, Rueden CT, Hiner MC, Eliceiri KW (2015) The ImageJ ecosystem: an open platform for biomedical image analysis. Mol Reprod Dev 82:518–529

Tam TW, Ang PO Jr (2008) Repeated physical disturbances and the stability of sub-tropical coral communities in Hong Kong, China. Aquat Conserv Mar Freshw Ecosyst 18:1005–1024

Vermeij MJA (2006) Early life-history dynamics of Caribbean coral species on artificial substratum: the importance of competition, growth and variation in life-history strategy. Coral Reefs 25:59–71

Vermeij MJA, Sandin SA (2008) Density-dependent settlement and mortality structure the earliest life phases of a coral population. Ecology 89:1994–2004

Veron JEN (1995) Corals in space and time: the biogeography and evolution of the Scleractinia. UNSW Press, Sydney

Veron JEN (2000) Corals of the World. Australian Institute of Marine Science, Townsville

Weber J, White E (1974) Activation energy for skeletal aragonite deposited by the hermatypic coral *Platygyra* spp. Mar Biol 26:353–359