

Rapid poleward range expansion of tropical reef corals in response to rising sea surface temperatures

Hiroya Yamano,¹ Kaoru Sugihara,¹ and Keiichi Nomura²

Received 11 December 2010; revised 10 January 2011; accepted 12 January 2011; published 17 February 2011.

[1] Rising temperatures caused by climatic warming may cause poleward range shifts and/or expansions in species distribution. Tropical reef corals (hereafter corals) are some of the world's most important species, being not only primary producers, but also habitat-forming species, and thus fundamental ecosystem modification is expected according to changes in their distribution. Although most studies of climate change effects on corals have focused on temperature-induced coral bleaching in tropical areas, poleward range shifts and/or expansions may also occur in temperate areas. We show the first large-scale evidence of the poleward range expansion of modern corals, based on 80 years of national records from the temperate areas of Japan, where century-long measurements of *in situ* sea-surface temperatures have shown statistically significant rises. Four major coral species categories, including two key species for reef formation in tropical areas, showed poleward range expansions since the 1930s, whereas no species demonstrated southward range shrinkage or local extinction. The speed of these expansions reached up to 14 km/year, which is far greater than that for other species. Our results, in combination with recent findings suggesting range expansions of tropical coral-reef associated organisms, strongly suggest that rapid, fundamental modifications of temperate coastal ecosystems could be in progress. **Citation:** Yamano, H., K. Sugihara, and K. Nomura (2011), Rapid poleward range expansion of tropical reef corals in response to rising sea surface temperatures, *Geophys. Res. Lett.*, 38, L04601, doi:10.1029/2010GL046474.

1. Introduction

[2] Sea-surface temperature (SST) is an environmental predictor closely linked with marine biodiversity [Tittensor *et al.*, 2010], and climatic warming is likely affecting species distribution ranges [Hoegh-Guldberg and Bruno, 2010]. Large-scale, long-term observations are needed to detect such changes, but compared to terrestrial studies, such research on marine species remains scarce, partly due to the size and complexity of the ocean, but also to the relative difficulty of taking measurements in marine environments [Hoegh-Guldberg and Bruno, 2010]. In this study, we show the first large-scale evidence of the poleward range expansion of corals, based on 80 years of national records from the temperate areas of Japan, where century-long measurements

of *in situ* sea-surface temperatures have shown statistically significant rises.

[3] Corals play a fundamental role in primary production and habitat formation for numerous other species in tropical and subtropical areas. Thus, their poleward range expansions due to climatic warming could cause fundamental modifications of temperate coastal ecosystems. Although most studies of climate change effects on corals have focused on temperature-induced coral bleaching in tropical areas, poleward range shifts and/or expansions may also occur in temperate areas, as suggested by geological records and present-day eyewitnesses in several localities [Greenstein and Pandolfi, 2008; Precht and Aronson, 2004]. In addition to their importance in ecosystem function, corals are also sensitive detectors of long-term climatic warming effects. Adult coral colonies are sessile, and several years after larval settlement are required for a colony to develop sufficiently to be recognized *in situ*. Corals are basically long-lived, but are extremely sensitive to temperature. Both high and low temperatures can lead to bleaching, which causes coral mortality [Hoegh-Guldberg *et al.*, 2005]. Therefore, detection of range shifts and/or expansions of corals would provide solid baselines to discuss changes of coastal marine biodiversity and ecosystems in temperate areas.

2. Setting

[4] Japan covers a wide latitudinal range, stretching from subtropical to temperate areas, and latitudinal limits of coral reefs and coral distributions are observed around the Japanese islands [Veron, 1992b; Veron and Minchin, 1992; Yamano *et al.*, 2001] (Figure 1). In addition to SST limits, other reasons why Japan provides a unique opportunity for examining baselines of species range shifts and/or expansions due to climatic warming over a large spatial scale include the following. First, the Japanese islands form an almost continuous chain, and corals are distributed in a stepping-stone sequence along a latitudinal gradient, due to the Kuroshio and Tsushima warm currents, which potentially transport coral larvae from south to north [Veron and Minchin, 1992]. Second, because of Japan's relatively small landmass in comparison with other temperate settings (e.g., the United States, Africa and Australia), distribution is likely to be less disturbed by terrestrial influence. Third, SSTs, which constrain coral distributions [Veron and Minchin, 1992], have risen in the last 100 years as indicated by the Japan Meteorological Agency [Takatsuki *et al.*, 2007]. This was revealed by analyses of *in situ* observations of SSTs from ICOADS [Diaz *et al.*, 2002] and the Kobe Collection [Manabe, 1999], along with *in situ* data collected by related agencies. Finally, corals have been observed periodically in Japanese waters since the 1930s. Our

¹Center for Global Environmental Research, National Institute for Environmental Studies, Tsukuba, Japan.

²Kushimoto Marine Park Center, Kushimoto, Japan.

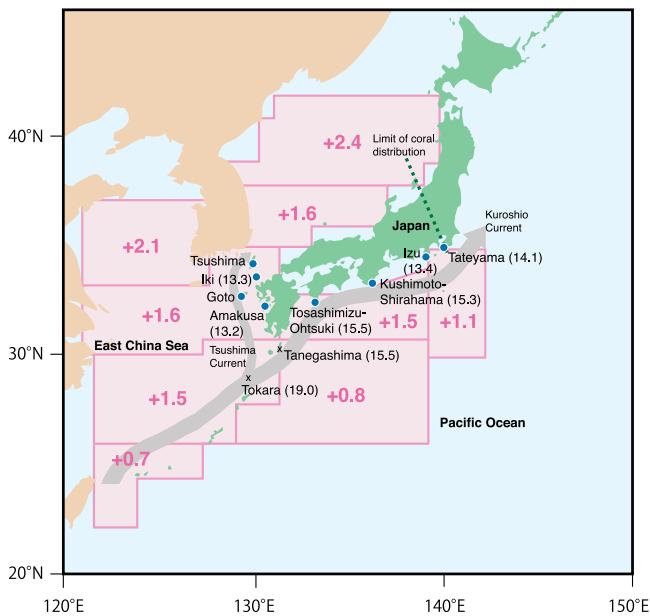


Figure 1. Locations of the eight regions examined (dots) and the regions additionally examined (crosses) in case the previous northern range margin was estimated to have been farther south than the eight regions. Numbers in parentheses indicate average *in situ* SST minima (°C) of coldest months [Veron and Minchin, 1992; Yamano et al., 2001], while numbers in rectangles indicate increases in winter SST (°C) over the last 100 years [Takatsuki et al., 2007].

dataset on corals is thus one of the largest-scale, longest-term records among marine species reported to date [Helmuth et al., 2006; Hoegh-Guldberg and Bruno, 2010].

3. Methods

[5] We collected records of coral species occurrence from eight temperate regions of Japan along a latitudinal gradient (Figure 1), where past coral occurrence records were available in the form of literature and specimens (auxiliary material).¹ When the previous northern range margin was estimated to have been farther south than the study regions, we also examined occurrence in the Tokara–Tanegashima region (Figure 1), based on literature (auxiliary material). Four distinct periods of coral exploration have occurred. The first period was in the 1930s and was undertaken by Drs Yabe and Sugiyama at Tohoku Imperial University (Tohoku University) of Japan. Some of the specimens collected by them were stored in Tohoku University Museum. The second period was from the 1960s and 1970s. Comprehensive surveys of marine environments and organisms were conducted as part of the designation planning of marine protected areas. Coral identification was performed mainly by Drs Utinomi and Eguchi. The third period was from the 1980s to 1990s, when Dr. Veron, who revised and integrated the recent taxonomic framework of corals, visited Japan and examined coral distribution [Veron, 1992b; Veron and Minchin, 1992].

¹Auxiliary materials are available in the HTML. doi:10.1029/2010GL046474.

The last period covers the late 1990s to the present. Japanese researchers, including the authors, conducted field surveys based on the recent taxonomic framework. In this work, we conducted additional field surveys in regions lacking detailed recent information. In addition to observing coral occurrence, colony sizes of the selected corals (Table 1) were measured to infer past occurrence. The eight study regions are all located in seas showing significant SST rises in winter (January–March) (1.1°C–1.6°C) [Takatsuki et al., 2007], which is critical for corals to survive at the latitudinal limits of their distribution [Veron and Minchin, 1992]. Since all the sites in these regions are remote from densely populated cities and most sites are located in marine protected areas, anthropogenic impacts are expected to be minor.

[6] Corals are one of the most difficult taxa to identify at species level. They have few taxonomically significant morphological characteristics because such characters show polymorphism, intraspecific variation and phenotypic plasticity in response to environmental factors [Veron, 2000]. In addition to the difficulties of identification, the coral taxonomic framework before 1990 differed greatly from that in current use. Therefore, careful examination is needed to establish consistent databases of coral records. Species for comparison were selected based on three criteria. First, species that were abundant in the regions of interest [Sugihara et al., 2009] were selected to avoid the possibility that past surveys had missed their occurrence. Second, species distributed typically at depths of less than 10 m were selected, as some past surveys used snorkeling or observation through a water glass from a boat. Finally, and most importantly, species with distinct growth forms that could be identified *in situ* were selected because in some previous reports, observers identified species *in situ* without collecting specimens. As a result, nine species categories were selected (Table 1 and auxiliary material). These species, except for *Acropora pruinosa/tumida*, *Caulastrea tumida* and *Lithophyllon undulatum*, are common in the Indo-Pacific region [Veron, 2000], and thus similar assessment is possible for other sites in the Indo-Pacific region by referring to these species. We revised species names from past literature based on the recent coral taxonomic framework formulated by Veron [1992b] (auxiliary material). We also examined descriptions and photographs available in the literature to confirm species names. One of the authors (KS) visited Tohoku University Museum and re-examined the 1930s specimens based on Veron’s framework. To minimize local effects, we pooled species lists from several sites in one region to represent occurrence in the region.

[7] We calculated the speed of coral range expansions along latitude based on the occurrence records. Although coral colonies may be recognized several years after larval settlement, we used the year when new colonies were found, in order to keep consistency in calculation based on the occurrence records. Past literature did not describe colony sizes, which made estimation of larval settlement years impossible. Thus, the expansion speed likely was underestimated.

4. Results and Discussion

[8] Four species categories of the nine selected showed poleward range expansion since the 1930s, whereas the other

Table 1. Characteristics of the Species Selected in This Study^a

| Species Category | Distribution [Veron, 2000] | IUCN Red List Category [Carpenter et al., 2008] | Growth Rate (cm/year) | Maximum Colony Diameter (cm) at the Northernmost Region of the Occurrence in the East China Sea and Pacific Coasts, Respectively | Settlement Year Estimated From Colony Sizes and Growth Rates | Reference for Growth Rates | Remarks |
|---|---|--|--------------------------|---|--|----------------------------------|--|
| <i>Acropora hyacinthus</i> (Dana, 1846) | Tropical to subtropical, Indo-Pacific One of the most abundant corals of exposed outer reef slopes of much of the western Pacific | Near Threatened | 2.09 | ~50 (Goto) and 300~ (Kushimoto-Shirahama) | 1996~ (Goto) and ~1938 (Kushimoto-Shirahama) | Harriott [1999] | Growth rate of <i>Acropora cytherea</i> at Solitary Islands (Australia) was applied. |
| <i>Acropora muricata</i> (Linnaeus, 1758) | Tropical to subtropical, Indo-Pacific Common and frequently a dominant species | Near Threatened | 3.7–7.6 | ~100 (Goto) and 250~ (Kushimoto-Shirahama) | 1995~ (Goto) and ~1994 (Kushimoto-Shirahama) | Harriott [1999] | Formerly called as <i>Acropora formosa</i> , which has been designated to be a junior synonym of <i>Acropora muricata</i> [Wallace, 1999]. Re- cords of <i>Acropora striata</i> from Tanegashima and Amakusa were reidentified as <i>A. mur- icata</i> based on the latest survey of the authors in the same re- gions. Growth rates at Houtman Ab- rolhos (Australia) were applied. |
| <i>Acropora pruinosa</i> (Brook, 1893)/ <i>Acropora tumida</i> (Verrill, 1866) | Subtropical to temperate, northwest Pacific Locally common in mainland Japan (<i>A. pruinosa</i>) Locally common (<i>A. tumida</i>) | Data deficient | 0.04–1.95 | 100~ (Tsushima and Tateyama) | ~1984 | Hagiwara [2003] | These two species have similar forms, which are difficult to distinguish from descriptions and photographs. Growth rate at Tateyama was applied. |
| <i>Acropora solitariaensis</i> (Veron & Wallace, 1984) | Tropical to temperate, eastern Indian Ocean and western Pacific Common at subtropical locations, rare elsewhere | Vulnerable | 0.9 | ~20 (Tsushima and Tateyama) | 1999~ | Yamano and Namizaki [2009] | This species has several morphological forms including a branching form and a disc (solid plate) form that has fused branches with nipple- like tips; the latter has been described in some previous literature (Table S2). Growth rate at Tateyama was applied. |

Table 1. (continued)

| Species Category | Distribution [Veron, 2000] | IUCN Red List Category [Carpenter et al., 2008] | Growth Rate (cm/year) | Maximum Colony Diameter (cm) at the Northernmost Region of the Occurrence in the East China Sea and Pacific Coasts, Respectively | Settlement Year Estimated From Colony Sizes and Growth Rates | Reference for Growth Rates | Remarks |
|---|---|---|-----------------------|--|--|-----------------------------|---|
| <i>Caulastrea tumida</i> (Matthai, 1928) | Tropical to temperate, eastern Indian Ocean and western Pacific | Near Threatened | N/A | 100~ (Tsushima and Kushimoto-Shirahama) | N/A | N/A | |
| <i>Favia speciosa</i> (Dana, 1846) | Common only in western Australia and Japan Tropical to temperate, Indo-Pacific | Least Concern | 0.461 | ~75 (Tsushima and Tateyama) | 1929~ | Ma [1934] | Growth rate at Tateyama was applied. |
| <i>Hydnophora exesa</i> (Pallas, 1766) | One of the most common faviids, especially in high latitudes Tropical to temperate, Indo-Pacific | Near Threatened | N/A | 100~ (Tsushima and Tateyama) | N/A | N/A | |
| <i>Lithophyllon undulatum</i> (Rehberg, 1892) | Tropical to temperate, eastern Indian Ocean and western Pacific | Near Threatened | N/A | ~50 (Tsushima and Kushimoto-Shirahama) | N/A | N/A | |
| <i>Pavona decussata</i> (Dana, 1846) | Usually uncommon Tropical to temperate, Indo-Pacific | Vulnerable | 0.598–1.939 | ~20 (Goto and Izu) | 1992~ | Glynn and Wellington [1983] | Growth rates of <i>Pavona clavus</i> at Galapagos were applied. |

^aGrowth rates are for relatively low SST settings in order to apply them to our study regions. In case the values were not available, those for corals with similar growth forms were applied. Maximum colony diameters observed in the recent survey are shown to estimate recent settlement years, though several size classes of the colonies were observed.

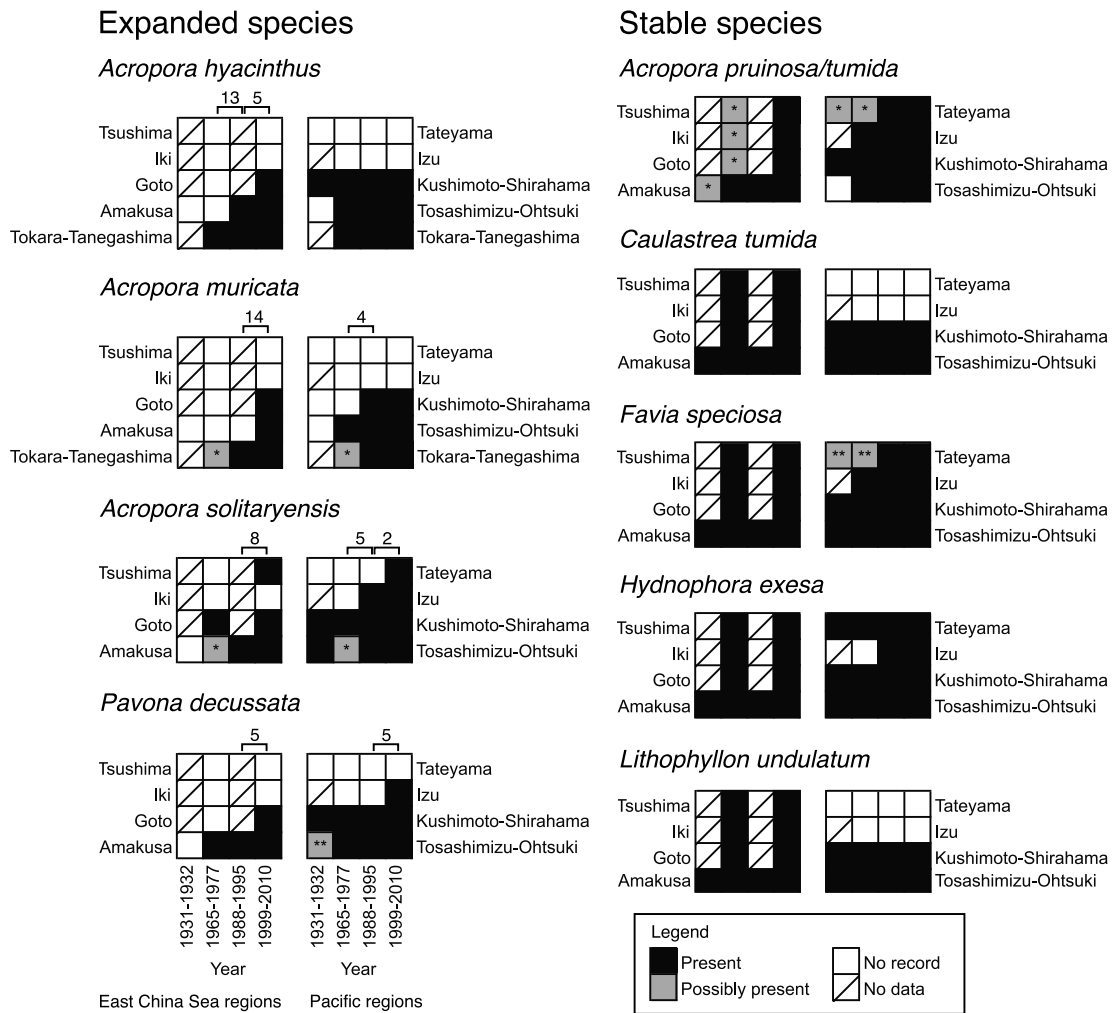


Figure 2. Changes in coral species occurrence in the eight regions since the 1930s. Numbers indicate minimum estimates of poleward expansion speed (km/year). For *Acropora hyacinthus* and *Acropora muricata*, previous northern distribution limits for the East China Sea region (Tokara and Tanegashima) are indicated. “Possibly present” means that more than two candidate species names, including the species of interest, were suggested based on our examination (asterisk) (auxiliary material) or existence of the colony was assumed according to sizes observed in recent surveys (double asterisk).

five remained stable (Figure 2), indicating no southward range shrinkage or local extinction. The estimated settlement years of the colonies of expanded species (Table 1) provide further evidence of recent expansions. Of the expanded species, *Acropora hyacinthus* and *Acropora muricata* are key species for reef formation in tropical Indo-Pacific regions [Hongo and Kayanne, 2011; Montaggioni, 2005], and clearly indicate the expansion of tropical species ranges to temperate areas. Note that all of the expanded species have been in IUCN (International Union for Conservation of Nature) extinction risk categories of “Near Threatened” or “Vulnerable” since 1998, when temperature-induced mass bleaching occurred [Carpenter et al., 2008] (Table 1). Adult colonies in these regions exhibited spawning [Mezaki et al., 2007; van Woessik, 1995], indicating that corals newly settled as a result of expansion have the potential to reproduce and expand farther northward. Thus, temperate areas may serve as refugia for tropical corals in an era of global warming, while corals in tropical areas suffer declines because of rising SSTs [Hoegh-Guldberg et al., 2007].

[9] These expansions could have major effects on temperate ecosystems. As the expanding *A. hyacinthus* and *A. muricata* have higher growth rates than other species (Table 1), several species around mainland Japan, including five endemic species [Veron, 1992a], could suffer declines as a result of competition caused by the invasion of the tropical species. *A. hyacinthus* and *A. muricata* generally occur with respective associated specific species that occupy a similar niche [Hongo and Kayanne, 2010]. This means that such associated species might also be expanding their ranges, as shown in Kushimoto, where two of species associated with *A. hyacinthus* (*Acropora gemmifera* and *Acropora microphthalma*) occurred recently [Nomura et al., 2008]. Furthermore, the range expansions of corals may cause range expansions in other tropical marine organisms associated with coral reefs. Recent findings in Japan, although not based on systematic surveys, suggest that such organisms (*Acanthaster planci*, reef fish and toxic microalgae that cause ciguatera) may also be expanding their ranges [Oshiro, 2008].

[10] The speed of coral range expansions presented in this study reached up to 14 km/year, which is far greater than that of other species, including terrestrial species (average 0.61 km/year) [Parmesan and Yohe, 2003], and generally greater than that of other marine benthic species (as much as 5 km/year) reported so far [Helmuth et al., 2006]. In addition to rising SSTs, the Kuroshio and Tsushima warm currents may be contributing to the quick expansions. Although range expansions of corals have not been detected, range expansions of reef fish were suggested in eastern Australia [Figueira and Booth, 2010], where the Eastern Australian Current, which flows from the equator poleward toward the south, may play a similar role as the Kuroshio and Tsushima warm currents.

[11] Collectively, these findings strongly suggest that fundamental modifications of temperate coastal ecosystems due to climatic warming could be in progress, and in regions with poleward current flows (east coast of the United States [Precht and Aronson, 2004], east coast of South America, east coast of Africa and east coast of Australia [Figueira and Booth, 2010]) the speed would be much greater. Our results not only provide evidence to serve as a baseline for the rapid range expansions of tropical reef corals but they also have strong implications for the potential range expansions of tropical species associated with coral reefs, which would contribute to changes in coastal marine biodiversity and ecosystems in temperate areas.

[12] **Acknowledgments.** Jun Nemoto at Tohoku University Museum helped to examine the coral specimens. The Oceanic Wildlife Society provided field support. Support for coral identification was provided by the Japanese Society for Coral Taxonomy. Comments from two anonymous reviewers helped improve the paper. This paper arises from a pilot project for monitoring global warming effects on ecosystems funded by the Center for Global Environmental Research, National Institute for Environmental Studies. Supported in part by the Global Environment Research Fund of the Ministry of the Environment, Japan (RF-082).

[13] P. G. Strutton thanks Benjamin Greenstein and Bernhard Riegl.

References

- Carpenter, K. E., et al. (2008), One-third of reef-building corals face elevated extinction risk from climate change and local impacts, *Science*, *321*, 560–563, doi:10.1126/science.1159196.
- Diaz, C., et al. (2002), Workshop on advances in the use of historical marine climate data, *WMO Bull.*, *51*, 377–380.
- Figueira, W. F., and D. J. Booth (2010), Increasing ocean temperatures allow tropical fishes to survive overwinter in temperate waters, *Global Change Biol.*, *16*, 506–516, doi:10.1111/j.1365-2486.2009.01934.x.
- Glynn, P. W., and G. M. Wellington (1983), *Corals and Coral Reefs of the Galapagos Islands*, Univ. of Calif. Press, Berkeley.
- Greenstein, B. J., and J. M. Pandolfi (2008), Escaping the heat: Range shifts of reef coral taxa in coastal Western Australia, *Global Change Biol.*, *14*, 513–528, doi:10.1111/j.1365-2486.2007.01506.x.
- Hagiwara, R. (2003), Distribution, environmental conditions and sexual reproduction of the zooxanthellae corals at the Banda area of Tateyama Bay, Chiba, Japan, *Midoriishi*, *14*, 24–30.
- Harriott, V. J. (1999), Coral growth in subtropical eastern Australia, *Coral Reefs*, *18*, 281–291, doi:10.1007/s003380050195.
- Helmuth, B., et al. (2006), Living on the edge of two changing worlds: Forecasting the responses of rocky intertidal ecosystems to climate change, *Annu. Rev. Ecol. Evol. Syst.*, *37*, 373–404, doi:10.1146/annurev.ecolsys.37.091305.110149.
- Hoegh-Guldberg, O., et al. (2005), Coral bleaching following wintry weather, *Limnol. Oceanogr.*, *50*, 265–271, doi:10.4319/lo.2005.50.1.0265.
- Hoegh-Guldberg, O., et al. (2007), Coral reefs under rapid climate change and ocean acidification, *Science*, *318*, 1737–1742, doi:10.1126/science.1152509.
- Hoegh-Guldberg, O., and J. F. Bruno (2010), The impact of climate change on the world's marine ecosystems, *Science*, *328*, 1523–1528, doi:10.1126/science.1189930.
- Hongo, C., and H. Kayanne (2010), Relationship between species diversity and reef growth in the Holocene at Ishigaki Island, Pacific Ocean, *Sediment. Geol.*, *223*, 86–99, doi:10.1016/j.sedgeo.2009.10.005.
- Hongo, C., and H. Kayanne (2011), Key species of hermatypic coral for reef formation in the northwest Pacific during Holocene sea-level change, *Mar. Geol.*, *279*, 162–177, doi:10.1016/j.margeo.2010.10.023.
- Ma, T. Y. H. (1934), On the growth rate of reef corals and the sea water temperature in the Japanese islands during the latest geological times, *Sci. Rep. Tohoku Imp. Univ. Second Ser.*, *16*, 165–189.
- Manabe, T. (1999), The digitized Kobe Collection, Phase I: Historical surface marine meteorological observations in the archive of the Japan Meteorological Agency, *Bull. Am. Meteorol. Soc.*, *80*, 2703–2715, doi:10.1175/1520-0477(1999)080<2703:TDKCP1>2.0.CO;2.
- Mezaki, T., et al. (2007), Spawning patterns of high-latitude scleractinian corals from 2002 to 2006 at Nishidomari, Otsuki, Kochi, Japan, *Kuroshio Biosphere*, *3*, 33–47.
- Montaggioni, L. F. (2005), History of Indo-Pacific coral reef systems since the last glaciation: Development patterns and controlling factors, *Earth Sci. Rev.*, *71*, 1–75, doi:10.1016/j.earscirev.2005.01.002.
- Nomura, K., et al. (2008), Progressive faunal inventory of hermatypic corals in Kushimoto, Wakayama Prefecture, Japan, *Nanki Seibutsu*, *50*, 191–200.
- Oshiro, N. (2008), Toxic fishes and food poisoning occurred in Nansei Islands, *Nippon Suisan Gakkaishi*, *74*, 915–916, doi:10.2331/suisan.74.915.
- Parmesan, C., and G. Yohe (2003), A globally coherent fingerprint of climate change impacts across natural systems, *Nature*, *421*, 37–42, doi:10.1038/nature01286.
- Precht, W. F., and R. B. Aronson (2004), Climate flickers and range shifts of reef corals, *Front. Ecol. Environ.*, *2*, 307–314, doi:10.1890/1540-9295(2004)002[0307:CFARSO]2.0.CO;2.
- Sugihara, K., et al. (2009), Latitudinal changes in hermatypic coral communities from west Kyushu to Oki Islands in Japan, *J. Jpn. Coral Reef Soc.*, *11*, 51–67, doi:10.3755/jcrs.11.51.
- Takatsuki, Y., et al. (2007), Long-term trends in sea surface temperature adjacent to Japan, *Sokko Jiho*, *74*, S33–S87.
- Tittensor, D. P., et al. (2010), Global patterns and predictors of marine biodiversity across taxa, *Nature*, *466*, 1098–1101, doi:10.1038/nature09329.
- van Woesik, R. (1995), Coral communities at high latitude are not pseudopopulations: Evidence of spawning at 32°N, Japan, *Coral Reefs*, *14*, 119–120, doi:10.1007/BF00303433.
- Veron, J. E. N. (1992a), Conservation of biodiversity: A critical time for the hermatypic corals of Japan, *Coral Reefs*, *11*, 13–21, doi:10.1007/BF00291930.
- Veron, J. E. N. (1992b), *Hermatypic Corals of Japan*, 234 pp., Aust. Inst. of Mar. Sci., Townsville, Queensland.
- Veron, J. E. N., and P. R. Minchin (1992), Correlations between sea surface temperature, circulation patterns and the distribution of hermatypic corals of Japan, *Cont. Shelf Res.*, *12*, 835–857, doi:10.1016/0278-4343(92)90047-N.
- Veron, J. E. N. (2000), *Corals of the World*, Aust. Inst. of Mar. Sci., Townsville, Queensland.
- Wallace, C. G. (1999), *Staghorn Corals of the World: A Revision of the Coral Genus Acropora*, CSIRO, Collingwood, Victoria, Australia.
- Yamano, H., et al. (2001), Highest-latitude coral reef at Iki Island, Japan, *Coral Reefs*, *20*, 9–12, doi:10.1007/s003380100137.
- Yamano, H., and N. Namizaki (2009), Corals on the front: change of *Acropora solitaryensis* colonies at Tateyama, Chiba Prefecture, Japan, *J. Jpn. Coral Reef Soc.*, *11*, 71–72, doi:10.3755/jcrs.11.71.

K. Nomura, Kushimoto Marine Park Center, Kushimoto, Wakayama 649-3514, Japan.

K. Sugihara and H. Yamano, Center for Global Environmental Research, National Institute for Environmental Studies, 16-2 Onogawa, Tsukuba, Ibaraki 305-8506, Japan. (hyamano@nies.go.jp)