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Ocean acidification limits temperature-induced poleward expansion of coral habitats around Japan

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Abstract

Using results from four coupled global carbon cycle-climate models combined with in situ observations, we estimate the combined effects of future global warming and ocean acidification on potential habitats for tropical/subtropical and temperate coral communities in the seas around Japan. The suitability of the coral habitats are identified primarily on the basis of the currently observed ranges for temperature and saturation states Ω with regard to aragonite (Ω_{arag}). We find that under the "business as usual" SRES A2 scenario, coral habitats will expand northward by several hundred kilometers by the end of this century. At the same time, coral habitats are projected to become sandwiched between the tropical regions, where the frequency of coral bleaching will increase, and the temperate-to-subpolar latitudes, where Ω_{arag} will become too low to support sufficiently high calcification rates. As a result, the area of coral habitats around Japan that is suitable to tropical-subtropical communities will be reduced by half by the 2020s to 2030s, and is projected to disappear by the 2030s to 2040s. The suitable habitats for the temperate coral communities are also becoming smaller, although at a less pronounced rate due to their higher tolerance for low Ω_{arag}.

1 Introduction

Today's distribution of hermatypic (reef-building) corals is confined to a relatively narrow range of sea surface temperatures (SST) and saturation states, with regard to the mineral carbonate aragonite (Ω_{arag}; Hoegh-Guldberg, 2005). These corals usually do not tolerate SSTs below 18 °C (e.g., Kleypas et al., 1999a) and are subject to bleaching if SST during the hottest months exceeds the climatological values by more than 2 °C for at least one month (Hoegh-Guldberg et al, 2007). Due to their dependence on the formation of an aragonite skeleton, corals are also sensitive to the carbonate ion concentration, $[CO_3^{2-}]$, and to Ω_{arag}. There is growing evidence that low pH and Ω_{arag} impact the coral's physiological processes negatively, especially their calcification rates (e.g., Gattuso et al., 1998; Kleypas et al., 1999a; Langdon et al., 2000, 2003), and their overall productivity (Anthony et al., 2008). Furthermore, such conditions tend to reduce the sperm's flagellar motility in broadcast spawners (Morita et al., 2009), which compromises recruitment success (Albright et al., 2010). Reduced recruitment success is further aggravated by the observation that the early life stages are particularly sensitive to low pH and Ω_{arag} conditions (e.g., Morita et al., 2009). Finally, experiments have also shown that exposure to low pH and Ω_{arag} makes corals more prone to bleaching (Anthony et al., 2011).

Although hermatypic corals do not have a single marginal threshold for Ω_{arag} and $[CO_3^{2-}]$, the current distribution of coral reefs in the Pacific Ocean is quite clear: no coral reef exists in waters with an Ω_{arag} of less than 3 (Kleypas et al., 1999b; Guinotte et al., 2003), indicating that this lower threshold is quite robust for these reef building warm water corals. Based on these Ω_{arag} thresholds, Guinotte et al. (2003) classified hermatypic coral habitats with an $\Omega_{arag} < 3$ as "extremely marginal", i.e., essentially not suitable for growth, habitats with $3 \leq \Omega_{arag} < 3.5$ as "marginal", and habitats with an $\Omega_{arag} \geq 3.5$ as "adequate to optimal". With regard to temperature, they defined the suitable range when SST > 18.4 °C in the coldest months, and when it does not exceed 31.1 °C during the hottest months of the year.

The human-induced increase in atmospheric CO_2 changes the distribution of suitable habitats for warm-water corals in at least two ways: first, rising sea surface temperatures in response to global warming will permit coral habitats to expand poleward (Precht and Aronson, 2004; Yamano et al., 2011), while at the same time possibly limiting their habitat in the tropics due to excessive bleaching (Guinotte et al., 2003; Meissner et al., 2012). Second, lowered Ω_{arag} due to the uptake of anthropogenic CO_2 from the atmosphere will affect the growth and fitness of corals everywhere, but particularly at higher latitudes, where the saturation state will reach critically low levels first (Kleypas et al., 1999b; Orr et al., 2005; Steinacher et al., 2009). The rise in atmospheric CO_2 of more than 30 % since pre-industrial times has increased global average SST by at least 0.5 °C (Trenberth et al., 2007) and has lowered surface ocean pH by about 0.1

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units and ocean Ω_{arag} by about 0.3 units (Feely et al., 2008). If CO_2 continues to rise unabatedly, much larger changes are in store, i.e., increases in SST of several degrees Celsius and drops in pH of up to nearly one unit and even more for Ω_{arag} (e.g., Feely et al., 2009).

Kleypas et al. (1999b) were first to systematically investigate the impact of future ocean acidification on coral habitats on a global scale. They highlighted that in a "business as usual" scenario with atmospheric CO_2 increasing to double its pre-industrial value in 2065, the drop in Ω_{arag} moves most of the current habitats for warm water corals outside the suitable range. Guinotte et al. (2003) extended this analysis by including also the effect of rising temperatures. They pointed out that the warming of the tropical Pacific puts much of the Western Tropical Pacific above the bleaching threshold of 31.1 °C, further stressing the coral communities. More recently, Meissner et al. (2012) revisited these findings by using a model of intermediate complexity and investigating a new set of emission scenarios. They confirm many of these previous findings, also emphasizing the combined stress by warming and decreased saturation states. They project that most of the tropical-subtropical coral reefs will experience severe bleaching events by the 2030s–2050s, but that the impact of the changes in Ω will tend to exceed the impact of the changes in SST.

In contrast to the reduction of the tropical habitats due to increased bleaching, the possible poleward extension of suitable habitats due to higher-latitude regions warming above the lower temperature threshold has received less attention (Precht and Aronson, 2004). Recently, Yamano et al. (2011) demonstrated on the basis of long-term coral reef observations that such a northward expansion has already occurred along the coastlines of Japan. Yara et al. (2009, 2011) investigated the potential future development of this northward expansion along the coasts of Japan, suggesting that this trend might continue for several decades. However, they took only the change in temperature into account, but not the changes in the saturation state.

Here, we build on this prior work and investigate the future development of potential habitats for coral communities in the seas close to Japan. In addition to warm water

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coral communities, we also focus on the habitat distribution of temperate corals, which do not form reefs and which have not been discussed extensively in the literature. Japan offers a unique opportunity to study the combined impacts of ocean warming (bleaching and poleward range expansion) and acidification, as it covers a wide latitudinal range, stretching from subtropical to temperate areas (Fig. 1). Furthermore, the coral distributions around the Japanese islands have been well studied and described, permitting researchers to assess future changes against a well established current state. In fact, some of the climate-change induced consequences have already been observed in Japan. A long duration (~ 1 month) of SSTs $\geq 30\,^{\circ}\mathrm{C}$ in summer caused severe bleaching in 1998 and 2007 in the southern part of Japan (e.g., Kayanne et al., 1999). Based on an in situ SST time series and an inventory of corals around Japan that dates back to the 1930s, Yamano et al. (2011) described a temperature-induced poleward range expansion of tropical coral species to temperate areas at speeds of up to $14\,\mathrm{km\,yr^{-1}}$. A final reason is that because of Japan's relatively small landmass in comparison with other settings, the coral distribution is likely to be less disturbed by terrestrial influences (Yamano et al., 2011).

The northern limit of coral reefs dominated by coral communities typically found in tropical-subtropical regions is currently situated at Tanegashima Island (30.7° N, 131.0° E) and Mageshima Island (30.4° N, 130.5° E), of Kagoshima Prefecture (Hori, 1980; Nakai, 1990; Kan et al., 2005; Ikeda et al., 2006), where the observed SST during the coldest months is $18\,^{\circ}\mathrm{C}$ and annual mean surface Ω_{arag} value is about 3.4, consistent with the Pacific-wide limits of the distribution of coral reefs (e.g., Kleypas et al., 1999a, 2006).

Corals are also frequently found in the temperate areas of Japan. They normally do not contribute to reef-building, though the world's most northerly coral reefs are found at Iki and Tsushima islands (34.1° N, 129.5° E) (Yamano et al., 2012). The northernmost coral (*Oulastrea crispata*) around Japan is currently found at Sadogashima Island (38.0° N, 138.2° E), of Niigata Prefecture (Honma and Kitami, 1978), where SST gets as low as $10\,^{\circ}\mathrm{C}$ during the coldest month. Also, the lowest Ω_{arag} there is around

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2.3, which is calculated from observed data of SST, sea surface salinity (SSS), and pH from Niigata Prefectural Fisheries and Marine Research Institute (2007, 2008, 2009 and 2010) and total alkalinity from Lee et al. (2006). Thus, Japan's two coral communities, i.e., the tropical-subtropical ones and temperate ones, have very different ranges for SST and Ω_{arag}, likely leading to differing responses to future climate change.

In order to quantify these differential responses, we examine the simultaneous effects of warming (bleaching and poleward range expansion) and ocean acidification until the end of this century for a "business as usual" CO_2 emission scenario (SRES A2).

We use simulation results from four fully-coupled global three-dimensional (3-D) atmospheric-ocean climate models that include complete carbon cycle modules (Steinacher et al., 2009, 2010). We then add the changes projected from these models to present-day climatologies in order to obtain a best estimate of the future trajectories of SST and Ω_{arag} in the near-surface ocean. We compare the speed of poleward range expansion of coral species to the speed of the change in the aragonite saturation state Ω_{arag}, and provide an updated projection of coral habitat marginality for the 21st century around the coast of Japan for both the tropical-subtropical and temperate coral habitats.

2 Methods

2.1 Climatological data and future projections

To project the combined effects of global warming and ocean acidification on coral habits for this century, we combine results from climate models for the coming decades with present-day climatological observations. In particular, we only use the information about the changes in SST and Ω_{arag} relative to today from the climate models, and add them to the present-day monthly climatological distributions to construct a more accurate description of the future projections. This method has been applied frequently

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in order to remove biases in the models' mean-states (e.g., Orr et al., 2005; Yara et al., 2009, 2011).

Given the lack of a surface ocean monthly climatology of Ω_{arag}, we computed monthly Ω_{arag} values on the basis of monthly fields of dissolved inorganic carbon (DIC), alkalinity (ALK), sea-surface temperature (SST), sea-surface salinity (SSS), phosphate (PO_4) and silicic acid ($Si(OH)_4$). The latter four (SST, SSS, PO_4 and $Si(OH)_4$) were taken from the World Ocean Atlas, version 2005 (WOA05), while we estimated the monthly surface climatologies of DIC and Alk using a combination of empirical relationships and the surface ocean $p\mathrm{CO}_2$ climatology of Takahashi et al. (2009). Namely, we computed surface ALK from monthly mean SST and SSS using the method detailed in Lee et al. (2006). We then calculated monthly mean DIC from monthly mean ALK and monthly mean sea surface $p\mathrm{CO}_2$ from Takahashi et al. (2009) using the OCMIP carbonate chemistry routines (http://www.ipsl.jussieu.fr/OCMIP/phase3/simulations/NOCES/HOWTO-NOCES-3.html) and SST, SSS, and the nutrients PO_4 and $Si(OH)_4$ from WOA05. All these monthly fields were then used to compute the monthly climatology of Ω_{arag} using the same OCMIP routines. The monthly DIC and Ω_{arag} fields correspond to a climatological year 2000, owing to the use of the surface $p\mathrm{CO}_2$ fields of Takahashi et al. (2009) which were adjusted to this reference year. All data were interpolated onto a $1^\circ \times 1^\circ$ grid for the Western North Pacific (area bounded by 24°–48° N, 118°–157° E).

To project the seasonal climatological distributions forward in time, we used annual mean SST and Ω_{arag} from four fully coupled global 3-D atmospheric-ocean climate models for 1980–2099. The models are the IPSL-CM4-LOOP model (IPSL; Friedlingstein et al., 2006), the Earth System Model employed at the Max Planck Institute for Mathematics (MPIM; Marsland et al., 2003; Maier-Reimer et al., 2005; Roeckner et al., 2006), the NCAR CSM1.4-carbon climate model (Fung et al., 2005; Doney et al., 2006), and the NCAR CCSM3 Biogeochemical Elemental Cycling Model (Moore et al., 2004). All models contain a carbon cycle module for both terrestrial and oceanic compounds, and three of the four models contributed to the IPCC Fourth Assessment Report (IPCC, 2007; Meehl et al., 2007; Solomon et al., 2007). The horizontal resolution of the models

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is $2^\circ \times 2^\circ$, $1.5^\circ \times 1.5^\circ$, $3.6^\circ \times 0.8$–1.8° and $3.6^\circ \times 1$–2° for IPSL, MPIM, CSM1.4, and CCSM3, respectively. The experimental setup for the future climate runs is described in Steinacher et al. (2010). Briefly, after a spin-up period of more than 1000 yr under pre-industrial conditions, the models were forced with prescribed CO_2 emissions from reconstructions over the 19th and 20th centuries and following the SRES-A2 "business as usual" emission scenario from 2000–2099 (IPCC, 2000). Carbonate ion concentration and the carbonate saturation state were calculated offline from modeled quantities using the standard OCMIP carbonate chemistry routines (see Steinacher et al., 2009 for details). All model data were interpolated on a regular $1^\circ \times 1^\circ$ grid to match the spatial resolution of the observational data described in the preceding section.

To produce the final monthly fields for SST and Ω_{arag} for the 21st century, we added the modeled annual mean SST and Ω_{arag} anomalies from 2000–2099 to the observation-based monthly climatologies. We thereby assumed constant seasonal cycles for SST and Ω_{arag} during the 21st century, which is generally supported by results from climate models (Steinacher et al., 2009), although there is a tendency for the seasonal cycle of Ω_{arag} to increase with time, due to the decreasing buffer capacity of the ocean (Rodgers et al., 2008). The modeled anomalies were computed by subtracting from the results the modeled climatological 20-yr mean SST and Ω_{arag} over the 1980–1999 period. From the seasonal envelope, we derived SST during the hottest and coldest months of each year, and the lowest monthly Ω_{arag} for each year. Finally, we calculated the decadal means of the bias-corrected SST of the hottest/coldest and annual lowest Ω_{arag} for each decade between 2000 and 2099.

2.2 Suitable coral habitats

We determine the potential future habitats for corals in terms of regions with a given annual range in SST and Ω_{arag}. For the tropical-subtropical (reef-building) coral community, we use the 18 °C isotherm during the coldest months of each year as the northern limit, and the 30 °C isotherm during the hottest months of each year as a southern limit (Kayanne et al., 1999). For the temperate coral community, the northern limit was

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set to the 10 °C isoline during the coldest month of each year. These thresholds are the same as those used by Yara et al. (2009, 2011) and reflect also today's distributional limits of coral reefs and corals in Japan, respectively.

Following Kleypas et al. (1999b) and Guinotte et al. (2003) we adopted the isoline of $\Omega_{arag} = 3$ at the annual lowest value of each year as the northern limit of the tropical-subtropical coral community. For the temperate coral community, the isoline of $\Omega_{arag} = 2.3$ at the annual lowest value of each year, was chosen as the northern limit. This latter threshold was chosen because it corresponds to the annual minimum at the current northern limit of coral occurrence at Sadogashima Island (Niigata Prefectural Fisheries and Marine Research Institute, 2007, 2008, 2009, 2010). The isoline of $\Omega_{arag} = 1$, below which aragonite dissolves, at the annual lowest value for each year, was also examined as a reference.

We calculated the percentage of coastal waters within a certain range of SST and Ω_{arag} as an indicator of habitat suitability for the two different coral communities (see Table 1). Tropical-subtropical coral habitats are defined as "suitable" when $18\,^{\circ}\mathrm{C} \leq \mathrm{SST} < 30\,^{\circ}\mathrm{C}$ and $\Omega_{arag} \geq 3.5$, "marginal" when $3 \leq \Omega_{arag} < 3.5$, and "unsuitable" when $\mathrm{SST} \geq 30\,^{\circ}\mathrm{C}$ or $\Omega_{arag} < 3$. The habitats for temperate coral communities were defined as "suitable" if $10\,^{\circ}\mathrm{C} \leq \mathrm{SST} < 18\,^{\circ}\mathrm{C}$ and $2.3 \leq \Omega_{arag}$, "marginal" when $1 \leq \Omega_{arag} < 2.3$, and "unsuitable" if $\Omega_{arag} < 1$. No observational evidence for a SST threshold between marginal and unsuitable regimes has been reported for the northernmost boundary of temperate coral occurrence, and the threshold will not be discussed in this study. These thresholds defining the suitability of the corals habitats are by necessity an approximation and will be used as a guide to document the changes rather than as absolute thresholds.

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3 Results and discussion

3.1 Data evaluation

Given the highly derived nature of the computed monthly climatological Ω_{arag} distribution around Japan, it is critical to evaluate this product with in situ observations. Two datasets were used to this end: first, winter cruise data from the Japanese Meteorological Agency (JMA)/Meteorological Research Institute (MRI) for 1983–1999 (Midorikawa et al., 2010; Ishii et al., 2011) along the transect at 24°–33° N, 137° E (Fig. 1) and second, monthly station data for Sadogashima Island (38.0° N, 138.2° E) for 2005–2009. The latter were measured at a depth of 2.5 m at 04:00 p.m. local time each day (Niigata Prefectural Fisheries and Marine Research Institute, 2007, 2008, 2009, 2010; Fig. 1).

The WOA05/Takahashi-based climatological SST during the coldest months and the annual lowest Ω_{arag} for each year correlate well with those measured in the JMA/MRI winter cruise data (Midorikawa et al., 2010; Ishii et al., 2011; Fig. 2a, b; $R^2 = 0.95$ and 0.96 for SST and Ω_{arag}, respectively). However, our WOA05/Takashashi-based SST and Ω_{arag} are biased low, on average, by 0.5 °C and 0.16 units. The WOA05/Takahashi-based SST and Ω_{arag} correlate also well with the in situ data at Sadogashima Island ($R^2 = 0.98$ for SST and 0.79 for Ω_{arag}, respectively; Fig. 2c, d). Almost no bias was observed for the WOA05-based SST with respect to these in situ observations (slopes of 1.00 and no offset), but Ω_{arag} is systematically biased low by about 0.9 units. This bias is largely due to a slope that is only half as large as the one of the 1 : 1 line, leading to high underestimations of Ω_{arag} at high Ω_{arag}, but low underestimations of Ω_{arag} at low Ω_{arag}.

Differences in Ω_{arag} may be due to the different temporal and spatial resolutions of the WOA05/Takahashi-based data with respect to in situ observations. Recognizing the partially substantial discrepancies between the WOA05/Takahashi-based data and the in situ observations, we nevertheless use the WOA05/Takahashi-based data for our subsequent analyses. This is mostly because they permit us to cover all areas, while

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the in situ data are available from only a highly limited number of places. However, we discuss the uncertainty arising from the model-data misfit in the discussion section.

3.2 Projected shifts in tropical-subtropical and temperate coral habitats

Over the course of the 21st century, the average isolines of SST = 18 °C and 10 °C during the coldest months, i.e. the isolines that define the northernmost boundaries of the tropical/subtropical and temperate coral communities, respectively, are projected to shift consistently poleward (Fig. 3). As the coral habitats move northward, the corals are increasingly immersed in waters with a low Ω_{arag}. The isolines of $\Omega_{arag} = 3$ and 2.3, which define the northernmost boundaries of the two coral communities, are progressively moving southward, due to ocean acidification, quenching the coral habitats. Next, we investigate these shifts in the suitable habitats in more detail, separately for the tropical/subtropical and the temperate coral communities.

3.2.1 Tropical-subtropical coral communities

In the 2000s, the calculated northern limit of the tropical-subtropical coral community is located in Southwest Japan (Fig. 3), which agrees with previous observations (e.g., Veron, 1995; Kleypas et al., 1999a; Buddemeier et al., 2004). All the habitats to the south of this line are bathed in waters with $\Omega_{arag} \geq 3$, i.e. they are all suitable for tropical-subtropical corals. With ocean warming, the 18 °C isotherm during the coldest month is moving northward along the eastern coast of Japan. By the end of this century, the entire eastern coast of Japan south of Tokyo has become suitable for growth for the tropical-subtropical corals on the basis of temperature (see also Yara et al., 2011).

At the same time, the 30 °C isotherm in the hottest months is moving northward as well. By the 2050s, the 30 °C isoline is projected to enter the domain from the south (Fig. 3). By 2070, large areas on the eastern coast of West Japan (Kyushu and Shikoku Islands; Fig. 1) are above this threshold, implying that these habitats are expected to experience severe and repeated coral bleaching events (Yara et al., 2009). Taken

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together, habitats suitable for tropical and subtropical corals identified solely on the basis of the temperature tolerance are moving northward, but increasingly become scarce, as the northern limit is moving northward more slowly (by $2.6 \pm 0.6\,km\,yr^{-1}$) than the southern boundary is (by $7.8 \pm 0.0\,km\,yr^{-1}$); number of models: $n = 1$.

Ocean acidification worsens this temperature-induced habitat restriction substantially. As the isotherms are moving northward, the isolines of Ω_{arag} are moving southward, pushing all habitats around Japan below the $\Omega_{arag} = 3$ threshold by the 2030s, i.e., within a few decades, there is no longer any habitat that is suitable for growth for the tropical and subtropical coral communities (Fig. 3). The changes in areal extent of the habitats suitable for these communities around Japan become even more evident in Fig. 4, highlighting that by the 2030s, all of the areas around Japan that have suitable temperatures for tropical-subtropical corals have an $\Omega_{arag} < 3$. Given the immediacy of this date, this projection is largely independent of the particular emission trajectory, as even substantially smaller emission trajectories are reaching the atmospheric CO_2 concentration of the A2 scenario in 2030 within the next 40 yrs.

Overall, the tropical-subtropical coral communities around Japan are projected to experience conditions far outside their present range. By the 2020s, the total area suitable for tropical-subtropical communities increases by only 5 % due to the elevated SST, but it decreases by 55 % due to the lower Ω_{arag} (Fig. 5). Given the combined effects of global warming and ocean acidification, the area of suitable habitats for tropical-subtropical coral communities around Japan will decrease by 55 % by the 2020s, and will disappear by the 2030s.

Figure 6 shows the projected SST and Ω_{arag} in the 21st century for Kushimoto-Shirahama (33.5° N, 135.7° E) and Tateyama (35.0° N, 139.8° E), where migration of the tropical-subtropical coral community starts and on-site monitoring of the poleward range expansion of coral habitats has been conducted (Yamano et al., 2011; Yara et al., 2011). Until the 2030s, both Kushimoto-Shirahama and Tateyama are projected to be located within the "suitable" regime in terms of SST, but in terms of Ω_{arag}, the sites will move out of the "suitable" and into the "marginal" regime in the 2010s. Therefore, the

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negative effects of ocean acidification precede the positive effect of global warming on tropical-subtropical coral reef formation at these two sites.

3.2.2 Temperate coral communities

The projected poleward expansion of habitats for temperate coral communities during the 21st century as indicated by the 10 °C isotherm imply a shift of the northern boundary from from Sadogashima Island (38.0° N, 138.2° E) to the Tsugaru Straits (41.3° N, 140.4° E; Figs. 1 and 3). Thus, the entire mainland of Japan will become a potential coral habitat in terms of SST by the end of the 21st century. While the Honshu Island west of Tokyo, and Northern Shikoku and Kyushu Iskands are currently habitats for temperate corals, they are projected to host both tropical-subtropical and temperate coral communities in the future, as projected by Yara et al. (2011).

However, coral communities are projected to experience unprecedented levels of Ω_{arag} due to ocean acidification. Figure 4b shows the projected temporal changes in Ω_{arag} for the temperate coral community. For the present period (in 2010s), the models simulate that 77 % of the temperate coral community habitats exists in waters with $\Omega_{arag} \geq 2.3$, i.e. within the limits of suitability. However, over the course of the 21st century, areas with $\Omega_{arag} \geq 2.3$ will decrease and areas with $\Omega_{arag} < 2.3$ will increase. In the 2080s, 8 % of the current temperate coral community is projected to experience undersaturation ($\Omega_{arag} < 1$). At the end of the 21st century, one fifth of the current temperate coral habitat is projected to experience undersaturation, indicating that also temperate coral habitats will become endangered due to ocean acidification, despite their substantially higher tolerance for low Ω_{arag} conditions.

3.3 Speed of coral habitat transitions

We averaged SST and Ω_{arag} longitudinally and projected the progression of critical Ω_{arag}- and SST-isolines onto the north-south (latitudinal) axis to estimate the speed of change in these variables. The poleward expansion due to changes in SST proceeded with a latitudinal speed of $2.6 \pm 0.6\,\mathrm{km\,yr^{-1}}$ for the 18 °C isoline (northern limit of the tropical-subtropical coral community) and at $1.2 \pm 0.8\,\mathrm{km\,yr^{-1}}$ for the 10 °C isoline (northern limit of temperate coral occurrence).

These estimated speeds are similar to those of $1\,\mathrm{km\,yr^{-1}}$ for the potential habitat expansion of tropical-subtropical coral communities and $4\,\mathrm{km\,yr^{-1}}$ for the poleward migration of temperate coral habitats, respectively, predicted by Yara et al. (2011). However, both model results are notably smaller than the observed speed of the recent expansion of tropical coral habitats of up to $14\,\mathrm{km\,yr^{-1}}$ (Yamano et al., 2011). The difference between this observed speed and our projected one is presumably caused by two factors (see also Yara et al., 2011): first, our speeds are based on decadal averages of the potential habitat expansion of an entire community, while Yamano et al. (2011) analyzed the speed of new colony settlements for a specific indicator species. Second, we only consider here the influence of SST, while the observed migration speed might have been enhanced due to other factors, such as water depth, salinity, nutrient concentration, and competition with large seaweeds, none of which we considered. Notwithstanding this difference, we conclude that if SST were the only factor, we would expect species to keep up with the rate of change, and that entire coral ecosystems would migrate poleward without major impediments.

However, the southward progression of the reduction in Ω_{arag} is likely to limit this expansion for those species sensitive to ocean acidification. The isolines of $\Omega_{arag} = 3$ and $\Omega_{arag} = 2.3$ move southwards with a latitudinal velocity of $21.1 \pm 1.7\,\mathrm{km\,yr^{-1}}$ and $28.2 \pm 11.6\,\mathrm{km\,yr^{-1}}$, respectively. The speed of these changes is of the order of or is even faster than the migration speeds observed by Yamano et al. (2011), suggesting that migration likely will not be a successful option for the affected coral communities. The migration could be additionally slowed down by the negative impacts of ocean acidification on a range of processes involved in coral reproduction, such as fertilization, settlement and growth of early life stages of *Acropora palmata* (Albright et al., 2010), and sperm flagellar motility in *Acroporidae* (Morita et al., 2009), any of which may decrease future migration speed. Additionally, coral migration towards the south will not be favored in parts of the east coast of Japan, due to the strong poleward Kuroshio Current.

3.4 Uncertainty in the SST and Ω_{arag} projections

Two sources of uncertainty and biases need to be considered for our projections. First, uncertainties associated with our present-day climatologies, and second, uncertainties associated with the model-based future projections.

For the latter, we use the range of the four model projections as an indicator of uncertainty. It turns out that the models simulated similar changes in annual mean SST in the seas close to Japan (Fig. 7a), whereas their Ω_{arag} projections deviated more strongly from each other (Fig. 7b). Deviations in SST and Ω_{arag} were largest in the Pacific Ocean south of Tokyo (35.4° N, 139.5° E; Fig. 1), because the monthly-mean isolines of SST = 18 °C during the coldest months and Ω_{arag} = 3 as the lowest annual value were predicted to be located south of the Kuroshio Current (Yara et al., 2011). In this region, the latitudinal SST and Ω_{arag} gradients are both small, so slight differences in the projected SST and Ω_{arag} among the models lead to large differences in the location of the isolines. Furthermore, the coarse resolution of the models results in a poor representation of small-scale features such as enclosed regions or strong narrow currents.

The differences between the models decreased after the 2030s when the monthly-mean isolines of SST = 18 °C during the coldest months shifted away from the Kuroshio Current in which the latitudinal SST gradient is relatively large (Yara et al., 2011). SST anomalies were highly consistent among the models for the 18 °C and 10 °C isolines. However, the models did not simulate the occurrence of high SSTs in the southern part of our domain consistently. The 30 °C isothermal line, one of the thresholds for an increased risk of coral bleaching (Kayanne et al., 1999), was predicted to reach our domain from the south in the 2030s by one model, but in the 2060s by another model (Fig. 7a). Hence, the uncertainty in the simulation of high SSTs by different models is larger than that for the lower SSTs. Similarly, the uncertainty in the simulation of Ω_{arag}

by different models increases with time. The location of the northern limit of the tropical-subtropical coral community and temperate coral occurance (defined by the isoline of Ω_{arag} = 3 and 2.3, respectively), is projected differently between models for the period after 2010s and after 2040s, respectively (Fig. 7b).

The uncertainties associated with the climatologies (see Sect. 3.1) also affect directly our estimates. While the comparisons with the in situ data revealed relatively small biases for SST, the biases for Ω_{arag} are considerable and negative (Fig. 2). This means that our projected transitions to low Ω_{arag} occur likely too early and that the suitable areas are in reality likely larger than projected. The impact of this bias on our estimates is difficult to evaluate given the very limited data available for the evaluation of our climatologies, but we consider it to be less than one decade. We consider this uncertainty by expanding the decades when certain transitions occur to at least two decades (Fig. 5).

4 Conclusions

Under unabated anthropogenic CO_2 emissions that are strongly dependent on current and future political and economic decisions, future coral habitats in seas surrounding Japan will be sandwiched between high temperature regions, where the frequency of coral bleaching is predicted to increase, and low aragonite saturation states that will reduce calcification rates and overall reproductive success.

The impact of these changes in habitats on the actual coral communities depends critically on their ability to adapt. While experiments for tropical-subtropical corals show their poor adaptation to changes in Ω_{arag} (e.g., Anthony et al., 2008; Diaz-Pulido, 2011), no such experiments with temperate coral communities have been reported in the literature. Hence, it is not clear whether temperate corals will be able to adapt to fast decreases in the $CaCO_3$ saturation state of their future habitats. However, several studies have reported survival of some coral species upon skeleton dissolution (e.g., Fine and Tchernov, 2007), thus confirming the naked coral hypothesis (Stanley and Fautin,

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2001). Whether or not corals in seas close to Japan will be able to survive decalcification is unclear, but it is certain that decalcification of coral reefs will alter reef biodiversity and ecosystems. Future studies must include the effects of combined factors on corals besides SST increase and Ω_{arag} decrease, such as changes in water depth, salinity, nutrient concentration, and competition with large seaweeds, and should focus not only on the tropical-subtropical coral community but also consider the temperate coral community. In particular, observational studies are necessary to determine the vulnerability of temperate coral species to low Ω_{arag} values.

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Table 1. Habitat characterization for the tropical/subtropical and the temperate coral communities.

	Tropical/subtropical corals				Temperate corals			
	SST	Source	Ω_{arag}	Source	SST	Source	Ω_{arag}	Source
Suitable	$18^{\circ}C \leq SST < 30^{\circ}C$	(1)	$\Omega_{arag} \geq 3.5$	(3)	$10^{\circ}C \leq SST < 18^{\circ}C$	(1),(4)	$\Omega_{arag} \geq 2.3$	(1)
Marginal	Undefined		$3 \leq \Omega_{arag} < 3.5$	(3)	Undefined		$1 \leq \Omega_{arag} < 2.3$	(1)
Unsuitable	$SST \geq 30^{\circ}C$	(2)	$\Omega_{arag} < 3$	(3)	Undefined		$\Omega_{arag} < 1$	(1)

Sources:
(1) Kleypas et al. (1999b);
(2) Kayanne et al. (1999);
(3) Guinotte et al. (2003);
(4) This study.

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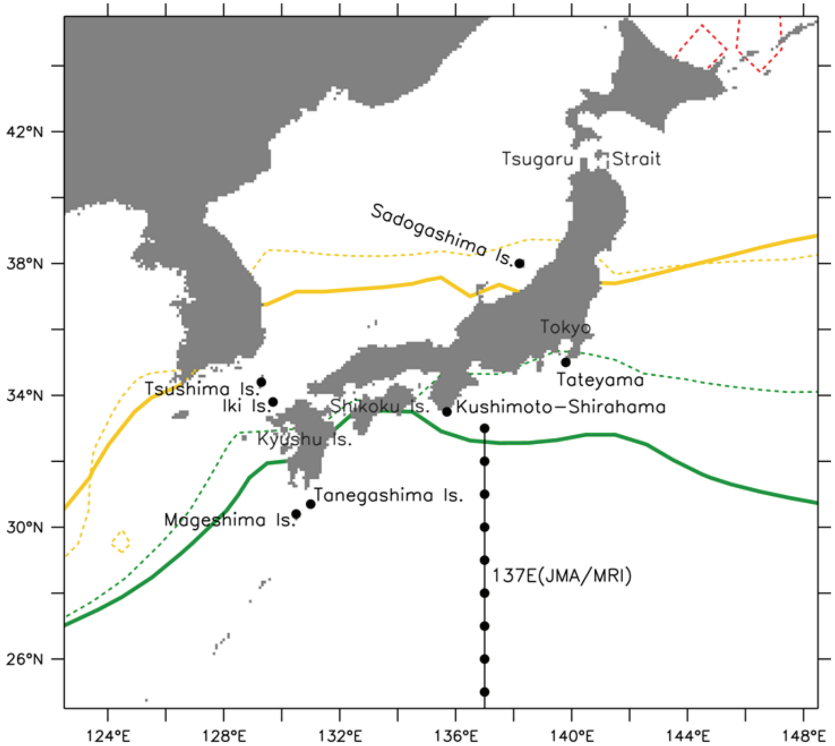

Fig. 1. Study site locations. At present, Sadogashima Island (38.0° N, 138.2° E) marks the northern limit of the temperate coral occurrence. Kushimoto-Shirohama (33.5° N, 135.7° E) and Tateyama (35.0° N, 139.8° E) are located in the current transition area of the tropical-subtropical coral community and the temperate coral community. The JMA/MRI cruise was a 137° E transect used to validate the projected SST and Ω_{arag}. Isothermal lines of SST = 18 °C (solid green line) and 10 °C (solid yellow line) and isolines of Ω_{arag} = 3.0 (dotted green line), 2.3 (dotted yellow line) and 1.0 (red dotted line) during the coldest months for the present period are also presented.

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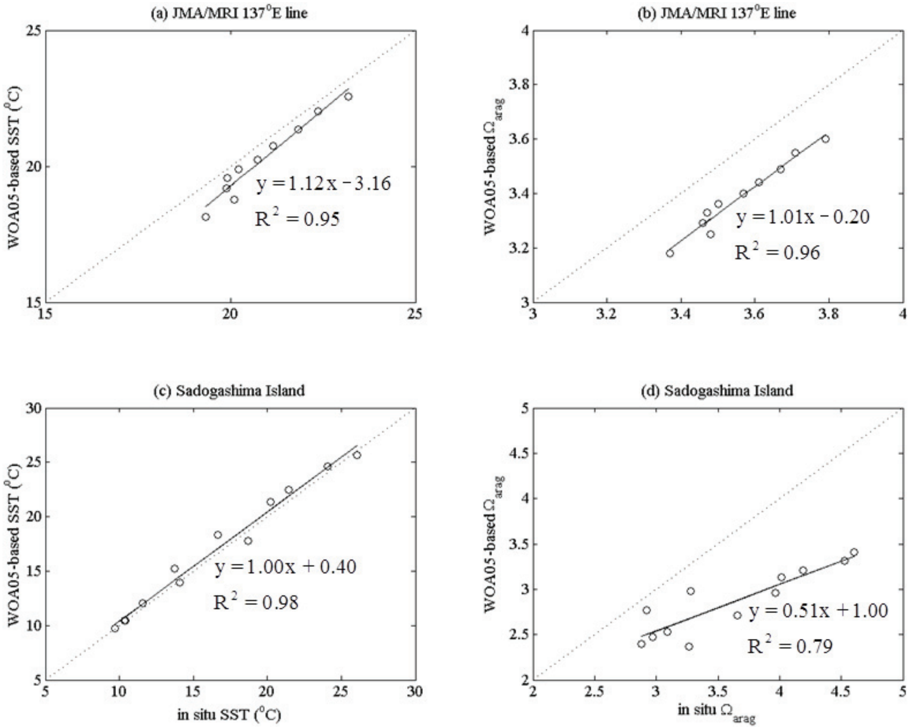

Fig. 2. WOA05-based monthly climatology vs. in situ diagram of **(a)** monthly SST and **(b)** monthly Ω_{arag} on the JMA/MRI transect from 24° N to 33° N along 137° E in winter (January and February), and **(c)** monthly SST and **(d)** monthly Ω_{arag} in Sadogashima Island (38.0° N, 138.2° E) for 2005–2009, respectively. In situ data are based on Midorikawa et al. (2010) and Ishii et al. (2011) for **(a)** and **(b)**, and Niigata Prefectural Fisheries and Marine Research Institute (2007, 2008, 2009, and 2010) for **(c)** and **(d)**, respectively. The dotted line in each figure is the 1 : 1 line.

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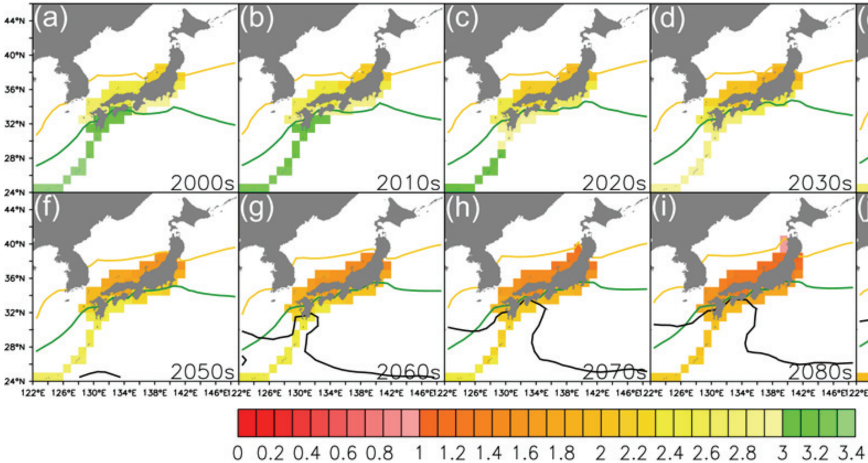

Fig. 3. Projected 10 yr average SST for the coldest months and Ω_{arag} as the annual lowest value during 2000s–2090s for the mean of four models. Lines depict the isolines of SST = 18 °C (green lines) and SST = 10 °C (yellow lines) during the coldest months, and the isoline of SST = 30 °C (black lines) during the hottest months. Shades denote the annual lowest Ω_{arag} values.

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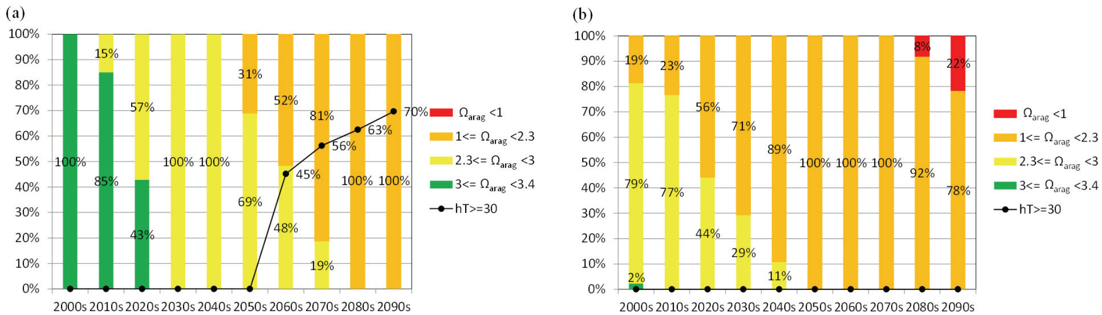

Fig. 4. Projected temporal changes in the surface area of coral habitats where the monthly-mean SST in the coldest months for 1990s–2090s is **(a)** ≥ 18 °C (tropical-subtropical coral community) and **(b)** 10–18 °C (temperate coral community), respectively. Colors represent the domain of $\Omega_{arag} < 1$ (in red), $1 \le \Omega_{arag} < 2.3$ (in orange), $2.3 \le \Omega_{arag} < 3$ (in yellow), and $3 \le \Omega_{arag} < 3.4$ (in green), respectively. Black lines show projected ratio of the surface area where the SST during the hottest months is ≥ 30 °C in each domain.

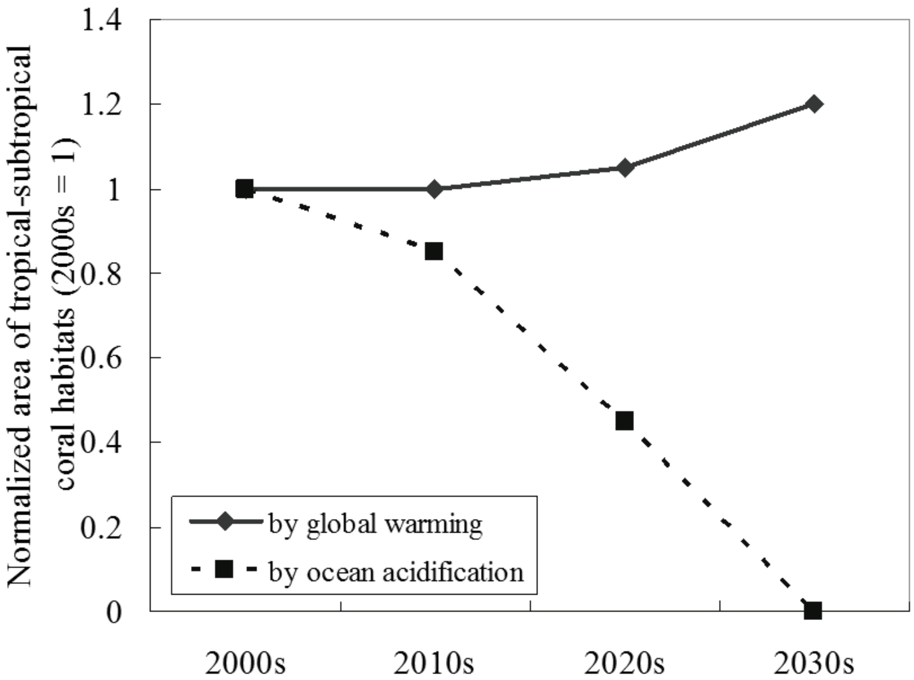

Fig. 5. Projected temporal changes in the normalized surface area of tropical-subtropical coral habitats in 2000s through 2030s (as of 2000s = 1). The solid line shows the area increase by SST warming due to global warming. The dotted line shows the decrease in area due to the decrease in Ω_{arag} as a result of ocean acidification.

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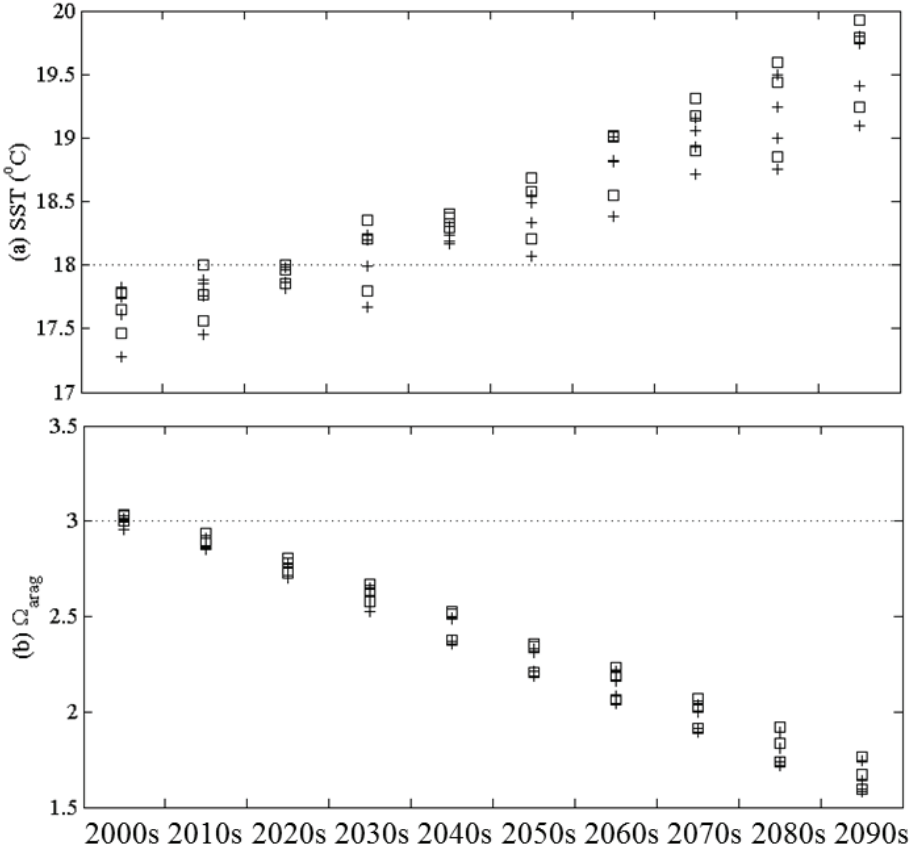

Fig. 6. Decadal-mean **(a)** SST (°C) during the coldest months and **(b)** annual lowest Ω_{arag} (2000s–2090s) at Kushimoto-Shirahama (33.5° N, 135.7° E) and Tateyama (35.0° N, 139.8° E) projected by the four climate models. Squares denote the projected SST and Ω_{arag} at Kushimoto-Shirahama. Crosses show the projected SST and Ω_{arag} at Tateyama. The dotted line in **(a)** and **(b)** denote the SST = 18 °C and Ω_{arag} = 3 line, respectively.

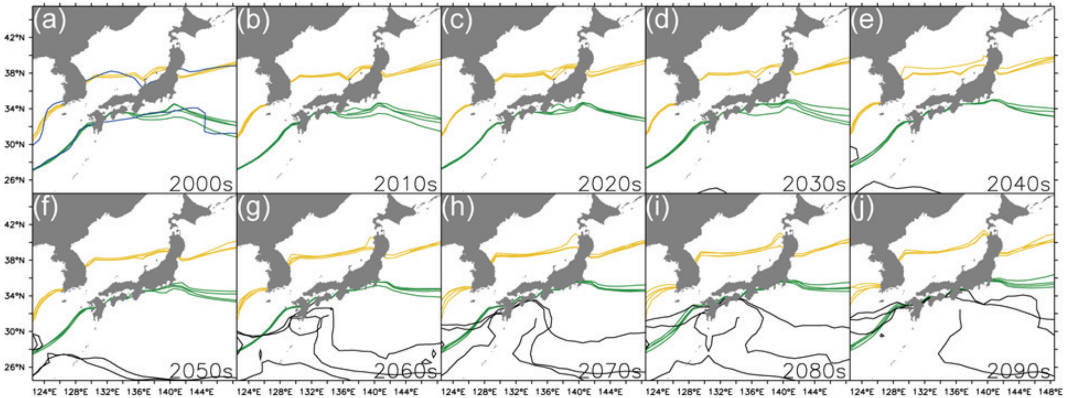

Fig. 7a. Projected 10-yr mean northern limit of the tropical-subtropical coral community (defined by the isothermal lines of SST = 18 °C; green lines) and temperate coral occurrence (defined by the isothermal lines of SST = 10 °C; yellow lines) defined by SST during the coldest months of each decade in seas close to Japan in 2000s–2090s, obtained by the four climate models. The blue lines in **(a)** denote the 10-yr mean observed monthly-mean isothermal lines of SST = 18 °C and 10 °C during the coldest months, estimated by NOAA OISST. The black lines denote isothermal lines of SST = 30 °C during the hottest months.

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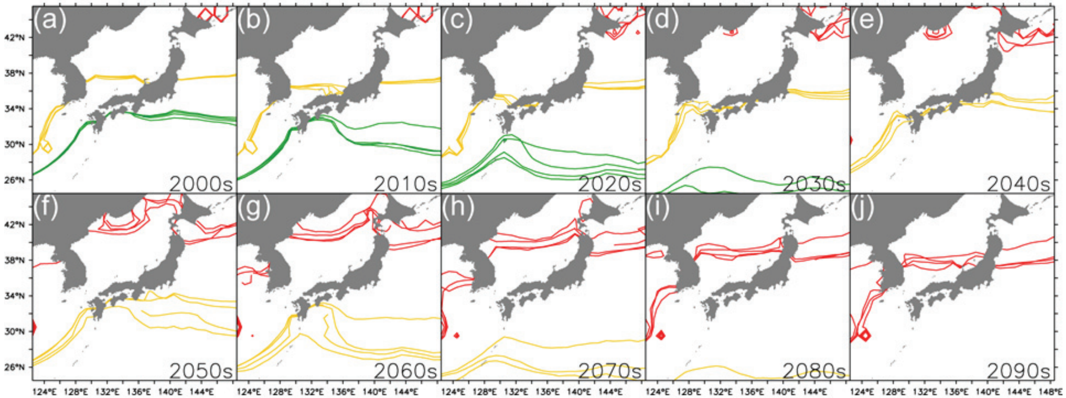

Fig. 7b. Same as in Fig. 7a, but for projected 10-yr mean northern limit of tropical-subtropical coral communities (defined by the isolines of $\Omega_{arag} = 3$; green lines) and temperate coral occurrence (defined by the isolines of $\Omega_{arag} = 2.3$; yellow lines), defined by Ω_{arag} as the lowest value in each decade. Red lines denote the isolines of $\Omega_{arag} = 1$ as a criterion for the aragonite undersaturation level.

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