Title: Spatio-temporal marine conservation planning to support high-latitude coral range expansion under climate change

Short running title: Marine reserve design under climate change

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Abstract

Aim Increasing sea-surface temperatures have resulted in poleward range expansions of scleractinian corals and declines in their core ranges. These changes may provide management opportunities for the long-term persistence of corals and associated species, but conservation science does not currently consider and anticipate these changes. We developed a spatio-temporal marine conservation plan in Japan that accommodates future coral range expansions based on projections of future sea-surface temperatures. Our aims were to (1) identify areas that consistently remain important for conservation through time and (2) determine the differences, if any, between priorities for marine protected areas that account for potential coral range expansions, and those that ignore them.

Location Japan

Methods We developed spatial planning approaches using temperature indices for coral habitat distributions in 2010, 2030, and 2100, and designed conservation plans for scenarios that incorporated different types of spatial and temporal connections between planning areas. Spatial connections are physical connections between adjacent and surrounding areas whereas temporal connections connect areas throughout time.

Results We found that protecting areas important for current and future coral habitat distributions is possible by incorporating temporal connections. This was accomplished with only a 6% increase in the overall reserve system costs, compared to reserve systems ignoring future coral habitat distributions. The attributes of priority areas (e.g. locations, outside boundary length, size) were substantially different when we varied the types of spatio-temporal connections.

Main conclusions This study demonstrated that areas with highest conservation priority now will not necessarily be optimal when planning for future change, such as coral range expansions. Furthermore, we showed that incorporating spatio-temporal connections into spatial prioritization achieves objectives of simultaneously conserving corals in the current climate and facilitating their expansions as sea-surface temperature rise.

Keywords climate change, climate model, conservation, marine protected area, range expansion, sea-surface temperature

Introduction

Coral reefs are in decline globally as a result of local and global-scale anthropogenic impacts such as eutrophication, coastal development, overfishing, and climate change related impacts such as warming sea water temperature, ocean acidification, and sea level rise (Anthony *et al.*, 2011, Burke *et al.*, 2011, Pandolfi *et al.*, 2011). About 32.8% of scleractinian (hard) coral species listed in International Union for Conservation of Nature Red List Categories and Criteria were classified as threatened (Carpenter *et al.*, 2008), and many are unlikely to persist in their current core ranges by 2050 under the most likely emission scenarios (Frieler *et al.*, 2013, van Hooidonk *et al.*, 2013). The current distribution of scleractinian corals is strongly influenced by water temperatures and also correlated with light availability and aragonite ion concentrations (Kleypas *et al.*, 1999). While exceeding upper temperature tolerances of 30 °C or a few degrees above long-term mean temperature during the warmest month results in coral bleaching and often mortality (Goreau *et al.*, 2000), low temperature mortality of the scleractinian corals has also been observed in high latitude communities in Japan and in the Carribbean (Veron & Minchin, 1992).

Global seawater temperatures measured on the surface have increased by 0.6°C during the past 100 years due to global warming (Pachauri & Reisinger, 2007). Increasing sea-surface temperatures are causing marine species range shifts, contractions, or expansions (Booth *et al.*, 2007, Figueira & Booth, 2010, Hoegh-Guldberg & Bruno, 2010, Yamano *et al.*, 2011). The poleward range expansion in relation to the increasing sea-surface temperatures has been reported recently in Japan using the data for the period from 1930s to 2010s (Yamano *et al.*, 2011), the Caribbean (Precht & Aronson, 2004), and in Australia (Hughes *et al.*, 2012). Poleward range expansions have also been reported for fish (Figueira & Booth, 2010, Last *et al.*, 2011), sea urchins (Ling *et al.*, 2009), seaweed (Wernberg *et al.*, 2011), and intertidal fauna (Pitt *et al.*, 2010).

Increasing water temperatures also threaten corals in the tropics, as they currently exist close to their physiological upper limit. Warm water events can cause widespread coral bleaching, where the symbiont dinoflagellate algae (zooxanthellae) are expelled from coral tissue, which can in turn lead to widespread coral mortality (Donner *et al.*, 2005, van Hooidonk *et al.*, 2013). As conditions on high-latitude reefs become tolerable with increasing water temperatures, poleward range expansions may provide refugia for scleractinian coral species, and their associated species (Riegl & Piller, 2003), although other ecological processes such as dependence on tropical propagule sources, increased rates of ocean acidification at higher latitudes and potentially the limiting light conditions may hinder long-term establishment of coral populations at high latitudes (Hoegh-Guldberg *et al.*, 2007). Given this uncertainty, combined with unknown potential adaptations of corals to the effects of climate change due to the lack of data (Baird & Maynard, 2008), it is important to identify high priority conservation sites for where corals can be protected both now, and in the future, as they expand their ranges towards potential refugia.

Marine protected areas are being implemented for coral reef conservation around the world (Mora *et al.*, 2006), but rarely consider the effects of climate change due to the lack of empirical scientific evidence or theory with supporting data (McClanahan *et al.*, 2012). An increasing number of marine reserve systems are established based on spatial prioritization. Spatial prioritization is an objective-driven systematic framework of where, when and how to allocate the resources and/or actions for conservation most efficiently (Margules & Pressey, 2000, Moilanen *et al.*, 2009), and the incorporation of climate change and potential climate refuges in these decisions is a rapidly growing area of research (Hannah, 2008).

There are numerous innovative prioritization approaches considering some aspects of climate change, including addressing the future declines in species in existing protected areas or current distribution (Araújo *et al.*, 2004, Carroll *et al.*, 2010, Carvalho *et al.*, 2010, Carvalho *et al.*, 2011, Hannah *et al.*, 2007), defining environmentally low variability areas (Iwamura *et al.,* 2010, Game *et al.,* 2011), considering temporal changes in water availability (Hermoso *et al.*, 2012), incorporating the threat of coral bleaching (Game *et al.*, 2008, Mumby *et al.*, 2011, Levy & Ban, 2013). However, none of these studies have incorporated the spatial and temporal connections of protected areas over time, and how these relate to range expansions.

It is important for marine protected area designs consider species range changes due to climate change if we want to be sure that the marine protected areas are protecting these species or habitats in the future (Araújo *et al.*, 2004). There are two ways to design conservation areas to ensure they protect coral species as their ranges expand or shift over time. First, protected areas can be designed based on current species distributions and then moved as these distributions change (Hyrenbach *et al.*, 2000, Soto, 2001). However, it can be politically challenging to move protected areas once they are established (Day, 2002). A second approach is to design protected areas that meet the needs of species both now and in the future – this is the focus of this paper.

Here, we develop spatio-temporal marine protected area networks that ensure corals are protected over time based on future projections of sea-surface temperatures. We demonstrate a spatial prioritization process which includes connections through time and space to facilitate coral expansion and addresses two main questions: (1) how different, if at all, are designs for marine reserves when climate change is accounted for, compared to ignoring future change?; and (2) are there areas that are consistently important for protecting both current and future coral habitat distributions?

(A) Methods

(B) Study region

Coral communities in Japan span subtropical to temperate areas. The highest latitude at which accreting coral reefs are located is at 34°N in Japan (Yamano *et al.*, 2012) and the highest latitude scleractinian coral population (*Oulastrea crispate* (Lamarck 1816)) observed is at 38°N at the Sadogashima Island, Niigata Prefecture (Honma & Kitami, 1978). In this study, we considered the rocky areas within 1 km along the Japanese coastline and less than 100m in depth to be potential sites for coral expansion (Fig. 1). We used the threshold for 100m to buffer the normal coral zonation depth due to the light limitation (Kleypas *et al.*, 1999). To carry out spatial planning we developed hexagonal planning units of 5 km^2 area for this entire region (n = 5457).

(B) Sea-surface temperature prediction data using a climate model

The future sea-surface temperature was obtained using a model MIROC3.2_hires under the Special Report on Emissions Scenarios A1B scenario, which assumed a rapid economic growth in the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC, 2007). The bias of the model was corrected by Yara *et al*. (2011). This model was one of the climate models from the World Climate Research Programme's phase 3 of Coupled Model Intercomparison Project performed for the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (Meehl *et al*. 2007).

We assumed that poleward range expansion of corals results solely from sea-surface temperatures rise and ignored other factors that could affect range changes, such as ocean acidification (Yara *et al.*, 2012). Three time slices were considered: 2010 to represent current conditions (Fig. 2a), 2030 for near future (Fig. 2b), and 2100 for distant future (Fig. 2c). We estimated sea-surface temperature values for these three time slices using the ten-year sea-surface temperature mean for February, since the coldest month of the year is the limiting factor for coral expansions (2000 to 2009 for 2010, 2020 to 2029 for 2030, 2090 to 2099 for 2100) (Fig. 2).

(B) Conservation features

We used the three sea-surface temperature-based indices for coral habitat distribution proposed by Yara *et al.* (2009) and (2011) that are monthly-mean isothermal lines of 10°C, 13°C and 18°C in the coldest months. These indices were based on the known low temperature limits for corals in Japan: 10°C marks the limit of existing coral occurrence (*Oulastrea crispata* in Sadogashima Island) (Honma & Kitami, 1978). A threshold of 13°C was considered viable for the establishment of coral communities as about 40 coral species established in locations where the average winter water temperature was 13.3 °C (Yamano *et al.*, 2001, Yamano *et al.*, 2012). A temperature of 18°C marks the lower limit to establish the majority of tropical hard corals and accreting reefs, where coral accretion of $CaCO_3$ out weights erosion (Kleypas *et al.*, 1999, Veron, 1995). Using these three sea-surface temperatures-based indices, we created three coral ecoregions in Japan, each defined by a different temperature range: “temperate” for 10-13°C, “subtropical” for 13-18°C, and “tropical” for 18-30°C, with 30 °C recognized as the high temperature limits for corals (Fig. 2) (Yara *et al.*, 2011, Yara *et al.*, 2012). The terms used to name ecoregions (temperate, subtropical, and tropical) represent temperature zones and not coral community types. We set these three coral ecoregions as our conservation features and aimed to protect 10% of the distribution of each in a network of protected areas.

(B) Spatial prioritization

We used Marxan (Ball *et al.*, 2009), a decision-support tool (http://www.uq.edu.au/marxan/), to design networks of protected areas that met our objectives. Marxan identifies areas that achieve specified conservation targets for a minimum cost. Marxan minimizes the objective function

$$\sum_{i=1}^{m} c_i x_i + CSM \sum_{i1}^{m} \sum_{i2}^{m} x_{i1}(1 - x_{i2})\, CV_{i1,i2} \quad (1)$$

subject to

$$\sum_{i=1}^{m} a_{ij} x_i \geq T_j \text{ , for } j = 1, \dots, n \qquad (2)$$

where m is the total number of planning units (i = 1, … , m), and c_i is the cost of selecting planning unit i. If planning unit i is selected for conservation, x_i= 1 and if not x_i= 0. The connectivity value matrix, $CV_{i1,i2}$, reflects the strength of the connection between planning units $i1$ and $i2$. The connectivity strength modifier, *CSM*, adjusts the importance of connectivity relative to planning unit costs and penalties for not meeting conservation targets (Watts *et al.*, 2009). Larger values of the *CSM* create a more connected reserve system, whereas smaller values create a less connected reserve system. In equation (2), T_j is the target amount for feature j (j=1, …, n) and a_{ij} is the amount of feature j in planning unit i.

In this study the cost of protecting each coral reef reflects the estimated amount of fishing occurring on a reef to represent the burden to fishers when an area is reserved. Ideally, we would estimate fishing pressure using fishing data depicting where people fish and how much they fish (Adams *et al.*, 2011, Scholtz *et al.*, 2011). As fishing data do not exist at a fine scale for our study region, we used human population to represent fishing pressure. We made the parsimonious assumption that fishing pressure is correlated with coastal population. The cost of each planning unit was calculated by adding up the number of people living within 20 km from its center point. We used a 20km buffer because it covers coastal towns or cities by providing a non-zero value for all planning units with the least overlapping between the buffers. We used the population count grid data for 2000 (CIESIN *et al.*, 2005).

(B) Definition of connections

The connections that we define here were applied for all of the planning units to calculate the connectivity value matrix, $CV_{i1,i2}$, in equation (1). We named planning units according to their position in space and time, where the first number in an ordered pair was the spatial location and the second number was the year, e.g. (1, 2010). We defined "spatial connection" as physical connections between adjacent and surrounding planning units within a time slice. For example, if the two planning units $i1$ = (1, 2010) and $i2$ = (2, 2010) shared a boundary then they are connected spatially within a single time slice and $CV_{i1,i2} > 0$. We defined "temporal connection" as connections between one planning unit and that same planning unit in the future. For instance, if planning units $i1$ = (1, 2010) and $i2$ = (1, 2030) are located geographically in the same place then they are connected temporally if $CV_{i1,i2} > 0$ (Fig. 3). Planning units are connected temporally only if one of the conservation features exists in the planning unit through time. Finally, planning units can be connected through time and space if the value in the connectivity matrix is positive and the indices differ in both time and space (Fig. 3). Spatial connections between planning units within a single time slice were calculated as the shared boundary length of adjacent planning units. Additionally, we calculated a connection between nearby planning units between time slices to represent easier migration of species to neighboring sites through time. For every planning unit in a time slice, we identified nearby planning units in the future at three spatial scales - near neighbors and neighbors that are two and three hexagon(s) away and used a weighting of 1/2, 1/4, and 1/8 for 1-3rd degree neighbors, respectively, to represent the declining likelihood of local dependencies with distance among neighboring sites (Fig. 3).

(B) Scenarios and Marxan analyses

We produced systems of marine protected areas for three different scenarios (Fig. 4) and compared their results. In scenario 1, “within a time slice adjacency connections”, we planned for each time slice separately (2010, 2030 and 2100), accounting for spatial connections between planning units in a single time slice but with no temporal connections (Fig. 4a). In scenario 2, “within a time slice adjacency + between time slices temporal connections”, we included all time periods (2010, 2030, and 2100) in one analysis, considering spatial connections between adjacent planning units in a single time slice and temporal connections between time slices (Fig. 4b). In this scenario, spatial connections were considered only within one time slice so that the spatially connected planning units in a year were not connected in multiple time slices. The spatial connection is independent for every time slice. Lastly, in scenario 3, “between time slices adjacency + between time slices temporal connections”, we planned the entire time range together incorporating spatial and temporal connections among multiple time slices (Fig. 4c).

We ran Marxan 100 times for each scenario. We chose a connectivity strength modifier, *CSM*= 10, by finding the trade-off point between the cost and connectivity using a method developed by Stewart and Possingham (2005). We kept the *CSM* value constant for all scenarios.

Each scenario produced solutions for marine protected area networks for the three time slices (2010, 2030 and 2100). We compared how the priorities changed over time in one scenario and overall reserve system costs across all scenarios using the best solutions (i.e. the reserve system with the minimum score from 100 runs) as well as the average of the best ten solutions. Differences in selection frequency across 100 runs were compared to contrast the spatial configurations of priority areas.

Results

When we planned for spatial connections within a single time slice (scenario 1 "within a time slice adjacency connections"), the selected planning units changed considerably over time (Table 1). In fact, only 29% of planning units were selected consistently through time. Moreover, there was very little overlap in the priorities for conservation in 2010 with those in 2100. Of the priority sites delineated in 2010, 88% will cover the conservation feature "tropical", 12% will include "subtropical" and none "temperate" in 2100. In addition, 15% of selected planning units were prioritized only in 2030 and not before or after, and conversely 6% of selected planning units were prioritized in 2010 and 2100 and not in 2030. When we considered temporal connections in the planning, we found that 93% (in scenario 2 "within a time slice adjacency + between time slices temporal connections") and 94% (in scenario 3 "between time slices adjacency + between time slices temporal connections") of planning units were selected in every time period in the best solutions, even though conservation features moved over time (Fig. 2) (Table 1).

Incorporating temporal connections (scenario 2) increased the overall reserve system costs by only 6% compared with the baseline scenario 1 (Table 2). However, there was 48% increase in the overall reserve system costs in scenario 3 when both adjacency connections between time slices and temporal connections were considered. The total number of selected planning units decreased by 5% in scenario 2 than that of in scenario 1 although more connection (temporal connection) was incorporated (Table 2). The largest reserve network system in terms of the number of planning units was designed in scenario 3 when the highest number of connections was considered (Table 2). The outside boundary length of the reserve networks of the best solutions through time was the smallest in scenario 3. The boundary length was approximately three times larger in scenario 2 and 19 times larger in scenario 1, compared with that of scenario 3. The overall selection frequency decreased in scenario 3 compared to other scenarios. In scenario 3, the number of high priority planning units (selected more than 50 times in 100 runs) was about 6 times and 5 times less than scenarios 1 and 2 respectively.

Spatial prioritization approaches that took into account predicted future sea-surface temperatures rise delivered substantially different spatial priorities compared with an approach that ignored the future, as seen in the differences in selection frequency between scenarios (Fig. 5). When the adjacency connections between time slices and temporal connections were considered (scenario 3), some planning units were more frequently selected than in scenarios that ignored the connections (red areas in Fig. 5b,c). These highly selected planning units were prioritized over all time slices. Overall solutions were similar between scenario 1 and 2 than between other pair of scenarios (Fig. 5). The spatial allocation of priority areas differed dramatically in the best solution of scenarios (Fig. 6). Priority areas moved through in scenario 1 (Fig. 6a) whereas priority areas were stable in scenario 2 and 3 (Fig 6b,c). Priority areas in scenario 3 were more clumped than that of scenario 2 by adding the spatial connection between multiple time slices (Fig. 6b,c).

Discussion

It is important that marine protected area designs reflect the dynamic physical and biological processes that change over time (Hughes *et al.*, 2010, Mumby *et al.*, 2011, Mumby & Steneck, 2008). Yet, there are few examples where spatial and temporal dynamics have been considered in marine spatial prioritization (Grantham *et al.*, 2008). To ensure that marine protected areas are protecting conservation features over time, it is necessary to account for species range changes due to climate change (Araújo *et al.*, 2004). Our study incorporated spatial and temporal connections between multiple time slices among locations to accommodate likely changes in climate and corresponding range expansions in spatial prioritization. We applied this idea to scleractinian corals in Japan, because these corals are already expanding their range poleward (Yamano *et al.*, 2011) and are vulnerable to climate change. It is uncertain how far or fast corals will change their distributions, and which species will be winners or losers. However, our approach has advantages because designing protected areas incrementally based on only current species distributions, with the aim of modifying protecting areas in the future as changes become evident, would be less cost-effective (Stewart *et al.*, 2007) and also politically difficult (Day, 2002).

Our results showed that priority areas were considerably different between scenarios that incorporated different types of connections. We demonstrated how to find places for protection that are important for conserving current and future conservation features. Finding these priority areas was achieved with a marginal increase in costs when we incorporated temporal connections and spatial connections within a single time slice (scenario 2). This scenario represented potential changes in coral communities over time in a single planning unit (area of 5 km^2), and spatially clustered priority areas in each time slice. Coral larvae can disperse poleward for long distances in strong boundary currents (Beger *et al*., 2011, Treml *et al*., 2008). However, larval transport between priority areas is not necessarily ensured, because the dispersal distance and survival dynamics of coral larvae differ significantly depending on the species and oceanographic factors (Cowen *et al*., 2000, Graham *et al*., 2008). In scenario 3, we represented species being able to move to adjacent planning units with time by adding the spatial connections between time slices. This may safeguard the short-distance dispersing corals and their associated species (Shanks *et al*., 2003). However, there was a substantial increase in costs and a decrease in outside boundary length when we added the adjacency connections between time slices (scenario 3).

Our approach made these trade-offs between costs and outside boundary length explicit, which can be used by planners to make informed decisions. Further, adding spatial connections between multiple time slices (scenario 3) decreased the overall selection frequencies of planning units, resulting in greater options for achieving the planning goals. Whether to incorporate spatial connection within a time slice or between time slices would also depend on the size of planning units and conservation objectives (i.e. to protect any particular species). Regardless, it is important to include not only spatial connections but also temporal connections (either within a time slice or between time slices) from the beginning when developing a marine conservation plan that allows for system dynamics. This is because it enables us to find priority areas that protect conservation features in the future.

It is important to design reserve networks for coral reef conservation that are robust to future impacts (Kennedy *et al.*, 2013). We delivered more spatially cohesive and stable solutions by considering spatio-temporal connections in the prioritization process. However, this study considered only one component of climate change, warming sea temperature. We focused on facilitating the expansion of corals, which is limited by sea-surface temperatures in the coldest month. However, sea-surface temperatures in summer could also affect suitable areas for coral, as elevated sea-surface temperatures in the hottest month can cause coral bleaching events (Fitt *et al.*, 2001), and have been reported from high-latitude reefs at Load

Howe Island, Australia (Harrison *et al.*, 2011).

Furthermore, ocean acidification caused by atmospheric carbon dioxide is likely to limit the distribution of coral reefs (Hoegh-Guldberg *et al.*, 2007, Meissner *et al.*, 2012, Yara *et al.*, 2012). Ocean acidification lowers calcification rates of corals (Anthony *et al.*, 2008), leading to a point where future rates of reef erosion may exceed rates of reef accretion (Hoegh-Guldberg *et al.*, 2007, McCulloch *et al.*, 2012). According to some future projections, ocean acidification could have a larger impact on coral habitats than sea-surface temperatures rise (Meissner *et al.*, 2012, Yara *et al.*, 2012). However, this may not be true for all species- the impacts of ocean acidification are different for hard coral species at the organismic scales (Rodolfo-Metalpa *et al.*, 2010). Moreover, coral calcification trends in massive *Porites* in high-latitude of Western Australia were a response to increasing temperature rather than ocean acidification (Cooper *et al.*, 2012). Coral species up-regulate pH internally (McCulloch *et al.*, 2012), which may lead to delayed responses to acidification and buy time for potential emission reductions to take effect. Research investigating the influences of the combined stress factors is emerging but not yet conclusive. For example, Madin *et al.* (2012) found that increases in storm intensity had a relatively minor effect on long-term population persistence of the table coral *Acropora hyacinthus* (Dana, 1846), compared to the ocean acidification. The combined effects of ocean acidification and temperature trends may limit the pole-ward expansion of corals. Considering multiple threats within the planning process, as well as information on coral ecology and environmental data such as ocean currents, will improve conservation outcomes. For example, in our study region the Kuroshio Current (the warm pole-ward currents flowing from the equator) is projected to extend and shift polewards due to global warming (Sakamoto *et al.*, 2005). This could result in higher speeds and latitudes of coral expansion (Yamano *et al.*, 2011).

Improving the spatial representation of socio-economic values of coral reefs to users, such as opportunity costs of reef fishing, using the field data and involving stakeholders would better represent social desires and minimize the impacts on stakeholders (Klein *et al.*, 2009, Yates & Schoeman, 2013). Especially in Japan, the fishing industry and markets are very large. There are approximately a thousand of marine managed areas where some kind of fishing is allowed (Yagi *et al.*, 2010), but our analysis is concerned with no-take areas that would exclude all fishing. Our study shows a novel way for addressing changing distributions in conservation plans, however, we used the population surrogate to represent fishing opportunity costs due to the lack of spatial data, and projections of how the distribution and intensity of fishing activity may change. Including such improved information to account for human impacts from fishing is an urgent research priority to improve planning approaches for the future.

Designing marine protected areas in the face of climate change means making management decisions in the face of uncertainty (Wintle *et al.*, 2011). Yet, social and political willingness to undergo repeated reserve designation processes is unlikely in most places, and whether such redesign processes can keep pace with changes in ocean climate is questionable. Finding areas that will fulfill conservation objectives now and in the future will thus help to avoid species or habitat losses. Our approach considering climate change by incorporating temporal and spatial connections into reserve planning overcomes this challenge. Our method can be applied to any dynamic conservation-planning problem not only for the sea but also on land. Our approach enables governments and planners to choose marine reserves that will be more robust to climate change as countries strive to expand the world's reserve system to fulfill the strategic plan for biodiversity 2011-2020, including Aichi Biodiversity Targets of the Convention on Biological Diversity by 2020.

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Biosketch

Azusa Makino is a PhD student at School of Biological Sciences, the University of Queensland, Australia. A.M. is developing a novel conservation planning methods for focusing on marine ecosystems, considering climate change, land-sea connectivity and effectiveness of differential zones in protected areas. A.M. belongs to the Australian Research Council Centre of Excellence for Environmental Decisions (www.ceed.edu.au) and is collaborating with the Center for Environmental Biology and Ecosystem Studies, National Institute for Environmental Studies, Japan (http://www.nies.go.jp/biology/eng/index.html).

Author contributions: A.M., H.Y., M.B., C.K., and H.P. conceived the ideas; A.M. and H.Y. collected the data; Y.Y. provided climate model output data; A.M. analyzed the data; A.M. led the writing of the manuscript, which includes contributions from all authors.

Tables

Table 1. Percentages of combination of selected planning units for three time slices in each scenario. For example, 29% of selected planning units were selected in all time slices and 15% of selected planning units are selected only in 2030 in scenario 1. Every planning unit can be selected (status of "1") as priority for conservation or not selected (status of "0") in every time slice (2010, 2030, and 2100).

	Time slice			Scenario		
	2010	2030	2100	1: within a time slice adjacency connections	2: within a time slice adjacency + between time slices temporal connections	3: between time slices adjacency + between time slices temporal connections
Planning unit state through time 1: selected 0: not selected	1	1	1	29%	93%	94%
	1	1	0	5%	0%	1%
	1	0	1	6%	1%	1%
	0	1	1	6%	1%	0%
	1	0	0	19%	0%	1%
	0	1	0	15%	1%	2%
	0	0	1	19%	4%	2%

Table 2. Average of the costs, human pressure, of each time slice of the best ten solutions of each scenario.

Scenario	Time slice	Costs (population within 20 km from the center point of each planning unit)	Total number of selected planning units
1: within time slice adjacency connections	2010	356,721	317
	2030	352,695	317
	2100	364,437	333
2: within time slice adjacency + between time slices temporal connections	2010	376,511	303
	2030	382,153	306
	2100	384,113	313
3: between time slice adjacency + between time slices temporal connections	2010	539,591	355
	2030	538,040	357
	2100	516,770	361

Figure legends

Figure 1. Rocky areas in our study region of Japan. Our study region includes areas 1 km from the coastline and less than 100m in depth (as potential sites for coral expansion).

Figure 2. Conservation features over time (2010, 2030 and 2100). The lines are in units of degree Celsius (°C). Our conservation features were different temperature ranges: “temperate” for 10-13°C, “subtropical” for 13-18°C, and “tropical” for 18-30°C. These conservation features change over time due to the climate change.

Figure 3. Concept of scenario 3 (between time slice adjacency + between time slices temporal connections). We term the format of a planning unit *i*1 = (1, 2010), where the first number in the ordered pair is the spatial location of the planning unit and the second number is the year. The “between time slice adjacency” connections are physical connections between adjacent and surrounding planning units within a time slice (e.g. planning unit *i*1 = (1, 2010) and *i*2 = (2, 2010)), as well as between time slices (e.g. planning unit *i*1 = (3, 2010), *i*2 = (6, 2030)). The latter “between time slices temporal” connections are between one planning unit and that same planning unit in the future (e.g. planning unit *i*1 = (1, 2010), *i*2 = (1, 2030)).

Figure 4. Illustration of three scenarios: (a) scenario 1 “within a time slice adjacency connections”; (b) scenario 2 ”within a time slice adjacency + between time slices temporal connections”; and (c) scenario 3 “between time slice adjacency + between time slices temporal connections”. Scenario 2 investigates how the temporal connections influence the spatial prioritization compared to the baseline scenario 1. Scenario 3 examines the effects of adding spatial connections between multiple time slices.

Figure 5. Comparison of selection frequency between scenarios: (a) scenario 1 (adjacency connections within a time slice) vs. scenario 2 (adjacency connections within a time slice and temporal connections), (b) scenario 1 vs. scenario 3 (adjacency connections between time slices and temporal connections), and (c) scenario 2 vs. scenario 3. The sum of selection frequency of all time slices in a scenario was calculated and the differences between scenarios were calculated by subtraction. For example, if the color is closer to red, the areas were more selected in scenario 3, whereas if the color is green these areas were more selected in scenario 1 (b) or 2 (c).

Figure 6. Spatial configuration of priority areas of the best solution (i.e. minimum reserve size out of 100 solutions) in Kyusyu, southwest Japan (see Fig. 1) for every time slices of each scenario: (a) scenario 1, (b) scenario 2, and (c) scenario 3.

Figures

Figure 1.

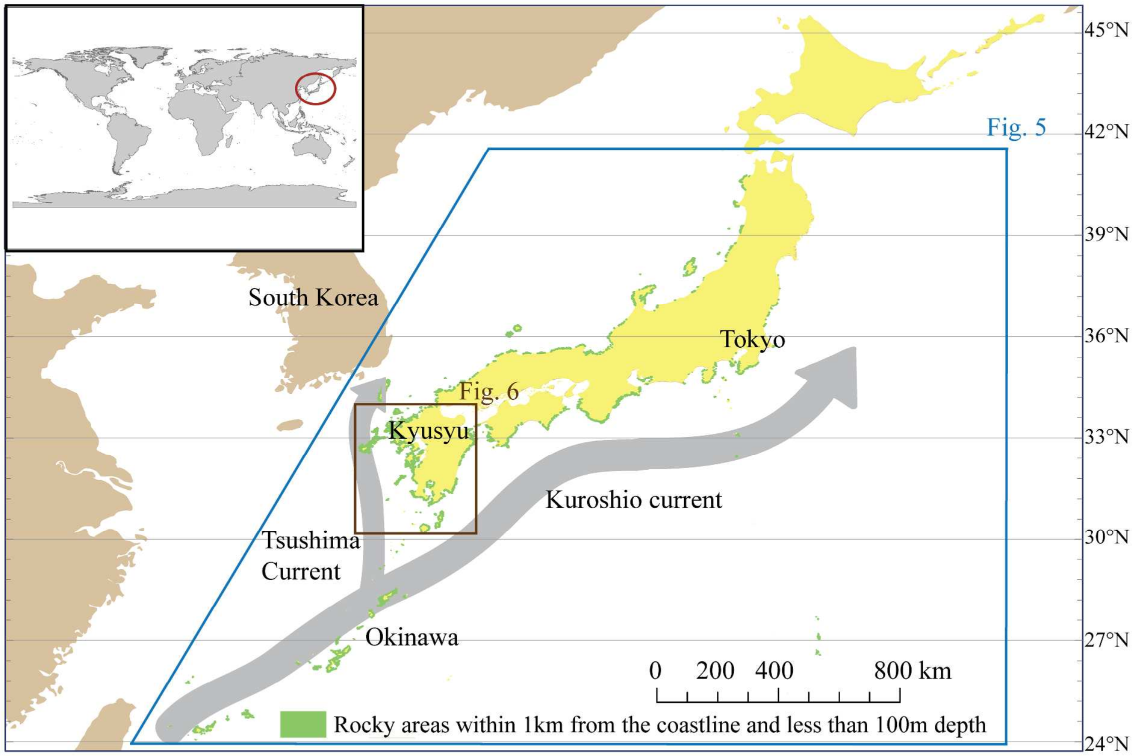


Figure 2.

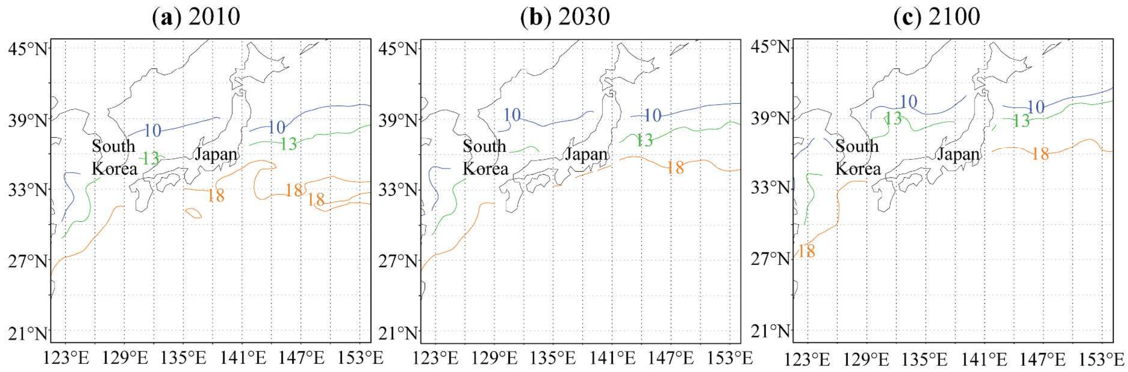
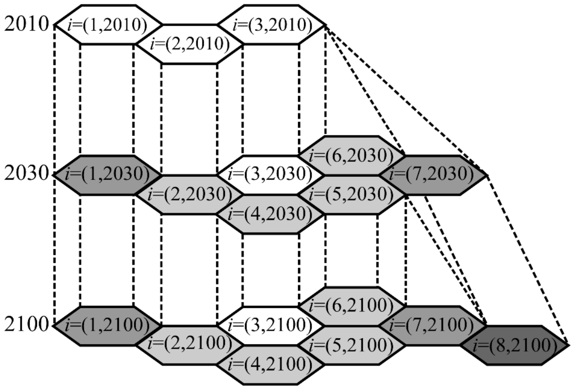

(a) 2010
(b) 2030
(c) 2100
45°N
39°N
33°N
27°N
21°N
123°E
129°E
135°E
141°E
147°E
153°E
South Korea
Japan
10
13
18

Figure 3.


2010
i=(1,2010)
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2030
i=(1,2030)
i=(2,2030)
i=(3,2030)
i=(4,2030)
i=(5,2030)
i=(6,2030)
i=(7,2030)
2100
i=(1,2100)
i=(2,2100)
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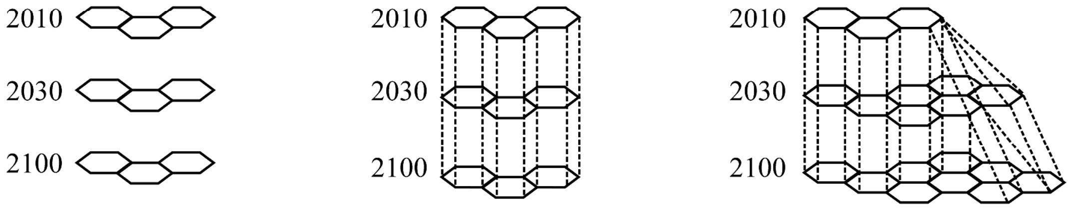
i=(8,2100)

Figure 4.

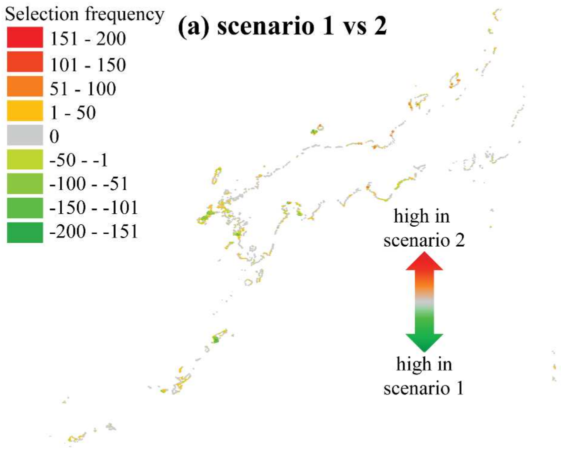


(**a**) scenario 1: within a time slice adjacency connections

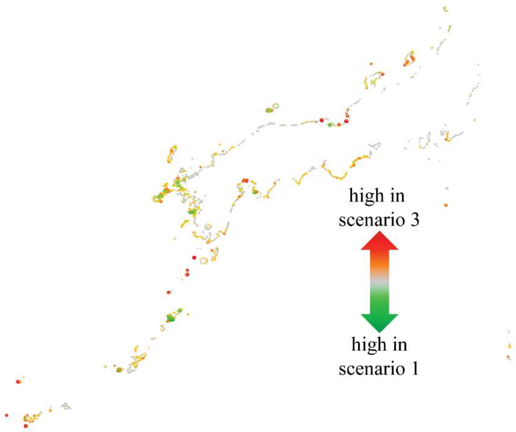
(**b**) scenario 2: within a time slice adjacency + between time slices temporal connections

(**c**) scenario 3: between time slices adjacency + between time slices temporal connections

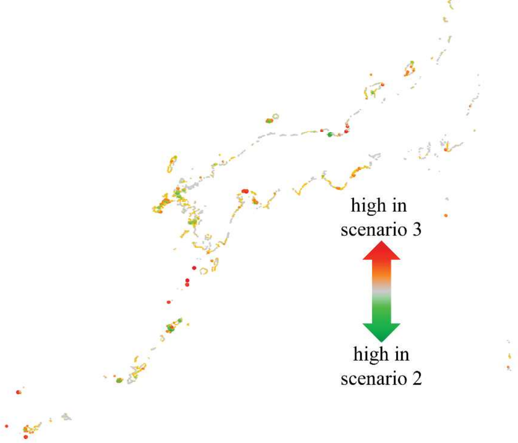
Figure 5.



(a) scenario 1 vs 2

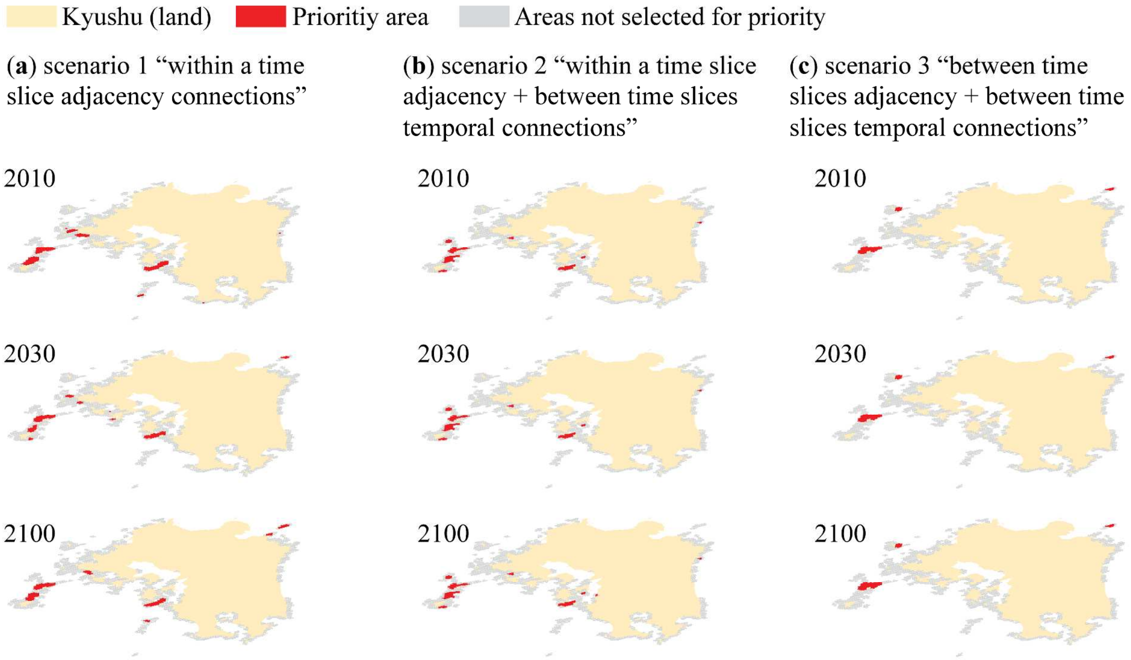


(b) scenario 1 vs 3



(c) scenario 2 vs 3

Figure 6.


Kyushu (land)
Prioritiy area
Areas not selected for priority
(a) scenario 1 “within a time slice adjacency connections”
(b) scenario 2 “within a time slice adjacency + between time slices temporal connections”
(c) scenario 3 “between time slices adjacency + between time slices temporal connections”
2010
2010
2010
2030
2030
2030
2100
2100
2100