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Climate-induced species range shift and local adaptation strategies in a temperate marine protected area, Ashizuri-Uwakai National Park, Shikoku Island, western Japan

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ABSTRACT

In temperate seas, expansion of reef-building coral distribution, decline of macroalgal beds, and changes in constituent species for coral communities and/or macroalgal beds mainly due to increase in sea surface temperature have been reported. Not only mitigation but also adaptive responses are important for the measures against climate change. Consideration of adaptive measures depends on local conditions such as the degree of environmental change and industrial structure is necessary when measures are implemented. This study focused on the marine protected area (Ashizuri-Uwakai National Park in Japan) and its surrounding area. This area is characterized by a very large north-south gradient in water temperature and the distribution of corals and macroalgae along it. The purpose of this study is to consider what adaptive measures are suitable for each region and industry in response to changes in coastal ecosystems (coral community and macroalgal bed). Future (assuming the end of this century under RCP2.6 and RCP8.5 scenarios) changes in the potential distribution area of coral, macroalgae, and their consumers were projected using simulated sea surface temperature with a high-spatial resolution. After projecting the coastal ecosystem changes and assessing the contemporary use of coastal ecosystem, we give examples of what specific adaptive measures should be taken in each area for three fields, i.e., biodiversity conservation, fisheries, and tourism. Assuming the 2090s, though drastic changes in coastal ecosystem are not projected compared to the present state under RCP2.6 scenario, as coral distribution shifts north, feeding damage by crown-of-thorn starfish is projected to become a problem. Therefore, expansion of protected areas and promotion of conservation activities are major challenges for coral ecosystem conservation. On the other hand, under RCP8.5 scenario, it is important to take appropriate conservation measures for macroalgae since coral growth becomes difficult to achieve and grazing pressure on macroalgae increases due to extreme elevated water temperature. Moreover, creation of alternate or new tourism resources will be needed. This research represents projected scenarios of coastal ecosystem changes with a high spatial resolution and adaptation measures based on the changes for each municipality.

1. Introduction

Coastal ecosystems are composed of a diverse community of organisms in many regions and both coral reefs (or coral communities) and seaweed beds have high ecosystem services such as via provision of shelter, nursery, as well as food and water quality control, and creating a superior landscape (Moberg and Folke, 1999; Costanza et al., 2014; Hicks and Cinner, 2014). Coastal areas are often adjacent to areas of human activities and are susceptible to local stresses (e.g., coastal development and sediment loading). Simultaneously, environmental changes due to global climate change have also been an issue in recent decades. Mass coral bleaching (Hughes et al., 2017) and decline of seaweed beds (Díez et al., 2012) have been reported in many tropical and temperate seas and it is well known that coral reefs (or coral communities) and seaweed beds are vulnerable to climate change (Hoegh-Guldberg, 2010; Harley et al., 2012; IPCC, 2019). In temperate

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seas, poleward range shifts in reef-building corals and macroalgae, with changes in constituent species for coral communities and macroalgal beds, have been a remarkable phenomenon (e.g., Yamasaki et al., 2014; Tuckett et al., 2017). Moreover, there are many areas where massive outbreaks of predators (coral-eating crown-of-thorns starfish and snails and for macroalgae herbivorous fish and sea urchins) have led to increases in grazing pressure becoming a major problem (Cameron et al., 1991; McClanahan, 1994; Yatsuya and Nakahara, 2004; Pratchett, 2010). In those areas, active ecosystem management such as control of the number of predators and installation of protective nets have been conducted by mainly diving guides and/or fishermen.

The necessity of the concept to adapt to climate change has been widely pointed out in various fields (e.g., Mawdsley et al., 2009; Sumaila et al., 2011). Structures of coastal ecosystems vary from region to region and the response to various environmental changes depends on the species or community. Therefore, it is important to consider the adaptive responses according to the characteristics of the industries and ecosystems and the degree of future change projected in each region. To project the future environment, many climate models have been applied and the degree of changes greatly differ depending on the emission scenario of greenhouse gases and/or target year (IPCC, 2019).

Establishment of marine protected areas (MPAs) including national parks is a useful strategy to protect as areas of rich biodiversity and outstanding landscape. The regulations in MPAs greatly differ between and within the region (Horta e Costa et al., 2016) and the background and management measures in Japanese MPAs have been reviewed in Yagi et al. (2010). Though biological conservation, securing habitat for animate beings and/or tourism use are often considered important among MPAs, coordination between stakeholders is necessary where MPA is adjacent to areas of human activity. Moreover, local communities play an important role in the use and conservation of coastal ecosystems in national parks (e.g., Fiallo and Jacobson, 1995; Pittman et al., 2019; Abe et al., 2021).

In this paper, one of the Japanese national parks located in temperate area (Ashizuri-Uwakai National Park in Shikoku Island; Fig. 1) was selected for the study area. The Ashizuri quasi-National Park was designated in 1955 and the protected area was expanded as the Ashizuri-Uwakai National Park in 1972, and this park is located in Kochi and Ehime prefectures (Fig. 1b). It is unique among Japan's national parks, excluding island areas, in that it covers a relatively extensive latitudinal range. We focused on the municipalities within the Ashizuri-Uwakai National Park and the area to its north (Fig. 1c). Part of the land area and most of the coastal area are designated as a national park (Fig. 1c). The main attractions of the sea area are scleractinian and soft corals and tropical fishes that congregate on the corals (MOE, 2017, Fig. 2). Remarkable changes in coastal ecosystems (especially reef-building corals and macroalgae) have occurred in part of the study area. For example, poleward range expansion of corals has been reported (Yamano et al., 2011). In addition, temperate species of *Sargassum* have been replaced by tropical species (Tanaka et al., 2012). As further environmental and ecological changes are expected in the future as a result of climate change, it is important to discuss what impacts will occur in each region and what measures should be taken to deal with them.

The purpose of this study was 1) to understand the north-south gradient of coral-macroalgal distribution, the spatial distribution of conservation and use of coastal ecosystems under the current situation, 2) to evaluate environmental and ecological changes from the past through quantitative data and local stakeholder perceptions and project future changes in the distribution of corals and macroalgae, 3) to project future changes in underwater landscapes/ecosystem services and propose local adaptation measures for each area and industry.

2. Study area

The study area is part of the temperate zone in terms of climate

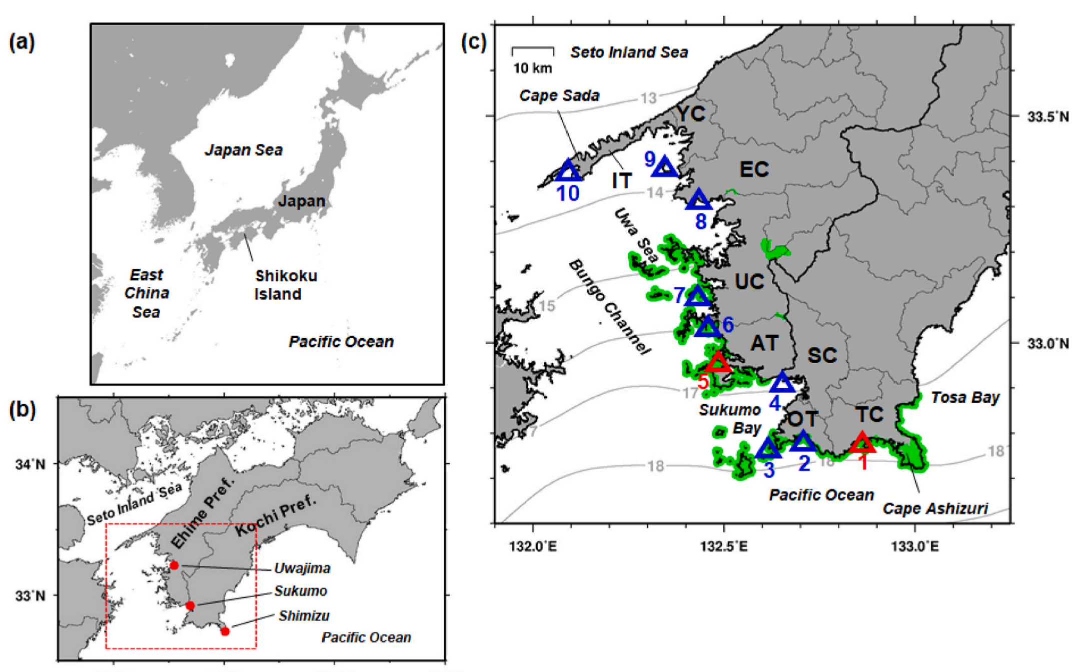

Fig. 1. Location of study area and municipalities (TC: Tosashimizu City, OT: Otsuki Town, SC: Sukumo City, AT: Ainan Town, UC: Uwajima City, EC: Seiyo City, YC: Yawatahama City, IT: Ikata Town). Green shaded area in (c) represents the Ashizuri-Uwakai National Park including land area. Municipalities TC-OT-SC and AT-UC-EC-YC-IT are part of Kochi Prefecture and Ehime Prefecture, respectively. Blue and red triangles represent the area where underwater observations were conducted. Red triangles indicate the areas where macroalgal biomass sampling was performed. The detailed coordinates of the survey sites are shown in the Supplement. Red circles in (b) denote the locations of meteorological stations (Uwajima, Sukumo, and Shimizu operated by the Japan Meteorological Agency). Contours in (c) denote mean sea surface temperature (°C) in February during 2009–2018 (Fig. 6). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

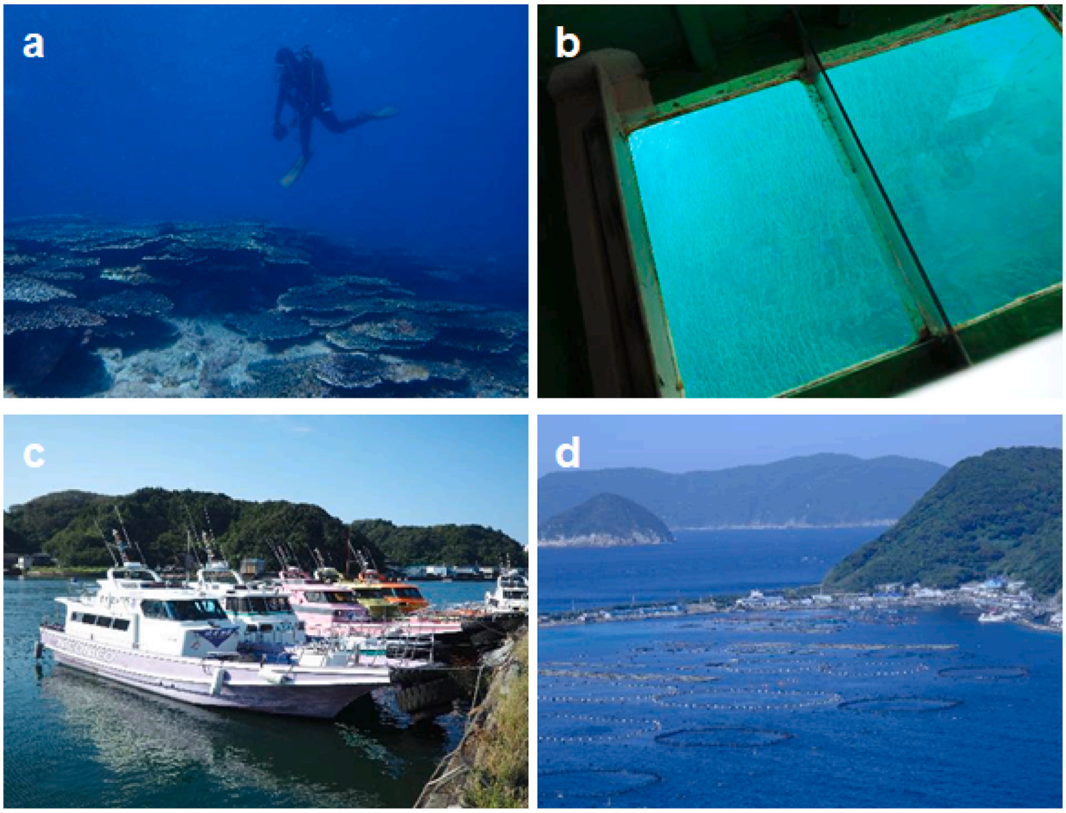

Fig. 2. Examples of usage situation of coastal areas in the Ashizuri-Uwakai National Park and its surrounding area (a: diving, b: glass boat, c: recreational fishing, and d: fish aquaculture). Photo was taken in Otsuki Town (a and d), Tosashimizu City (b), and Sukumo City (c) in 2019.

region. Monthly minimum and maximum temperatures are 8.7 and 27.5 °C at Shimizu (Tosashimizu City) and 6.8 and 27.5 °C at Uwajima (Uwajima City), respectively. Annual precipitation ranges from ca. 1600–2500 mm, with more in the southern regions. Several typhoons approach Shikoku Island during a year, with a seasonal increase in frequency between July and September (https://www.jma.go.jp/jma/menu/menureport.html; accessed 21 October 2020). The Kuroshio Current, the western boundary current with relatively warm waters, flows eastward off the Cape Ashizuri in Pacific Ocean, and strongly influences the hydrodynamics, water quality and biological community (e.

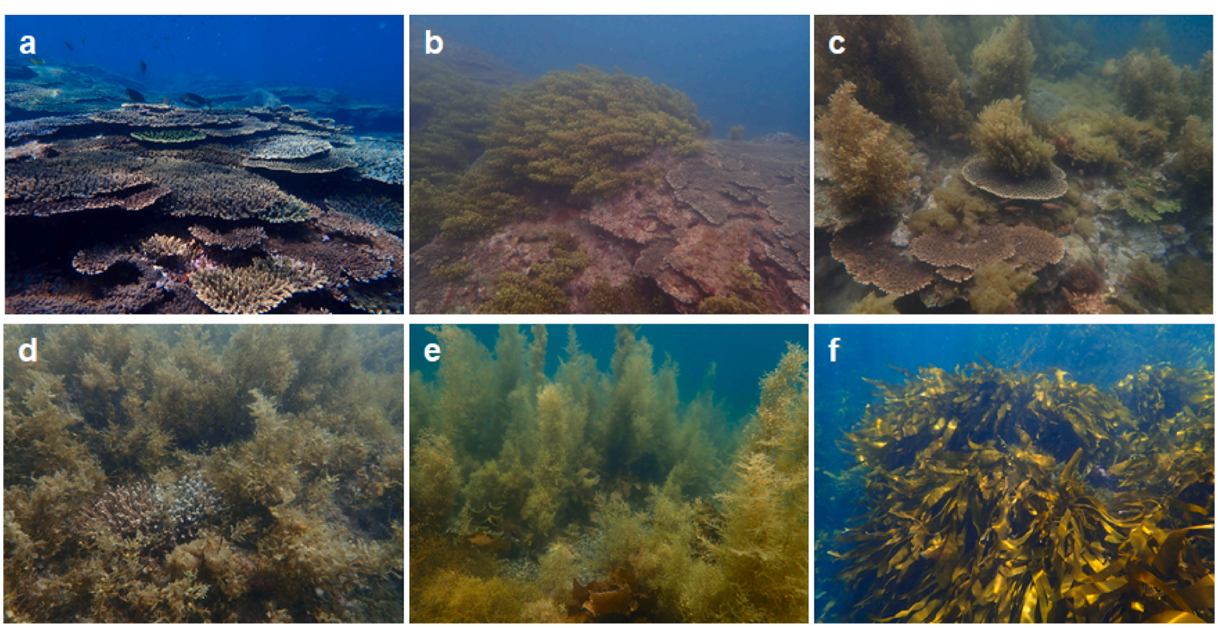

Fig. 3. Examples of typical underwater photographs showing reef-building coral communities and macroalgal beds during May to June in the study area. a: coral community at Kashiwajima in OT (Otsuki Town), b: coral and tropical *Sargassum* community in TC (Tosashimizu City), c: coral and temperate/tropical *Sargassum* community in UC (Uwajima City), d: few corals (mainly branched) and temperate/tropical *Sargassum* community in EC (Seiyo City), e: temperate *Sargassum* and few Laminariaceae community in YC (Yawatahama City), and f: Laminariaceae and temperate *Sargassum* community in IT (Ikata Town).

g., Isobe et al., 2010; Yamazaki et al., 2016; Morioka et al., 2019). A large water temperature gradient is formed between Pacific Ocean and Seto Inland Sea (i.e., along the west coast of Shikoku Island; Bungo Channel) especially in winter (Sakamoto et al., 2016).

In the Ashizuri-Uwakai National Park and its northern area, field observations of underwater landscape, assemblage of use and conservation of coastal ecosystem, and interviews with local stakeholders were conducted in our previous research study (Abe et al., 2021). Shallow (<5 m) underwater landscape (coral community and macroalgal bed) of the study area are mainly constituted from coral community (including tabular coral) and tropical *Sargassum* in the southern area (Fig. 3a and b), coral community (including tabular coral) and temperate/tropical *Sargassum* in the central area (Fig. 3c), and sparse branching coral, temperate *Sargassum*, and Laminariaceae in the northern area (Fig. 3d–f). Though Yoshida et al. (2019b) have evaluated the climate change impacts on the macroalgae bed ecosystem for the Seto Inland Sea (Fig. 1b), the dynamics of the coral community and local adaptive measures were not presented in the study.

3. Methods

3.1. Field observations of corals and macroalgae

Six observation areas inside the national park and four observation areas outside the park were established (Fig. 1c). Field observations of underwater landscape focusing on corals and macroalgae have been conducted from May to June through 2018–2020 (Abe et al., 2021). The distribution of corals and macroalgae was surveyed at several points in each observation area (Supplement Table S1). Two to four researchers swam in depths shallower than 5 m at several stations in each area for about 1 h per site by SCUBA or snorkel. The presence or absence of *Acropora solitaryensis* complex and *A. hyacinthus* complex (Kitano et al., 2020) for coral communities, and the species of macroalgae found were recorded.

In addition, to compare the character between tropical and temperate *Sargassum* species, *Sargassum* thallus length and biomass were investigated from May to June 2020 at three stations in Nishiumi (Ainan Town: AT) and at two stations in Tatsukushi (Tosashimizu City: TC) (Fig. 1c; Table S1). This sampling period corresponds to the peak growing season of *Sargassum* in and around study area (Choi et al., 2006; Haraguchi et al., 2018). The biomass of *Sargassum* species was measured by quadrat sampling using scuba diving. At least five 50 cm × 50 cm or 25 cm × 25 cm square quadrats were placed in the *Sargassum*-dominated assemblage in each site ($n = 3$–8). In cases where *Sargassum* was densely distributed in rocky areas near the intertidal zone, the smaller quadrat was used. All *Sargassum* species present in each quadrat were collected from holdfast. The collected samples were carried to the laboratory in cold storage and rinsed by freshwater after removing epiphytes. Individual thallus length and biomass (wet and dry weight) were measured for emerging *Sargassum* and mean thallus length and standing stock of each species were obtained.

3.2. Present status of conservation and use of coastal ecosystems

To understand the status of monitoring, conservation, and utilization of coastal ecosystems in the study area, data on 1) locations for monitoring of corals and macroalgae and control of the number of their predators and 2) use of space for tourism (diving points, glass boat routes, sea bathing, and leisure fishing) and coastal fisheries (area of fish or bivalve aquaculture) were collected from the Internet or paper reports. The obtained data were used to organize the spatial distribution on GIS software. The details of the dataset were shown in our previous study (Abe et al., 2021).

3.3. Analysis of environmental and ecosystem changes and local stakeholder perceptions

To clarify the trends in climate change from the past, meteorological data on air temperature, precipitation, and typhoon until 2020 were obtained from the Japan Meteorological Agency (https://www.data.jma.go.jp/gmd/risk/obsdl/index.php; https://www.data.jma.go.jp/fcd/yoho/typhoon/statistics/accession/shikoku.html; accessed 21 April 2021). Mann-Kendall tests were performed for trend analysis of time series data using XLSTAT statistical software.

Annual monitoring of coral community ecosystem has been conducted by Reef Check (http://reefcheck.jp/; accessed 21 April 2021) and Monitoring sites 1000 project (https://www.biodic.go.jp/moni1000/coral_reef.html; accessed 21 April 2021) inside the national park area, e.g., Tatsukushi (Tosashimizu City), Kashiwajima (Otsuki Town), and Nishiumi (Ainan Town). We obtained the time series of coral cover at each monitoring station.

In addition to the quantitative environmental data analysis, we conducted a questionnaire survey. To understand the perceptions of tourism, fisheries, and local government towards coastal ecosystems, we interviewed tourism operators (mainly dive shops) ($n = 21$), fishermen ($n = 8$), local government offices (prefectural, municipality, and fisheries experimental stations) ($n = 24$), and experts ($n = 8$) from 2017 to 2020. The interview items were broadly divided into the following categories: "characteristics of the study area", "current problems and past changes in coastal ecosystems", "expectations and concerns about future changes in coastal ecosystems", and "whether there are conflicts between tourism and fisheries". The results of the interviews were summarized in terms of perceptions of the distribution and use of coral and macroalgae in each region from the standpoint of the tourism industry and fishermen.

3.4. Future water temperature and range shift of coral and macroalgae

Simulation results with high spatial resolution are essential to evaluate ecosystem changes on a local scale (e.g., each municipality). Since models for global scale simulations (i.e., Global Climate Model) have a coarse resolution, the dataset of future physical environment having ca. 2 km resolution (FORP-JPN02 ver. 1; Nishikawa et al., 2021) were obtained and only water temperature data was used in this study. This data is based on downscaling simulation around Japan. Sea surface temperatures (SSTs) under two representative concentration pathways of greenhouse gases (RCP2.6 and RCP8.5) at the end of this century (2091–2100) were used after bias correction of water temperature by adding the difference of monthly climatology between the observed SSTs, Multi-scale Ultra-high Resolution Sea Surface Temperature (MUR SST) Analysis version 4.1 (JPL MUR MEaSUREs Project, 2015), and modeled SSTs. The detailed method of temperature bias correction was described in Kumagai et al. (2018b).

Water temperature is one of the major factors controlling biological activity and water temperature as a guide to survival and reproduction may be different among species. For instance, rising water temperature in winter may promote the establishment of tropical species, while summer elevated temperature may limit the survival of temperate species. *Acropora solitaryensis* complex and *A. hyacinthus* complex for tabular coral, *Acanthaster* cf. *solaris* for coral predator, *Ecklonia cava kurome* for kelps, *Sargassum hemiphyllum* for temperate *Sargassum*, *S. ilicifolium* for tropical *Sargassum*, and *Siganus fuscescens* for herbivorous fish were selected as typical species in the study area and a water temperature threshold accounting for distribution or activity was established for each species based on previous studies (Table 1). The changes in biological distribution and/or activity were projected using surface water temperature field in the future. Resource competition between corals and macroalgae (Tanner, 1995; McCook et al., 2014) and the possibility of egg or larval coral recruitment (Tay et al., 2012) were not considered in our projection.

Table 1
The effects of water temperature on biological activity conditions for reef-building corals, macroalgae, and their predators used in future projections.

Target species	Significance	Activity	Water temperature	Reference
Acropora solitaryensis complex and *A. hyacinthus* complex	tabular corals	survival	14 °C <	Yamano et al. (unpublished), Takao et al. (2015)
			<30 °C	Yara et al. (2012)
Acanthaster cf. *solaris*	predator of corals	survival	15 °C <	Yamaguchi (1987)
		reproduction	28 °C <	Yokochi and Ogura (1987)
Ecklonia cava kurome	kelps	growth	<28 °C	Tanaka et al. (2008)
Sargassum ilicifolium	tropical *Sargassum*	growth	13 °C <	Suto (1992)
		growth	<34 °C	Low et al. (2019)
Sargassum hemiphyllum	temperate *Sargassum*	growth	<30 °C	Baba (2014)
Siganus fuscescens	herbivorous fish	feeding activity	15 °C <	MERI (2012)

4. Results and discussion

Sections 4.1 to 4.3 show the present distribution, conservation, and conflict, 4.4 shows the changes from the past, and 4.5 to 4.7 shows the projected future changes. In order to understand the characteristics of each municipality, the distribution of corals, macroalgae, and their predators, as well as their conservation and use in each region, is summarized in Fig. 4. The detailed location is given in our previous study (Abe et al., 2021).

4.1. Present occurrence of corals and macroalgae and comparison of sargassum biomass

This section describes the characteristics of the distribution of corals and macroalgae obtained from the field survey. In addition, section 4.5 presents future water temperature changes through numerical simulations and evaluates distributional changes based on knowledge of the optimal temperature range of survival and activity of corals, macroalgae, and their predators.

From south to north of the study area, a decrease in the number of reef-building corals and tropical *Sargassum* species present and an increase in the number of temperate *Sargassum* and kelps were observed. Coral species were extremely limited north of Seiyo City (EC in Fig. 1c) in terms of both number and cover, but tabular coral *Acropora solitaryensis* and *A. hyacinthus* were abundant south of Uwajima City (UC). Macroalgal beds in the study area were located in a transition zone consisting of temperate species (e.g., *Ecklonia cava kurome* and *Sargassum hemiphyllum*) and subtropical species (*S. ilicifolium*). *Ecklonia cava kurome* was found north of Yawatahama City (YC), *S. hemiphyllum* north of Sukumo City (SC), *S. ilicifolium* south of Seiyo City (EC), and *S. crispifolium* south of Sukumo City (SC).

Quantitative collection of *Sargassum* was conducted at Nishiumi (Ainan Town) and Tatsukushi (Tosashimizu City). *S. hemiphyllum* and *S. ilicifolium* were found at Nishiumi and *S. ilicifolium* and *S. crispifolium* were present at Tatsukushi. These three species were not mature at the time of sampling. Considering the present main distribution area, *S. hemiphyllum* and *S. ilicifolium* are classified as temperate and tropical species, respectively (e.g., Kumagai et al., 2018), and *S. crispifolium* is a warm water species (Tanaka et al., 2013). The comparison of thallus length and biomass of three *Sargassum* species between Nishiumi, Ainan Town and Tatsukushi, Tosashimizu City are shown in Fig. 5. While most *Sargassum hemiphyllum* reached over 100 cm in thallus length, thallus lengths of *S. ilicifolium* and *S. crispifolium* were around 10–20 cm. Mean biomass of *S. hemiphyllum* was higher than that of *S. ilicifolium* and *S. crispifolium*.

Subsequently, thallus length and biomass of the three *Sargassum* species focused on the present study are compared with other studies. In *S. hemiphyllum,* the mean thallus length was roughly equal to and the biomass tended to be higher than those in temperate areas of Japan (Umezaki, 1984; Yokoyama et al., 1999). For *S. crispifolium,* there are few studies however, thallus length was considerably short, and biomass was about two times as large as those in Kagoshima, southern part of Japan (Tsuchiya et al., 2011). For *S. ilicifolium,* the mean thallus length was shorter than and the biomass was relatively larger than that in the tropical coral reefs (Low et al., 2019, and references therein). In comparison between the present study and the temperate region in Japan (Shimabukuro et al., 2007; Haraguchi et al., 2018), the biomass was slightly less, and the thallus length was relatively short. Because the thallus length and biomass of *Sargassum* species are affected by the wave exposure and growing depth and vary among or between local or regional spatial scale, we could not compare them uniformly. Morphological characteristics of *Sargassum* beds are supposed to change by the replacement of temperate species such as *S. hemiphyllum* with tropical species such as *S. ilicifolium*.

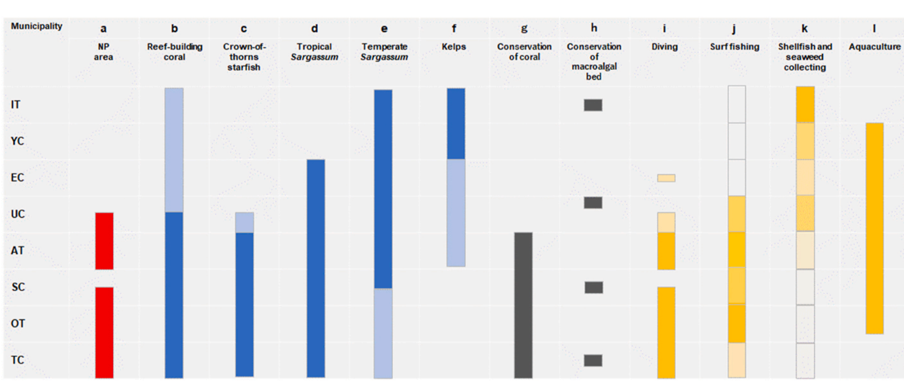

Fig. 4. Schematic view showing geographic distribution gradient of (a) coastal national park area (Ashizuri-Uwakai National Park), (b) reef-building coral (assuming tabular coral *Acropora solitaryensis* complex and *A. hyacinthus* complex), (c) crown-of-thorns starfish (COTS) *Acanthaster* cf. *solaris*, (d) tropical *Sargassum* (assuming *S. ilicifolium*), (e) temperate *Sargassum* (assuming *S. hemiphyllum*), (f) kelps (assuming *Ecklonia cava kurome*), (g) coral conservation (mainly control of the number of COTS), (h) macroalgae conservation (mainly control of the number of sea urchins), (i) leisure diving, (j) recreational fishing (mainly surf fishing), (k) coastal fisheries for shellfish and macroalgae, and (l) aquaculture for fish and bivalve. The darker color of the color bar from b to f represents that the distribution of each of the envisioned species was confirmed by our field observations and the lighter color means the distribution has been reported or the distribution of different species assumed was confirmed by field observations. The shading of the color bar from i to l represents frequency of use and darker color indicates a higher use frequency. The detailed distributions are shown in our previous study (Abe et al., 2021). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

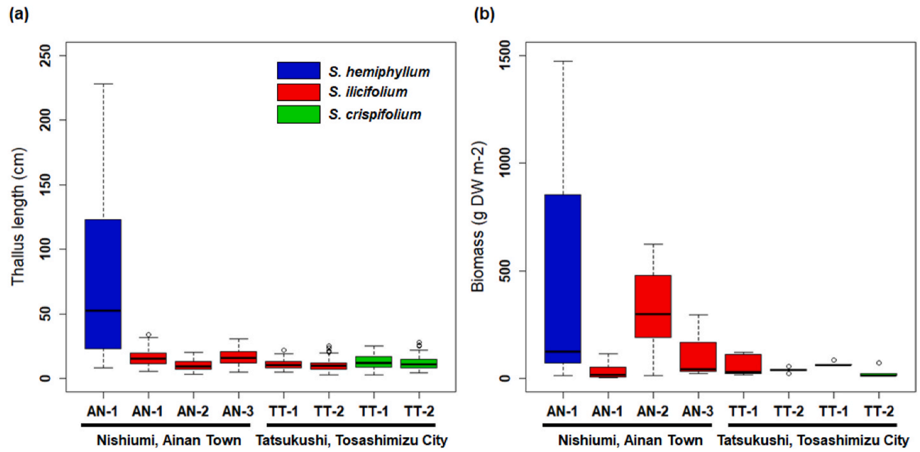

Fig. 5. Box plots of (a) thallus length and (b) biomass of *Sargassum hemiphyllum*, *S. ilicifolium*, and *S. crispifolium* at each station at Nishiumi (Ainan Town; AN-1, AN-2, AN-3) and Tatsukushi (Tosashimizu City; TT-1, TT-2) collected during May to June 2020.

4.2. Present conservation structure for coral and macroalgae

Prevailing predators of corals in the study area are crown-of-thorn starfish (COTS) and snails (*Drupella* spp.). In recent years, outbreaks of COTS have been a serious problem between TC and AT (Table 2). Though the distribution of COTS greatly depends on the presence of coral and winter water temperature, outbreaks have not been reported north of Uwajima City where tabular corals are growing (Figs. 3c and 4). The majority of coral conservation measures conducted in the study area are management of the number of COTS. The management measures are implemented between Tosashimizu City and Ainan Town through program by the Ministry of the Environment and Fisheries Agency (some are subsidized by prefecture and municipality) (Fig. 4g).

Although the species of herbivore of macroalgae are different from region to region, the main ones are sea urchins, rabbitfish (*Siganus fuscescens*), and parrotfish. Management of sea urchin populations is a major conservation measure. The conservation is mainly conducted supported by the Fisheries Agency, while the magnitude and implementation area are very limited compared to that of coral conservation (Fig. 4h).

In the study area, local dive stores and fishermen are the main stakeholders in the implementation of coral and macroalgae conservation. Although overuse by diving in coral reef areas is often a problem and is mainly reported to have negative impacts (e.g., Zakai and Chadwick-Furman, 2002; Barker and Roberts, 2004), dive stores are highly conscious of preserving coral communities as one of the major tourist resources. On the other hand, macroalgae rarely function as a diving resource, but conservation activities are basically carried out by fishermen because they may be directly related to coastal fisheries. This system of implementation has been reported in various regions of Japan (Sekine, 2015; Shinbo, 2016; Yamashita, 2021).

4.3. Present conflict between marine leisure and fishery

Coastal areas are important space not only for tourism, but also as a place for fishery production and biodiversity. If there are conflicts among various stakeholders, there is a concern that it may become an obstacle in the use and conservation of coastal ecosystems and even in the implementation of adaptation measures, and it is necessary to identify the existence of conflicts in each region. As for four representative categories (diving, leisure fishing, coastal fisheries, and aquaculture) that actively use the coastal zone, relationships concerning conflicts asked at the hearing are briefly summarized in Fig. 6. The relationships greatly varied from region to region (Table 2). Deterioration of water quality due to fish aquaculture was a problem in one limited area (Kashiwajima in Otsuki Town) and it caused a decline in the quality

Table 2
Brief summary of (a) experienced changes and perceptions in the coastal ecosystem (especially seaweed beds and coral communities) from the past, (b) expectations and concerns about future changes in the coastal ecosystem for fishermen, and (c) conflicts concerning space utilization among leisure diving, recreational fishing, aquaculture, and coastal fisheries based on an interview survey with local related parties. “isoyake” means decrease or disappearance of upright seaweed beds resulting in the formation and maintenance of poorly vegetated areas on shallow bedrock and boulder areas (Fujita, 2010).

Topic	Municipality	Example of comments
a	IT YC	There is no real sense of “isoyake”. Recognition on the presence of corals in this area must be rare.
	EC UC	The seaweed beds have clearly declined. Though corals are definitely increasing, it seems that macroalgae and corals are competing with each other from year to year recently.
	AT	The seaweed beds have clearly declined. Though corals can be seen since long ago, coral cover has seemed to decline due to predation by COTS.
	SC OT TC	The seaweed beds have clearly declined. Though corals can be seen since long ago, coral cover has seemed to decline due to effects of heavy rain, typhoon, and predation by COTS.
b	IT YC	There is no good feeling about the increase in corals. Meanwhile, there is no sense of urgency about “isoyake”.
	EC UC	Though ecosystems constituted by macroalgae are more desirable as fishing grounds than corals, we do not believe that the increase in corals is a problem for fisheries in the future.
	AT	Corals get tangled in the gill nets, but it does not mean that increase in coral is the problem. We do not believe that a decline in corals is desirable for fisheries in the future.
	SC OT TC	Though corals get tangled in gill nets, we think that it is inevitable.
c	IT YC	Basically, there is no leisure diving going on since fishermen are diving for the harvest of rocky living resources.
	EC UC	Recreational fishing (boat fishing), coastal fisheries, and diving use points that may overlap, but it has not been a major problem.
	AT	Recreational fishing (surf fishing), coastal fisheries, and diving use points that may overlap, but it has not been a major problem.
	SC OT TC	Recreational fishing (surf fishing), coastal fisheries, and diving use points that may overlap, but it has not been a major problem. Although major diving sites are managed with mooring buoys in place, it is difficult to significantly increase the number of the buoys because of the relationship with the local fisherman. In some areas, leftover feed (wet fish) from fish farming deteriorates the water quality and it affects the quality of diving and bathing.

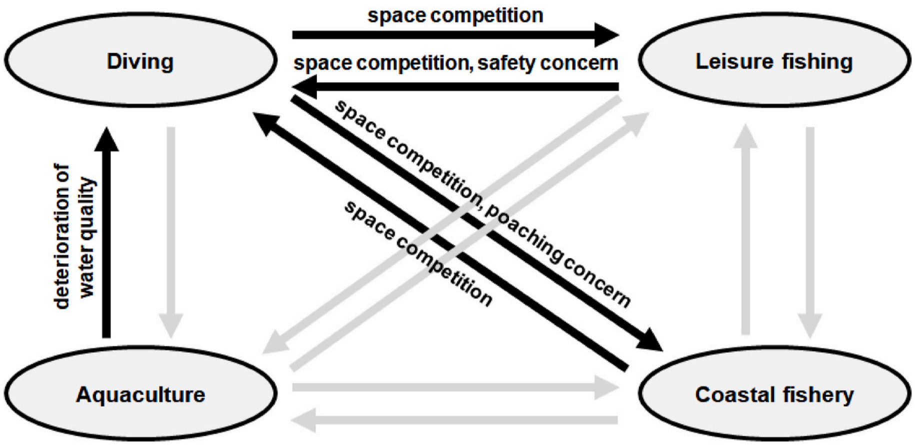

Fig. 6. Conceptual diagram of conflict concerning space utilization among leisure diving, recreational fishing, aquaculture, and coastal fisheries in the study area. Gray arrows indicate that no conflicts were reported in the interviews.

of the diving. Looking at the whole study area, issues such as competition for space, safety, and poaching concerns exist among diving, surf fishing, and coastal fisheries. However, it is not a major problem within the community since the magnitude and frequency of coastal use were not so large at present. In addition, there is no diving as a marine recreation in places where shellfish and macroalgae are harvested by coastal fisheries, and a structure has been formed that is less likely to cause conflicts (Fig. 4i, k).

Horizontal distributions of examples of diving points, glass boat routes, and designated aquaculture areas for three areas within the national park zone (Nishiumi in AT, Kashiwajima in OT, and Tatsukushi in TC) are shown in Fig. 7 to illustrate the competition for space use. At Nishiumi in AT, most of the dive sites are concentrated and distributed around a small island on the west side and aquaculture is not conducted in such an area (Fig. 7b). At Kashiwajima in OT, fishes are cultured in the most secluded area, and the aquaculture area and some diving points are

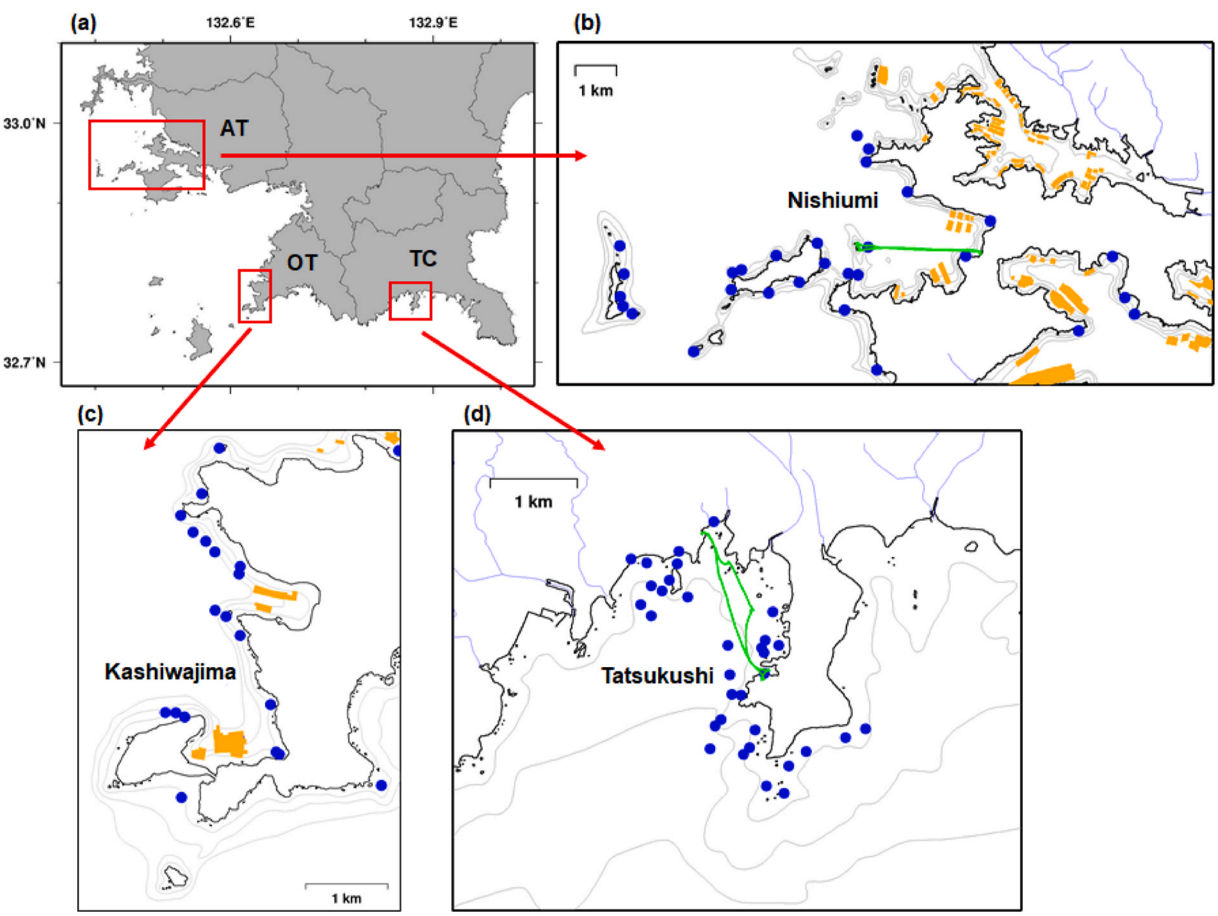

Fig. 7. Examples of space usage in (a) southern part of the Ashizuri-Uwakai National Park, (b) Nishiumi in Ainan Town (AT), (c) Kashiwajima in Otsuki Town (OT), and (d) Tatsukushi in Tosashimizu City (TC). Aquaculture area (orange polygon), diving point (blue circle), and glass boat route (light green line). Aquaculture areas were obtained from GSI Maps (https://maps.gsi.go.jp/; accessed 21 April 2021) provided by the Geospatial Information Authority of Japan. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

in close proximity (Fig. 7c). As mentioned above, deterioration of water quality caused by leftover feed from fish farming is a problem in this area. There are no fish aquaculture facilities, and many dive sites are constructed outside of the glass boat route at Tatsukushi in TC (Fig. 7d).

4.4. Environment and coastal ecosystem changes from the past

Long term variations in monthly mean air temperature from 1942 to 2019 at the meteorological stations of Uwajima, Sukumo, and Tosa-shimizu (Fig. 1b) were confirmed. Monthly mean temperatures were on the rise at all stations (Mann-Kendall test, $p < 0.01$) and the rate of increase was more pronounced in February (0.017–0.023 °C $year^{-1}$) than in August (0.010–0.022 °C $year^{-1}$). Long-term trends in annual precipitation and the number of days recording over 100 mm daily precipitation were not detected at the three meteorological stations described above. Moreover, there was no significant trend for the number of typhoons approaching Shikoku Island (Mann-Kendall test, $p = 0.848$).

Concerning long-term changes in seawater temperature in coastal areas, annual increasing rate of water temperature in Uwa Sea (Uwajima City) during 1982–2004 was ca. 0.03 °C yr^{-1} (Suzuki and Takeuchi, 2007). In addition, the rates of increase in surface temperature in southwestern part of Kochi Prefecture during 1976–2006 were ca. 0.02–0.03 °C yr^{-1} (NIES, 2008) and the increase rate was the same level as in Uwa Sea. Though there was a great deal of interannual variability as for surface water temperature, the temperature increased in every area in the long term.

At Kashiwajima, the coral cover decreased significantly in the mid-2000s, but has been recovering since then. Coral cover at Tatsukushi has remained at the same level and Nishiumi has seen a downward trend in coverage since 2002. As shown here, coral cover is not on the rise in the southern areas and there are various factors (e.g., sediment loading from land, storm surge, and feeding damage by COTS) that can significantly reduce coral cover.

Questionnaire survey was conducted for fishermen and diving operators using the coastal zone and the changes in the coastal ecosystem from the past were summarized by region (Table 2). Decline in seaweed bed ("isoyake") was widely reported in southern area (south from Uwajima City), while the comment was that they did not feel the effects of "isoyake" in the two northern municipalities outside of the national park area (Ikata Town and Yawatahama City). In addition, divers remarked that though the coral community has been seen for a while in the southern part of the study area, coral cover has greatly declined due to outbreak of predators, mortality due to sediment loading, and storm surge in the recent decade. On the other hand, fishermen and divers were aware of the steady increase of coral cover in the central area (Uwajima City and Seiyo City). Decline of seaweed beds and changes in their constituent species (Tanaka et al., 2012) and the northward shift of coral distribution (Yamano et al., 2011) were reported in the southern part of the study area, and the results of interviews were consistent with previous studies mentioned above. For fishermen in Ikata Town, the coral distribution was completely unrecognized, while our field observations found a few branch corals.

4.5. Future environment and ecosystem

The present and future SSTs in February and August during 2009–2018 and 2091–2100 are shown in Fig. 8. The increasing rate was higher in February than in August, and the range of the rise was ca. 1–2 °C under RCP2.6 and ca. 3–4 °C under RCP8.5 in February and ca. 1 °C under RCP2.6 and ca. 3–3.5 °C under RCP8.5 in August.

Our previous study (Abe et al., 2021) has shown that the species distribution estimated from the water temperature and the threshold values (Table 1) were generally consistent with the present actual habitat area. In the 2090s, the lowest and highest water temperature is projected to be ca. 15–20 °C and 27–29 °C, respectively, under RCP2.6 and northward shifts of tropical *Sargassum*, coral, and COTS are assumed. In addition, the lowest and highest temperature will rise to ca. 17–21 °C and 30–31 °C, respectively. Under this situation, the risk of coral bleaching and mortality due to high summer water temperature (over 30 °C) will be higher. Moreover, the distribution of temperate *Sargassum* (*S. hemiphyllum*) will be greatly limited in a narrow part of the northern part and survival of kelp (*Ecklonia cava kurome*) will be severe in the whole region. When we focus on the distribution and activity of predators, though the large populations of COTS have been confirmed in

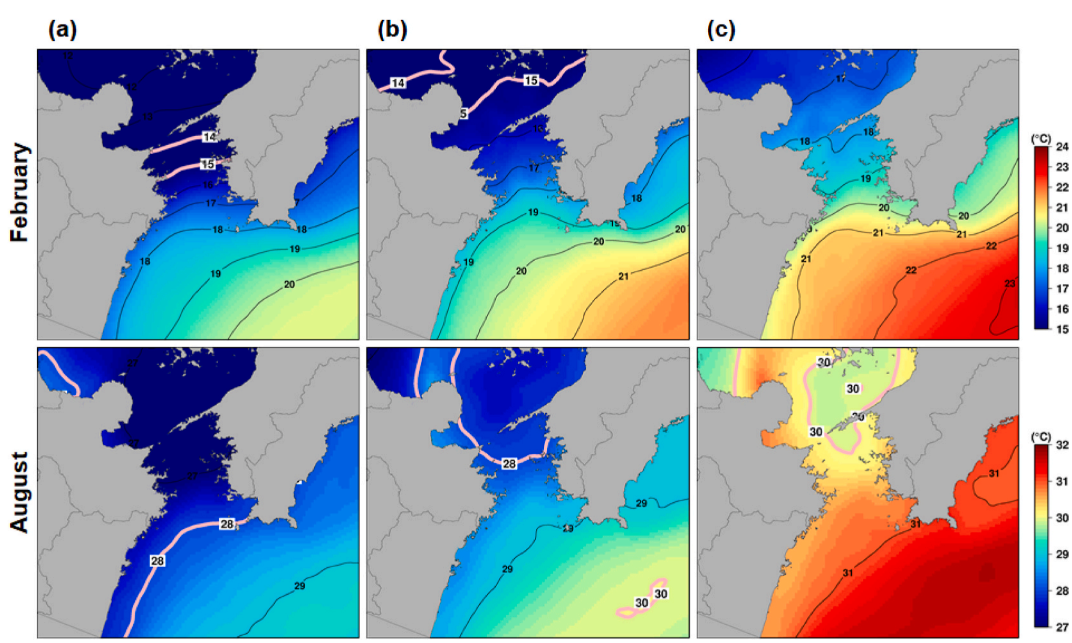

Fig. 8. Horizontal distribution of (a) observed and (b, c) simulated sea surface temperatures in February (upper panels) and August (lower panels) during (a) 2010s (2009–2018), (b) 2090s (2091–2100) under RCP2.6 and (c) 2090s under RCP8.5 simulations. The values were expressed as 10-year mean. The values were obtained from (a) the reanalysis dataset of MUR SST (JPL MUR MEaSUREs Project, 2015) and (b, c) the simulation of FORP-JPN02 (Nishikawa et al., 2021). Bias correction was conducted for the simulated temperatures.

areas south of Ainan Town at the present condition, overwintering and spawning will be possible in more northern areas as well in the future. In addition, grazing pressure of *S. fuscescens* will be higher since the minimum water temperature will never go below 15 °C and this will lead to prolonged period of feeding damage for macroalgae.

4.6. Future changes in the underwater landscape

Future changes in distribution of typical species constituting the coral community and macroalgal beds by increasing water temperature were presented in the previous section. How the underwater landscape (coral communities and macroalgal beds constituted from tropical and temperate *Sargassum* and kelps) will change based on these distribution projections are discussed here. Basically, as shown in Fig. 3, the ecosystem transitions are likely to occur depending on the water temperature. In detail, dominant of coral community (Fig. 3a), coral community and tropical *Sargassum* (Fig. 3b), coral community (mainly tabular) and tropical/temperate *Sargassum* (Fig. 3c), tropical/temperate *Sargassum* and sparse coral community (mainly branch) (Fig. 3d), temperate *Sargassum* and sparse kelps (Fig. 3e), and dominant of kelps and temperate *Sargassum* (Fig. 3f) will occur.

In our study area, dominant kelp such as *Ecklonia cava kurome* produces year-round macroalgal beds. On the other hand, *Sargassum* species have a seasonal fluctuation in biomass; the thallus length increases from winter to early summer, then the whole thallus including the holdfast (annual species such as *S. hemiphyllum* and *S. ilicifolium*) or except for holdfast (perennial species such as *S. patens*) disappear. The decline of kelp forest in the future and shift to *Sargassum* beds will induce a limited duration of a dense growth of seaweed beds. Moreover, the thallus length of tropical *Sargassum* species is characterized as shorter than that of temperate *Sargassum* species (Terazono et al., 2012, Fig. 5a). Therefore, when temperate species are completely replaced by tropical species, it will cause a decrease in the three-dimensional structure provided by *Sargassum* beds.

Exposure to high water temperature causes coral bleaching and mortality (Brown, 1997). Coral (symbiotic zooxanthellae) growth will be inappropriate when the water temperature rises to extremes and tropical macroalgae that are more adapted to high temperatures than corals may dominate in such cases (Table 1). However, the vegetation could be close to bare ground due to limited growth of macroalgae through annual feeding damage since increase in water temperature enhance grazing pressure by herbivorous fishes (Zarco-Perello et al., 2017).

4.7. Future changes in ecosystem services

In the previous section, projected future changes in the underwater landscape in response to elevated seawater temperatures are described. Ecosystem services are the benefits people derive from nature (Liquete et al., 2013). Possible future changes in ecosystem services in the study area are qualitatively discussed in Table 3. Provisioning (e.g., food provision), regulating and maintenance (e.g., water purification), and cultural (e.g., recreation and tourism) services were assumed as ecosystem services by the coral community and seaweed bed according to Liquete et al. (2013).

Dense distribution of corals or macroalgae can attenuate waves or currents and these effects prevent sediment resuspension on a local scale (Hardy and Young, 1996; Madsen et al., 2001). In addition, coral community and seaweed beds can serve as a nursery ground for various invertebrates and juvenile fish (Nagelkerken et al., 2000; Evans et al., 2014). These vegetations are widely accepted as fishery grounds. Though we seldom use kelps and *Sargassum* (except for *S. fusiforme*) distributed in the study area as human food, kelp forests and *Sargassum* beds can become a good food source for shellfish like abalones, turban shells and sea urchins (Imai and Arai, 1986; Yoshiya et al., 1987).

Macroalgae can contribute as a large sink of carbon (DIC) and nutrients (DIN and DIP) (Gao and McKinley, 1994; Mai et al., 2010; Krause-Jensen and Duarte, 2016; Yoshida et al., 2019a). Production can be an indicator of potential for carbon fixation and water purification and annual production by macroalgae can be estimated roughly using the P/B ratio (ratio between production and biomass) (Pedersen et al., 2005; Quartino and Boraso de Zaixso, 2008). Our field observations on *Sargassum* have indicated that there was significant difference between temperate *S. hemiphyllum* and tropical *S. ilicifolium* with respect to the standing stock per unit area (Fig. 5b). If we focus only on *Sargassum* species, transition from temperate to tropical species may decrease the fixed amount of biophilic elements (e.g., carbon, nitrogen, and phosphorus). Moreover, disappearance of kelp forests may greatly affect the material cycle in coastal areas since kelps have an especially high biomass and production (Gao and McKinley, 1994).

Various marine leisure activities are conducted in coastal areas and coral communities and seaweed beds may contribute to the leisure directly or indirectly. The tourist value of coral reefs is well known (Spalding et al., 2017). Therefore, it is assumed that the touristic value based on the coral community must be higher than that based on seaweed beds. According to the results of interviews with dive shops, the coral itself is rarely the main attraction for divers but the ecosystem that

Table 3
A brief summary of assumed changes in ecosystem services due to water temperature increase in the study area. The classification of ecosystem services was followed according to Liquete et al. (2013).

Species	Change	Major factors of the change	Examples of changes in ecosystem services		
			Provisioning service	Regulating and maintenance services	Cultural service
Reef-building corals	increase	temperature increase in winter	increase in target species for fisheries from coral community	improvement of wave attenuation effect	increase in recreational opportunities and quality
	decrease	increase in summer temperature and feeding damage by COTS	decrease in target species for fisheries from coral community	decrease in wave attenuation effect	decrease in recreational opportunities and quality
Tropical *Sargassum*	increase	temperature increase in winter	increase in target species for fisheries from seaweed bed	improvement of fixation capacity of nutrients and carbon, wave attenuation effect	not available
	decrease	increment of feeding damage by herbivorous fish	decrease in target species for fisheries from seaweed bed	decrease in fixation capacity of nutrients and carbon, wave attenuation effect	not available
Temperate *Sargassum*	decrease	temperature increase in summer and increment of feeding damage by herbivorous fish	decrease in target species for fisheries from seaweed bed	decrease in fixation capacity of nutrients and carbon, wave attenuation effect	not available
Kelps	decrease	temperature increase in summer and increment of feeding damage by herbivorous fish	decrease in target species for fisheries from seaweed bed	decrease in fixation capacity of nutrients and carbon, wave attenuation effect	not available

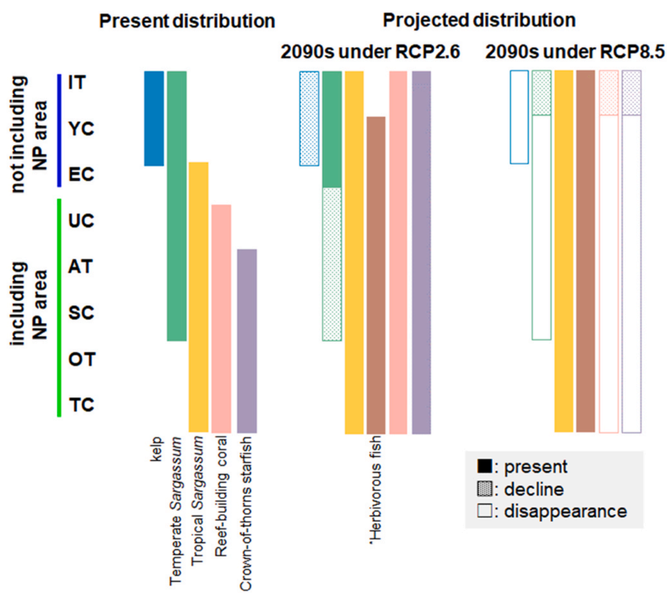

Fig. 9. Schematic view of future changes in coastal ecosystem (present, 2090s under RCP2.6 and RCP8.5) in the Ashizuri-Uwakai National Park and its northern surrounding area (TC: Tosashimizu City, OT: Otsuki Town, SC: Sukumo City, AT: Ainan Town, UC: Uwajima City, EC: Seiyo City, YC: Yawatahama City, and IT: Ikata Town). Asterisk indicates the extent to which feeding activity of herbivorous fish is not limited by water temperature in winter.

lives around the coral community is an attractive feature of the underwater landscape. Moreover, glass boats operate around areas with high coral cover. Thus, increase in the coral community may promote coastal use as one of the tourism resources. Meanwhile, recreational fishing targeting fishery resources gathered in seaweed beds (e.g., the squid *Sepioteuthis lessoniana*) is popular in the study area.

5. Consideration of adaptation strategy

5.1. Concept

Consideration and/or execution of adaptation measures should be conducted depending on the degree of environmental and ecological change. Here, examples of adaptation measures assuming the end of this century (2090s) under RCP2.6 and RCP8.5 are described for each municipality. Ecosystem services can be divided into the capacity of the ecosystems to deliver services to society (the supply-side) and the social demand for using a particular ecosystem function (the demand-side) (García-Nieto et al., 2013). The supply-side and the demand-side mainly imply conservation measures as promoting adaptation in terms of organism and cultural adaptive responses (promotion of use) on the human side, respectively, in this section. Although there are a wide range of realms that need to be considered for adaptive responses to future climate change, we focused on the adaptive measures based on two viewpoints, “conservation” and “utilization” (coastal fisheries and tourism), against the range shifts in corals, macroalgae, and their predators.

5.2. Application to study area

Examples of ecosystem changes for each simulation scenario (in the 2090s under RCP2.6 and RCP8.5) and proposed adaptive measures for each municipality are summarized in Fig. 9 and Table 4. Significance of each measure divided into “conservation” and “utilization” are reviewed and described in this section. Though extraterritorial management could be a last measure if the target species will not be expected to grow *in situ* field due to rising water temperature, we did not consider *ex situ* conservation since there will be northern habitat (e.g., Kumagai et al., 2018).

5.2.1. Conservation

- Implementation and/or continuation of monitoring for coastal ecosystem and growth environment

Monitoring of coastal ecosystems and their growth environment is essential in cases that there will be no immediate impacts by climate change. In Japan, the consecutive monitoring systems such as by government (*Monitoring sites 1000* project; Kawagoe, 2017) and NPO (*Reef Check Japan*) are constructed for the coral community. In addition, Sango Map Project (https://www.sangomap.jp/; accessed 21 April 2021; Namizaki et al., 2013; Kumagai et al., 2018b) through citizen participation is collecting examples of observation of coral growth,

Table 4
Examples of proposed adaptive measures in each municipality assuming in the 2090s under RCP2.6 and RCP8.5 scenarios based on Fig. 9. Adaptive measures are shown from two perspectives, *conservation* of corals and macroalgae and *utilization* (coastal fisheries and tourism) considering present conservation and utilization status (Fig. 4). *: The necessity of *ex situ* conservation of corals under RCP8.5 depends on the status of coral in other regions.

Emission scenario	Municipality	*Conservation*		*Utilization*
		Coral	Macroalgae	
RCP2.6	Ikata Town Yawatahama City	Implementation of coral ecosystem monitoring and management of the number of nuisance species, setting up protected area	Assisted dispersal of kelps	Changes in the species to be fished, use of coral as a tourism resource and development of facilities for this
	Seiyo City Uwajima City		Management of the number of herbivorous fish and implementation of macroalgae monitoring	
	Ainan Town Sukumo City Otsuki Town Tosashimizu city	Continuation of coral ecosystem monitoring and management of the number of nuisance species, expansion of protected area and regulation change		Changes in the species to be fished
RCP8.5	Ikata Town Yawatahama City	Alleviation of local stresses	Assisted dispersal of temperate *Sargassum* species	Changes in the species to be fished
	Seiyo City Uwajima City Ainan Town Sukumo City Otsuki Town Tosashimizu City	*NA**	Management of the number of herbivorous fish	Changes in the species to be fished and promotion of aquaculture, tourism use of tropical *Sargassum* beds

bleaching, and spawning. On the other hand, data on continuous monitoring of seaweed beds is very limited in the study area and it is difficult to grasp the long-term changes in benthic vegetation on a broad scale. As for water quality, seasonal observations since the 1970s have been implemented by each prefecture.

- Expansion of protected area and regulation change

Much of the coastal area of the study area is designated as a national park area by the Ministry of the Environment, Japan. Most of the area is ordinary zone that has few regulations. A total of 22 areas (179.1 ha) have been designated as a marine park zone and many actions are regulated within these areas. Coral conservation activity such as extermination of COTS are preferentially implemented in the national park area (especially the marine park zone). It is well known that the establishment of marine protected areas play a key role in the conservation of marine life (Magris et al., 2017). Therefore, increase in marine park zone and/or extending the national park area to the north can be important for conservation of the coastal ecosystem. Spatial placement of protected areas considering the balance among biodiversity conservation, fisheries, and tourism and genetic connectivity (Botsford et al., 2009; Christie et al., 2010) is also required.

- Management of the number of nuisance species

Building a system (budget and personnel) is essential for the implementation of coral predator management. For example, management of the number of predators and coral monitoring have not been conducted in Uwajima City since outbreak of COTS have not been reported. However, increase in COTS will be simulated in the future (Fig. 9) and it is important to have a system for the implementation of conservation activities in advance in such places.

Increase in water temperature enhances grazing pressure on macroalgae by herbivorous fishes (Zarco-Perello et al., 2017) and the duration of damage will be longer than ever before. Taking measures against feeding damage in accordance with local conditions is necessary (Masuda et al., 2000). Moreover, actively harvesting and utilizing herbivorous fishes is effective in conserving seaweed beds.

It is necessary to consider carefully what to target for conservation activities in areas where macroalgae and corals are growing in the same habitat since increase in feeding pressure of sea urchins on seaweed have been shown to promote coral recruitment (Coma et al., 2011; Nozawa et al., 2020).

- Assisted dispersal of kelps and temperate *Sargassum* species

The potential of distributional expansion of kelps and fucoids is dependent on the dispersal of zoospores (kelps) or propagules (fucoids), however, dispersal of kelps and fucoids is said to occur largely within short distances (Schiel and Foster 2006). Therefore, even if the range of distributional possibility shifts toward the north in the future, it is suggested that the distribution of kelps or fucoids cannot move due to their limited dispersal ability. Moreover, the deeply indented coastlines in our study area also cause local differences in topographical features and wave exposure and limit the smooth dispersal of kelps and fucoids. In the above case, assisted dispersal which assisted gene flow and artificially expand the distribution is one of the effective approaches to maintain biodiversity and underwater landscape. The assisted dispersal is paid attention to adaptive measures recently, however, there are no actual examples for seaweed beds (Coleman and Goold, 2019; Eger et al., 2020). In Ikata town to recover from isoyake, construction of artificial seaweed beds has been conducted using spore bag that were packed with fertilized kelps and *Sargassum* species and introduce the bag to the artificial reef (Choi et al., 2000). The assisted dispersal may be technically possible in our study area but, ethical problems and cost, necessity should be discussed.

- Alleviation of local stresses

Sediment inflows from rivers and extreme eutrophication are not favorable for corals and macroalgal growth/survival (Umar et al., 1998; Nugues and Roberts, 2003; Fabricius, 2005), especially under global warming (Wooldridge et al., 2012). In some of the waters in the study area, burial (mortality) of coral and macroalgae due to the inflow of sediment from heavy rains have occurred. Moreover, although coral bleaching caused by exposure of high water temperature have been a serious phenomenon in tropical and subtropical seas, reduction in land load and shading the light can mitigate bleaching risks (Wiedenmann et al., 2012; Coelho et al., 2017). As just described, effects of climate change on coastal ecosystem can be mitigated through alleviation of local stresses such as watershed management and *in situ* environment control.

5.2.2. *Utilization*

- Changes in the species to be fished in coastal fisheries

Shifts in benthic vegetation may alter the types of useful fishery species that live there. Simultaneously, water temperature increase itself will lead to changes in fish fauna. Harvest of abalone and sea urchins are expected to decrease significantly as global warming progresses in areas where kelps and temperate *Sargassum* are dominant at the present time. Moreover, increment of coral communities lead to increased fisheries damage such as breaking of gill nets (Table 2). Specific projections concerning changes in harvest are a difficult issue, but it is important for the coastal fisheries sector to prepare for climate change by referring to fish species and fishing methods currently used in more southern regions. In addition, it may be possible to promote the cultivation of fish and bivalves that are resistant to high water temperatures.

- Utilization of ecosystem by amplification of marine leisure facilities in tourism

Currently, most of the dive shops and dive points are located south of Ainan Town (Fig. 4i). If the distribution area of large coral communities moves northward in response to global warming, it may lead to diving in areas that have not been used before. The development of tourist facilities (e.g., dive shop, glass boat) is essential to utilize new marine resources. It is necessary to coordinate the interests of different industries (e.g., Toyoshima and Nadaoka, 2016) when starting new tourism activities. Furthermore, a tool for optimizing the use of space between different industries has been developed (Villa et al., 2001), thus the construction of a framework for spatial layout and regulatory content needs to be considered in the future.

- Utilization of ecosystem around tropical *Sargassum* beds

With respect to fisheries, the importance of tropical seaweed beds is widely recognized (Tano et al., 2017). On the other hand, though we have no quantitative data on touristic value for macroalgae species and/or macroalgal beds have lower scenic attractiveness compared to the coral community. However, diverse organisms inhabit associate with tropical *Sargassum* beds (Chaves et al., 2013; Tano et al., 2016) and it is important to promote its value as a place for diving and other marine activities.

6. Conclusions and future tasks

This research focused on an area with a high spatial temperature gradient and simulated changes in coral and macroalgae distributions based on future water temperature. Perceptions of coral and macroalgae distribution, use, and conservation varied greatly from region to region. Subsequently, adaptive measures to be taken in each municipality under two different climate scenarios are proposed for three realms (conservation of biodiversity, fisheries, and tourism). Indeed, the projection method of biological distribution applied in this study was not the state-of-the-art and the number of projected species was limited, but it is worthy of note that local adaptive measures corresponding to ecosystem changes are presented with high spatial resolution.

Though we presented the qualitative evaluation of ecosystem services, the projection of financial benefits is a major future task. Sato et al. (2020) have reported the decline of ecosystem services through the changes in fish community in subtropical coral reefs after mass coral bleaching in 2016. As for macroalgae, CO_2 emission permits and benefit amount with sewerage maintenance costs owing to high photosynthesis activity can be estimated based on macroalgal biomass and production.

In this study, future changes in coral and macroalgae were simulated using the surface water temperature obtained from a regional hydrodynamic model. As shown in Kumagai et al. (2018), various environmental factors in addition to water temperature (such as light extinction coefficient, chlorophyll *a* concentration) should be considered in the simulation for distribution. Moreover, consideration of thermal adaptation in coral symbionts (Rowan, 2004; Howells et al., 2016) may make the coral distributional changes a little more gradual. Ecosystem functions such as carbon storage by primary producers is highly dependent on the organism's biomass. Thus, in addition to presence or absence of living things, the projection of changes in the biomass should be performed.

Growth and survival of organisms are affected by not only gradual changes in temperature but also short-term events such as surge due to typhoons and sedimentation by floods. Increase in the frequency of severe tropical cyclone and slowing down of translation speed of cyclone have been projected (Yoshida et al., 2017; Yamaguchi et al., 2020). Therefore, it may be necessary to select sites that are less susceptible to extreme events and to conserve coastal ecosystems.

Contributors

HY designed the research; HA, SH, YFK, NHK and SM performed research; HA and NHK analyzed the data; and HA wrote the paper.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ocecoaman.2021.105744.

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