Geoscience Letters

RESEARCH LETTER

Open Access

Coral distribution and diversity in Sakiyamawan–Amitoriwan nature conservation area of Iriomote Island in Japan

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Abstract

Sakiyama and Amitori bays of Iriomote Island in Japan are adjacent, but their coral distributions differ significantly. This study investigates the differences in the coral distribution and diversity between both bays from the diversity index and intermediate disturbance hypothesis (IDH) perspective. In Amitori Bay, tabular and branching corals dominate the mouth and inner part of the bay, respectively. Coral diversity is maximum in the intermediate part of the bay, realizing the IDH. In Sakiyama Bay, branching and massive corals dominate the reef edge and coast sides of the bay's intermediate part, respectively. Coral diversity is maximum in the reef edge part of the bay, and IDH is not realized. The difference in the soil inflow and geographical characteristics between both bays significantly affects their coral distribution and diversity.

Keywords Coral diversity, Intermediate disturbance hypothesis, Soil inflow, Sakiyamawan, Amitoriwan nature conservation area, Iriomote Island

Introduction

The Sakiyamawan–Amitoriwan nature conservation area of Iriomote Island is Japan's only oceanic nature conservation area (Fig. 1a). The area has included Sakiyama Bay since 1983 and the adjacent Amitori Bay since 2015. It retains a natural environment without significant human influence because it is uninhabited and inaccessible by land. Furthermore, it has various geographic and environmental gradients, such as differences in the water depth, bay length, and bay shape between the bays and inputs of soil particles and fresh water from rivers at the innermost bays (Fig. 1a, Table 1). Changes in physical variables, such as the current, wave, water temperature, and soil inflow with the geographic and environmental gradients, influence the coastal ocean ecosystems distributed in the area, such as corals and *Enhalus acoroides*[1]. For example, a coral community cannot develop in a muddy environment (e.g., Sheppard et al. 2009), but an *E. acoroides* community can grow because its roots or rhizomes can easily settle on the muddy seafloor (Komatsu et al. 2004). That is, the soil inflow affects coastal ocean ecosystems in this area. Thus, the area with various geographic and environmental gradients is suitable for investigating the relationship between coral distributions and physical variables. In addition, a chain of islands in southwestern Japan with dense subtropical forests, including Iriomote Island, was added to the list of Natural World Heritage sites in 2021. On the other hand, Iriomote Island has witnessed an increasing number of tourists

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[1] *E. acoroides* is a large sea grass with underground rhizomes and long strap-like leaves, primarily distributed in coastal areas of the tropical–subtropical Indian and Western Pacific Oceans. The northern limit of its range is the Yaeyama Islands, including Iriomote Island. The leading communities of *E. acoroides* on Iriomote Island are in Sakiyama Bay.

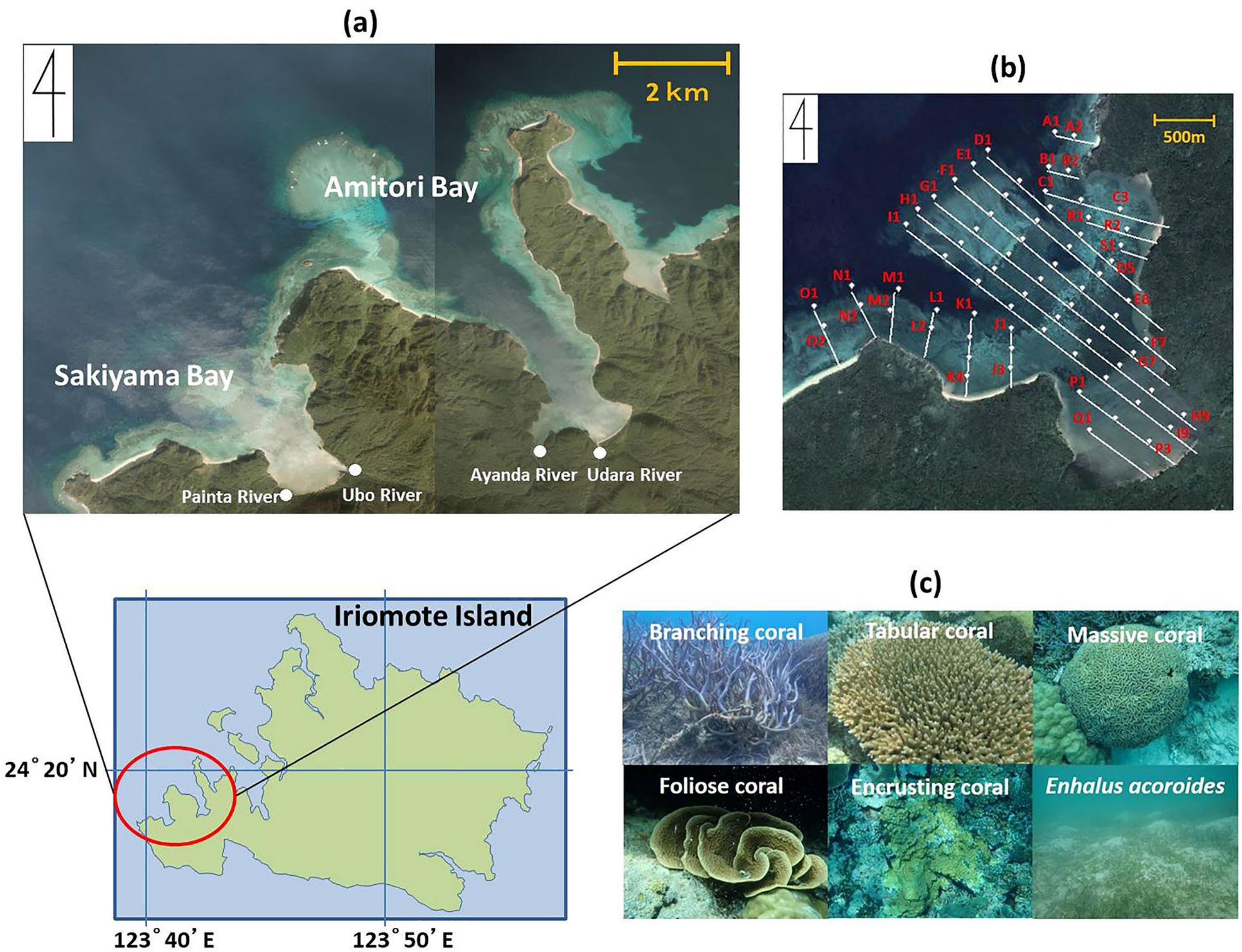

Fig. 1 **a** Iriomote Island and the Sakiyamawan–Amitoriwan nature conservation area. The Painta and Ubo rivers are at the innermost part of Sakiyama Bay. The Ayanda and Udara rivers are at the innermost part of Amitori Bay. **b** Investigation points for coral distributions in Sakiyama Bay. **c** Coral life forms treated in this study and *E. acoroides*

Table 1 Difference in coastal ecosystems (coral and *E. acoroides*) and geographic environments between Amitori Bay and Sakiyama Bay (Kawana 1990, Shimokawa et al. 2014a, Ministry of the Environment, Government of Japan 2015, Shimokawa et al. 2016, Minami et al. 2017)

	Amitori Bay	Sakiyama Bay
Coral	Tabular and branching corals are dominant in the bay's mouth and inner parts, respectively. Coral diversity is the maximum in the bay's intermediate part	Branching and massive corals are dominant in the reef edge side of the bay's intermediate part and the coast side of the bay's intermediate part, respectively. Coral diversity is the maximum on the bay's reef edge
E. Acoroides	*E. acoroides* are rare, and no large community exists	*E. acoroides* is distributed over a wide area of the bay's inner part
Bay length	Around 3.9 km	Around 1.4 km
By mouth length	Around 2.0 km	Around 1.3 km
Water depth where corals mainly exist	From a few to 6 m. The seafloor is uneven	A few meters. The sea floor is almost flat
Maximum water depth	Around 70 m at the center of the bay	Around 40 m at the outside the reef edge
Rivers	Ayanda and Udara rivers at the innermost part of the bay	Painta and Ubo rivers at the innermost part of the bay

in recent years after the inauguration of a new airport on the adjacent Ishigaki Island, and concerns regarding the impacts on the natural environment are intensifying. Therefore, elucidating the relation between the coastal ocean ecosystem in Iriomote Island and the physical variables and the environmental impact assessment based on it are valuable immediate requirements.

Since 2009, we have investigated the relationship between coral and *E. acoroides* distributions and physical variables in this area (Shimokawa et al. 2016 for coral and *E. acoroides* distributions in Sakiyama Bay; Shimokawa et al. 2014a, 2015 for coral distributions in Amitori Bay; Nakase et al. 2015, 2016 for *E. acoroides* distributions in the northwest region of Iriomote Island). A book including English versions of our previous studies written in Japanese was published in 2020 (Shimokawa et al. 2020). It covers an overview of organisms in Iriomote Island, the observation equipment used to obtain the physical variables, the numerical model used to replicate the oceanic flow, wave height and sediment transport fields, the relations between the retention and dispersion of eggs, larvae, seeds, and fruit of marine organisms and the physical variables, and the relationships between the distribution of coral and *E. acoroides* and the physical variables.

Corals thrive in warm tropical and subtropical coastal oceans with temperatures reaching 30 ℃ (Sheppard et al. 2009). Over 450 different types of corals can be found in an ocean area surrounded by Indonesia, the Philippines, and New Guinea. Coral species decline in a direction away from this ocean area. The same types of corals inhabit the Indian and Pacific Oceans, but the Atlantic Ocean has different kinds of corals that are smaller than those in the Indian and Pacific Oceans. Subtropical regions, such as the Ryukyu Islands, including Iriomote Island, frequently become the north or south limits of various oceanic organisms (i.e., under marginal survival conditions for such organisms), which differ from tropical regions even in the same Pacific Ocean. In such subtropical regions, physical environments, including oceanic and atmospheric events, significantly affect the distribution of organisms. For example, strong currents and waves by growing typhoons in subtropical regions can destroy corals (Woodley et al. 1981; Dollar and Tribble 1993; Hongo et al. 2012), but if typhoons have not hit in such regions for a long period, a high water temperature can be maintained, causing coral breaching (Murakami et al. 2017; Nakamura et al. 2022). This is also one of the reasons for studying the relationship between coral distributions and physical variables in such a region.

Sakiyama and Amitori bays are adjacent, but their coral distributions differ significantly (Shimokawa et al. 2014a, 2016). This study will try to investigate the differences in the coral distribution and diversity between both bays from the diversity index and intermediate disturbance hypothesis (IDH) perspective (Connel 1978; see also "Diversity index and IDH" Section) based on the results of investigations of coral and *E. acoroides* distributions, observations of physical variables, and numerical simulations using the observations as initial and boundary conditions.

We summarize here the results obtained from Amitori Bay (Shimokawa et al. 2014a, b) to compare them with those from Sakiyama Bay provided in "Results in Sakiyama Bay" Section. In Amitori Bay, the coverage (Fig. 14 of Shimokawa et al. 2014a) of tabular and branching corals is the highest, followed by massive coral. Tabular corals are dominant in the bay's mouth, whereas branching corals are dominant in the bay's inner part. In addition, there are places, where only massive corals exist in the bay's innermost part. *E. acoroides* is rare, and no large community exists. The diversity index (Fig. 23 of Shimokawa et al. 2014a), H', has a large value in the bay's intermediate part and a small value in the mouth and inner part because only a few types of coral can exist in the mouth with a high wave height and the inner part with a high soil particle number. Diverse types of corals can co-exist in the intermediate part with intermediate disturbances. In Amitori Bay, the intermediate part becomes intermediate to its position in the bay and the strength of the disturbances. The wave height (Fig. 24 of Shimokawa et al. 2014a) is more significant in the order of the reef edge, intermediate part, and inner part of the bay. The number of soil particles (Fig. 25 of Shimokawa et al. 2014a) is larger in the reverse order. H' is large at intermediate wave height (Fig. 24 of Shimokawa et al. 2014a) and an intermediate number of soil particles (Fig. 25 of Shimokawa et al. 2014a). Consequently, the IDH is realized in Amitori Bay. Tabular corals have higher coverage in areas with low diversity than branching corals (Fig. 26 of Shimokawa et al. 2014a). That is, tabular corals are dominant in many areas in Amitori Bay.

Materials and methods

Investigation of coral distributions

Coral distributions were investigated at 44 points (Fig. 2 of Shimokawa et al. 2014a) in Amitori Bay in 2009 and 2011 (Shimokawa et al. 2014a) and 72 points (Fig. 1b) in Sakiyama Bay in 2015 (Shimokawa et al. 2016). Their life form (i.e., colony) and coverage were examined. The coral life form types considered in this study were branching, tabular, massive, foliose, and encrusting corals (Fig. 1c). Furthermore, *E. acoroides* distributions were investigated in Sakiyama Bay. Then, the coral diversity index

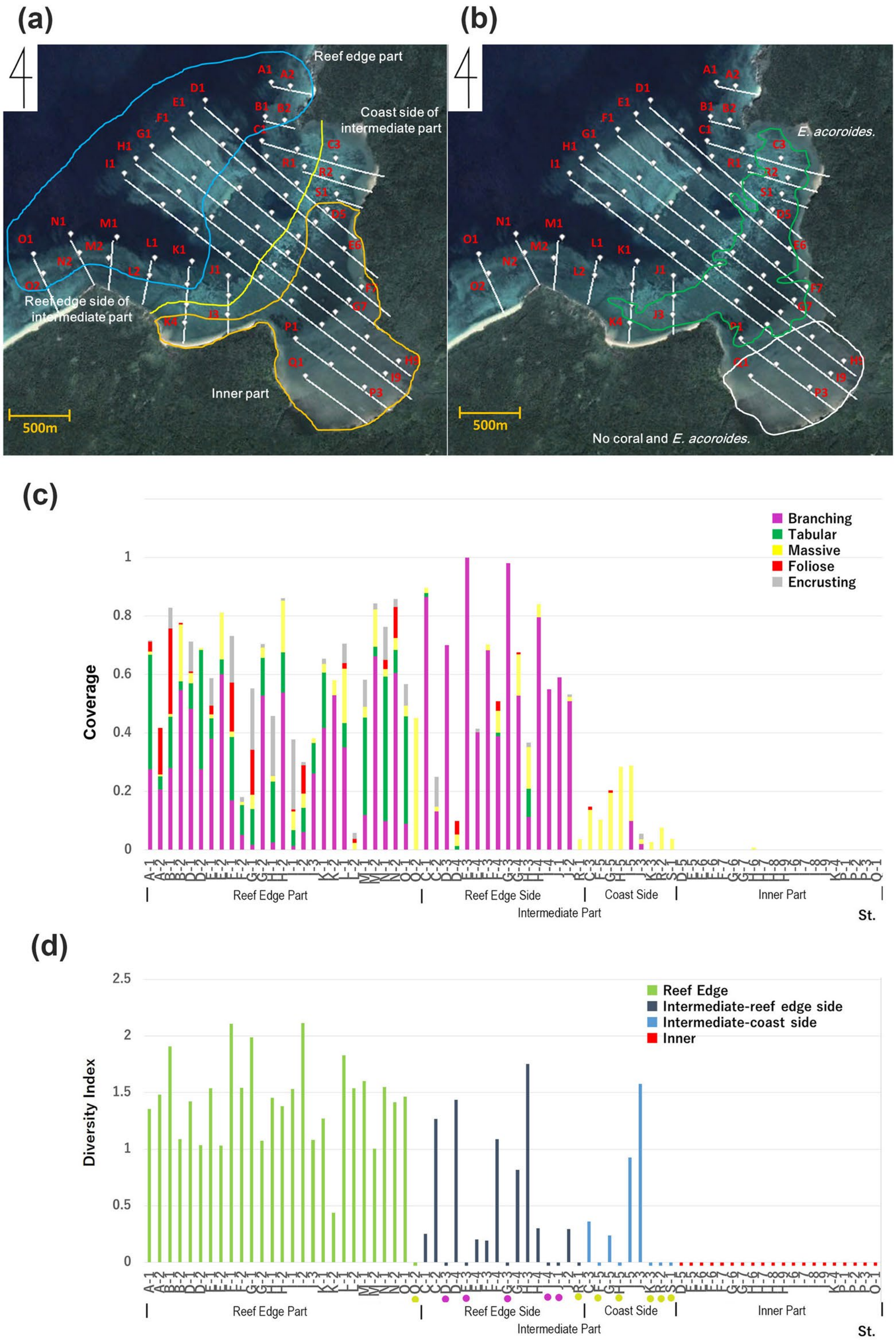

Fig. 2 **a** Classification of parts in Sakiyama Bay. The reef edge part is surrounded by a blue line. The inner part is surrounded by an orange line. The intermediate parts are between them. The reef edge and coast sides are divided by a yellow line. **b** Distribution region of *E. acoroides*. *E. acoroides* is distributed in the region surrounded by a green line. No coral and *E. acoroides* are distributed in the region surrounded by a white line. **c** Coral coverage classified by coral life forms. **d** Diversity index of corals. The zero values of the diversity index in the bay's intermediate part show the existence of only one type of coral (branching or massive). The pink and yellow circles under the station numbers show branching and massive corals, respectively. The zero values of the diversity index in the bay's inner part show no coral, except for St. H-6, where small massive corals exist (see **c**)

(e.g., Clarke et al. 2014) was calculated from the results obtained from the above investigations.

Observations and numerical simulations of physical variables

Physical variable observations of current speed, wave height, water temperature, salinity, and river flow rate were conducted in Amitori Bay in 2008, 2009, and 2011 (Shimokawa et al. 2014a) and Sakiyama Bay in 2011 and 2013 (Shimokawa et al. 2016). Numerical simulations were conducted using the results obtained from these observations as initial and boundary conditions of the physical variables to calculate the temporal and spatial distributions of ocean current, wave height, and soil particles for typical summers and winters in the Sakiyama and Amitori bays. For the calculation, the periods that can be considered normal states of the seasons at Iriomote Island were chosen. For the numerical simulations, our original ocean general circulation model (Murakami 2005; Shimokawa et al. 2014b) for ocean currents, the wave energy balance model (Isobe 1987), the simulating waves nearshore model (Booji et al. 1999) for the wave height, and Lagrangian particle tracking analysis (e.g., Bennett 2006) for the number of soil particles were used.

Finally, the relationships among coral distribution, diversity index, wave height, and the number of soil particles were analyzed using the results obtained from the above. The wave height and the number of soil particles averaged under the typical weather periods in the summer and winter in Iriomote Island were used for the analysis. The details of investigations of coral and *E. acoroides* distributions in (1) and the physical variable observations in (2) were described by Shimokawa et al. (2014a, 2016). Those of the diversity index calculations (1) are described in "Diversity index and IDH" Section. Those of the numerical simulations in (2) were described by Shimokawa et al. (2014a, 2016) for ocean current and wave height and Shimokawa et al. (2017) for the number of soil particles.

Diversity index and IDH

This section explains the diversity index and IDH, which are crucial concepts in this study.

The diversity index, H', (e.g., Clarke et al. 2014) is defined as

$$H' = -\sum r_i \log_2 r_i. \quad (1)$$

Here, i represents the number of species for living things or a biotic community and r_i represents the rate of the ith species count to the total count. It represents the degree to which living things or a biotic community contain various species. It increases with an increase in the number of species and/or evenness. For a given number of species, it reaches a maximum when each species has the same count. It can be zero or positive values with no upper limit. In this study, species and count represent the coral life form and its coverage, respectively. Overall, the value of H' for living things or a biotic community has a large dispersion that decreases with an increase in the total count (Clarke et al. 2014). Therefore, discussions related to H' should be done for the maximum or average values.

The IDH (Connell 1978) asserts that the local diversity of living things or a biotic community reaches the maximum when environmental disturbances to them are neither too strong (frequent) nor weak (rare). It is typically cited to discuss the relationship between the diversity of living things or a biotic community and environmental disturbances. When the disturbances are strong (frequent), only species resistant to them can survive and become dominant. When the disturbances are weak (rare), competitive exclusion of some species by stronger ones occurs (e.g., species with a fast growth speed), and they become dominant. That is, diversity decreases whether disturbances are too strong (frequent) or weak (rare) and reaches a maximum when disturbances are intermediate.

Moreover, the IDH indicates that the state of living things or a biotic community is in non-equilibrium (i.e., the rapid changes by disturbances and the slow recovery processes from them), and diversity is retained when the state is in non-equilibrium because strong (frequent) disturbances can provide a survival occasion for species that cannot survive when the state is in equilibrium. The disturbance here includes physical variables, including current, wave, water temperature, soil inflow, invasion frequency of large-scale atmospheric and/or oceanic events, such as strong typhoons, the lengthening of high water temperatures in summer with global warming and/or no typhoon event, natural enemies to corals, such as Crown-of-thorns starfish, and artificial changes in water quality due to land development. In this study, among them, the physical variables are focused on.

Results in Sakiyama Bay

Coral coverage

We classified Sakiyama Bay into four parts by location (the part with a significant wave effect, the part with a significant soil effect, the reef edge side of the intermediate part, and the coast side of the intermediate part) (Fig. 2a). In Sakiyama Bay (Fig. 2c), the coverage of branching and massive corals is the highest, followed by tabular corals, and foliose and encrusting corals have moderately low coverage. Branching corals are dominant on the reef edge side of the bay's intermediate part, but massive corals are dominant on the coast side of the bay's intermediate part. Tabular, foliose, and encrusting corals primarily inhabit the bay's reef edge. *E. acoroides* exists over a wide area from the bay's intermediate part to the inner part (the region surrounded by a green line in Fig. 2b). In the bay's innermost part, no coral and *E. acoroides* exist (the region surrounded by a white line in Fig. 2b).

Diversity index

In Sakiyama Bay (Fig. 2d), H' is large on the bay's reef edge. In the intermediate part, H' can be zero because there are points in which only one type of coral (branching or massive) exists (Fig. 2c). The pink and yellow circles under the station numbers in Fig. 2d represent branching and massive corals, respectively. In the bay's inner part, H' is zero at most points because no coral exists, except for St. H-6, where small massive coral exists (Fig. 2c). The difference in the diversity index between Sakiyama and Amitori bays is discussed with respect to IDH in "Discussions: differences between Amitori and Sakiyama bays" Section.

Diversity index and physical variables

In Sakiyama Bay, the wave height (Fig. 3a) is more significant in the order of the reef edge, intermediate part, and inner part of the bay, as in Amitori Bay. This is consistent with a general property that the wave height in a region with a coral reef reaches its maximum at the reef edge because the height of waves from an open ocean increases with a decrease in the water depth (e.g., Holthuijsen 2007) and energy of waves is lost considerably at the reef edge by wave breaking (e.g., Sheppard et al. 2009). The number of soil particles (Fig. 3b) in the inner part is higher than that in the intermediate and reef edge parts, and the difference between those in the intermediate and reef edge parts is slight. That is, in Sakiyama Bay, the intermediate part does not become intermediate to the number of soil particles.

For wave height (Fig. 3a), in the reef edge part and the coast side of the intermediate part, H' increases slightly with the increase in the wave height. The correlation coefficient, R, on the reef edge part and the coast side of the intermediate part are 0.51 and 0.21, respectively. On the coast side of the intermediate part, H' is high only at a few points (I5, J3) with high wave height even though H' is zero at most points (F5, H5, K3, R2, S1). Thus, the linear fit is strongly affected by the few points on the coast side of the intermediate part. Conversely, in the reef edge side of the intermediate part, the correlation to H' is small. R on the reef edge side of the intermediate part is 0.013. For the number of soil particles (Fig. 3b), in the reef edge part and the reef edge side of the intermediate parts, H' decreases slightly with the increase in soil particle number. R in the reef edge part and the reef edge side of the intermediate parts are −0.37 and −0.19, respectively. Conversely, on the coast side of the intermediate part, H' increases with an increase in the number of soil particles. R on the coast side of the intermediate part is 0.23. On the coast side of the intermediate parts, H' is large only at a few points (I5, J3) with high soil particle number even though H' is zero at most points (F5, H5, K3, R2, S1). Thus, the linear fit is strongly affected by the few points on the coast side of the intermediate parts as well as the case of wave height. These points I5 and J3 can be considered special locations, where both large wave and soil effects co-exist. In any case, H' is not large at locations with an intermediate wave height and number of soil particles. Thus, IDH is not realized in Sakiyama Bay.

Diversity index and coral coverage

In Sakiyama Bay (Fig. 4), the average H' is 1.19, higher than that in Amitori Bay. High H' values (more than 1.6) correspond to coverage from 0.05 to 0.4, and higher coverage (more than 0.6) corresponds to H' values lower than 1.0. In addition, branching corals have higher coverage in areas with low diversity than tabular corals. That is, branching corals are dominant in many areas in Sakiyama Bay.

Discussions: differences between Amitori and Sakiyama bays

This section discusses the differences in the distribution and diversity of corals and *E. acoroides* between the Amitori and Sakiyama bays, which are difficult to explain using only a specific factor. The difference in the soil inflow and geographical characteristics between both bays (see Table 1) is thought to have a considerable influence.

Amitori Bay has a long bay length compared to the bay mouth, and the water depth ranges from a few to 6 m for the region, where corals mainly exist, and reaches 70 m at the bay's center, and the sea floor is uneven, namely, the geographic and environmental gradients are large from the bay's mouth to the bay's inner part (Kawana 1990, Ministry of the Environment, Government of Japan 2015, Minami et al. 2017; see also Table 1). Due to these geographical characteristics, the effect of soil input from rivers (Fig. 1a; Ayanda and Udara rivers) can be significant only in the bay's innermost parts and the submarine canyon region of the bay's center and is relatively small at the bay's coast side, where corals primarily exist. Conversely, Sakiyama Bay has a short bay length and a wide-opened bay mouth, the water depth is a few meters for the region, where corals primarily exist, and the sea floor is almost flat even though the water depth is around 40 m

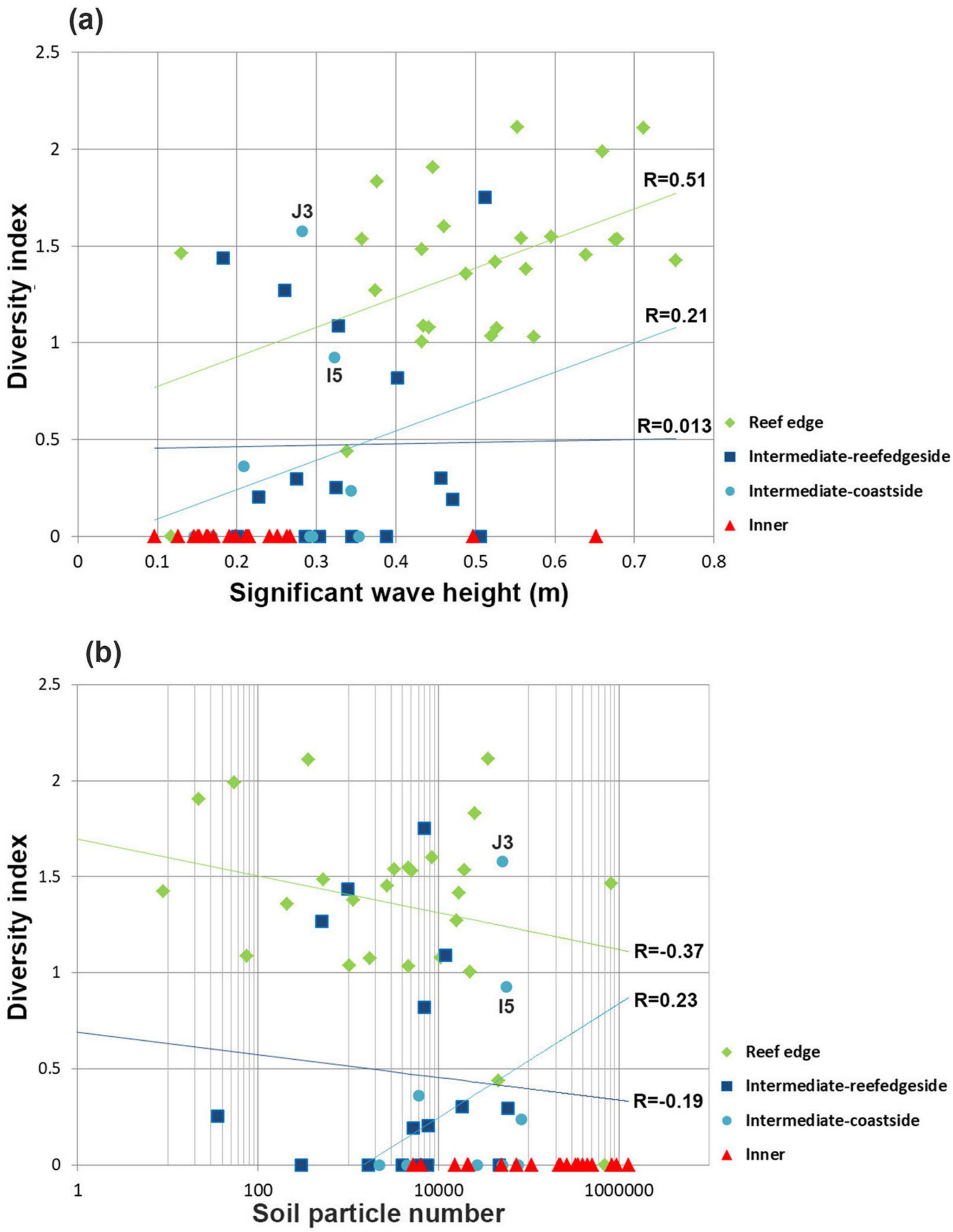

Fig. 3 **a** Relationship between the diversity index and significant wave height (m) in Sakiyama Bay. The significant wave height is shown by values in winter, which is much more significant than in summer. The linear fits are calculated by the parts. R values show the correlation coefficients to the correspoding lines. The calculation details were described by Shimokawa et al. (2014a, 2016). **b** Relationship between the diversity index and the number of soil particles in Sakiyama Bay. The numbers show averaged values for the number of soil particles virtually released from river mouths and arrived at the sea bottom in a day in numerical simulations. The calculation details were described by Shimokawa et al. (2017)

at the outside the reef edge, namely, the geographic and environmental gradients are smaller than those of Amitori Bay (Kawana 1990, Ministry of the Environment, Government of Japan 2015, Minami et al. 2017; see also Table 1). Due to these geographical characteristics, the effect of soil input from rivers (Fig. 1a; Painta and Ubo rivers) can easily spread over the entire bay. Specifically, in the bay's innermost part, sediments comprising fine brown sand and gray-black mud cover the majority of the seafloor (Shimoji et al. 1990). Therefore, in Sakiyama Bay,

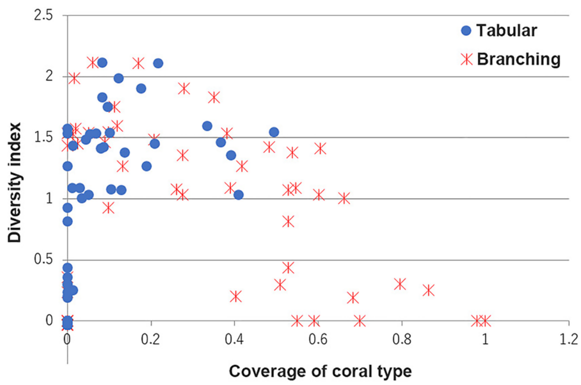

Fig. 4 Relationship between the diversity index and coverage of tabular and branching corals in Sakiyama Bay

the effect of soil input from the rivers can easily cover a wide area by ocean current and diffusion due to the small geographic and environmental gradients.

In each disturbance to corals (i.e., wave height and soil particle number in this study), the intermediate zone can be defined. In the case of Amitori Bay (Shimokawa et al. 2014a, b), the wave height is high at the bay mouth, low at the inner bay, and then becomes intermediate at the intermediate of the bay. The number of soil particles is high at the inner bay, low at the bay mouth, and then becomes intermediate at the intermediate of the bay. In this sense, IDH is discussed. It is the same in the case of Sakiyama Bay. However, in Sakiyama Bay, soil disturbance to corals is small only at the reef edge with high waves because the decrease in the number of soil particles from the inner bay to the bay mouth is small based on the above geographical characteristics.

A coral community cannot develop in Sakiyama Bay's inner part because corals are difficult to grow in muddy environments (e.g., Sheppard et al. 2009). However, an *E. acoroides* community can grow because its roots or rhizomes can easily settle on the muddy seafloor (Komatsu et al. 2004). Massive corals are more tolerant of soil particles than other corals because of their high ability to remove soil particles by mucus (e.g., Coffroth 1985, Bessel-Browne et al. 2017). Therefore, they are thought to inhabit the coast side of the bay's intermediate part (i.e., the second closest region to the river mouths). Branching corals are moderately tolerant of soil particles (e.g., Chappell 1980; Duckworth et al. 2017) because soil particles do not readily accumulate on them, and even when soil particles accumulate on them, they can be easily removed by ocean waves and currents. Therefore, they are thought to develop on the reef edge side of the bay's intermediate part (i.e., the third closest region to the river mouths). In this region, massive corals cannot win the competition for space and survive in environments, where other corals with a fast growth rate (i.e., branching coral in this case) inhabit, because the growth rate of massive corals is slow (e.g., Sheppard et al. 2009). Consequently, in Sakiyama Bay, the distribution according to the distance from the river mouth is in the following order: *E. acoroides*, massive corals, and branching corals.

In Sakiyama Bay, branching corals with a fast growth rate (e.g., Sheppard et al. 2009) are dominant on the reef edge side of the bay's intermediate part (Fig. 2a). However, other corals can be inhibited in the bay's reef edge part because branching corals are negatively affected by waves due to their form (e.g., Chapell 1980, Montaggiouni 2005). Furthermore, in Sakiyama Bay, the effect of soil particles on corals can be small at the bay's reef edge because high waves at the reef edge can remove soil particles from corals when soil particles accumulate on them. Consequently, an environment, where various corals can co-exist, is realized only at the bay's reef edge part with high waves and the diversity is high (Fig. 2b). Therefore, IDH is not realized in Sakiyama Bay. The increase in diversity at the reef edge can be related to edge effects (Lidicker and William 1999; Potts et al. 2016). Edge effects are the changes in biodiversity that occur inside the space surrounding the shared edge of two or more habitats. This transitional zone rich in biodiversity is known as the ecotone; examples are between woodlands and plains, forests and mountains, and land and water. This necessitates further coral investigation in the open ocean zone outside the reef edge in Sakiyama Bay. In addition, in the reef edge part, the coverage of encrusting corals is significantly higher at the first site (such as B1) than at the second site (such as B2). The difference in the water depth between the first and second sites may influence the coverage of encrusting corals. Thus, the reef edge part may be divided into two parts.

Finally, the difference in the dominant coral type between the two bays is discussed. As stated in the "Introduction" and "Results in Sakiyama Bay" Sections, tabular and branching corals are dominant in many places with low diversity in Amitori and Sakiyama bays, respectively. This means that for both bays, high coverage of a specific coral type (i.e., tabular corals in Amitori Bay and branching corals in Sakiyama Bay) in a region does not show high diversity because the region is a niche for only that coral. Furthermore, high coral diversity in a region does not show high coverage of a specific coral because the region is not a niche for only that coral.

Summary

Sakiyama and Amitori bays of Iriomote Island, Japan, are adjacent, but their coral distributions differ significantly. This study investigated the differences in the coral distribution and diversity between both bays from a diversity index and IDH perspective based on the investigation results of coral and *E. acoroides* distributions, physical variable observations, and numerical simulations using the observations as initial and boundary conditions.

In Amitori Bay, although various corals are distributed over a wide area, tabular corals are dominant in the bay's mouth, and branching corals are prevalent in the bay's inner part. Coral diversity is maximum in the bay's intermediate part, and IDH is realized. *E. acoroides* is rare, and no large community exists. In Sakiyama Bay, although various corals can be observed, branching corals are dominant on the reef edge side of the bay's intermediate part, and massive corals are dominant on the coast side of the bay's intermediate part. Coral diversity is maximum on the bay's reef edge, and IDH is not realized. *E. acoroides* is distributed over a wide area of the bay's inner part. The differences in the soil inflow and geographical characteristics between the two bays significantly influence their coral distribution and diversity.

This study is based on coral distributions in Sakiyama and Amitori bays before 2015. In 2016, large-scale coral breaching occurred globally, including in Sakiyama and Amitori bays (Biodiversity Center of Japan 2017). Murakami et al. (2017, 2018, 2019, and 2020) and Nakamura et al. (2022) have reported the cause of the coral breaching and the recovery processes in Sakiyama and Amitori bays. The change in the coral diversity with the recovery of a coral state is an exciting topic, especially from a non-equilibrium state perspective ("Diversity index and IDH" Section), and further studies will be required.

Finally, we would like to state the relation of this study's theme to climate change. As stated in the introduction, in subtropical regions, such as Iriomote Islands, physical environments, including oceanic and atmospheric events, such as typhoons, significantly affect the distribution of organisms there. IPCC (2015) reported that the number of typhoons can decrease, but the number of strong typhoons can increase with future global warming. Such changes in typhoons will affect the distribution of corals in the Amitori and Sakiyama bays. In particular, with a decrease in the number of typhoons, coral distributions in Sakiyama Bay may be more affected than those in Amitori Bay because the water temperature in Sakiyama Bay with a shallow water depth can easily increase compared with that in Amitori Bay with a deep water depth when no typhoon hits (i.e., strong wave and current do not occur) for a long period. In some cases, large-scale coral breaching can occur and cause fatal damage to corals. On the other hand, typhoons strengthened by global warming can destroy corals and cause fatal damage to corals in both bays (Hongo et al. 2012). For corals, typhoons are necessary existence, but very strong typhoons are not. More studies will also be required in this regard.

Abbreviation
IDH Intermediate disturbance hypothesis

Acknowledgements
The authors give their gratitude to Prof. K. Sugihara of Tsukuba University for his kind suggestions and Ms. S. Kota for her technical supports.

Author contributions
SS and TM mainly carried out the coral investigations, physical observations, and numerical simulations. All authors discuss the obtained results and drafted the manuscript in cooperation. All the authors read and approved the final manuscript.

Funding
This work is supported by the Japan Society for the Promotion of Science (No. 20K04069 and 22K03743).

Availability of data and materials
The datasets during and analyzed during this study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests. The authors declare that they have no issues relating to the journal policies and no competing interests and confirm that all the authors read and approved the manuscript for submission and the content of the manuscript has not been published or submitted.

Received: 11 July 2022 Accepted: 10 January 2023
Published: 19 January 2023

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