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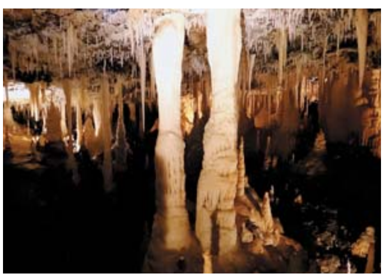
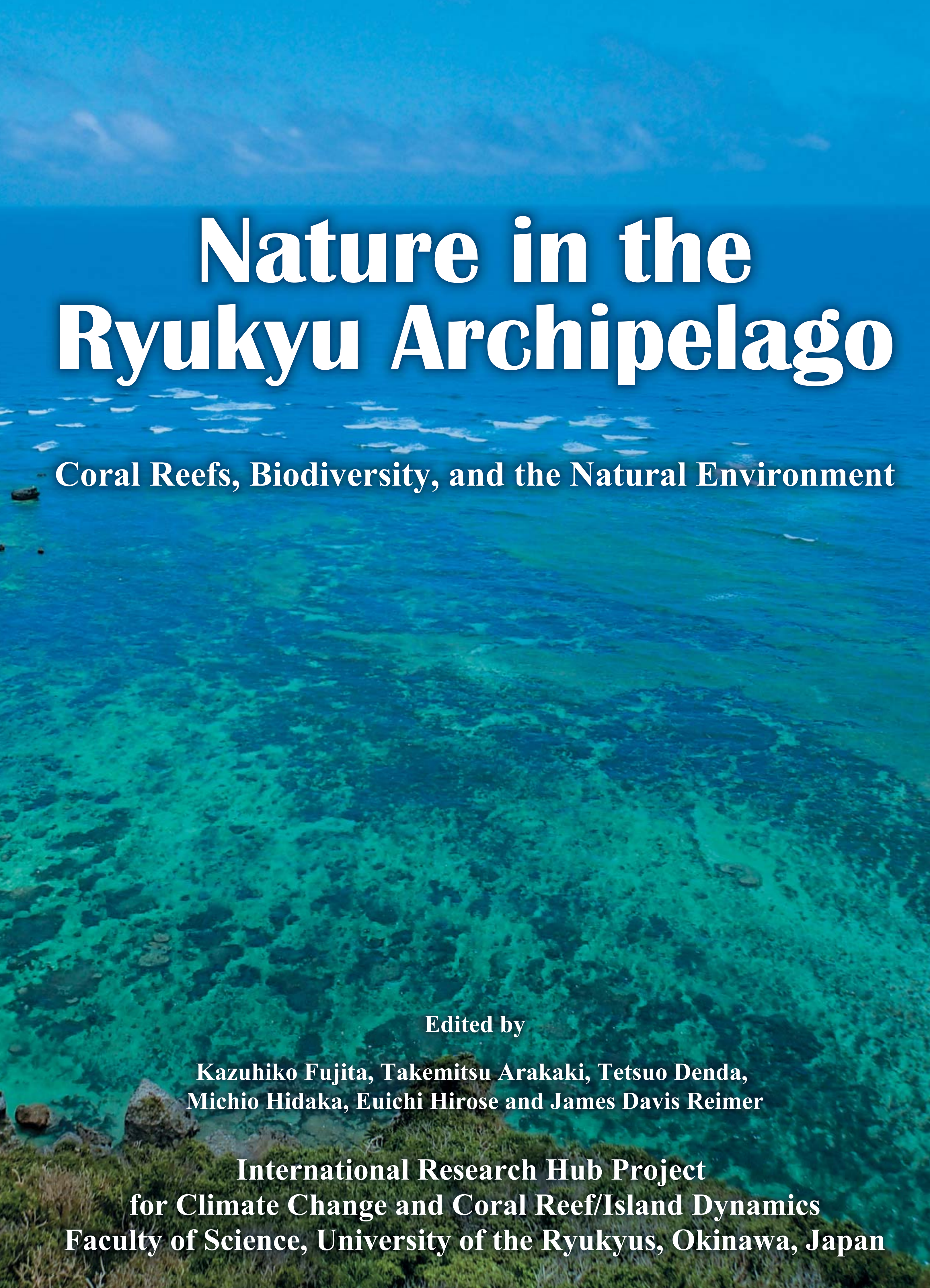
Nature in the Ryukyu Archipelago







Nature in the Ryukyu Archipelago

Coral Reefs, Biodiversity, and the Natural Environment

Edited by

Kazuhiko Fujita, Takemitsu Arakaki, Tetsuo Denda,
Michio Hidaka, Euichi Hirose and James Davis Reimer

International Research Hub Project
for Climate Change and Coral Reef/Island Dynamics
Faculty of Science, University of the Ryukyus, Okinawa, Japan

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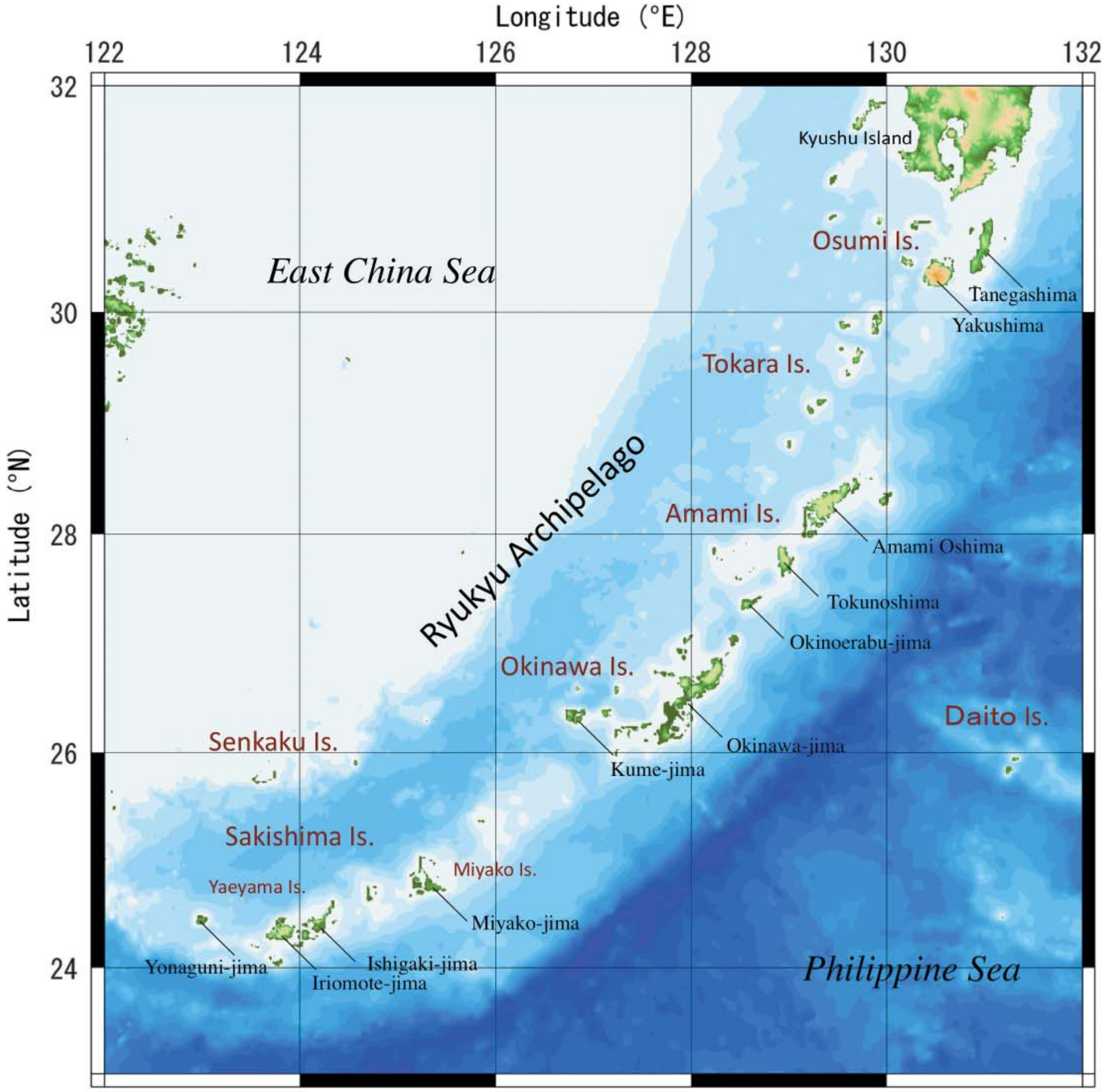


Map of the Ryukyu Archipelago. The terms “the Ryukyu Archipelago”, or “the Ryukyu Islands”, and “the Ryukyus” are defined as the island chain from Tanegashima Island to Yonaguni-jima Island, which includes the Osumi Islands, Tokara Islands, Amami Islands, Okinawa Islands, Sakishima Islands, Senkaku Islands and Daito Islands, and is the same as the term “Nansei-shotou Islands”, which are used administratively. The term “Okinawa” in this book means “Okinawa Prefecture.”

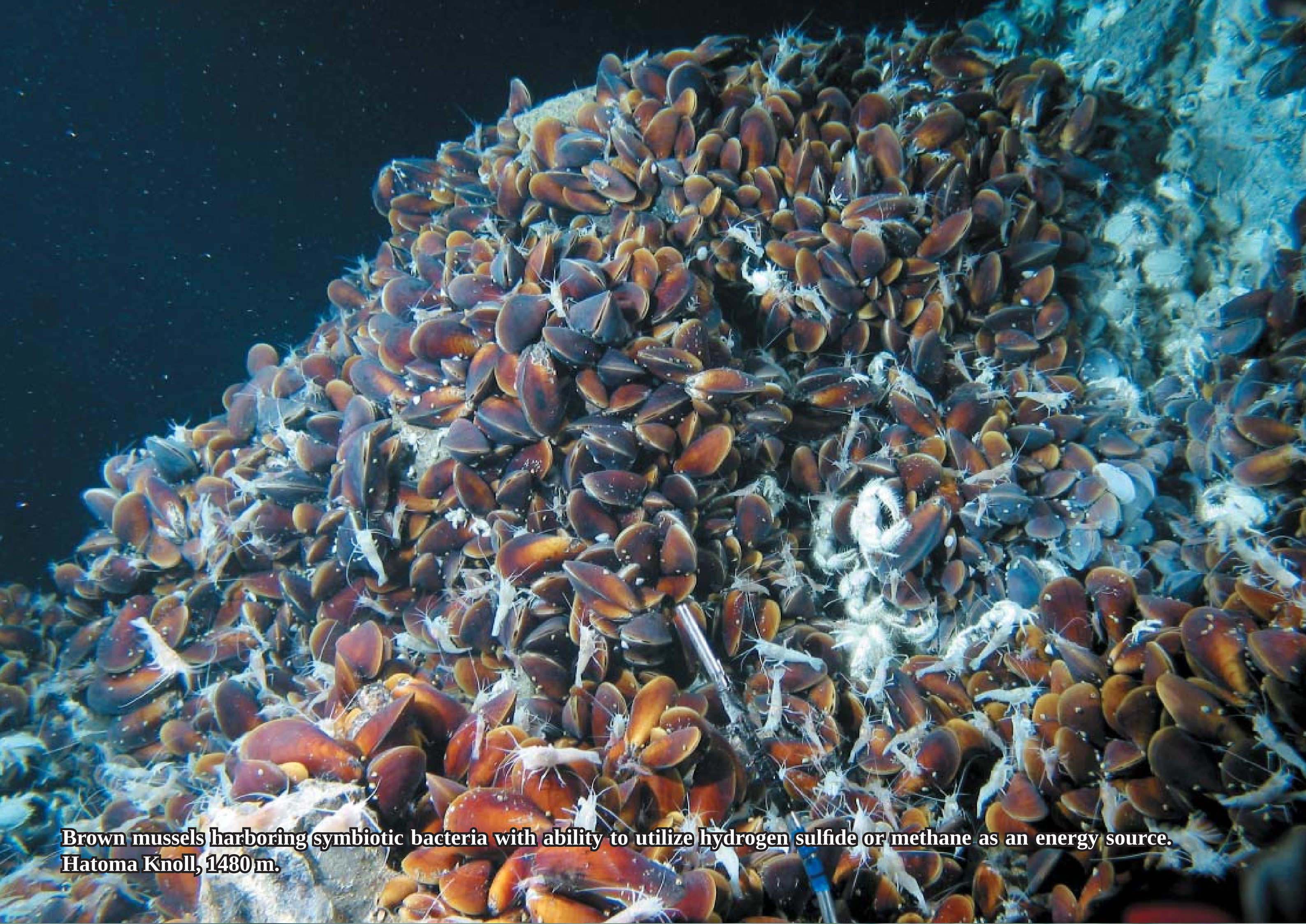
Dense community of *Acropora* corals and soft corals. Patch reef north of Sesoko-jima Island.

Acropora colony with yellow axial polyps. Zampa, Okinawa-jima Island.

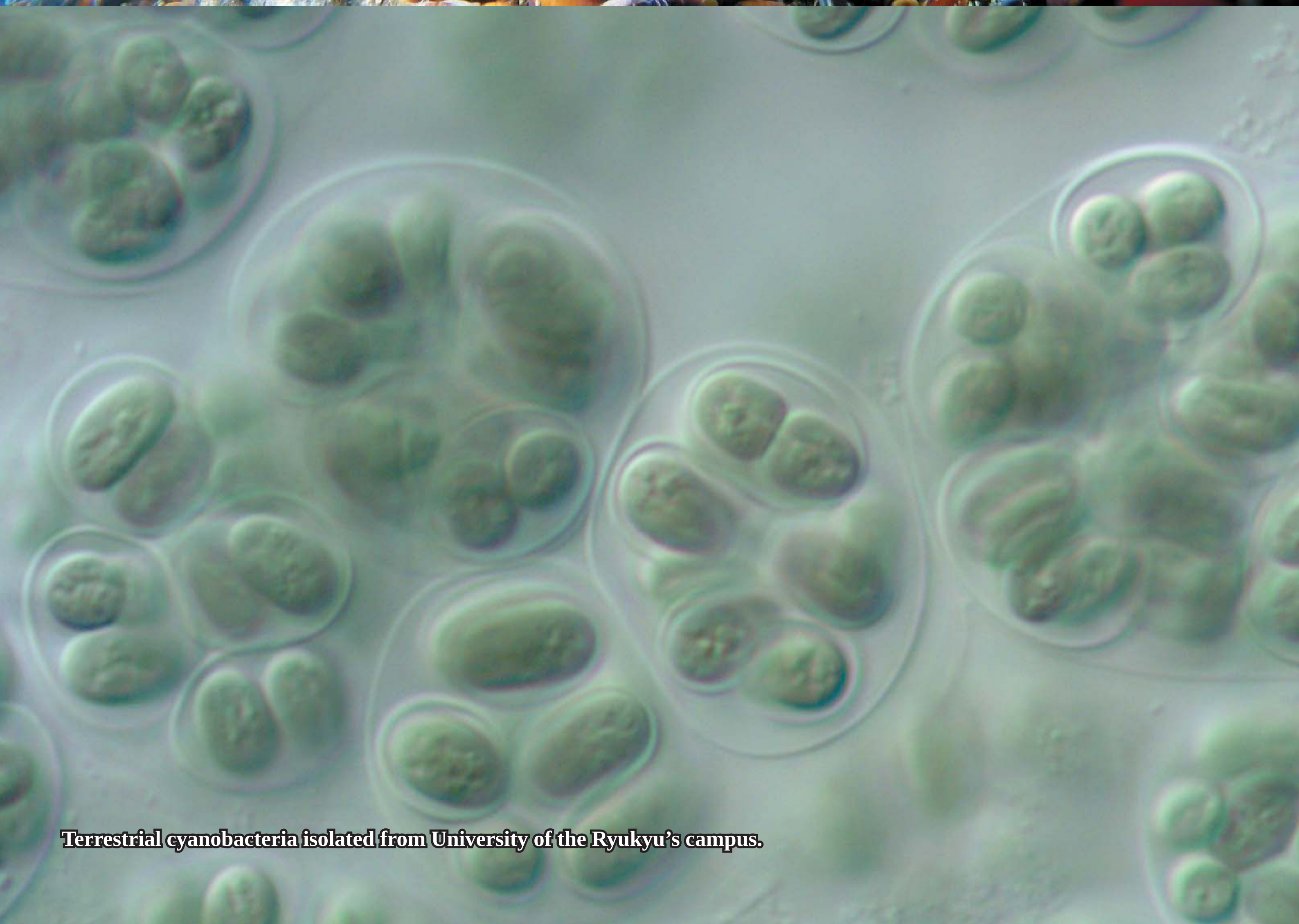
A massive colony of a brain coral, *Symphyllia* sp. Zampa, Okinawa-jima Island.

A living star sand (foraminifer) attached to algal turf, Aka-jima Island.

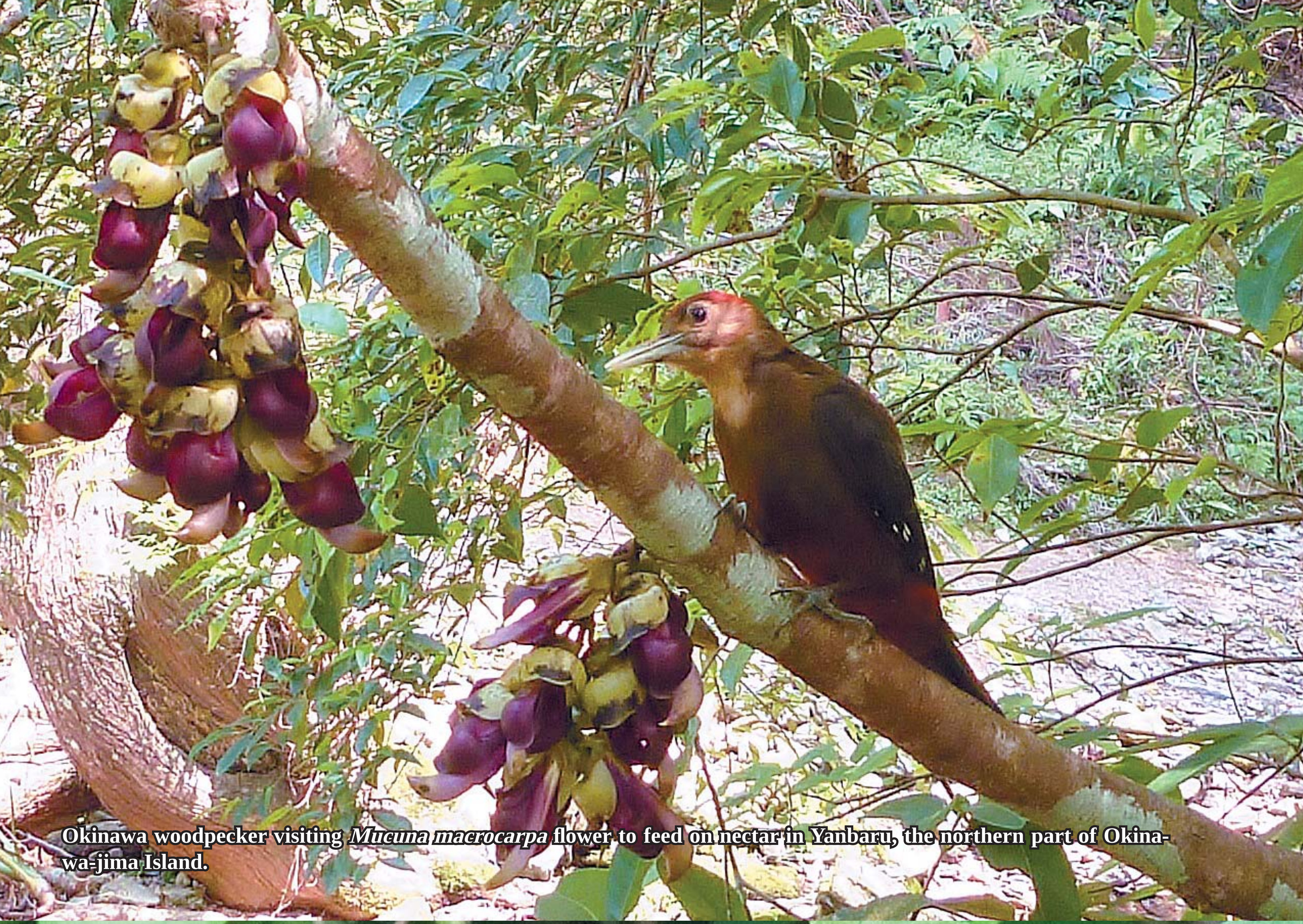
Different colors of one species of encrusting anemone in shallow waters of Okinawa-jima Island.



Brown mussels harboring symbiotic bacteria with ability to utilize hydrogen sulfide or methane as an energy source. Hatoma Knoll, 1480 m.



Terrestrial cyanobacteria isolated from University of the Ryukyu's campus.



Okinawa woodpecker visiting *Mucuna macrocarpa* flower to feed on nectar in Yanbaru, the northern part of Okinawa-jima Island.

The orange oakleaf or dead leaf butterfly at Mt. Yae, Okinawa-jima Island.

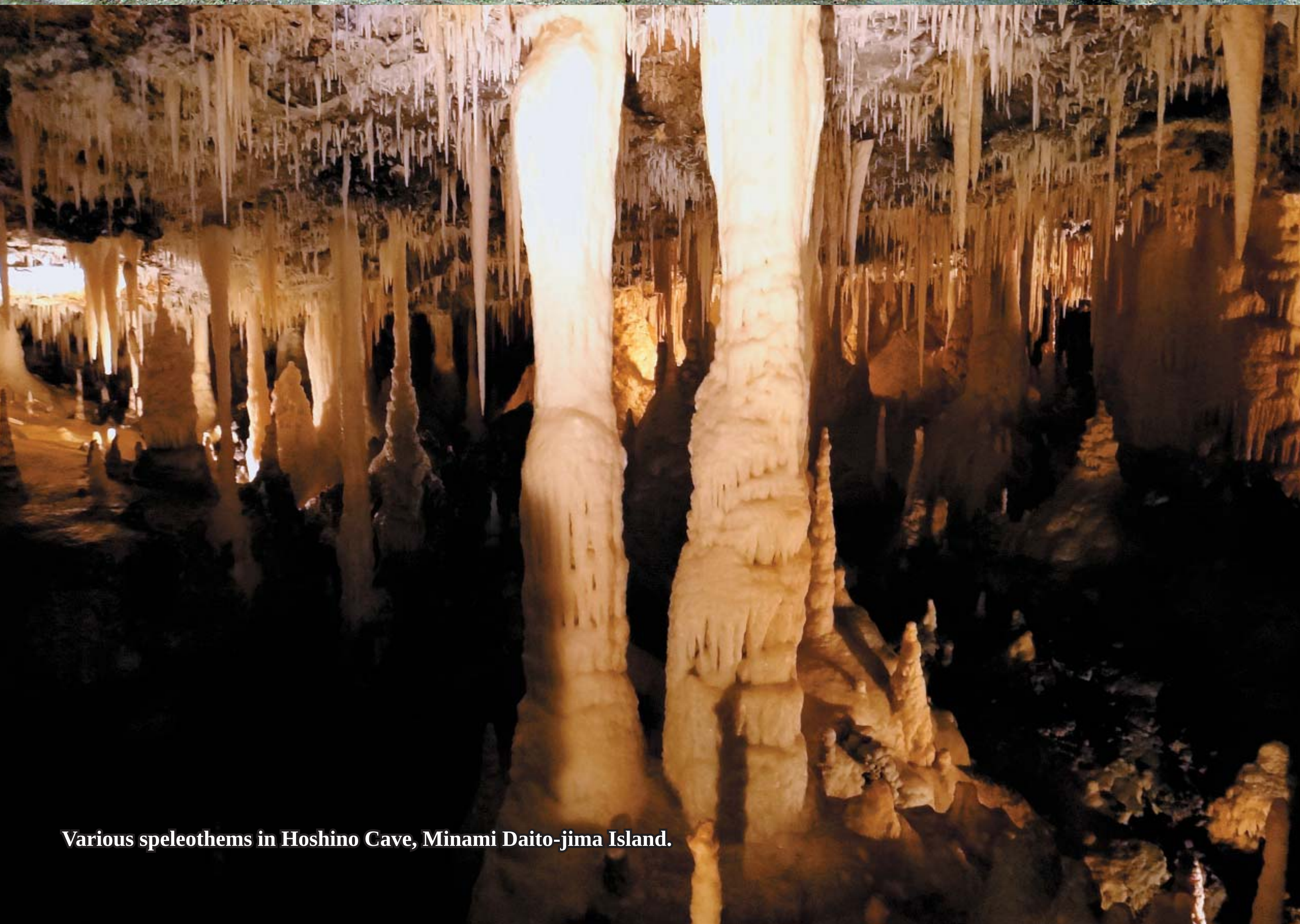
The Chinese guger tree blooming in a subtropical evergreen forest of Okinawa-jima Island.

The Iriomote cat, an endangered small felid endemic to Iriomote-jima Island.

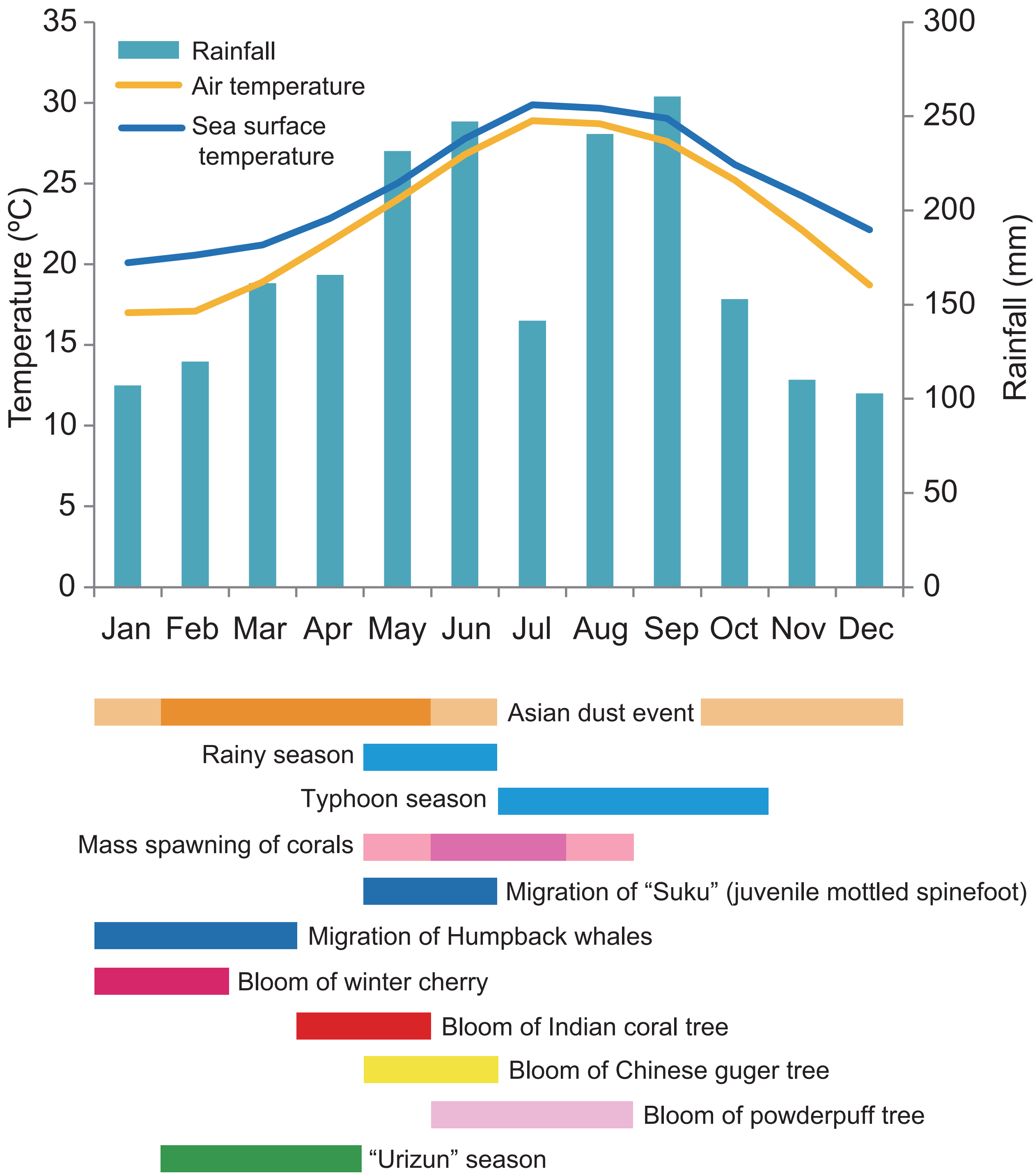
Cumulus clouds growing over Motobu Peninsula, Okinawa-jima Island.

Inclined folded strata exposed along the Kayo Coast, Okinawa-jima Island.

Beach rocks formed in the intertidal zone of the Bise Coast, Motobu Peninsula, Okinawa-jima Island.



Various speleothems in Hoshino Cave, Minami Daito-jima Island.



Environments and seasons of the Okinawa Islands. Air temperature and precipitation data are from monthly average values at Naha City from 1981 to 2010, provided by the Japan Meteorological Agency. Sea-surface temperature data are from 2010 to 2012 at coasts in front of Sesoko Station, Tropical Biosphere Research Center. “Urizun” is a word in the Okinawan dialect that means the season from February to April, during which trees sprout new green leaves and flowers start to bloom.

Contents

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Preface: Enjoying the Nature of the Ryukyu Archipelago

Makoto Tsuchiya

Emerald green colored coral reefs are dazzling, shining in the sun that pours down brightly. The southern islands of Japan look beautiful with their coral reefs in midsummer. The strange morphology of mushroom type rocks and geological characteristics of coral reef shores tell us the earth's history.

In 'Urizun' season, which is an old Okinawan term meaning the season when the ground starts to be covered with many plants after winter, we feel the breath of young leaves in full flush, or the flowers of 'Yanbaru', the northern part of Okinawa-jima Island. In Iriomote-jima Island, covered with dense subtropical forests, we are reminded of the wonder of nature from birds' song and insects' chirping. The singing of insects is common even in winter season in Okinawa, and cherry blossoms can be seen in late January. When tourists visit these southern islands and meet these experiences, they make no attempt to hide their surprise.

Although the Kuroshio Current has the characteristics of oligotrophic waters, it gives many blessings to Okinawa. When the islands of the Ryukyu Archipelago, a chain of islands stretching from Tanegashima Island in the north to Yonaguni-jima Island in the south, were a part of the Asian continent, many plant and animal species from the continent were distributed in this area. These species have adapted to the environment of each island after the Ryukyu Archipelago formed. We are now standing on the stage of evolution and have the opportunity to observe these processes with our own eyes.

People living in these islands have friendly and inseparable relationships with this fantastic nature. This area is characterized by a large and vibrant tourism industry. In order to sustain these important natural resources, we must pay strong attention to the conservation and sustainable management of nature. The 21st century is the time for discussion on the coexistence between nature and humans, which should be permanently kept healthy.

In the Faculty of Science, University of the Ryukyus, Okinawa, much research has been conducted on the analyses of interesting and unique topics and for solutions of environmental issues. Undoubtedly, one of the current important environmental issues is the effects of climate change on islands and coral reef ecosystems of the world. Coral reef bleaching caused by global warming has been observed frequently, and this is an indicator of the earth's changing environment. Moreover, we can recognize the changes of the earth's environment by the observation of other coral reef organisms. Biomineralization, which is the process by which organisms such as corals and molluscs synthesize inorganic materials such as shells and skeletons, has been the subject of a variety of research in the fields of chemistry, geology and biology. This process may also be affected by the climate change, resulting in the degradation of coral reef environments. Ocean acidification caused by climate change has also been reported to affect the lives of many animals synthesizing hard tissues, such as corals, urchins, molluscs and foraminiferans.

Island ecosystems surrounded by coral reefs are strongly affected by climate change and their environments are quite delicate. Conservation of island organisms and their environments is an important theme in the discussion of coexistence of nature and human beings. After recognizing the characteristic nature of the Ryukyu Archipelago, we have to accumulate scientific information on these environments. In this book, we try to make clear the characteristics and importance of this from integrated viewpoints of different fields such as biology, geology and chemistry.

In Chapter 1, current topics of coral reef ecosystems, one of the representative environments of Okinawa, will be introduced. Coral reefs are systems constructed by organisms over a very long time and diverse organisms inhabit these reefs. Recently, corals, the most important component of a coral reef ecosystem, are under accumulating stresses and abnormal phenomena have been observed. How do corals react against the stresses of abnormal environments? These abnormal reactions of coral will be explained. As well, past environmental conditions are recorded in the skeletons of corals. We can get important hints for the future from getting information on past coral reef environments.

Chapter 2 describes some interesting topics on the lives of organisms. We strongly recommend you observe these organisms in forests or seashores on your own. Diverse organisms showing their interesting behavior live close to us. You may be surprised to know that some algal species live on the guardrails of roads. Analyses have also been made on biodiversity, which is a current important research topic. We also introduce the endemic wildcat species of Iriomote-jima Island, which cannot easily be observed in the field. Additionally, we address the difficult question of how many species are living in the sea. The answers and information in this chapter will surprise you.

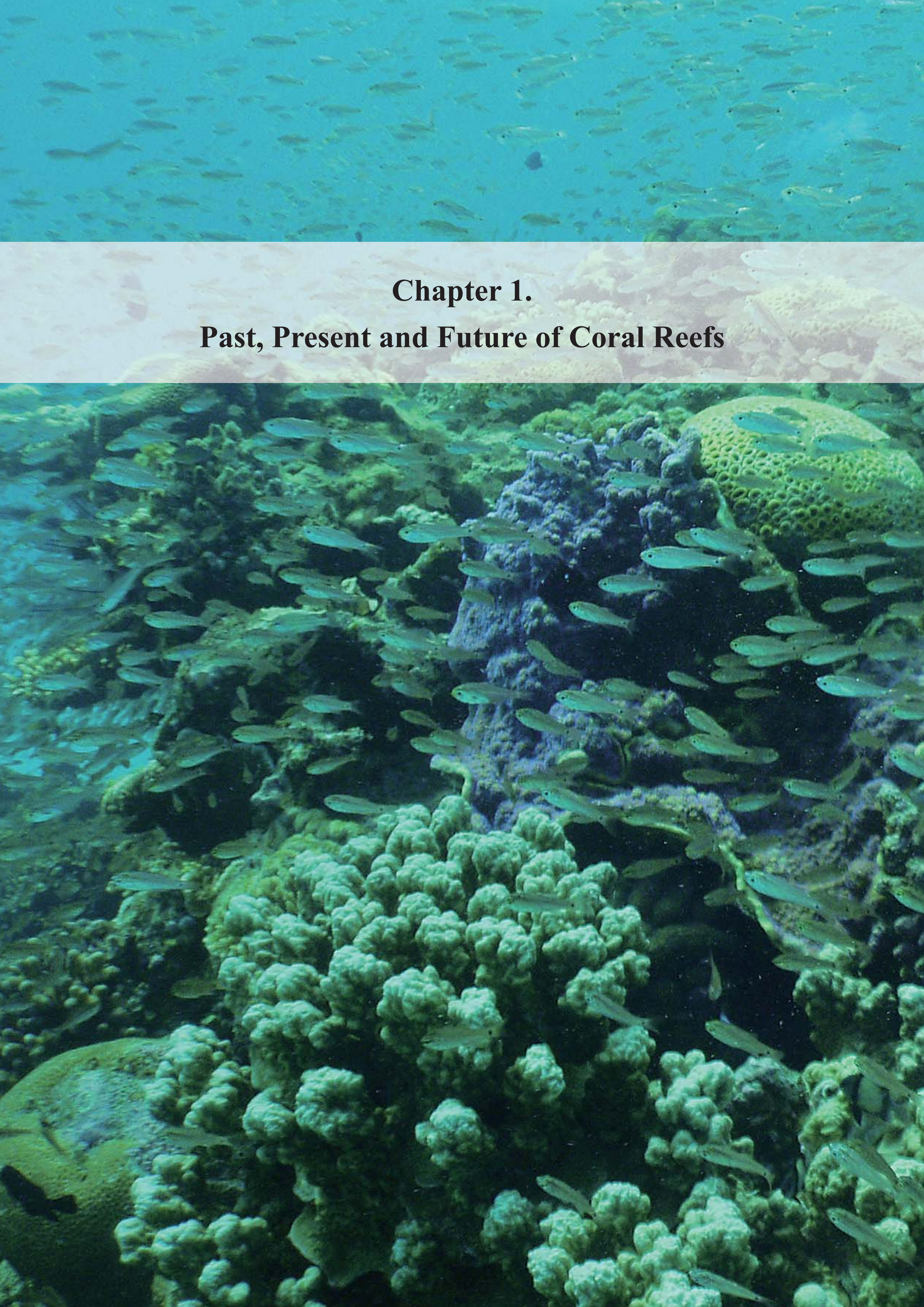
Geological aspects of the Ryukyu Archipelago are introduced in Chapter 3. The complex structure of limestone caves is the result of a long and mysterious process. Recognizing the geological characteristics of each island, we can feel wonder for each island's history, and this leads to a better understanding of island organisms. When we recognize the characteristics of tropical or subtropical environments with reference to the Kuroshio Current, we can understand the wide relationships between our environment, and the continent of Asia, and the southern ocean. Some materials in the air of the Ryukyu Archipelago are carried from eastern Asia. How do these materials affect the environment of these islands? The biogeochemical cycles in the atmosphere and ocean should be analyzed from a various angles.

Abundant and beautiful nature is our treasure. We should share these treasures with many people on this planet, and with our descendants. We have published this book for many people, including people living on the islands of the Ryukyu Archipelago, Japanese tourists from outside of the islands, and for those from abroad. If readers can discover the interesting and important points of the nature of the Ryukyu Archipelago through this book, we will be extremely happy.

This book is a part the discussion and research results of the International Research Hub Project for Climate Change and Coral Reef/Island Dynamics at the Faculty of Science, University of the Ryukyus, which has been supported by the Ministry of Education, Culture, Sports, Science and Technology, Japan, between 2011 to 2016.

November 2015

Makoto Tsuchiya, *Professor Emeritus*



Chapter 1.
Past, Present and Future of Coral Reefs

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1—1. Corals: reef-building animals

Michio Hidaka and Dwi Haryanti

What are corals?

Most of the Ryukyu Archipelago are surrounded by reefs formed by calcifying animals and plants. Corals are the most important contributors to coral reef formation. What do we know about them?

‘Corals’ are kin to sea anemones and jellyfish. These organisms possess minute stinging capsules called ‘nematocysts’ or ‘cnidae’ that are used to capture zooplankton or defend themselves against predators. Accordingly, this group of animals has been assigned to a single phylum, the Cnidaria. The coral cnidarians secrete external calcium carbonate skeletons, while sea anemones and jellyfish do not.

Scleractinian corals (also called stony corals or true corals) are the major reef-builders. The tentacles of these corals are produced in multiples of six (24, 48, and so on). Accordingly, members of this group are classified into the subclass Hexacorallia, which also contains the sea anemones. Soft corals, blue corals, organ-pipe corals, and most precious corals belong to the subclass Octocorallia, members of which have eight pinnate tentacles (Fig. 1).

The life cycles of cnidarians often comprise two stages, the polyp and the medusa (Fig. 2), both of which may be considered as bags with a single opening, the mouth. The polyp is attached to the ocean floor and

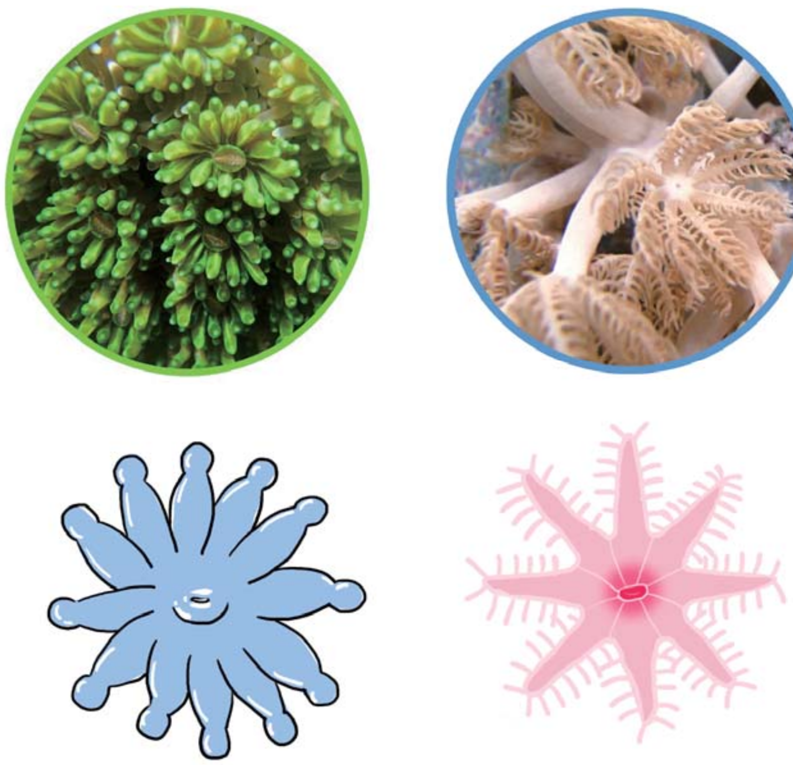

Figure 1. Polyps of a hexacoral (left) and an octocoral (right). Tentacles of hexacoral polyps usually occur in multiples of six, while octocoral polyps have eight pinnate tentacles.

has a mouth facing upward, while the medusa is free-swimming and has a mouth facing downward. In many cnidarians, part or all of the polyp body transforms into a medusa, which is the sexual phase that develops eggs or sperms. Zygotes formed by gamete fusion develop into polyps.

Both hexacorals and octocorals belong to the class Anthozoa. The medusa phase is absent in this class (Fig. 2); the polyps reproduce sexually. Below, we consider the lives of the major reef-builder stony corals (hereafter, ‘corals’).

The polyp of a coral is essentially a sea anemone surrounded by the external calcium carbonate skeleton that it has secreted. Tentacles surrounding the mouth protrude from the polyp and capture prey. Rather than forming a simple opening, the mouth is equipped with a tube, which functions as an esophagus. Cilia on the surface of the tube help move captured plankton into the stomach (gastrovascular cavity), where they are digested and ingested by the epithelial cells lining the cavity.

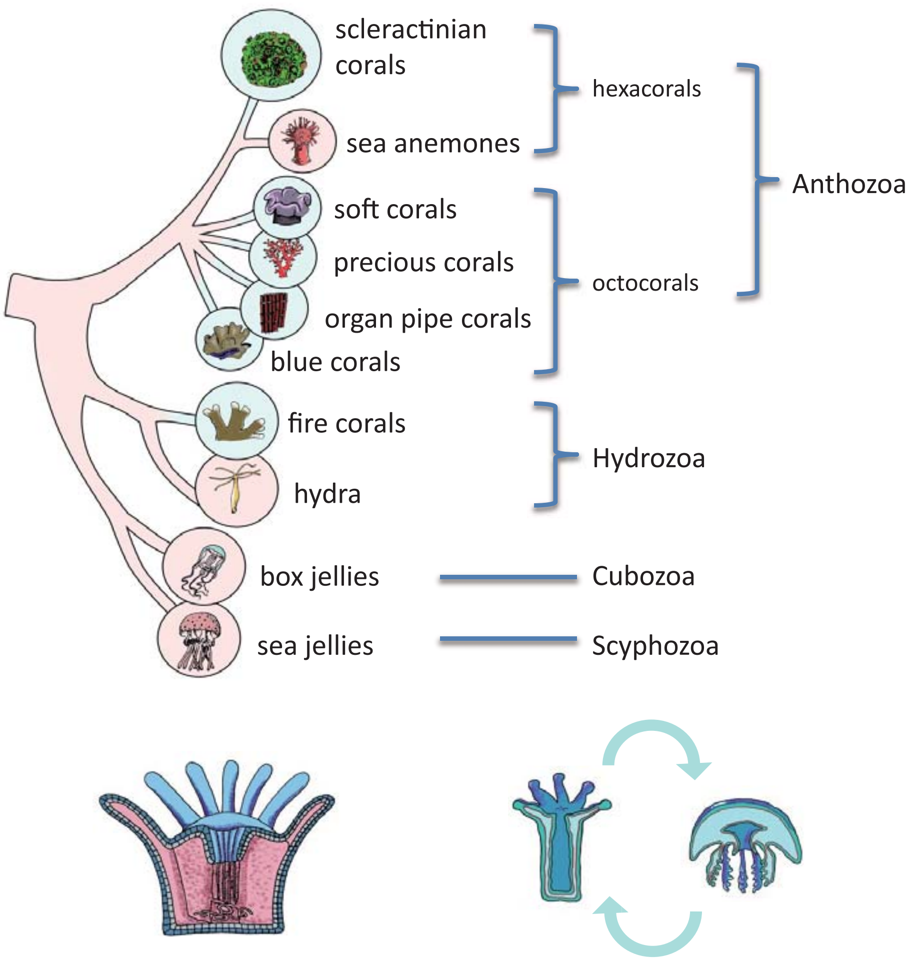

Figure 2. Phylogenetic tree of corals and related cnidarians. Upper panel: most corals belong to the class Anthozoa, but some are members of the class Hydrozoa. Blue circles represent corals. Lower panel: Anthozoans occur only as polyps (lower left); hydrozoans, scyphozoans, and cubozoans have polyp and medusa stages during their life cycles (lower right).

How corals become so massive

Most corals are 'colonial.' All colonies originate from a founder (primary) polyp. A single swimming coral larva that has developed from a zygote settles on the bottom and metamorphoses into a polyp. As the polyp grows, new polyps are formed by budding (Fig. 3). Colonial corals comprise very large numbers of

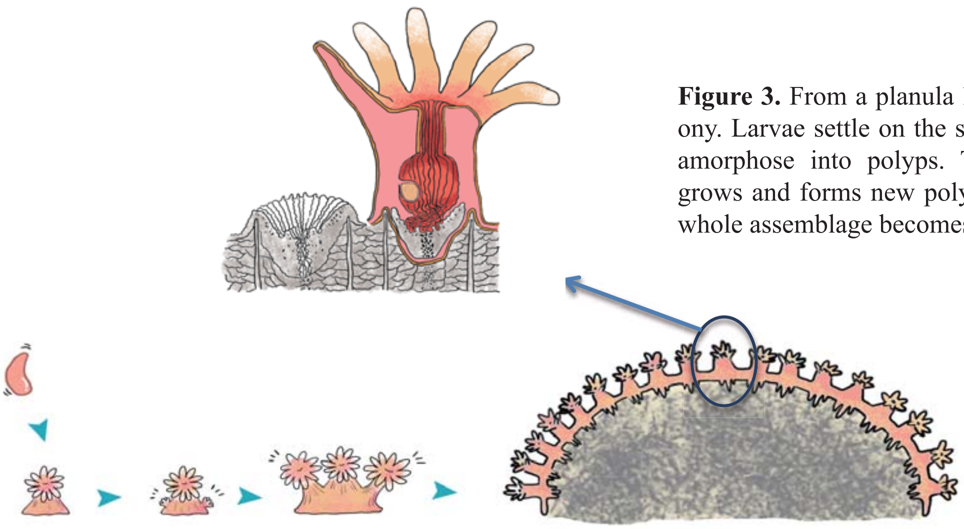

Figure 3. From a planula larva to a coral colony. Larvae settle on the substratum and metamorphose into polyps. The founder polyp grows and forms new polyps by budding; the whole assemblage becomes a coral colony.

Figure 4. Corals with various growth forms. Massive, plate, branching, and encrusting growth forms of colonial corals. Solitary corals with ellipsoid forms are also shown (top left). Images by Takashi Nakamura.

polyps connected by common tissues. A whole colony can be considered as a digestive bag with many openings (mouths) sitting on the skeleton. Colonies can become very large, although individual polyps are very small, ranging in size from a few millimeters to a few centimeters. Individual polyps are similar in shape, but the forms of colonies vary remarkably (Fig. 4). Even colonies of the same species can assume different growth forms depending on environmental conditions in the habitat, such as illumination and water turbulence. Many corals assume a plant-like form so that photosynthetic symbiotic algae living in their tissues, zooxanthellae, can efficiently capture light.

Birth of new corals: sexual reproduction

About 70% of coral species are hermaphroditic. Polyps within single colonies (or a polyp in case of solitary corals) develop both eggs and sperm. The remaining species are gonochoric; their colonies (or individuals in case of solitary corals) are either male or female. About 90% of coral species are broadcast spawners, which release eggs and sperm into the water column. The remaining species brood planula larvae within their stomachs (Fig. 5).

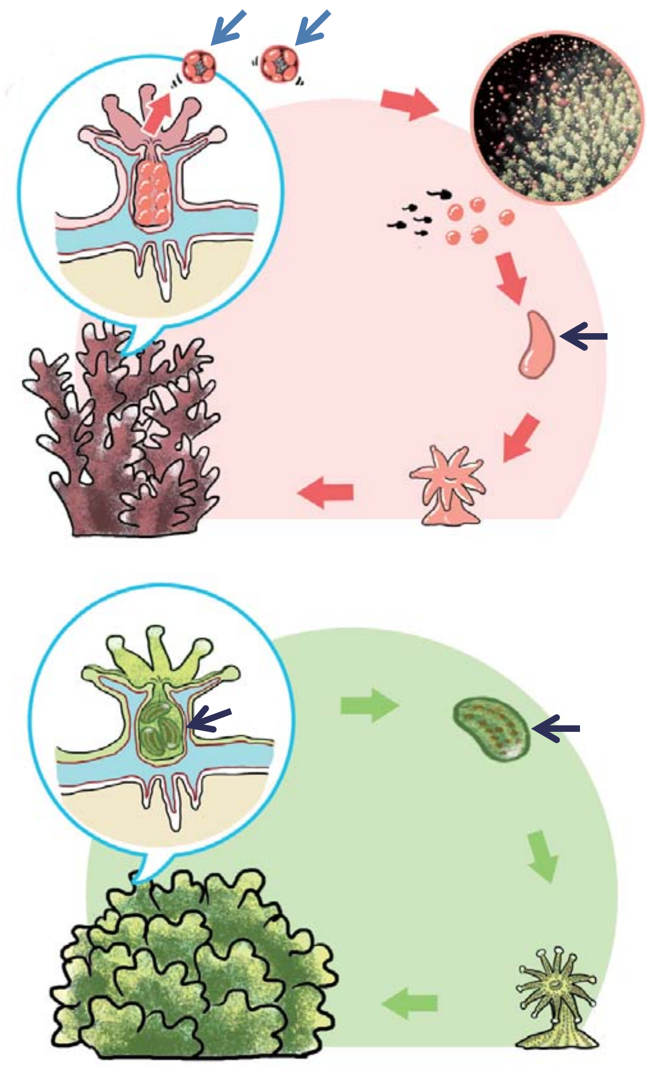

Figure 5. Reproduction of corals. The top shows broadcast spawning corals releasing gametes (egg-sperm bundles in case of hermaphroditic spawners, blue arrows) into the sea. When eggs are fertilized by sperm, they develop into larvae called planulae (black arrow). Larvae settle on the substratum and metamorphose into polyps. The lower part indicates brooding corals releasing larvae after fertilized eggs have developed into larvae within the mother polyps. Image by Takashi Nakamura.

Most corals (about 60% of species) are hermaphroditic spawners that release eggs and sperm (as egg-sperm bundles) into the sea once per year. Male and female gonochoric spawners release their gametes during the breeding period. In reefs around the Ryukyu Archipelago, multiple species spawn gametes during early summer evenings around full moon. Eggs are fertilized by sperm released from different colonies of the same species. Fertilization takes place in the water column, mainly close to the ocean surface. Zygotes develop into planula larvae that settle on the substratum and metamorphose into polyps after a few days.

In brooding corals, fertilization takes place within the stomach, and zygotes develop into larvae within the mother polyp. Some Okinawan brooder species, such as *Pocillopora damicornis* and *Stylophora pistillata*, release planulae in the night during certain lunar phases in every summer month. Corals may be able to sense changes in seawater temperature, sun and moonlight, which function as environmental cues to regulate the timing of spawning or planula release.

Corals have a high capacity for asexual reproduction and regeneration

Corals with branching growth forms often suffer mechanical damage caused by water turbulence. Breakage results in the production of unattached branch fragments. Fragments, if not buried by sand, may regenerate to form new colonies (Fig. 6A). In stressful environments, individual polyps may separate from the rest

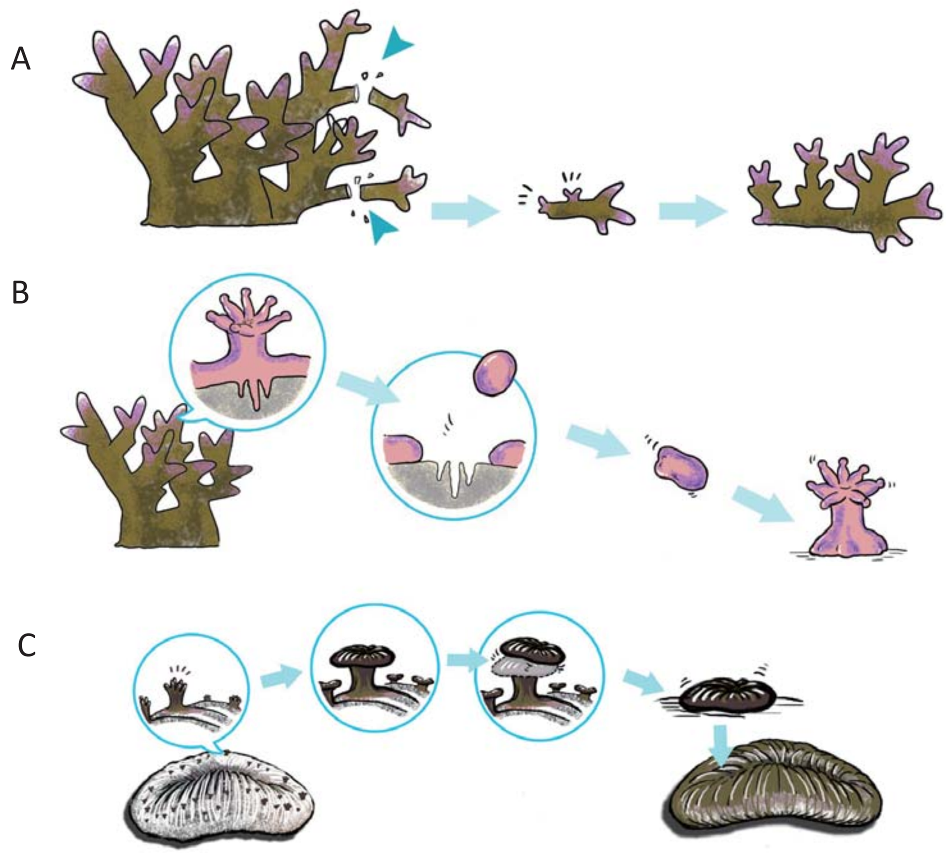

Figure 6. Asexual reproduction of corals. A, fragmentation; i.e., regeneration of colonies from fragments. B, polyp bailout; polyps detach from a colony and transform into planula-like structures, which settle on the substratum and form new polyps. C, regeneration from a tissue fragment; if small viable tissue pieces remain on the skeleton of an apparently dead *Fungia* (mushroom coral) individual, polyps may regenerate from the live fragments and produce new individuals.

of the colony, transform into a planula-like structure that swims, and finally settle on substratum in a new environment (Fig. 6B). Polyps are able to regenerate from small tissue pieces remaining on an apparently dead coral skeleton (Fig. 6C). Thus, corals have a high capacity for regeneration and proliferation through asexual reproduction. Asexually produced corals derived from a single colony are genetically identical to the parent colony and to one another. Such genetically identical colonies are called clonemates.

Corals have long life spans

Massive *Porites* colonies may form huge structures several meters in height (see Column 3). The annual linear growth rate of massive *Porites* colonies is <1 cm/yr, indicating that large colonies of this genus must be more than several hundred years old. Other coral species, such as *Pocillopora damicornis*, grow quickly but do not attain such large sizes. These corals may have relatively short life spans (decades).

Do long-lived corals have high value?

If regulations were enacted to ensure that anthropogenic damage to coral reefs incurred payment of compensation, how would the fees be set; i.e., how might we best estimate the value of corals? “Time to recreate the colonies” (or “time to replace”) could be used as a natural currency in fee setting. Thus, long-lived corals would possess intrinsically high value.

Long-lived coral colonies consist of huge numbers of cells. It is likely that somatic mutations occur among these cells and might sometimes confer benefits on the whole colony during periods of adaptation to new environments. Some coral cells may be totipotent. If such stem-like cells were to acquire beneficial mutations during adaptation to new environments, they might proliferate and replace other cells within the coral colony, thereby facilitating adaptation to changing conditions. If this were the case, long-lived corals may have an enhanced capacity for adaptation to environmental change. Organisms generally adapt to environmental change through the production of genetic diversity by sexual recombination. Among the diversity of genotypes emerging via this process, some may be better suited to new conditions and come to represent an increased proportion of the population due to the process of natural selection. Somatic mutation in corals would also provide genetic diversity to be worked over by the forces of selection and might generate unexpected responses to global climate change.

Column 1.
Corals of the Ryukyu Archipelago

Michio Hidaka

Coral species off the Ryukyu Archipelago are similar to those in other tropical regions, such as the Philippines and Indonesia. However, temperate regions in Japan, such as Kyushu, Shikoku and the Kii Peninsula, share few species with the Ryukyu Archipelago (Fig. 1). Pelagic larvae of corals usually settle on the sea floor within a few days and rarely disperse far from their original colonies.

The life histories and ecology of corals inhabiting deep waters off the Ryukyu Archipelago are not well understood. Corals living on sand/mud bottoms in deep-water bays have unique life histories that are different from species on shallow reefs (Fig. 2). Large coral reefs have been found recently in deep waters (approximately 30 m) around the Ryukyu Archipelago. The few species on these reefs are characteristic of deep waters. Large areas of the reefs are sometimes covered by a single species of coral (Fig. 3). Some of the deep-water coral species are also found on shallow reefs. It is possible that deep reefs provide refugia for shared species during times of environmental stress in shallow waters; e.g., stresses imposed by typhoons or high temperatures.

Shallow seawater temperatures remain equable in some tropical locations because of cold-water upwelling related to topographic features of the sea floor. Other shallow areas are shaded from excessive insolation on the lee sides of islands. Shaded corals do not suffer severe bleaching, even when corals in neighboring areas shed their pigmented symbionts. Upwelling and shading sites may provide refugia for Ryukyuan corals and such areas should be conserved for the preservation of reefs in the archipelago.

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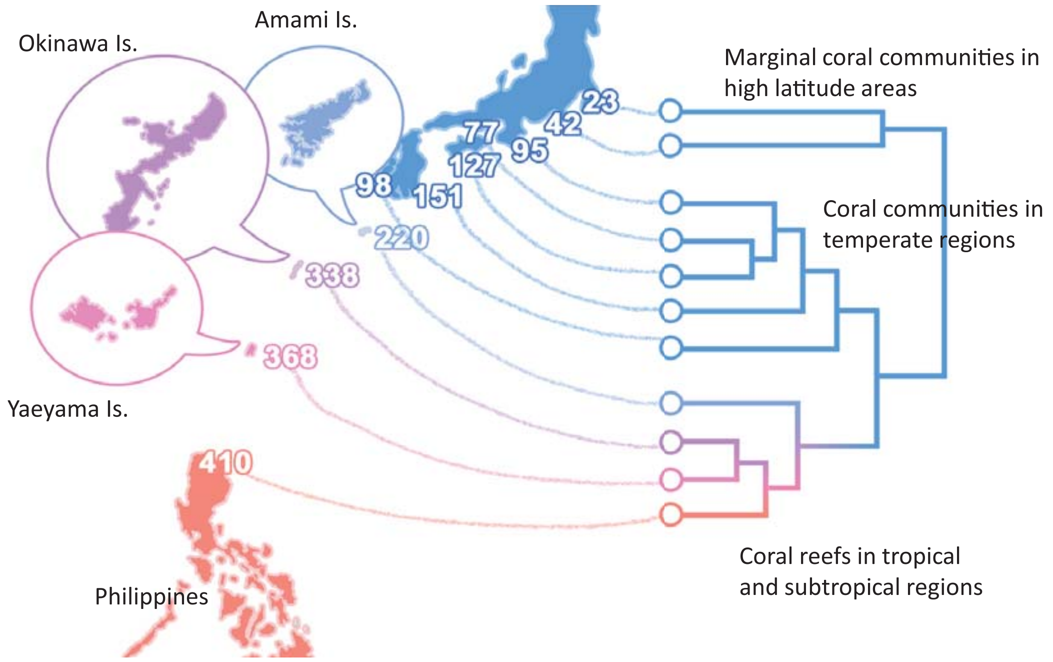

Figure 1. Tropical and subtropical coral reefs have species compositions that are different from those in temperate regions. The dendrogram on the right side depicts species similarities between sites; if two sites share a high proportion of common species, they are connected by short branch lines. Numbers indicate species richness at each site (graphic by Dwi Haryanti, modified from Veron 2000).

Figure 2. Corals in deep bays have unique life history traits. Left side: *Goniopora stokesi*. This coral does not settle on rocky bottoms, and produces daughter colonies that eventually detach from the mother colony. Right side: *Diaseris* sp. This coral develops radial invaginations and divides into several sectors, each of which regenerates to form a circular individual. These species have unique modes of asexual reproduction (Oura Bay; images by Naoko Yasuda).

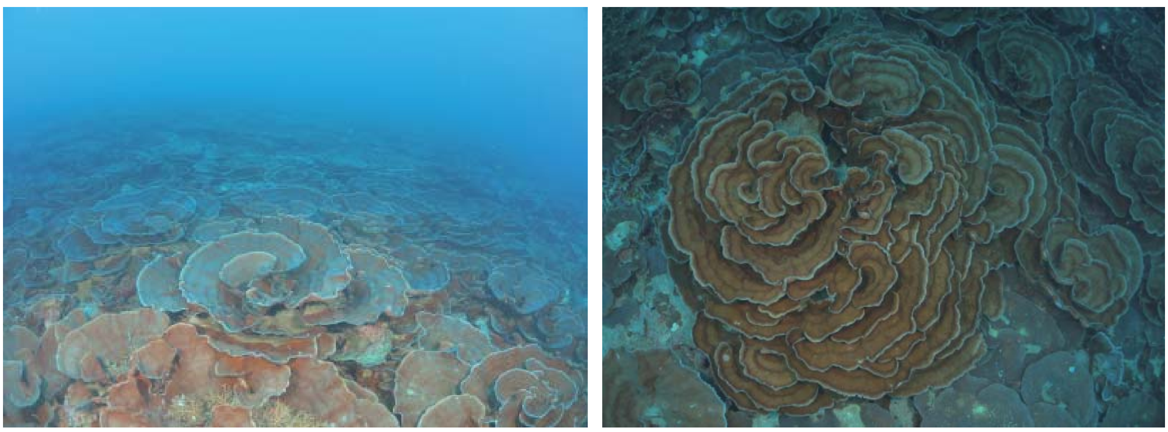

Figure 3. Deep-water coral reef community dominated by *Pachyseris* sp. (30-m depth off Iriomote-jima Island; images by Tohru Naruse).

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1—2. Are corals stressed by hot summers?

The advantages and disadvantages of symbiosis with zooxanthellae

Takashi Nakamura

Have you observed healthy live corals in their natural marine environment? If you look carefully, you may see a range of organisms associated with them, such as shrimps and crabs eating the mucus secreted by corals, small fishes hiding among branches, and the eggs laid by a diversity of marine species (Fig. 1). Moreover, you might also see serious conflicts between coral-eating organisms, such as the crown-of-thorn starfish, and those animals inhabiting corals.

When studying the colors of corals, you may notice that many are brown to greenish-brown. “Zooxanthellae” are responsible for this dark pigmentation. Symbiotic algal cells occur at densities of millions per square centimeter of coral surface. In this section, we will explore the symbiotic relationship between the corals and zooxanthellae, paying particular attention to the photosynthesis of these algae.

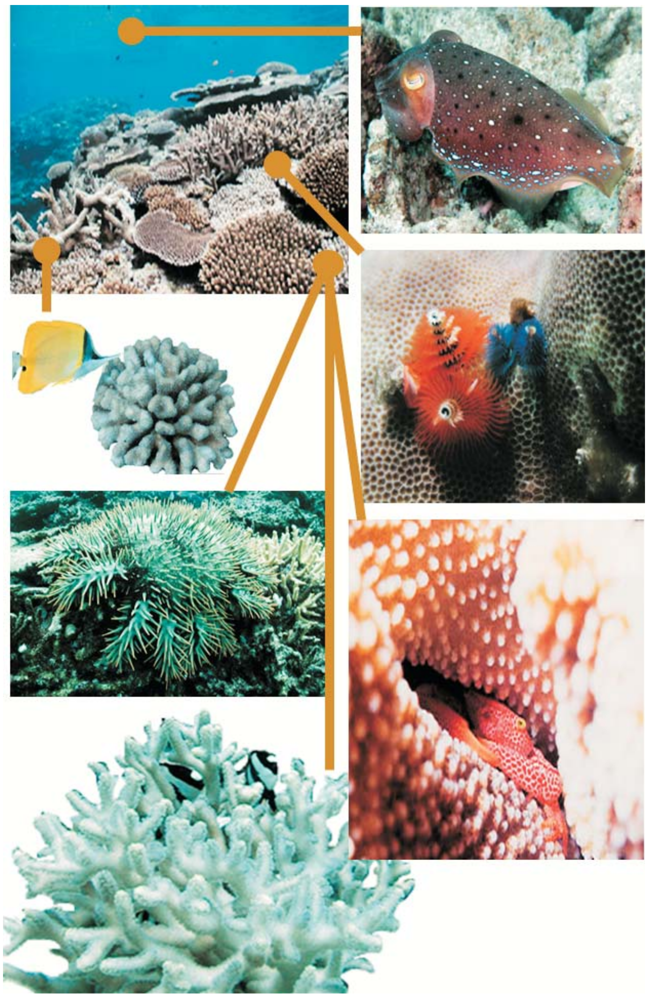

Figure 1. Organisms found around coral colonies. Clockwise from the right upper image: giant cuttlefish (laying eggs between coral branches); Christmas tree worm (excavates residential holes in the coral matrix); coral crab (lives between coral branches); white-saddled reef fish (uses branches as hiding place from predators); white collar butterfly fish and crown-of-thorns starfish (both eat corals).

What are the optimum conditions for healthy coral growth?

Transparent waters and abundant sunlight are important for healthy coral growth. Around the subtropical Ryukyu Archipelago, surface waters are heated by powerful insolation, especially during the summer. Warm waters are less dense than cooler, deeper layers, and essentially float near the surface. Shallow waters are soon stripped of mineral nutrients by planktonic algae, which sink into deeper waters as they die. The rain of bodies falling from the surface is rapidly mineralized by microbes, but stratification of the water column ensures that the minerals are not returned to the shallow layers, which become progressively more nutrient-deficient (Fig. 2). Photosynthetic production is minimal in waters stripped of minerals in this manner, and production in the whole food chain supported by algae is correspondingly reduced. Thus, food supplies for benthic organisms that depend on plankton production, such as corals, become very limited. Low productivity waters like these are termed "oligotrophic"; they are essentially disadvantageous environments for benthos. How then do corals maintain healthy growth under such conditions?

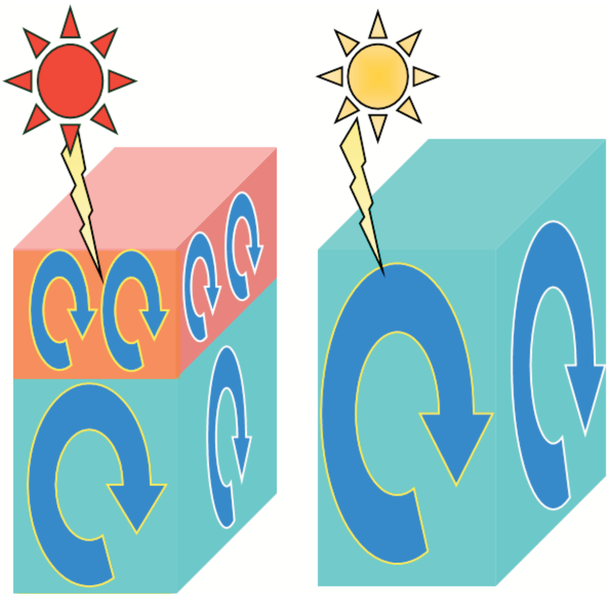

Figure 2. The ocean around the Ryukyu Archipelago in summer (left) when the water column is strongly thermally stratified, and around Honshu (largest main island of Japan) at higher latitude (right), where the thermal gradient in the water column is less steep and vertical mixing by wind forcing is frequent.

Secrets of coral growth in oligotrophic waters

Their symbioses with zooxanthellar algae allow corals to flourish in nutrient-limited environments. These algae are photosynthetic, but they are not mineral or nutrient-limited because the host coral's metabolism provides what they need: carbon dioxide (a waste product of respiration), ammonium, nitrate, and phosphate ions. Tropical waters are transparent and the energy source for photosynthesis (photons) is abundant in the surface tissues of corals where the algae live. A significant proportion of algal photosynthesis is transferred to the host polyp; the products transferred include glycerol, glucose, and amino acids (Fig. 3). In fact, as an example, most (approximately 90%) of the energy required by the cauliflower coral (*Pocillopora damicornis*) is provided by the photosynthesis of symbiotic zooxanthellae. This is the secret to healthy coral growth in oligotrophic waters.

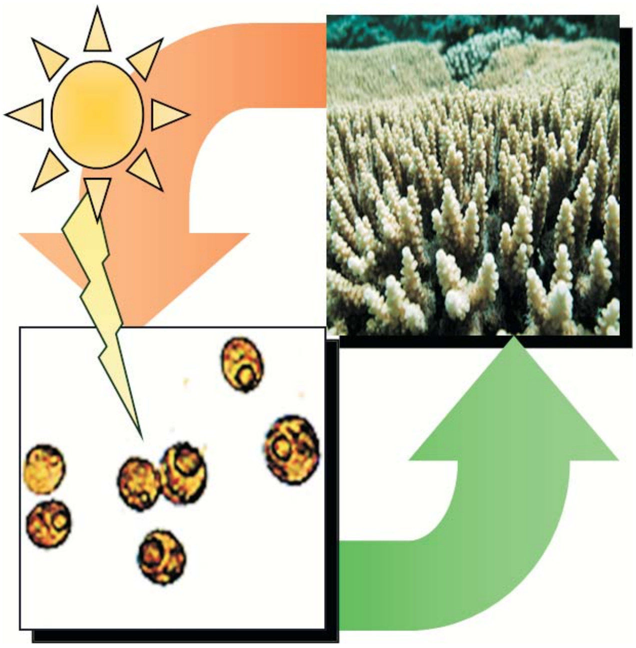

Figure 3. Symbiotic relationship between coral polyps (upper right) and zooxanthellae (lower left).

Are dysfunctional zooxanthellae responsible for coral bleaching?

Persistent high water temperatures during summer are associated with a variety of problems in the resident biota; "coral bleaching" is one of these. Bleaching occurs when zooxanthellar density in coral tissues declines and photosynthetic pigment concentrations (e.g., chlorophylls) in the remaining algal cells fall to low values. These reductions in the quality and quantity of symbiotic zooxanthellae lead to a pale appearance of corals; the white-colored skeletons can be seen through the transparent tissue of corals (Fig. 4). Around the Ryukyu Archipelago, water temperature usually rises rapidly after the end of rainy season when the duration of strong insolation increases. When cloud cover during the rainy season is less than normal, a higher amount of sunlight than normal reaches the sea surface and warms the waters even before the onset of summer. Under these circumstances, full summer solar radiation often raises water temperature above 30°C in July and August, causing large-scale coral bleaching. For example, the ginger coral (*Stylophora pistillata*) bleaches during periods when water temperatures exceed 30°C.

When a moderate strength typhoon approaches the Ryukyu Archipelago, seawater temperature drops rapidly due to wind-driven mixing. Thus, coral bleaching tends to be suppressed in years when typhoons are frequent. When corals remain bleached for prolonged periods, they suffer from energy deficiencies due to the reduction in photosynthetic production by the algal symbionts. Although the few zooxanthellae remaining in the bodies of bleached corals are able to recover to their original densities when environmental stress subsides, the polyps may have already been weakened by the nutrient deficiencies, and they readily succumb to disease. Growth rates of corals also decline after a bleaching event has ended, even when the colonies have returned to their original, darker pigmentation (Fig. 5).

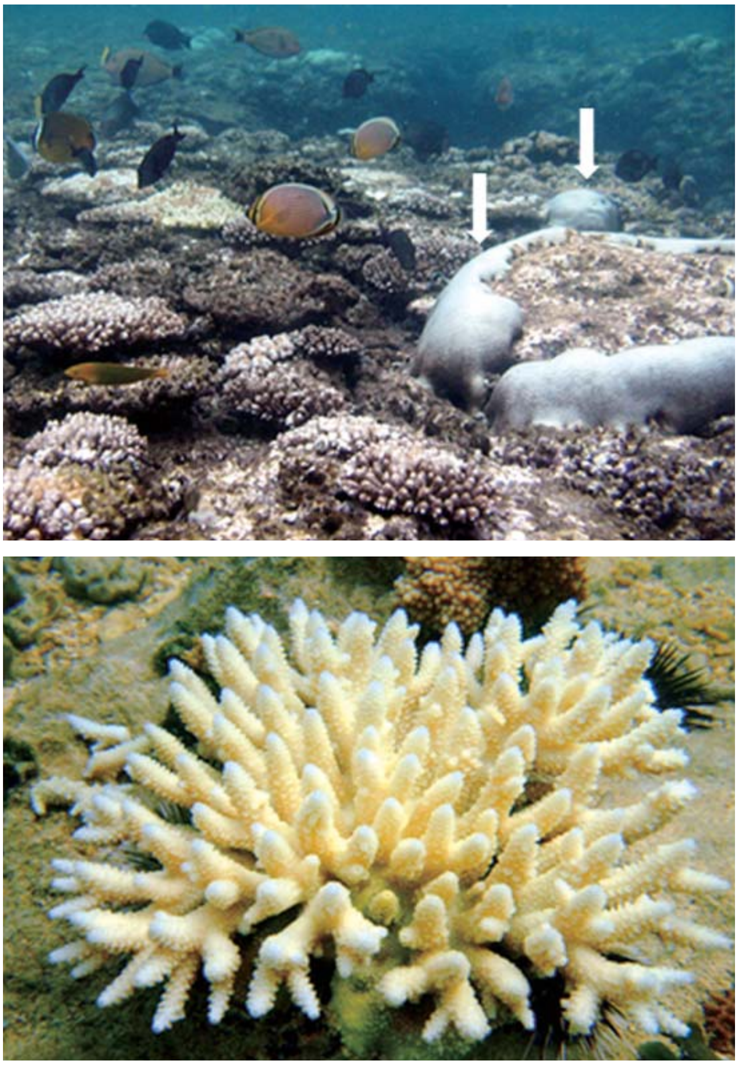

Figure 4. Bleached colonies of massive corals (upper image) and branching corals (lower image).

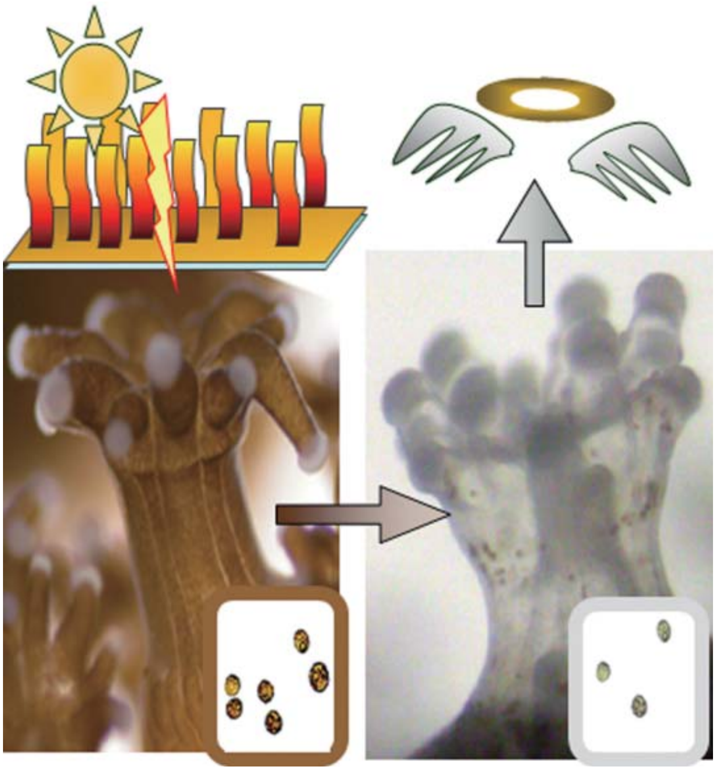

Figure 5. Bleaching as a result of light-induced stress responses in many zooxanthellate corals exposed to high water temperature. A prolonged bleached status results in coral death.

Safety systems in zooxanthellar metabolism

The photosynthetic machinery of any primary producer is able to absorb only a finite number of photons. Excessive photon irradiance may cause damage to the photosystems arrayed on the chloroplast membranes. When corals (and their symbiotic zooxanthellae) are exposed to excessive light for considerable durations, a component of the chloroplast (the D1 protein) deforms, causing a shutdown of photosynthesis, preventing irreversible damage to other components of the light-absorbing apparatus. This is one of the major processes of "photoinhibition", which operates like a breaker fuse in an electrical circuit that prevents system overload. D1 proteins are regenerated immediately when suitable light levels are restored. Disruption and regeneration of these breaker fuses allow zooxanthellae to maintain optimal photosynthesis under dynamic light conditions with minimal risk of irreversible damage. However, high water temperature may disrupt this finely balanced mechanism by slowing down the repair process of damaged photosynthesis. Are zooxanthellae stressed by high water temperature?

Thermal stress impacts on the coral symbiosis emerge when stress-sensitive corals, such as branching coral (e.g., *Acropora* sp.) and ginger coral (*Stylophora* sp.), are experimentally exposed to excessive light to suppress photosynthesis, and then allowed to recover under a range of water temperatures. Recovery of photosynthesis in these coral species is markedly slowed by temperatures exceeding 30°C, but this effect is not apparent in stress-tolerant corals (e.g., *Pavona* sp.). Thus, zooxanthellar sensitivity to high temperature during recovery from excessive insolation is likely a determinant of relative bleaching sensitivity in corals.

Conclusions

Increased frequencies of mass bleaching events around the world indicate that the modern marine environment is becoming unsuitable for corals. Predicting the future of coral reef ecosystems will require improved understanding of (i) the optimal environmental conditions for the coral-algal symbiosis, and (ii) the responses of corals to environmental perturbations.

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1—3. Coral biomineralization

Hiroyuki Fujimura, Sylvain Agostini, Azizur Rahman and Tamotsu Oomori

Skeleton produced by coral

Many marine organisms that live in the tropical and sub-tropical ocean, such as corals and foraminifers, have skeletons or shells of calcium carbonate. The production of such skeletons and shells by organisms is called “biomineralization”, and the minerals produced are called “biominerals.” As a familiar example, human bone is a biomineral. While coral skeletons are made from calcium ions and carbonate ions, human bone is made from calcium ions and phosphate ions. Calcium carbonate skeletons or shells are formed from the calcium and carbonate ions in seawater. One kilogram of seawater contains 0.4 grams of calcium; this amount corresponds to about one third of that in milk (1.1 grams per kilogram of milk). The other component, carbonate ions, which are produced by dissolving CO_2 in water, is found in three forms: carbonic acid, bicarbonate ions, and carbonate ions. These chemical substances are called “carbonate species” and are present at 0.024 grams carbon per kilogram of seawater. Among these carbonate species, bicarbonate and carbonate ions are used for the formation of coral skeletons. Two main mineral forms of calcium carbonate are produced by marine organisms, “aragonite” and “calcite” (Fig. 1). Most scleractinian corals, which can

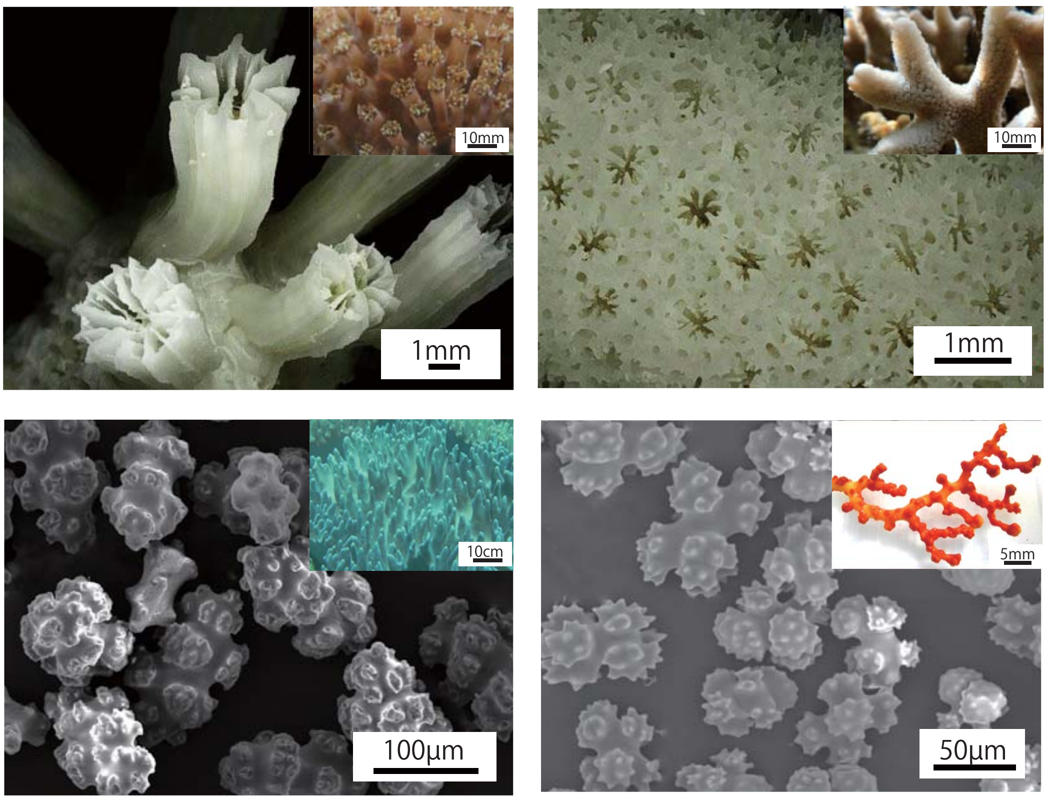

Figure 1. Two forms of calcium carbonate produced by corals: aragonite (upper) and calcite (lower).
Upper left; *Galaxea* sp., Upper right: *Montipora* sp., Lower left: Soft coral, Lower right: Deep sea coral (precious coral).

build coral reefs, produce aragonite. On the other hand, soft corals and deep-sea corals produce mainly calcite. Precious coral, a deep-sea coral, is made of calcite mineral.

Why do scleractinian and precious corals produce skeletons composed of different mineral forms of calcium carbonate? The accepted reason is related to the chemical composition of seawater and its variation throughout history. Modern seawater contains more magnesium than calcium, and the aragonite preferentially precipitates in seawater; however, if seawater contains more calcium, then calcium carbonate tends to precipitate as calcite. Therefore, it is the ratio of these two elements in seawater that controls the mineralogy of calcium carbonate, with magnesium acting as a catalyst for the production of aragonite. The ratio of magnesium to calcium in seawater has varied since the dawn of time. High magnesium and calcium periods have alternately occurred during the Earth's history (Fig. 2). High-magnesium periods (in which aragonite precipitates preferentially) are generally referred to as the "aragonite sea", as opposed to the "calcite sea." Marine organisms that evolved in the aragonite sea, such as modern scleractinian corals, which appeared during such a period approximately 230 million years ago (Ma), tend to have acquired the ability to produce an aragonite skeleton. In contrast, calcifiers that appeared in periods of calcite seas may have evolved the ability to produce calcite skeletons.

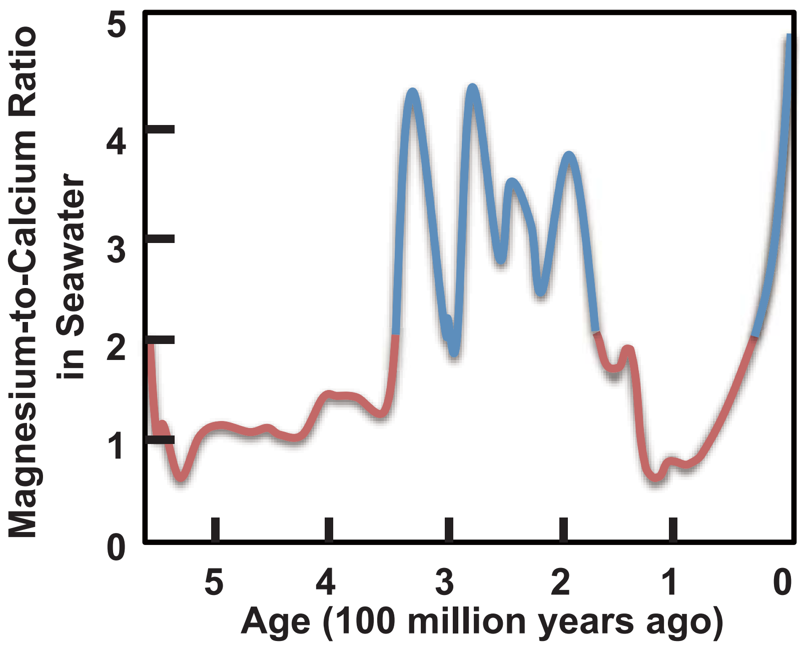

Figure 2. Historical variations in the magnesium-to-calcium ratio in seawater.
Red lines indicate periods of "calcite sea", and blue lines "aragonite sea"(based on Hardie, 1996).

Coral biomineralization

How do corals form their skeletons? Usually, coral grows more rapidly during the daytime because of the photosynthetic activity of symbiotic algae, zooxanthellae, that live in the coral (see Section 1-2). Corals obtain nutriments produced by these symbionts through photosynthesis, and produce the energy required to operate a pump that transports calcium into the narrow space between the coral body and its skeleton; the pump simultaneously removes acids (hydrogen ions) from that space in exchange for calcium. Photosynthesis by the symbiont not only provides the energy source for the pump but also makes the coral body more alkaline, leading to neutralization of the acid produced during biomineralization. The decomposition of nutriments through respiration produces CO_2, which dissolves in water and is transformed into carbonate species, as mentioned above. These carbonate species, bicarbonate and carbonate ions, then react with calcium to produce the skeleton. In this way, coral gradually builds up very small “bricks” (biominerals) of calcium carbonate onto the existing skeleton (Fig. 3).

Coral, as an architect, builds up artistic, sophisticated bricks, making skeletons of various shapes and structures with a growth rate of a few millimeters to a few centimeters per year. Coral can add bricks over several hundred years to become several meters in size; finally, as a result of this activity these corals can produce coral reefs over a long span of years (see Section 1-4 and Column 3).

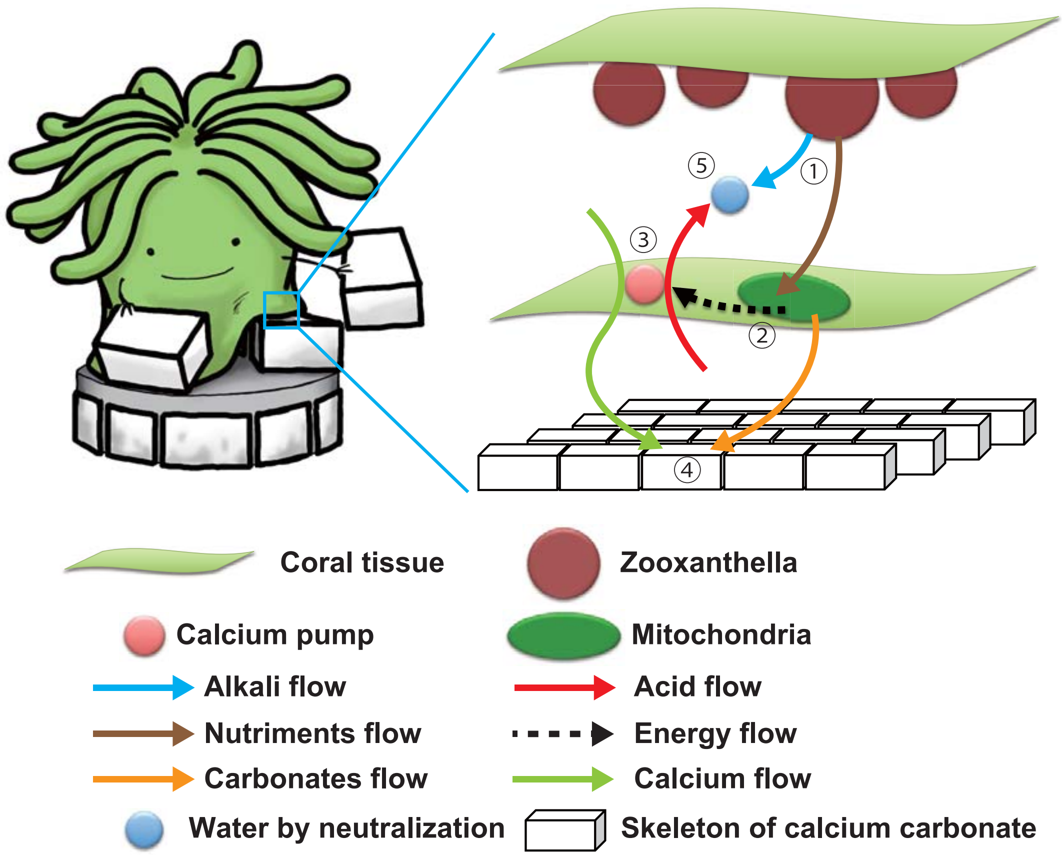

Figure 3. Mechanism of coral calcification.
1) Zooxanthellae provide nutriments produced by photosynthesis to coral mitochondria and result in making the coral an alkaline environment. 2) Mitochondria decompose the nutriments, release carbonate species by respiration, and produce energy for operation of a calcium pump. 3) The pump transports calcium ions into the narrow space beneath the coral polyp and transfers acids (hydrogen ions) to the coral body. 4) Calcium ions react with carbonate species to produce calcium carbonate. 5) Transferred hydrogen ions, which are acidic, are neutralized by the alkaline environment of the coral body.

Coral reefs and the global environment

Because coral grows very slowly but produces enormous amounts of calcium carbonate, it contributes significantly to the global carbon cycle. How do corals and/or coral reefs contribute to the global environment? And in particular, what role does coral play in protecting against the threat represented by the increasing levels of atmospheric CO_2, which are expected to lead to global warming and ocean acidification?

At first, some may believe that coral reefs absorb CO_2 as does a forest. However, the organic matter produced by corals and their symbiotic algae consists of mainly sugars and proteins, which are biodegradable materials, but not cellulose, which decomposes very slowly. Because the organic materials produced by coral and algae decompose rapidly, the fixed CO_2 is released back to the atmosphere, resulting in a balance between CO_2 input/output.

Moreover, it was thought that because corals produce calcium carbonate using carbonate species derived from dissolved CO_2, CO_2 is fixed in the skeleton itself. However, skeletal formation using the dissolved CO_2 does not reduce atmospheric CO_2 levels because the dissolved CO_2 used for skeletal formation is only removed from the atmosphere into the ocean on a geological time scale (i.e. thousands of years), and the ocean itself is a significant sink for atmospheric CO_2. Conversely, on a biological (human) time scale, CO_2 in the ocean will increase as a result of the acid that is produced during the calcification process because calcification leads to an increase in the acidity of seawater. Therefore, coral reefs cannot be expected on a short time scale (e.g. within 100 years) to absorb the anthropogenic CO_2 that is now being released at high rates.

Thus, one might think that corals play a negative role by releasing CO_2; however, this is not so. We must consider the role of coral reefs in the global carbon cycle on a longer time scale; e.g., a few thousands to millions of years. Coral reefs eventually become limestone on land through movements of the Earth's crust (see Sections 1-4 and 3-1). Released CO_2 dissolves in rainwater, which precipitates to the surface of the land. Rain, which is a weak acid, gradually dissolves limestone. This process can absorb CO_2 and is known as "chemical weathering." Limestone dissolved by CO_2 becomes carbonate species in the water and is transported back to the ocean through groundwater and river systems (Fig. 4). Coral skeletal formation and weathering of limestone occur simultaneously in the natural carbon cycle. The amount of CO_2 that is released by the production of calcium carbonate is almost equivalent to the amount that is absorbed by the weathering process. However, during the formation of calcium carbonate skeletons, the amount of calcium carbonate produced is slightly greater than the amount of released CO_2. Therefore, by accumulating enormous amounts of calcium carbonate, corals function as regulators of atmospheric CO_2 on a geological time scale.

This absorption process in the natural carbon cycle occurs at a much slower pace than the rate of anthropogenic CO_2 release and so is not a solution to global warming. Nevertheless, corals play an important role in the natural carbon cycle, and in this way contribute to controlling the global environment.

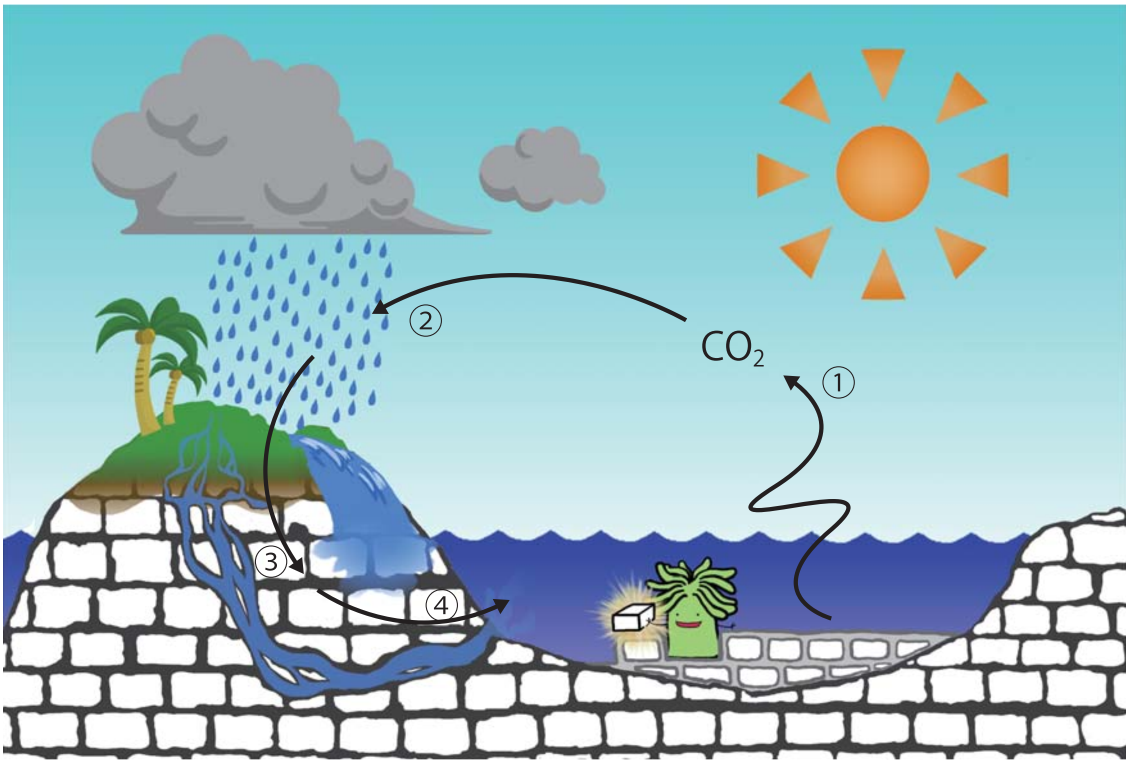

Figure 4. The carbon cycle and role of coral reefs.
1) Coral produces a skeleton (calcium carbonate) and releases CO_2. 2) Released CO_2 dissolves in rainwater during circulation in the atmosphere. 3) Rainwater containing CO_2 falls to the ground and dissolves limestone (chemical weathering process). 4) Dissolved limestone returns to seawater through rivers and groundwater systems in the form of calcium and carbonate species. As the amount of calcium carbonate produced is slightly greater than the amount of released CO_2, the whole process from 1 to 4 leads to the removal of CO_2 from the atmosphere.

Column 2.
Another problem threatening coral reefs: ocean acidification

Haruko Kurihara

Climate change is causing tremendous changes in coral reef ecosystems. As we have seen, warming has caused coral bleaching, but there is another threat: ocean acidification (OA), a recently discovered phenomenon caused by increasing concentrations of CO_2 in the atmosphere. When CO_2 dissolves in seawater, seawater becomes more acidic (pH decreases) and accelerates calcium carbonate ($CaCO_3$) dissolution. We therefore performed experiments to determine whether calcareous marine organisms, including corals, sea urchins, and bivalves, are affected by increasing levels of OA (Fig. 1). We found that both calcification rates and the expression of some calcification-related genes were suppressed by OA in some of these organisms, but some species were completely tolerant of OA. How will coral reefs change as OA increases? In 2013, we discovered a CO_2 vent site off Iwotorishima Island that was dominated by soft corals bearing small $CaCO_3$ spicules; hard corals were completely absent (Fig. 2). Thus, available evidence indicates that (i) coral reefs will lose much of their biodiversity, and (ii) the community will shift to be dominated by the few species that are highly tolerant to OA as concentrations of CO_2 increase. Now is the time to plan for the management and conservation of coral reefs facing threats from global warming and ocean acidification.

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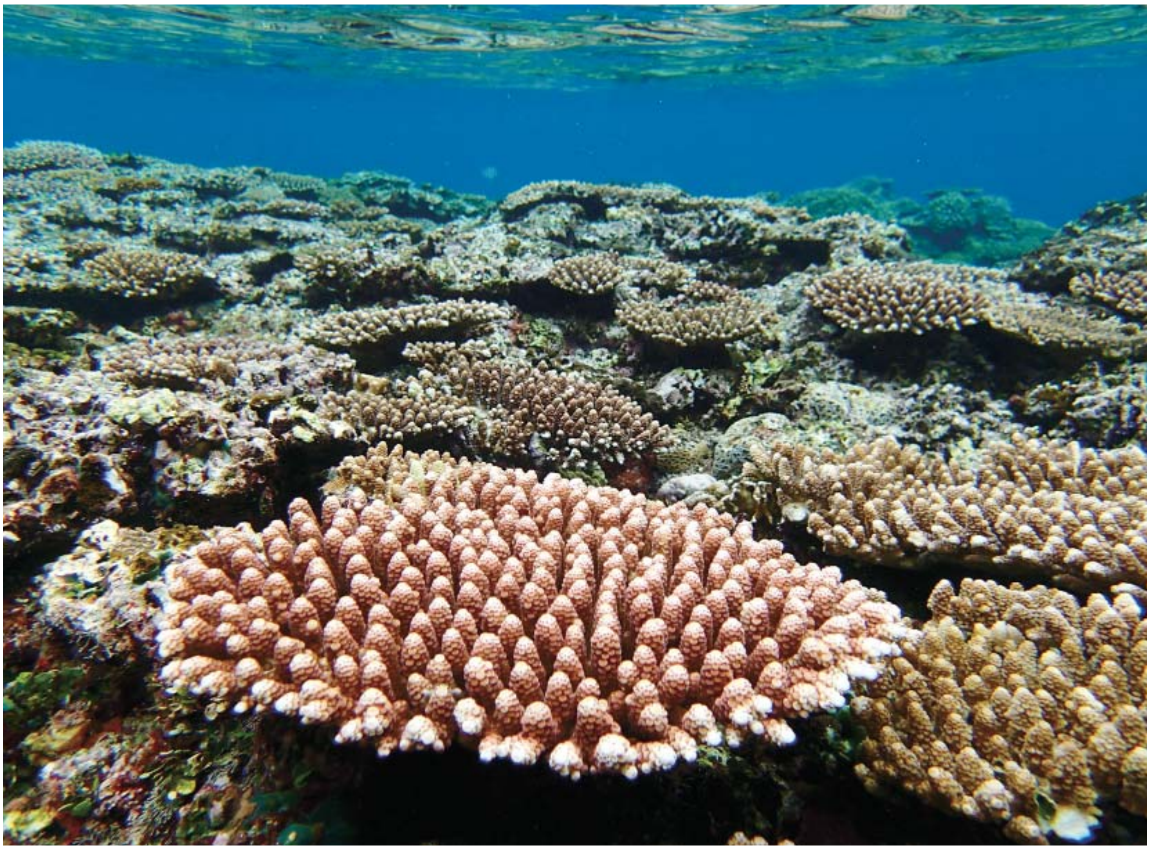

Figure 1. Image of a coral reef off Iriomote-jima Island in the Ryukyu Archipelago. A highly diverse community of hard corals with calcium carbonate skeletons is visible.

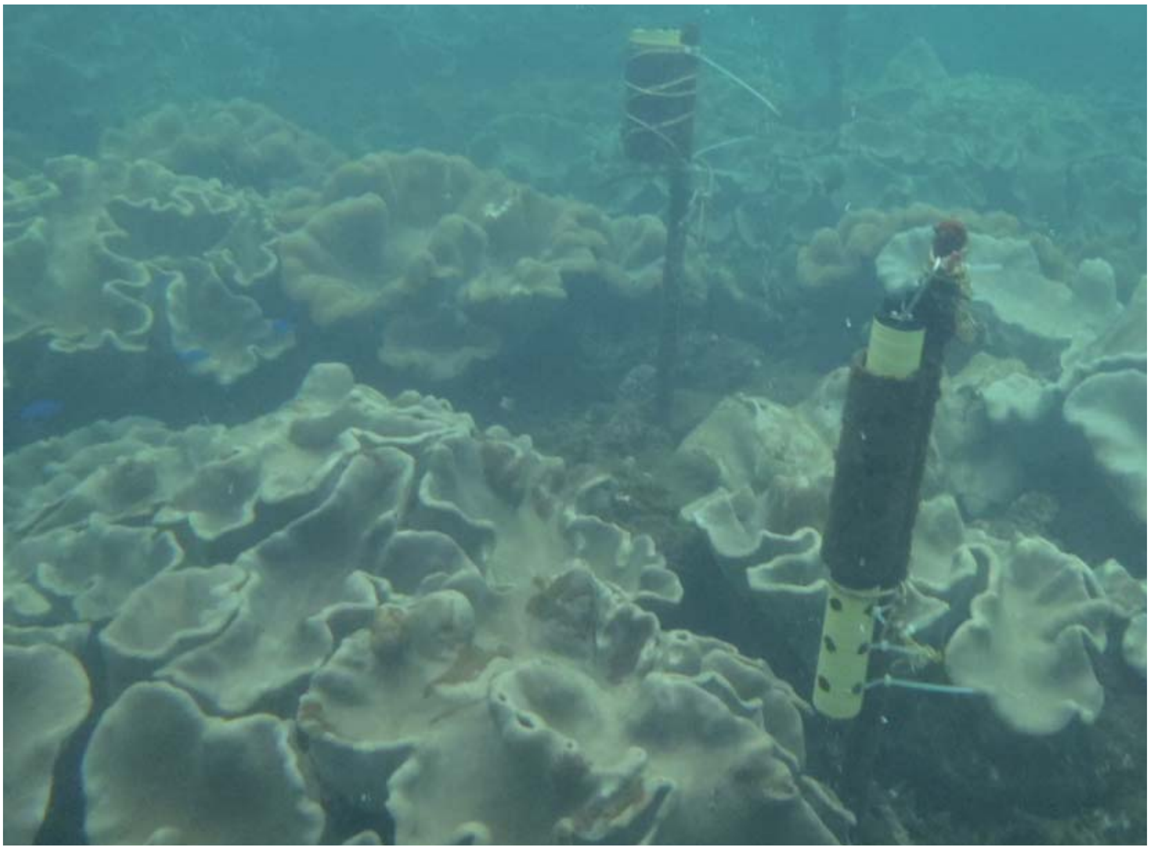

Figure 2. CO_2 vent off Iwotorishima Island (Ryukyu Archipelago) dominated by soft corals.

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1—4. Islands and coasts formed by biominerals

Kazuhiko Fujita and Chuki Hongo

You can imagine the Ryukyu Archipelago as a beautiful place with white sandy beaches surrounded by an ocean of many colors of blue (Fig. 1). Sandy beaches are important places for tourists' and local people's recreation. When visiting these sandy beaches, you can see offshore surf enclosing light-blue shallow waters, called "reefs." You may also see large grayish rocks and vertical cliffs along the coast. If you walk to a village near the coast, you will see traditional houses enclosed by stone walls built from rocks found on the coast. How did these beautiful coasts and rocks form?

Figure 1. Seascape of a typical coast of the Ryukyu Archipelago (Kudaka-jima Island).

Coasts formed by biominerals

Imagine picking up and observing some of the gravel along the coasts. Some pieces have a white color and are either branching or hemispherical in shape. If you observe these more closely, you see small polygonal depressions with radial plates on their surfaces. These pieces of gravel are pieces of coral skeletons. You may also find many types of shells of different colors and shapes, which reflect the high diversity of shell-producing organisms living in the Ryukyu Archipelago.

Figure 2. Coral-reef sands typically found in the Ryukyu Archipelago.

Next, imagine observing the sand on the beach. You may find white- and orange-colored grains (Fig. 2). White sand grains are mainly fragments of coral gravel and shells. You may also find very smooth particles. These are fragments of calcareous algae, which are algae that precipitate calcium carbonate.

Now, let's observe the orange-colored sand grains (Fig. 3). You may find many star-shaped grains. This is "star sand" ('Hoshi-no-suna' in Japanese), a famous souvenir of the Ryukyu Archipelago, the only place in Japan where star sand is found. Although they have an unique shape, these grains are shells of common unicellular organisms called Foraminifera. Living star sands contain cytoplasm inside the shell, and are attached to seaweed and rocks in intertidal pools. You may also find grains that look like the sun in a cartoon, which are called "sun sand" ('Taiyou-no-suna' in Japanese). This is also a type of Foraminifera. Compared with star sand, grains of sun sand are larger, more spherical, and have more rounded spines.

There are also disc-shaped grains that look like coins, which are called "coin rocks" ('Zeni-ishi' in Japanese). Although these are larger than star sand and sun sand, they are also a type of Foraminifera. You can also find dark-green, striped sticks with a hat on top, which Okinawan people call "dwarfs" ('Kobito' in Japanese). These are spines of sea urchins.

The gravel and sand found along the coasts of the Ryukyu Archipelago are made from skeletons and shells of many marine calcareous organisms. In the ocean around the Ryukyu Archipelago, corals and many other calcareous organisms produce either skeletons or shells ("biominerals") with diverse and unique shapes.

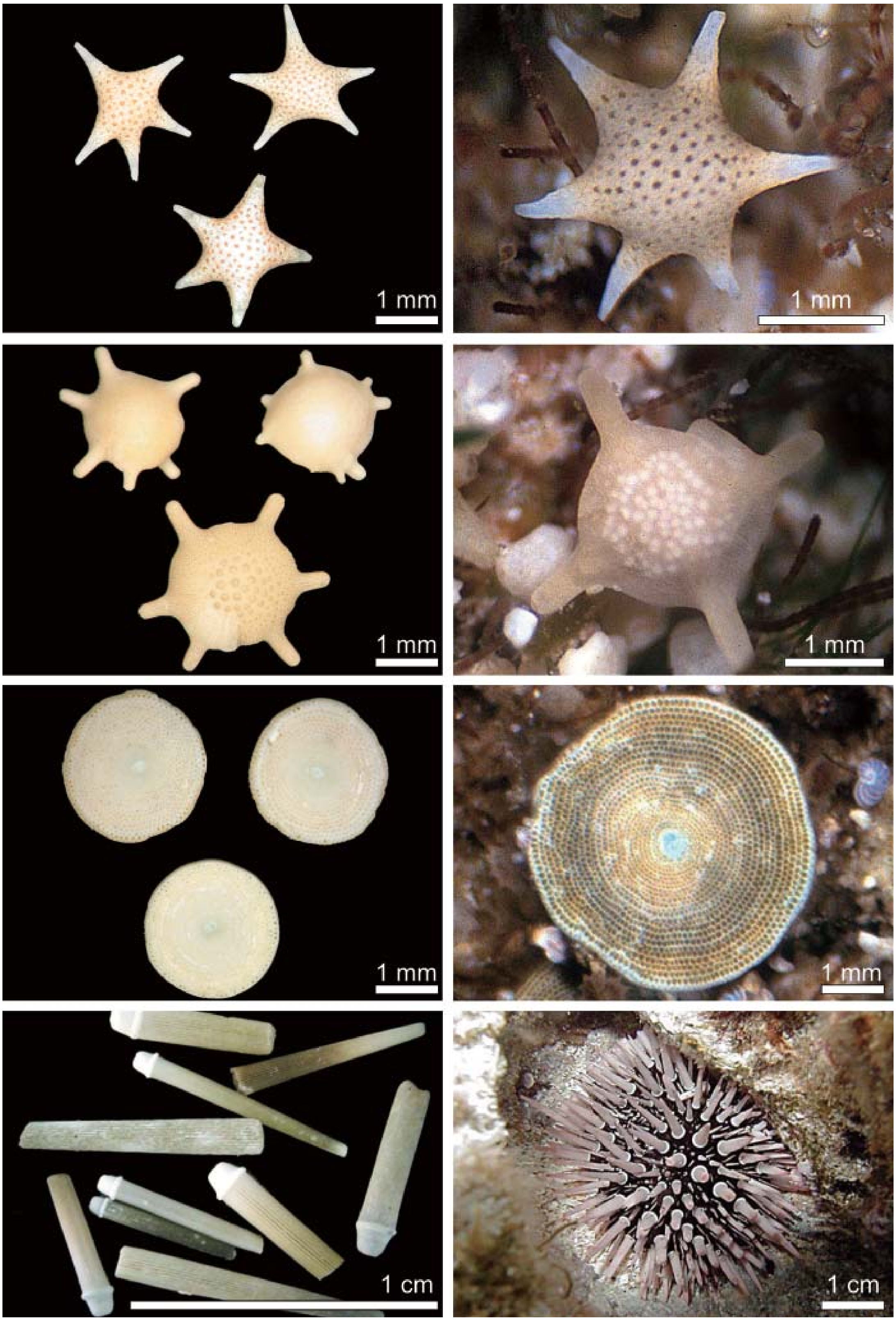

Figure 3. Gravel and sand with unique shapes that are typically found in beach sediments of the Ryukyu Archipelago (left) and living sand-producing calcareous organisms (right). From the top: star sand ('Hoshi-no-suna' in Japanese), second: sun sand ('Taiyou-no-suna'), third: coin rock ('Zeni-ishi'), fourth: sea urchin spines.

Coral reefs constructed by calcareous organisms

Look now at the ocean in front of you (Fig. 4). You see emerald green water 1 to 2 m deep that extends for several hundred meters. This zone is called the shallow lagoon or moat ('inou' in Okinawan dialect). Beyond the shallow lagoon, the intertidal flat zone extends for one hundred meters. This zone is called the reef crest ('hishi' in Okinawan dialect). Beyond the reef crest, the deep blue water is open to the outer ocean. This type of coast, called a coral reef, cannot be seen along coasts of the Japanese Islands. Coral reefs around the Ryukyu Archipelago typically develop close to shore and "fringe" the coastlines, so they are called fringing reefs. How do these reefs develop?

Coral reefs cannot form by only deposition of coral fragments and foraminiferal sands. Sea-level rise is necessary for coral reefs to develop. Corals live just beneath the surface of the sea. If sea level rises, corals grow upward to keep pace with the rising sea. The corals gradually pile up on each other, forming a structure with vertical relief (a coral reef).

Let's examine the development of coral reefs in more detail. In the Ryukyu Archipelago, corals started to grow at locations near the present reef crest about 8,000 years ago (Fig. 5). Then, reefs developed gradually by the piling up of corals in response to rising sea levels. From 6,000 to 4,000 years ago, the upward coral growth stopped as sea level stabilized. After this time period, the reef expanded laterally to form flat shallow

Figure 4. Typical coral reef of the Ryukyu Archipelago (Ibaruma, Ishigaki-jima Island). Zones marked by red and yellow lines show the shallow lagoon and reef crest, respectively.

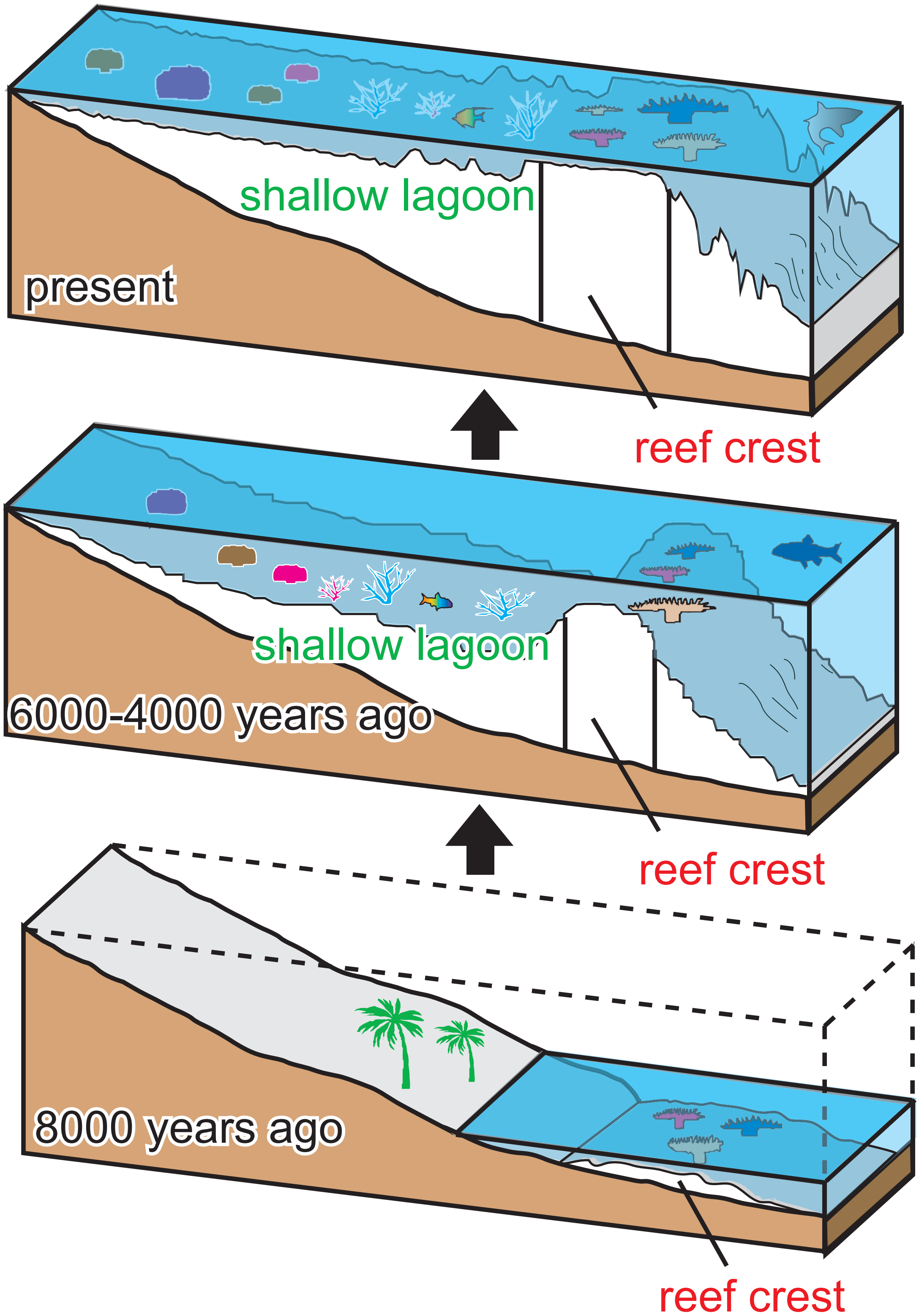

Figure 5. Process of coral reef formation. Blue surface is the surface of the sea.

zones (reef crest). Corals and other calcareous organisms on the reef crest were continually affected by ocean waves. Fragments of their skeletons and shells were transported landward to the lagoon, and the lagoon was gradually covered by sand and gravel until it became shallow. This process of coral reef formation was revealed by drilling the reefs and analyzing fossil corals.

If you were swimming in the shallow lagoon and saw a coral shaped like a stump more than 1 m in diameter (Fig. 6), it would be a microatoll. When a coral reaches the sea surface by upward growth, the coral on top dies from exposure to air during low tides but the coral on the sides is still alive and continues to grow laterally. The formation process of microatolls is similar to that of coral reefs.

Coral reefs and microatolls are constructed by calcareous organisms in response to long-term changes in the global climate.

Figure 6. A microatoll formed by corals.

Limestone of fossil coral reefs

Let's observe the rocks and cliffs along the coasts. Although the surfaces of the rocks are dissolved and have many holes and depressions, you may be able to find fossils of coral (Fig. 7). You may also find white balls. These are also fossils called rhodoliths (algal balls), which consist of many concentric layers. The concentric layers form as a gravel-sized core is covered many times by calcareous algae and encrusting organisms. You may also see large flat fossils that look like "potato chips." These are a type of Foraminifera, as is the star sand. The largest of these attain diameters of 5 cm, making it one of the largest unicellular organisms in the world. The rhodoliths and large foraminifers live in water up to 100 m deep around coral reefs. The presence of these fossils means that the rocks and cliffs were formed from skeletons and shells of calcareous organisms that once lived in coral reefs in shallow water. These rocks formed of calcareous fossils are called limestone. Limestone is found in most of the islands of the Ryukyu Archipelago (Fig. 8). In particular, most parts of Miyako-jima Island are covered with limestone (see section 3–1).

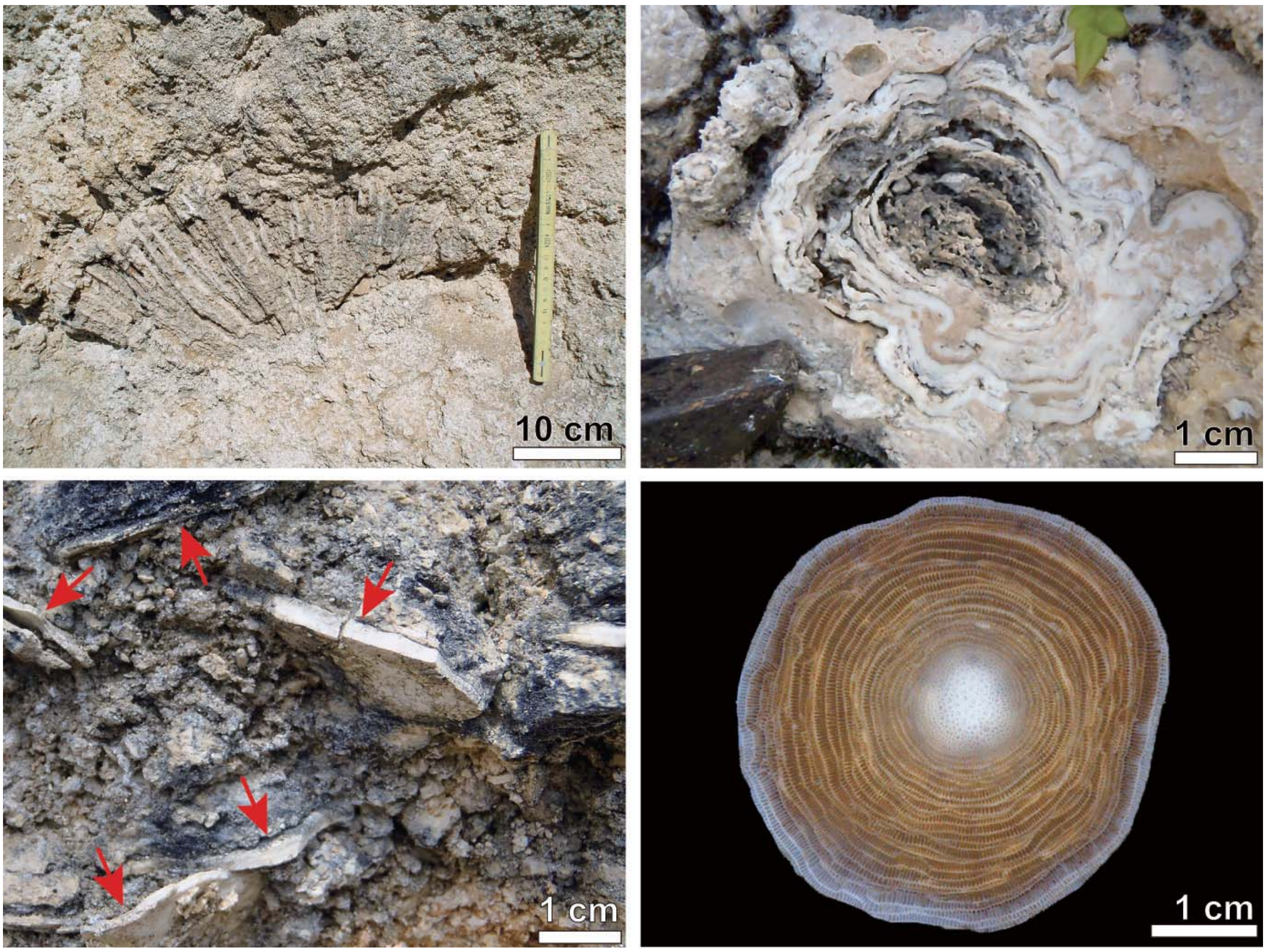

Figure 7. Fossils typically found in limestone in the Ryukyu Archipelago. Top left: corals, top right: rhodoliths (algal balls), lower left: large foraminifers (red arrows), lower right: a large living foraminifer.

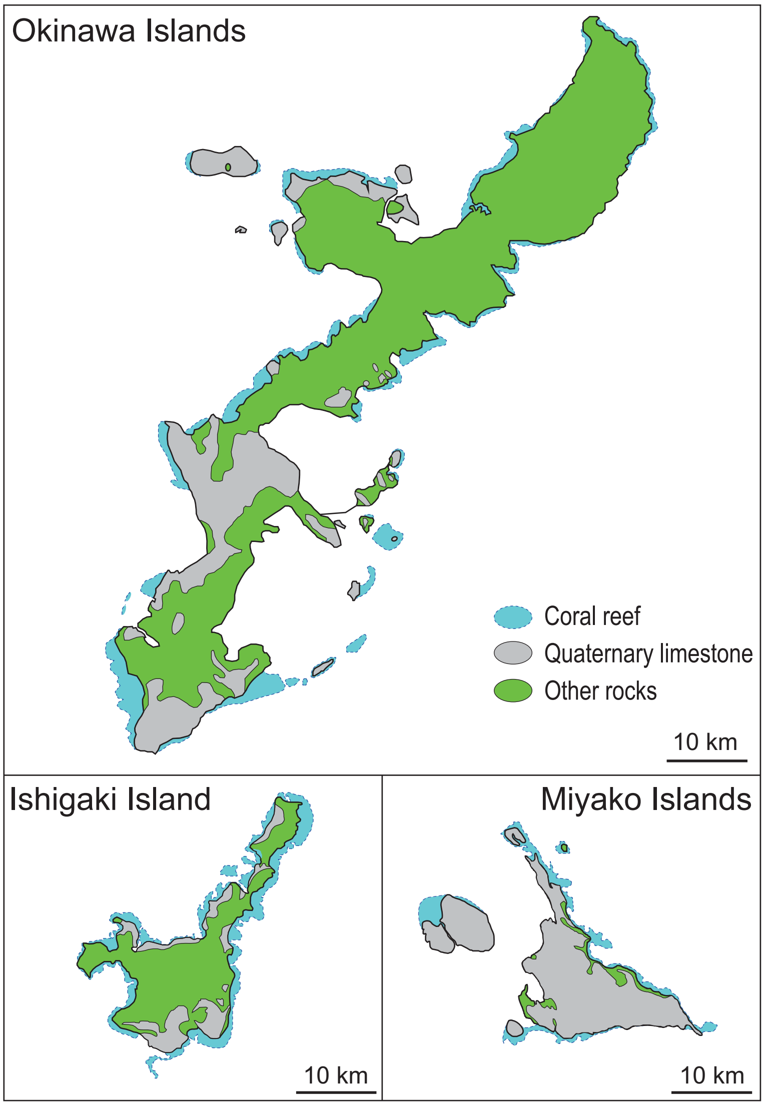

Figure 8. Distribution of coral reefs and Quaternary (from approximately 2.6 million years ago to the present) limestone in the main islands of the Ryukyu Archipelago.

The future of islands and coasts formed from biominerals

Environmental changes such as global warming, ocean acidification, and coastal pollution result in deterioration of corals and other calcareous organisms and hence a decrease in the amounts of sand and gravel made of biominerals. At long time scales, this means the loss of sandy beaches, coral reefs, and limestone, which are the foundation of the islands and coasts. To save these beautiful islands and coasts of the Ryukyu Archipelago, it is important for us to minimize the effects of our (human) influences and global changes on these calcareous organisms.

Column 3.
Large corals can record past climate change

Ryuji Asami

Massive corals of one coral genus (*Porites* sp.) grow hemispherically to become broccoli-shaped and sometimes to be as large as several meters in diameter (Fig. 1, left). Such large corals have lived for several hundred years and they commonly grow about 1 cm each year. The inside of the coral structure is composed of white-colored coral skeleton of calcium carbonate (Fig. 1, right). If this coral-skeleton structure was radiographed, you would see a pattern of light and dark stripes, similar to tree rings (Fig. 2, left). The stripes are annual growth bands of coral with seasonal variations in skeletal density.

Coral skeletons include a variety of elements and organic matter. The concentrations of these elements and compositions vary with changes in the ocean environment; therefore, it is possible to learn how the ocean environment has changed from several hundred years ago until today by chemically analyzing long-lived, large corals. For example, the seawater temperature warming trend since the Industrial Revolution (late 18th century) (Fig. 2, above), the history of radioactive fallout released by nuclear weapons testing (Fig. 2, middle), and the seawater acidification trend (Fig. 2, below) since the mid-20th century can all be delineated.

Recently, there has been growing concern about global environmental issues such as temperature warming and ocean acidification. Predicting how ocean environments will change in the future is an important subject from social and scientific points of view, and understanding past environmental changes is a key challenge in this endeavor. Notably, annual skeletal bands of large corals can be “observing stations in the oceans” that provide long-term time series of environmental changes extending beyond meteorological weather and satellite data that will help us diagnose climate changes in the past, present, and future.

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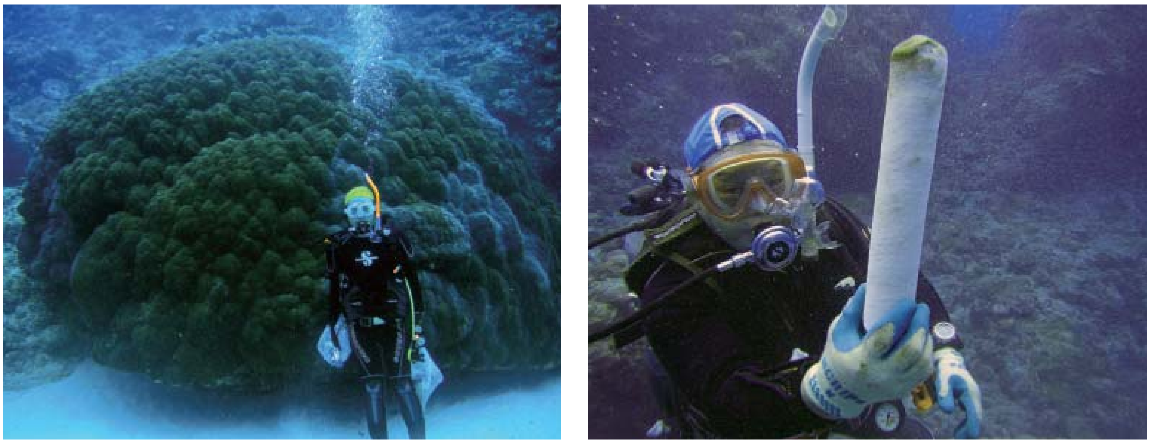

Figure 1. Underwater photograph of a large massive stony coral (left) and the columnar core of a coral skeleton (right).

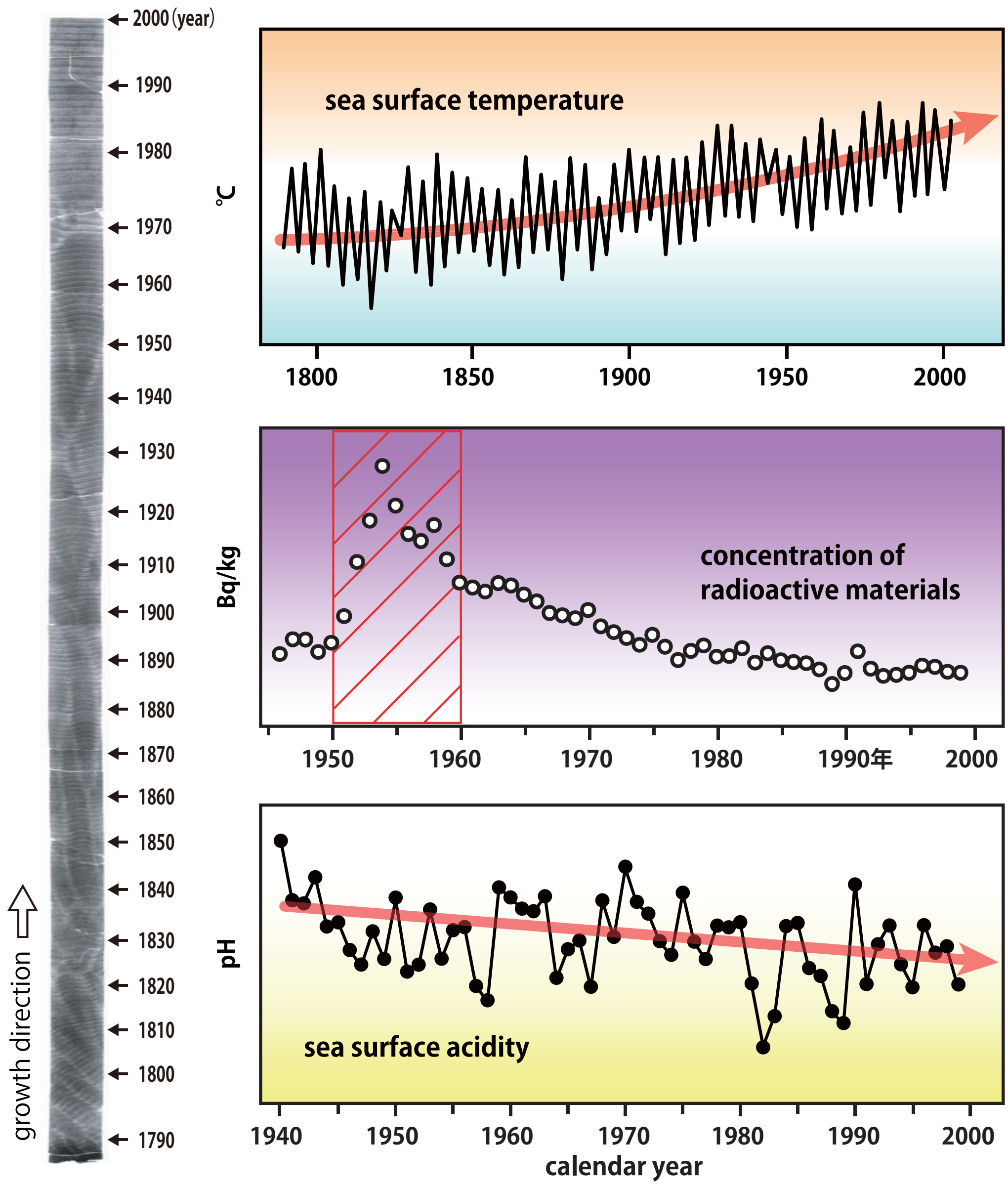

Figure 2. X-ray image of a 3-m coral skeleton core showing annual growth bands with a mean width of about 1 cm (left) and time-series graphs of ocean environmental changes recorded in coral skeletons (top, water temperature; middle, concentration of radioactive material; bottom, water pH).

Column 4.
“Tsunami boulders” as records of devastating ancient tsunamis in the Miyako and Yaeyama Islands

Mamoru Nakamura

A small house-sized boulder is located in the park near Ohama Elementary School in the south of Ishigaki-jima Island (Fig. 1). Small trees grow on the top of the boulder and offer shade from the sun. Based on observations of the surface of the boulder, it is evident that it contains fossil coral, indicating that the boulder was originally part of a coral reef. This reef fragment was removed from the reef by a large tsunami that occurred about 2,000 years ago and was transported by subsequent large tsunamis to its present location. Such boulders are typically known as “tsunami boulders,” and have been found at various places in the Miyako and Yaeyama Islands (Fig. 2). Dating of coral fossils within various tsunami boulders indicates that large devastating tsunamis have struck this region several times, approximately 200, 400, 600, 900, 1,200, and 2,000 years ago.

The Yaeyama tsunami (or Meiwa tsunami), which occurred in AD 1771, struck both the Miyako Islands and the Yaeyama Islands, with maximum run-up heights (*i.e.*, the maximum height on land to which the tsunami reached) exceeding 30 m in the southeastern part of Ishigaki-jima Island. There were approximately 12,000 total deaths in the Miyako and Ishigaki Islands, and approximately one-half of the people on Ishigaki-jima Island were killed by this tsunami. The resulting social damage lasted for 100 years. In particular, despite an increasing population before the tsunami, the population of the Yaeyama Islands decreased for the next 100 years following the tsunami.

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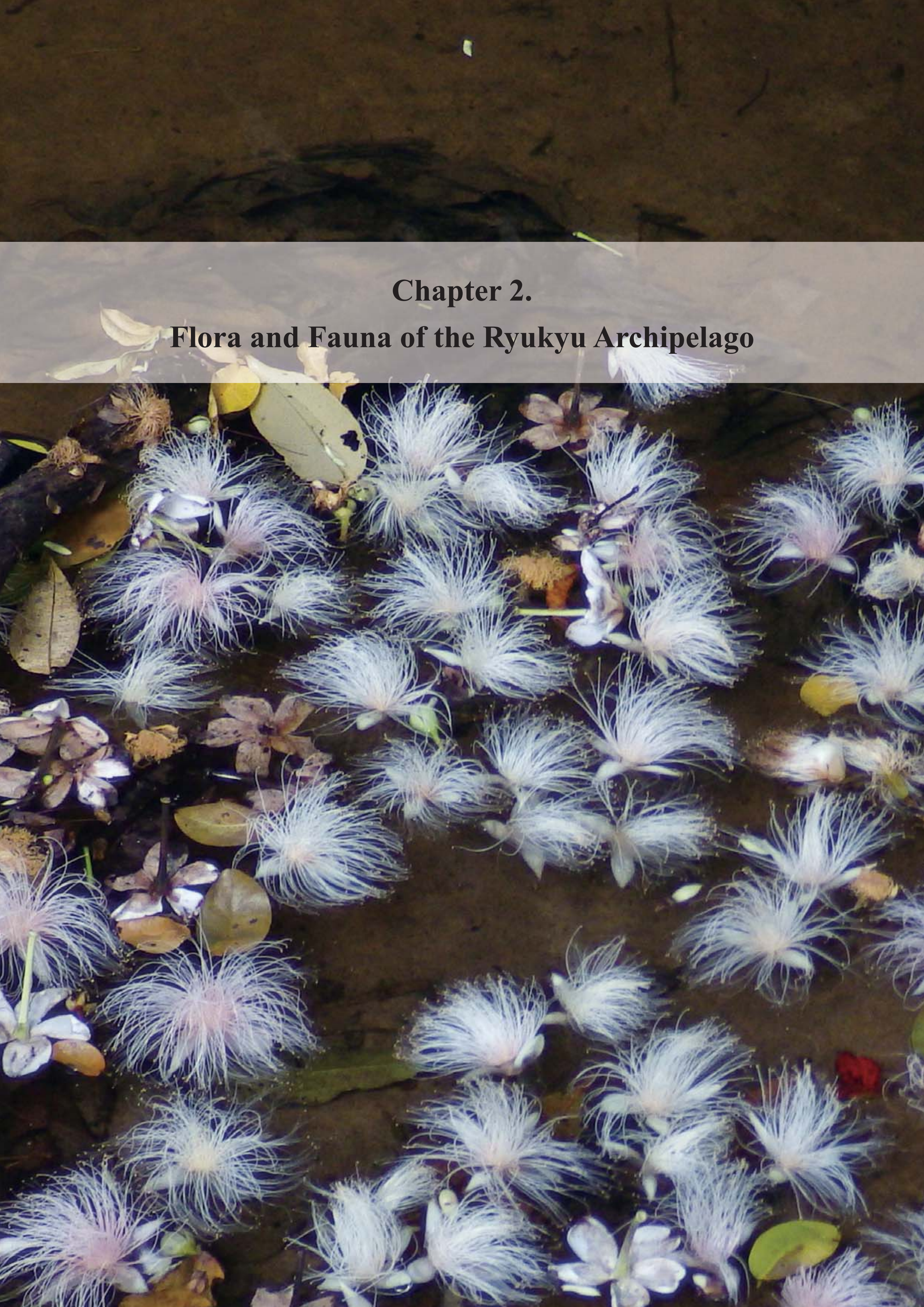
Figure 1. Tsunami boulder (known as "Tsunami-Ufu-Ishi") at Ohama, Ishigaki-jima Island. Diameter: 12 m, height: 6 m.

Figure 2. Tsunami boulder (known as "Bari-Iwa") at Ibaruma, Ishigaki-jima Island. Diameter: 9 m, height: 4 m. Moved by the 1771 tsunami.

Chapter 2.
Flora and Fauna of the Ryukyu Archipelago



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2—1. Subtropical forest and biodiversity conservation in the Ryukyu Archipelago

Yasuhiro Kubota

Threats to endemic biodiversity in the Ryukyu Archipelago

Biota in the Ryukyu Archipelago are characterized by high diversity and uniqueness. Geography including geohistory is a predominant factor in shaping biodiversity patterns in this region. Most of the islands that make up the archipelago are continental islands that were connected to one another and to the Asian continent through a land-bridge and intermittently isolated due to sea level changes that occurred during glacial oscillations. Therefore, biological communities in this region have coalesced through the formation of land-bridge corridors and have been repeatedly fragmented in response to insularity. Such geohistorical processes act as an evolutionary driving force to diversify the islands' endemic organisms.

On the other hand, narrow and closed environments on islands can be a factor that concentrates human activities. One can construct farmlands, build dams on rivers, or cut down forests and, because of the small areas of islands, the influence of these activities may be more serious than anticipated. Artificially modifying what few rivers and forests are available on islands can have negative consequences on the living organisms. Therefore, the Ryukyu Archipelago are listed as a biodiversity hotspot, defined as (despite their high biodiversity) areas where many organisms are on the verge of extinction due to anthropogenic impacts. For the above reasons, developing conservation measures for the endemic biota in the Ryukyu Archipelago is an urgent challenge for evolutionary ecologists.

In this chapter, we focus on the forests, which are the foundation of biodiversity in the Ryukyu Archipelago. Subtropical forests in this region harbor large amounts of wildlife, including endemic species. At the same time, the forest has been extensively used by humans. Indeed, forestry is still one of the local industries today. Forestry practices directly influence the degradation and conservation of biodiversity. We first explain potential patterns of subtropical forests and the current situation of forest management, and then indicate the importance of scientific-based evidence (ecological research) to effectively conserve biodiversity of the subtropical forest.

Diversity of the subtropical forest

For a typical subtropical forest in the Ryukyu Archipelago, the number of tree species is about 100 species per hectare. In contrast, warm-temperate forests in the south-western Japanese archipelago support 50 to 70 tree species. Subtropical forests are apparently similar to the evergreen broad-leaved forest of the warm temperate zone, but tree species diversity is much higher (Fig. 1). In addition, they are characterized by the co-occurrence of numerous shrub species, e.g., Rubiaceae, which are mostly distributed in the tropics. The dominant canopy species of subtropical forests are *Castanopsis sieboldii* and *Schima wallichii*, which are

Figure 1. Landscape of the subtropical forest in the Ryukyu Archipelago (upper column). *Castanopsis sieboldii* (middle column). *Schima wallichii* (lower column).

evergreen broad-leaved trees.

Typhoon disturbances and their ecological role

Typhoon disturbances have a significant impact on forest ecosystems and diversity. In the Ryukyu Archipelago, typhoons are common through May to October; large typhoons have strong wind speeds, reaching 60 meters/second. Such typhoons often destroy the forest canopy. At first glance, this may appear destructive of the forest but, in fact, periodic disturbances by typhoons play an important role in the maintenance of tree species diversity in the subtropical forest (Fig. 2).

Each tree species has different physiological and ecological traits. Some species can grow even in shady conditions under the canopy, but others do not have shade tolerance and grow only in sunny locations. Typhoon disturbances drastically change the light environment in the forest. The forest floor, with large trees

Figure 2. Typhoon disturbance and tree species coexistence.

overhead, is typically shady. However, typhoon disturbances turn such areas into a bright environment, a so-called “canopy gap”. In addition, such environmental changes in light conditions depends on the severity/magnitude of the typhoon disturbance: large gaps are created by several tens of giant trees falling or being uprooted, while small gaps can be created when branches break. As a result, typhoons create a variety of light environments in the forest.

In addition, the scale and frequency of disturbances by typhoons vary depending on the terrain. Although there are few high mountains in the Ryukyu Archipelago, because of small ridges and valleys, the topography is complex. Forests along ridges experience strong winds, while forests in valleys are not strongly affected by wind, but are stable and maintain shady conditions on the forest floor. Spatial variation in light environments associated with typhoon disturbances leads to a diversity of habitats (ecological niche diversity), which allows for the coexistence of tree species with different characteristics.

Logging impacts on the biodiversity of subtropical forests

As mentioned above, the maintenance mechanisms of biodiversity in subtropical forests may be unique. However, the question remains of how human activities have impacted these potential processes. In the Ryukyu Archipelago, large-scale deforestation occurred both before and after World War II and, in parts of the islands, timber production in natural forests continues today. The canopy of subtropical forests is essentially kept low by the influence of typhoons; the height of the forest is usually about 10 ~ 20 m. Because individual trees are relatively small in relation to the cost of logging (thus, providing lower profit), it is important for foresters to increase the timber harvest per area. As a result, clear-cutting to a relatively large extent is performed. In the context of nature conservation, clear-cutting has ecological impacts. Therefore, the trade-off between forestry and ecology leads to serious disputes involving logging and protection between forestry officials and nature conservationists. To address such controversy, scientific information is essential for both sides. In the following sections, we explain the impact of clear-cutting on the forest structure.

Simulating forest dynamics and assessments of logging impacts

Based on data obtained in field surveys, we can simulate forest dynamics after clear-cutting on a computer and evaluate the effects of clear-cutting on structure and diversity of the subtropical forest (Fig. 3). The lifespan of trees is typically more than a hundred years and, thus, field experiments take a long time. Therefore, it is difficult to verify anthropogenic impacts on forest dynamics. “Experiments on the computer” are a promising methods in ecological studies. We simulated clear-cutting in a variety of forests and predicted

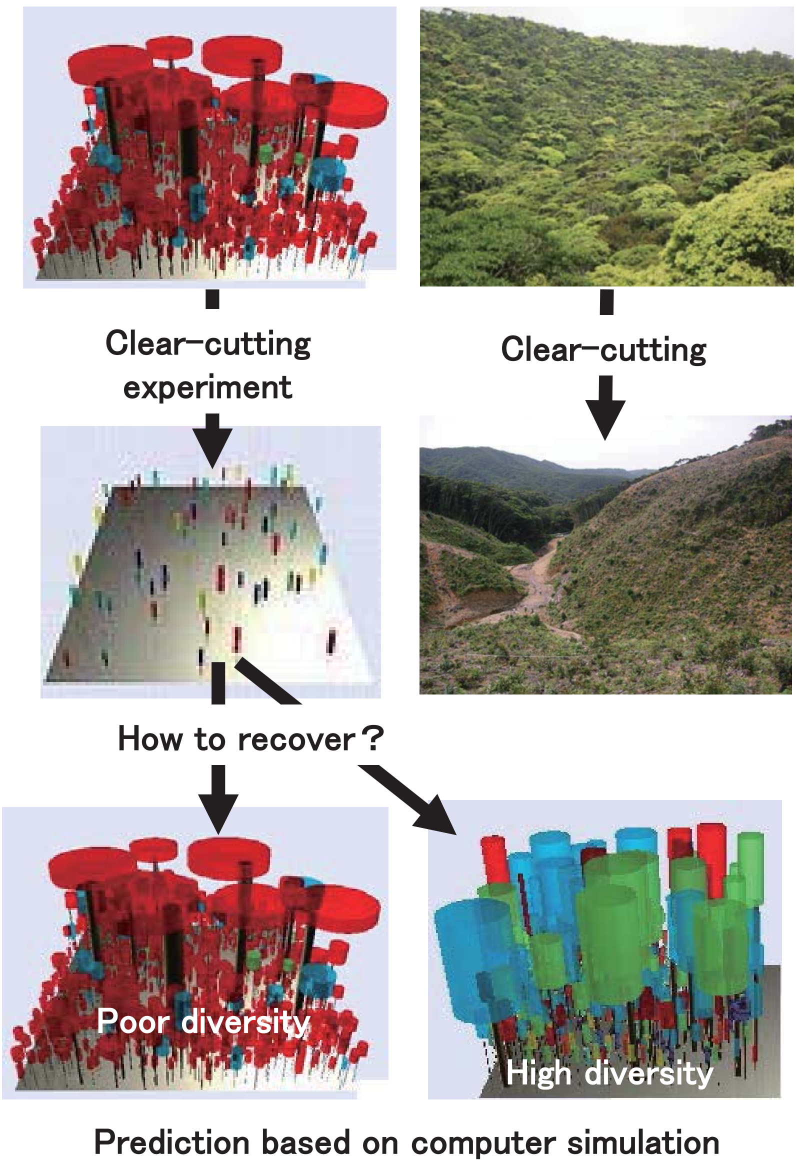

Figure 3. Simulation of forest dynamics: clear-cutting experiments on the computer.

the subsequent recovery process of biomass and tree species diversity for each forest. In Figure 4, every line shows the trajectory of forest recovery along with time development. Some forests have restored species diversity in response to the regeneration of biomass. However, there are also forests that do not rapidly recover species diversity.

Biodiversity loss in relation to logging

The recovery pattern of species diversity differs greatly between forests. Such differences in logging impacts on the recovery of biodiversity reflect regeneration processes of the subtropical forest. Most subtropical tree species have "sprouting capability"; some trees are able to regrow by sprouting due to clonal growth. The dominant species, *Castanopsis*, is a typical sprouting tree. Thus, when clear cutting a forest with a high dominance of *Castanopsis*, their dominance substantially increases by the vigorous growth of sprouting stems, and ends up being greater than before logging. As a result, secondary forests that have been regenerated after clear-cutting shift to forests dominated by *Castanopsis*, as compared to the previous harvest. In other words, we can predict that clear-cutting, through the sprouting regeneration of *Castanopsis*, may decrease the

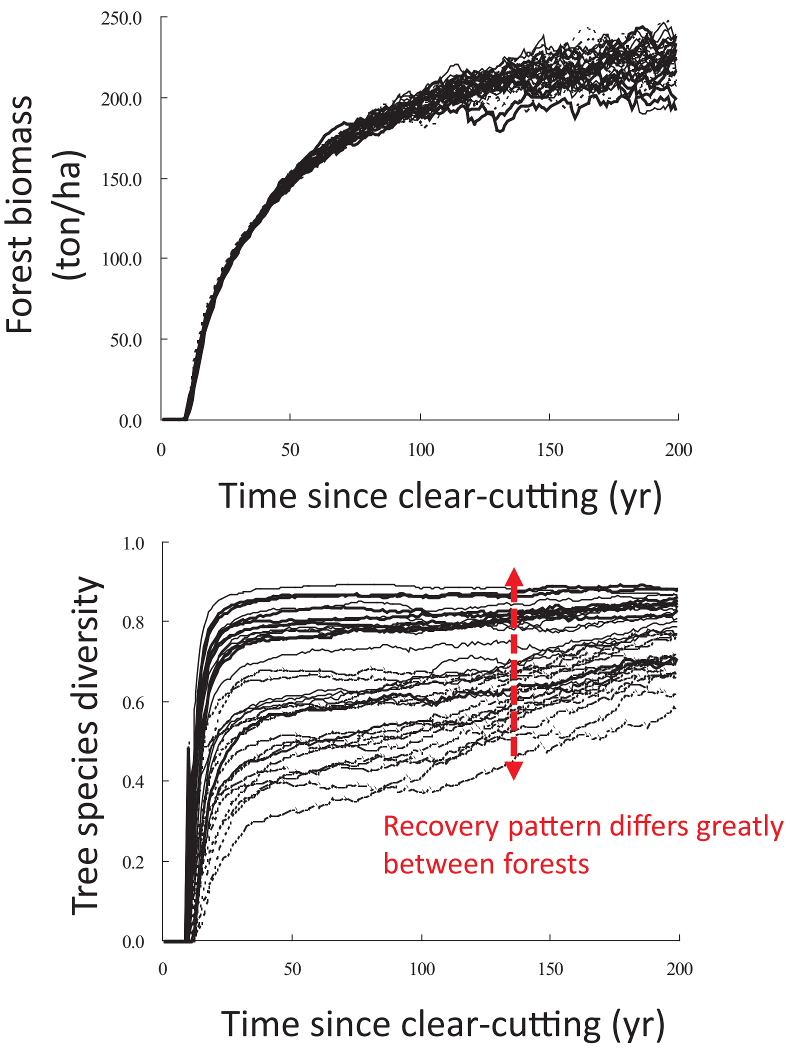

Figure 4. Simulating recovery processes of forest biomass and tree species diversity.

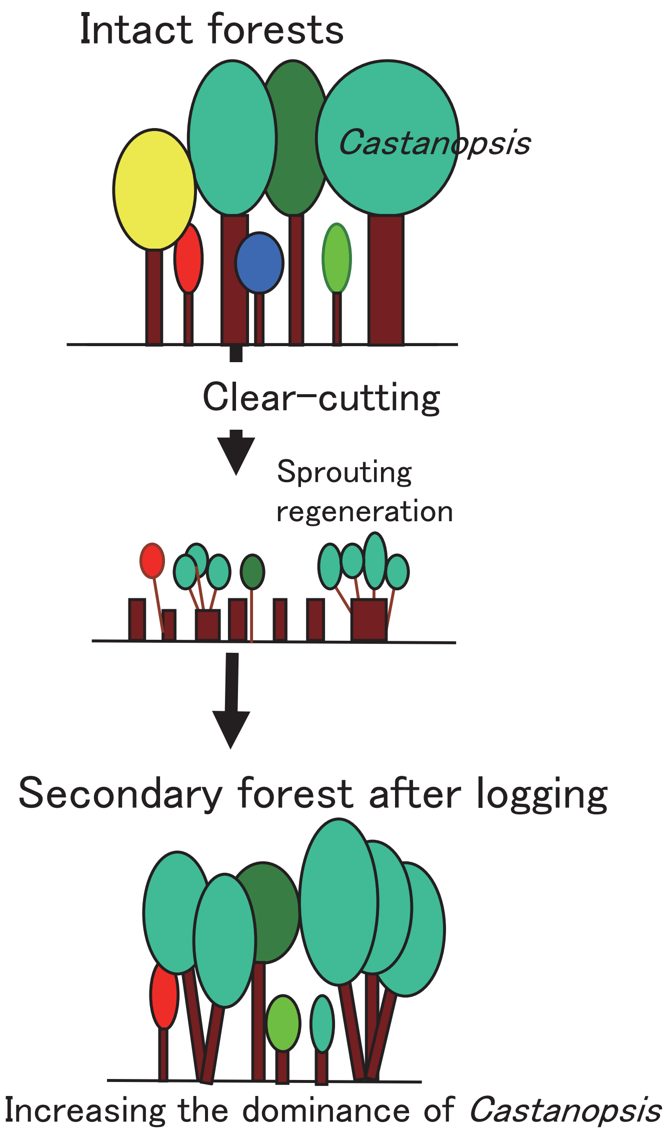

Figure 5. Mechanism of the dominance of *Castanopsis sieboldii* in response to clear-cutting.

diversity of subtropical forests (Fig. 5). As shown in Figure 4, the inter-forest difference in recovery patterns of species diversity is related to the dominance ratio of *Castanopsis* before cutting.

Our simulation analyses of forest dynamics revealed that clear-cutting accelerates the dominance of *Castanopsis*. In addition, when simulating for a longer time, the dominance of *Castanopsis* will slowly lessen and various species can regenerate and, finally, secondary forests gradually recover their species diversity. These simulation results suggest that currently, the observed forests dominated by *Castanopsis* may have been formed under the influence of past deforestation. It is possible that the forest dominated by *Castanopsis* represents original features of the subtropical forest, but human activity in the past may have impacted the forest structure in this region. Furthermore, from the viewpoint of biodiversity conservation these analyses suggest that forests of *Castanopsis* should be cut down with care.

Toward ecological forestry

Deforestation has been performed in forests across all regions in Japan, not only in subtropical forests in the Ryukyu Archipelago. The methods of forest management are mainly based on many years of empirical knowledge rather than scientific quantitative evidence. For example, to improve the appearance and productivity of forests, understory thinning (e.g. weeding the forest floor) is being done in the subtropical forest of the Ryukyu Archipelago.

In the northern part of Okinawa-jima Island ('Yanbaru'), understory thinning has been performed from the 1970s to the present. Scientific validity of such a management method based on empiricism can be assessed based on simulation analyses, as mentioned above. Figure 6 demonstrates an assessment of whether forest growth managed by understory thinning was enhanced. We can see there are few differences in the recovery of forest biomass between managed and intact forests. More importantly, Figure 7 indicates that the number of tree species (surrogating as biodiversity) is significantly reduced by understory thinning.

Experienced management techniques commonly used have been shown to have no effect in forestry, and can actually decrease the biodiversity based on these analytical results.

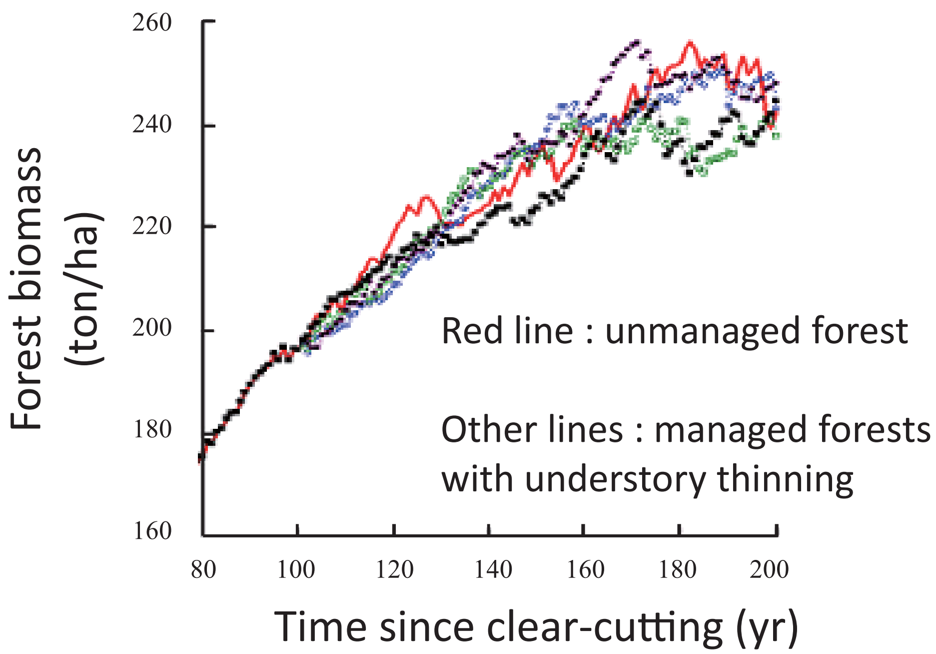

Figure 6. Simulating understory thinning and its influence on biomass recovery.

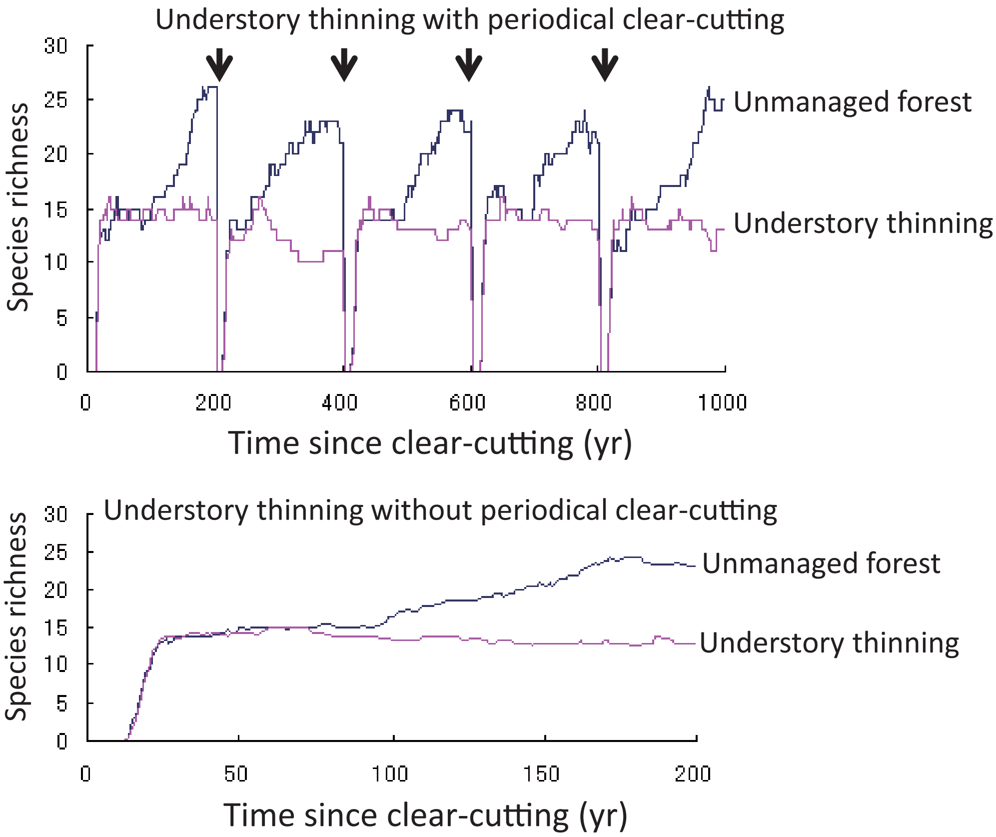

Figure 7. Simulating the impacts of understory thinning on tree species richness in managed forests.

Our results explicitly illustrate the loss of biodiversity due to deforestation. By advancing such analyses, we can improve the methods of forest management and consider how to maximize forestry revenue while minimizing biodiversity loss based on scientific evidence. Studies on ecology constitute a promising approach to provide basic knowledge on the maintenance of biodiversity, and also for examining controversies involving the question of how to use forest ecosystems. Further ecological studies should contribute to developing improved methods of biodiversity conservation.

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2—2. Exploring mangrove forests, tidal flats and seagrass beds

Makoto Tsuchiya

Okinawan mangrove forests (mangals) develop wherever tidal flats form around river mouths and the inner reaches of bays fringing the island. Seagrass beds are often located on the seaward margins of these intertidal flats. What are the connections between these ecosystems, and are they important in the lives of human beings?

Mangroves are intertidal tree species growing on soft sediments and sometimes on hard substrata in sheltered marine locations of tropical and subtropical regions. They are very well adapted to the stressful life at the interface between land and sea. Mangroves have several defining characteristics: 1) they do not occur in terrestrial environments, 2) some species have specialized root systems and produce seedlings via viviparous reproduction, and 3) they are adapted to saline environments, and are able to survive even when their roots and lower trunks are submerged in seawater at high tide.

Among the mangroves species found around Okinawa, *Bruguiera gymnorrhiza, Rhizophora stylosa, Kandelia obovata* and *Avicenia marina* produce viviparous propagules (Fig. 1) and have specialized aerial root systems called pneumatophores (Fig. 2). The other two species, *Lumnitzera racemosa* and *Sonneratia alba*, also have pneumatophores, but do not produce viviparous propagules.

Several mangrove forests in the Ryukyu Archipelago are under protection as conservation areas: stands

Figure 1. Propagules of the mangroves *Bruguiera gymnorhiza* (left), *Rhizophora stylosa* (middle) and *Kandelia obobata* (right).

Figure 2. Landscapes in mangrove ecosystems. Top: forest of *Bruguiera gymnorrhiza* on Ishigaki-jima Island. Knee roots of this species are conspicuous. Lower left: stilt roots of *Rhizophora stylosa* are visible in the Gushi District of Naha City. Lower right: aerial roots (pneumatophores) of *Avicenia marina* on the Iriomote-jima Island tidal flat.

around the mouths of the Sumiyo and Yakugachi Rivers fall within the Special Protection Zone of the Amami-Gunto Quasi National Park; large mangrove forests around the mouths of the Nakama, Urauchi, Fukido and Nagura Rivers are within the boundary of the Iriomote-Ishigaki National Park; mangals located within the inner part of Gesashi Bay have been registered under the Japanese Natural Monument category; and the Manko National Wildlife Sanctuary, which is located at the confluence of the Kokuba and Nuha Rivers, has been registered as an important wetland under the 1999 Ramsar Convention.

Intertidal areas covered by soft substrata, such as sand or mud, are known as tidal flats (Fig. 3). On these flats you may find huge populations of small crabs and/or snails. The behaviors of crabs are extremely interesting.

Figure 3. Range of plant and animal species on tidal flats.

Mangrove species supply food to animals living on tidal flats

Inside the mangrove forest, you can see large volumes of fallen leaves on the mud (Fig. 4). These are shredded and fragmented into small pieces over time. The resulting particles accumulate in large quantities as fine organic particles in and on the mud, where they are used as food by animals in the benthos and swimming species that enter the forest during flood tides. Particles are carried out of the forest as the tide ebbs and onto the lower tidal flats, where they may be eaten by crabs, gastropods and other small animals. Organic fragments derived from parts of animals and plants are known as detritus. Bacteria grow abundantly on detrital particles. Microscopic examination of the surface substrata from intertidal flats reveals fine sandy particles and amorphous materials, which are the detrital component. Detritus is colonized by myriad microscopic organisms, such as diatoms, nematodes, and bacteria, all of which are eaten by crabs and snails. This organic debris decays slowly in the forests and on the lower flats, where large volumes of detritus accumulate. These accumulations are vast reservoirs of organic materials.

The large gastropod snail *Terebralia palustris* (Fig. 5) and large crab species feed directly on fallen mangrove leaves. Each *T. palustris* (10 cm long) specimen consumes about 3 grams dry weight of *R. stylosa* leaves per day. A proportion of the leaves consumed by the snail is assimilated by the animal's metabolism, and the remaining fraction is deposited in feces containing large amounts of partially processed organic matter. These feces are pulverized into small fragments by waves, and then consumed by small crabs and gastropods living on the tidal flats.

Figure 4. Fallen mangrove leaves on a tidal flat. The darkly pigmented area is an accumulation of fragmented or decomposing leaves, which may be used as foods by crabs and gastropods on the tidal flat.

Figure 5. The gastropod *Terebralia palustris* occurs on mangrove forest floors of Iriomote-jima Island. The snail directly consumes unprocessed mangrove leaves.

Tidal flats are restaurants for birds

Tidal flats are feeding and resting sites for many birds. Huge flocks of migratory species gather on the sediments, where they rest, feed and then fly onward to their next destination. All of these activities occur simultaneously as new migrants arrive and others depart. Tidal flat shores are preferred sites for many bird species, but only when benthic organisms are abundant and diverse. Biodiversity is a major issue in our changing world because so many of nature's benefits depend on the integrity of the taxonomic complexity in wild communities. The rich benthic diversity on tidal flats provides a bounty for the range of bird species that are either resident or transient.

You may have a chance to see a large longbill bird capturing a fiddler crab on the tidal flat. Survival of longbill populations over the long term depends on an adequate supply of crabs, which in turn depends on the sustainability their food supplies. Other species of birds feed mostly on worms. It is likely that crabs and worms eat different diets, which are available in different habitats. Environmental heterogeneity underpins the provision of diverse food sources to different consumer species, which in turn support diverse populations of higher trophic level predators, such as shorebirds. The value of diversity in natural systems is made abundantly clear by this simple example.

Many of the shore bird species that you see on the tidal flats in Okinawa are long-distance migrators. Some fly between Siberia and Southeast Asia twice a year and need multiple resting/feeding sites along the routes they travel. Accordingly, the many countries along the flight paths have come to common agreements for the conservation of migratory bird species and are working to preserve their natural habitats.

Environmental purification by the benthos in mangrove and tidal flat ecosystems

Benthic animals in tidal flat environments collectively operate as a purification mechanism. They consume vast quantities of organic materials that would otherwise accumulate and rot through microbial degradation.

When large amounts of organic matter transported seaward by the flow of rivers accumulate on tidal flats or in the mangrove forests, the microbes get to work, releasing a pervasive stench of hydrogen sulfide, which is an indicator of dead zone formation. However, when benthic animals are abundant, they will reduce the content of organic matter through their feeding behavior. Several groups of benthic animals, such as deposit feeders (which eat fine sediments deposited on the tidal flat surface; Fig. 6 left) and suspension feeders (which filter suspended matter and plankton from water column; Fig. 6 right, Fig. 7), co-occur on tidal flats, where they collectively regulate the physicochemical environment. The feeding behavior of the benthos ensures the health of the tidal flats.

Is it possible to quantitatively calculate the purification capability of the benthos? As a first step, we estimated the food consumption rate of the fiddler crab *Uca vocans*. One individual of this species consumed 5.3 g of organic carbon and 0.46 g of total nitrogen over three summer months. One individual of the bivalve *Cyclina sinensis* (30 mm long) (Fig. 7 right) filtered out particles at a rate of 7 mg/h from a water column containing 7 mg/l of suspended matter. These are the kinds of data that are needed to evaluate the environmental purification capability of benthic animals on tidal flats.

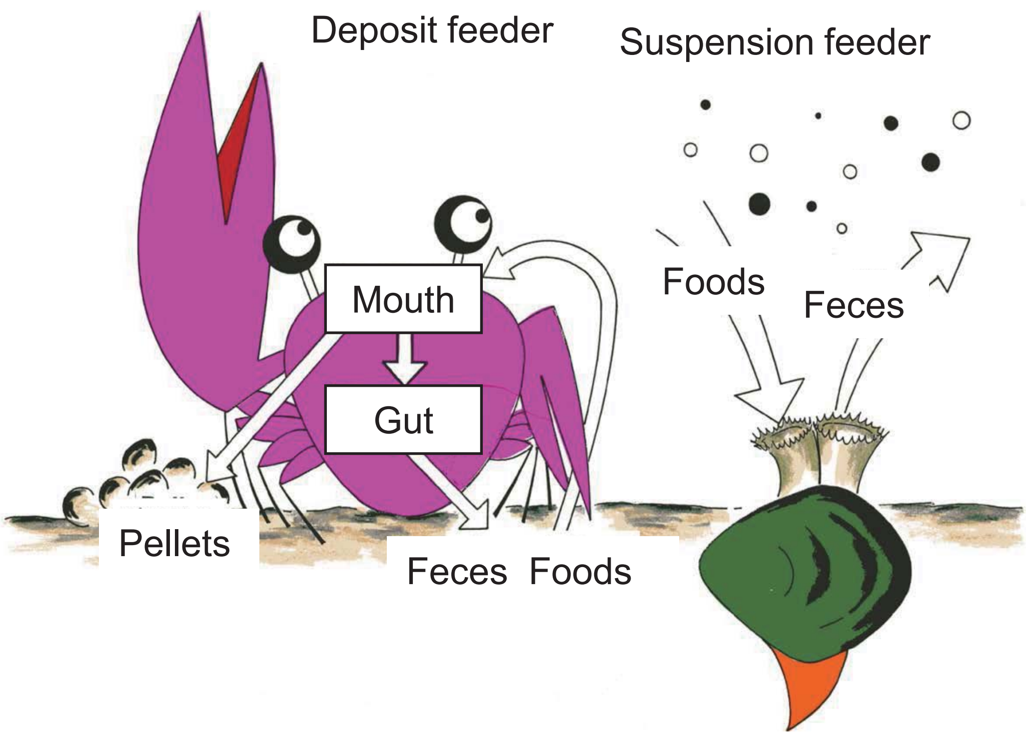

Figure 6. Feeding processes of a deposit feeder (left, fiddler crab) and a suspension feeder (right, bivalve). The fiddler crab is taking sediments from the surface of the tidal flat; a proportion of collected material is transported to the gut. The remaining portion is deposited as pellets on the tidal flat.

Figure 7. The gastropod *Batillaria zonalis* (middle) and the bivalve *Cyclina sinensis* (right) that have been transferred to beakers containing a medium containing cultured unicellular algae. The animals captured the algae by filtration of the medium, which became transparent one hour later.

Sites for human health and wellness

An extensive tidal flat extending seaward and covered by many beautiful bird species is a tranquil scene that brings peace to human observers. We derive incalculable benefits from the peace of mind that comes when we stand before beautiful natural landscapes. Even within urban landscapes, populations of wild animals have a calming effect on our minds, and surely promote human health. These wellness benefits provided by natural scenes are most abundant where there is wilderness, but not all wild landscapes are readily accessible. Getting into a mangrove forest is especially difficult, but can be done at high tide in kayaks or canoes.

Mariculture of seaweeds and shellfish gathering

Tidal flats are used as recreation sites. Many members of the public enjoy shellfish collecting, but the flats are also used for commercial seaweed mariculture. In Okinawa, the flats are suitable for culture of the green alga *Monostroma nitidum.* Farms culturing this species are distributed in the vicinity of Onna Village and around Nakagusuku Bay. The light green seaweed stands are very attractive and a special feature of the winter months between December and February (Fig. 8).

Seagrass beds develop in offshore sectors of some tidal flats. In these beds, you can observe a diversity of sea cucumbers, mollusks, crustaceans and other benthic animals. Several fish and shrimp species use the beds as nursery habitats.

Mangrove forests and tidal flats as sites for environmental education

Education is important for the learning and teaching of environmental ethics. Mangrove forests and tidal flats have often been used for environmental education. Among locations used for this purpose, the Ramsar site at Manko is especially important (Fig. 9). This region spans the Okinawan mangroves and tidal flats in the vicinity of Naha and Tomigusuku cities. Eco-tours are available for organized visits to these mangroves and/or tidal flats.

Figure 8. The green alga *Monostroma nitidum* cultured on tidal flats off Okinawa. Upper: preparation of the nursery system in September. Lower: lush green carpet of *M. nitidum* on the nets in winter.

Figure 9. Manko tidal flat located at the mouths of the Kokuba (Naha City) and Nuha (Tomigusuku City) Rivers. This important mangrove ecosystem is located within a large municipality. This area is registered in the 1999 Ramsar Convention.

One more benefit

Mangrove forests and tidal flats have often been targeted for reclamation projects to build infrastructure, mariculture farms, breakwaters, and other construction. All of these do confer benefits to the human population, but come with environmental costs because we lose the goods and services previously provided for free by the natural ecosystems that were removed. Nature cannot be rebuilt as it once was (Fig. 10).

Losses and gains of benefits through development activities are central issues considered by the new discipline of environmental economics. The consenting party for a particular development will emphasize the economic merits for humans, while conservationists will emphasize losses of free benefits that cannot be recovered. Progress in this field requires the accurate estimation of the monetary value of ecosystem goods and services.

Figure 10. Diverse types of breakwaters have been constructed recently in Okinawa. Such structures should be built in harmony with nature (Onna Village).

Friends of mangrove forests and tidal flats

Several ecosystems, such as coral reefs, seagrass beds, and sandy beaches are distributed around mangrove and tidal flat habitats. Connectivity among these ecosystems should be taken into consideration when compiling information on natural habitats and should be incorporated into management planning for the future.

Organic materials or nutrients produced in mangroves support populations of organisms on tidal flats, and also those in coral reefs. Coral reef fish visit mangroves at high tide to obtain food, and many fish species migrate between coral reefs and seagrass beds. Seagrass beds provide desirable habitats for small animals, such as crustaceans, mollusks, and ascidians. Seagrass beds are consumed directly by the dugong, a very large marine mammal. Decomposing or fragmented seagrass leaves may be carried to deeper environments where they provide food to a large number of animals. Seaweeds, which are algae, also obtain mineral nutrients derived from seagrass beds. Shallow water ecosystems in the ocean are linked in a tight network of nutrient and energy exchange.

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2—3. The Iriomote cat: a discussion

Masako Izawa and Nozomi Nakanishi

Animal species found only in the Ryukyu Archipelago

In our faunistic study of the Ryukyu Archipelago, we encountered a curious phenomenon. Some animal species occur on only one or two islands. Some species are found on single small islands and nowhere else on the planet. The Amami rabbit, which is found on Amami Oshima and Tokunoshima Islands, the Okinawa Rail (Fig. 1) on Okinawa-jima Island, and the Okinawa Woodpecker on Okinawa-jima Island are all good examples.

"Subspecies" are populations of the same species that are recognizably differentiated in appearance and have distinct geographical occurrences. Geographic separation of different populations belonging to the

Figure 1. The Okinawa Rail, a flightless bird endemic to Yanbaru (northern part of Okinawa-jima Island). Photo credit: Tatsuya Hiragi.

Figure 2. The Daito flying-fox, a subspecies of the Ryukyu flying-fox endemic to the Daito Islands. A whitish body color is characteristic of this subspecies. Photo credit: Mammal Ecology Laboratory, University of the Ryukyus.

same species promotes differentiation in structure and ecological attributes over time, leading to the formation of taxonomic units that we refer to by separate subspecific names. Consider the megabat known as the Ryukyu flying-fox. This species is divided into the following subspecies in the Ryukyu Archipelago: the Erabu flying-fox on Kuchinoerabu-jima Island, Orii's flying-fox on the Okinawa Islands, the Daito flying-fox on the Daito Islands (Fig. 2), and the Yaeyama flying-fox on the Yaeyama and Miyako Islands.

Differentiation of rare subspecies has taken place over long periods of time. The component islands of the Ryukyu Archipelago are continental; they were once connected by land bridges to the Southeast Asian continental land mass. Many animals migrated to these islands across the land bridges. The sea level has risen since this immigration occurred, forming these offshore islands. Some fauna became extinct while other taxa persisted on the islands, and we now can observe those that survived. When populations are very small, the fate of a species (extinction or persistence) is often determined by accidental (stochastic) events.

Are carnivorous animals able to survive on the islands?

Among animals with very restricted distributions, the Iriomote cat (*Prionailurus bengalensis iriomotensis*) is the most striking example: it lives only on Iriomote-jima Island (Fig. 3). Although many animal species are distributed from the Tokara Islands to the Yaeyama Islands, the Iriomote cat is the only carnivore.

How has this cat species persisted on this island? DNA analyses shows that it was segregated from a population on the continent approximately 200,000 years ago. Perhaps its insular persistence for such a long period of time is entirely fortuitous.

Figure 3. The Iriomote cat, endemic to Iriomote-jima Island. Photo credit: Mammal Ecology Laboratory, University of the Ryukyus.

Generally, carnivorous mammals cannot survive on small islands because their foraging range is large. Carnivores are positioned at the top of food chains that are supported by primary producers (plants) at the base. Energy is transferred upward from plants through the food chain in a stepwise sequence from herbivores to primary carnivores, and then to secondary carnivores, which may include cats. The efficiency of energy transfer is only approximately 10% at each step. Therefore, each carnivore must be supported by a much larger biomass of species lower in the food chain. Small islands have limited areas for the production of species low in the food chain, and that is why carnivores are absent on almost all islands in the Ryukyu Archipelago.

Diet of the Iriomote cat

There are 37 known species of wildcats (Felidae) throughout the world. Some live on continental landmasses, while others live on islands. Iriomote-jima Island is the smallest landmass that supports a wildcat species. Wildcat food supplies on this island are limited. More than half of the 37 felid species are small (about the same size as the Iriomote cat). They feed on smaller mammals such as rats, mice, and small hares, and birds. However, no native rats, mice, or hares have been found on Iriomote-jima Island. How did the cats survive through these approximately 200,000 years? To answer this question, we examined animal remains in the scat of cats on the island and discovered that they eat a diversity of animals (Fig. 4), such as flying-foxes, birds including waterhens (Fig. 5) and thrushes, reptiles such as lizards and snakes, frogs, insects, and crustaceans such as freshwater prawns. This very wide diversity of prey species distinguishes the Iriomote cat from other felids in the world.

The Iriomote cat has another unique feature: it is not afraid of water. Bathing a reluctant domestic cat is dangerous, difficult work. Almost all wild felids live in forests and generally avoid immersion in water. However, there are certain exceptions. For example, tigers immerse themselves in water to cool off during hot summers; sometimes they pursue sambar deer through standing water. The fishing cat, true to its name, is skilled in catching fish in rivers. The Iriomote cat has the same ability. As ascertained by radio-tracking surveys, the Iriomote cat moves not only through forests, but also along rivers and streams, through wetlands, and mangrove forests (Fig. 6). It can swim well, and is able to cross the Urauchi River on Iriomote-jima Island, which is the longest river in Okinawa Prefecture.

Figure 4. Prey remnants in the scat of the Iriomote cat. Photo credit: Mammal Ecology Laboratory, University of the Ryukyus.

Figure 5. The white-breasted Waterhen, one of the major prey species of the Iriomote cat. Photo credit: Tetsuya Iwasaki.

The story of the Iriomote cat

In summary, the Iriomote cat was separated from the continental population approximately 200,000 years ago and began life on this island. The island was small and did not contain any of the animals that the wildcat had previously preyed on. Under normal circumstances, the wildcat would have become extinct. However, under the humid, subtropical conditions on this island there was a diversity of species of herpetiles and insects. Many migratory birds visit the island during winter as the Ryukyu Archipelago is located on their migratory routes. The wildcat apparently adapted to these conditions and broadened its diet, but to do this it also had to enter water and swim. The cat developed ecological traits that enabled persistence and facilitated its evolution into the unique Iriomote cat that we see today. The presence of this unusual species is attributable to the biodiversity of Iriomote-jima Island.

Figure 6. The Iriomote-jima Island forest. This island has abundant water in its many rivers, streams, and wetlands. Photo credit: Shun Kobayashi.

Column 5.
Secrets of the “Irukanda” flower

Shun Kobayashi

From late February to April, after winter has ended on Okinawa-jima Island and the days grow warmer, purple flowers with a strong, unique odor come into bloom. These are the flowers of *Mucuna macrocarpa* (Japanese name: Irukanda or Ujirukanda), which is a woody vine in the pea family. The inflorescence clusters of Irukanda are over 30 cm long and hang down from thick vines that sometimes exceed 10 cm in diameter.

The flower of Irukanda has a somewhat unusual morphology. Each flower has stamens and a pistil enclosed by a pair of tough petals (carinas) that are pale purple in color (Fig. 1, left). When the flower is in this configuration, pollen that has already been released from the stamens is not transferred to other flowers and the pistil is unable to receive pollen because both pollen and pistil are trapped inside the tightly closed carina. A flower like this will wither without producing seeds.

However, when the Ryukyu flying-fox (a megabat) visits the flower and feeds on nectar (Fig. 2), the carinas are opened, exposing the stamens and the pistil (Fig. 1, right). Pollen grains from another flower that are attached to the flying-fox are introduced and spread over the pistil. Why does the carina open like this when it was previously locked shut? The Irukanda flower has a pale green petal (banner) with a pair of hooks at its base. These hooks function to “plug” to the carina, preventing a potentially large amount of sweet nectar from leaking out from the base of the flower. The flying-fox pushes the banner upward, releasing the hooks to feed on the nectar within the calyx. In addition to preventing nectar leakage, these hooks prevent carinas from opening. When the flying-fox lifts the banner, the carinas open, exposing the stamens and pistil.

Other insects and birds also visit Irukanda flowers to feed on their nectar, but only the flying-fox on Okinawa-jima Island is able to open the flower. The flying-fox is an indispensable partner for Irukanda plants. The unique odor of the Irukanda flower may be a special attractant that brings the flying-fox to the flowers, thereby ensuring pollination.

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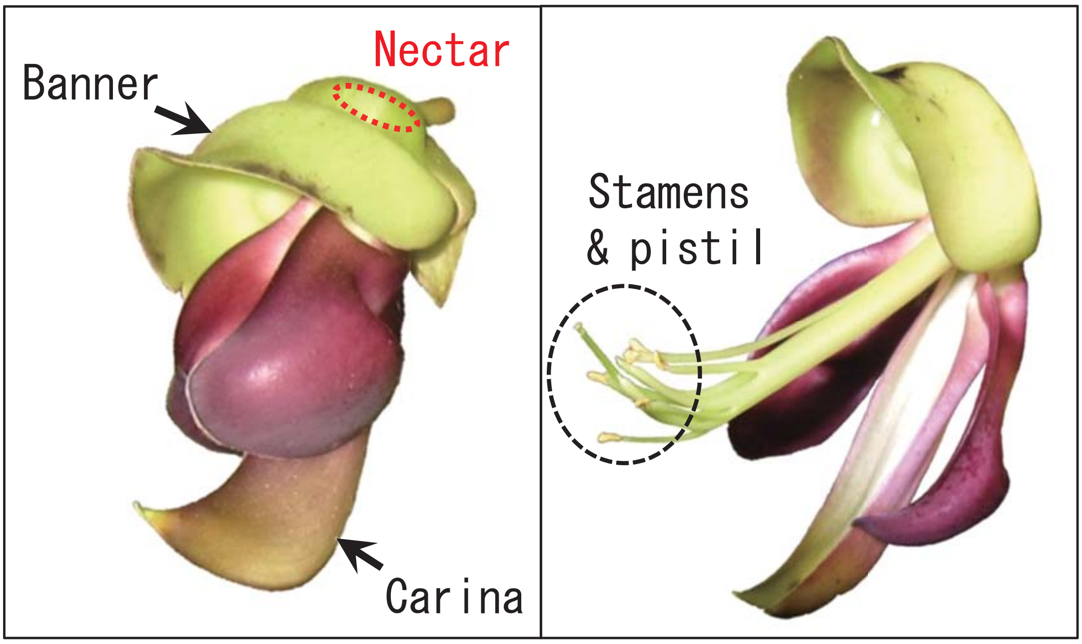

Figure 1. *Mucuna macrocarpa* flower. left: before opening, right: after opening.

Figure 2. A flying-fox visiting a *Mucuna macrocarpa* flower to feed on nectar.

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2—4. Diversity of butterflies and environmental issues in the Ryukyu Archipelago

Joji Otaki and Wataru Taira

Diversity of butterflies in the Ryukyu Archipelago

In Okinawan dialect, butterflies are affectionately called "*haberu*" or "*habiru*", indicating that they are popular insects on the islands. An old article in a journal published in the Meiji Era by the Zoological Society of Japan informs us that preparation of butterfly specimens for display was a popular activity among merchants in Naha. Merchants were interested in butterflies in the Ryukyu Archipelago as marketable products, because many of the species in Okinawa are not found on Japan's main islands and had rarity value for most mainland Japanese. Butterfly species in the Ryukyu Archipelago are indeed different from those on Japan's mainland. What makes them unique?

Records list 182 species of butterflies in the Ryukyu Archipelago (from the Yaeyama Islands to the south of the Tokara Islands). This number is about 56% of the 323 species listed for the whole country. High species richness (and therefore high ecological diversity) is one of the features of the Ryukyuan butterflies. Furthermore, the species composition of the Ryukyu Archipelago is unique and likely a product of unique geographical conditions. Three important terms underpin this uniqueness: "stray butterflies", "northern range-margin species", and "endemic species". We will explain each of these with some examples.

Stray butterflies

Many of the butterflies of the islands can be called strays. These insects are not regular residents. They are occasionally swept into the archipelago from the south (e.g., from Taiwan or the Philippines) by typhoons and seasonal winds. Thus, the strays tend to be southern species.

The strays in the Ryukyu Archipelago include many danaid butterflies, such as the Swinhoe's chocolate tiger (*Parantica swinhoei*) and the Malayan crow (*Euploea camaralzeman*) (Figs. 1, 2). In total, more than 50 stray butterfly species have been identified in the Ryukyu Archipelago. The islands are located at the southern end of the long Japanese archipelago where they pick up wind-blown species from more tropical regions. Thus, the geographical location of the Ryukyu Archipelago plays a key role in determining the unique butterfly species composition on the islands.

Northern range-margin species

Some of the strays may occasionally lay eggs and propagate on the Ryukyu Archipelago. Species that do this are termed accidental butterflies on the islands. Accidental butterflies include the brown pansy (*Junonia hedonia*), the plains cupid (*Chilades pandava*), and the tiny grass blue (*Zizula hylax*) (Fig. 3). Some may repeatedly propagate in summer months, only to die out during the following winter periods. Others, how-

Figure 1. The common tiger (*Danaus genutia*) (left) and Swinhoe's chocolate tiger (*Parantica swinhoei*) (right) drinking nectar. May 2010; Ishigaki-jima Island. Photo credit: Akino Miyagi.

Figure 2. The Malayan crow (*Euploea camaralzeman*) drinking nectar. May 2013; Ishigaki-jima Island. Photo credit: Akino Miyagi.

Figure 3. Copulating pair of the tiny grass blue (*Zizula hylax*), the smallest butterfly in Japan (female, left; male, right). November 2013; Hamahiga-jima Island. Photo credit: Akino Miyagi.

Figure 4. Copulating pair of the crow eggfly (*Hypolimnas anomala*) (top, female; bottom, male). November 2009; Iriomote-jima Island. Photo credit: Akino Miyagi.

ever, have persisted over time, thereby expanding their distribution ranges. Protracted persistence requires adaptation to the different climate regime on the islands. Temperature conditions are especially important. Most stray southern butterflies are unable to endure the cold of winter. The much colder winters on Kyushu, one of Japan's main islands, prevent invasion by southern strays.

The Ryukyu Archipelago is the northern range margin for many southern butterflies, which are termed northern range-margin species on the islands. This group includes the common rose (*Pachliopta aristolochiae*), the common Mormon (*Papilio polytes*), the paper kite (*Idea leuconoe*), and the banana skipper (*Erionota torus*). Almost half of the butterflies found on the Ryukyu Archipelago are categorized as northern range-margin species.

The northern range margins of the peacock pansy (*Junonia almana*) and the blue pansy (*J. orithya*) were previously located within the Ryukyu Archipelago, but these species have gradually moved north, and they are now found on Kyushu and even Honshu. Many more species are similarly expanding their distributions northward, a phenomenon that may be attributable to a rise in temperature caused by global climate change.

Accidental butterflies that reach the Ryukyu Archipelago from more southern areas, such as the crow eggfly (*Hypolimnas anomala*) (Fig. 4) and the plains cupid, have begun to overwinter and propagate during the summers in recent years. If this trend continues, these species may become residents on the islands and perhaps expand their ranges even further northward.

Endemic species

The last key category is the endemic species. As mentioned, many butterflies on the islands are of southern origin. However, there are some species called endemics that uniquely evolved on single islands or in small isolated regions. Thus, an endemic is a species that is distributed across only a limited geographical range. The Asahina's skipper* (*Ochlodes asahinai*) (Fig. 5), the Yaeyama four-ring* (*Ypthima yayeyamana*), and the Masaki's three-ring* (*Y. masakii*) (Fig.6) are endemic species that inhabit only the Ishigaki-jima and Iriomote-jima Islands. The Ryukyu three-ring* (*Y. riukiuana*) and the Okinawa peacock (*Papilio okinawensis*) are endemic to the Okinawa Islands, and the Ryukyu bushbrown* (*Mycalesis madjicosa*) is endemic to the Ryukyu Archipelago. These butterflies are of special value, because they are found in no locations outside of the Ryukyu Archipelago. The evolution of these species in the Ryukyu Archipelago may have been inherently driven by the geographic history of these islands. These endemics are key species in studies of butterfly evolution and the geographical history of the islands.

In summary, the Ryukyu Archipelago is rich in stray butterflies, northern range-margin species, and endemics, which in combination contribute to the magnificent butterfly fauna of the islands. The archipelago hosts precious environments that are unique both nationally and globally.

Ryukyuan butterflies and environmental issues

Despite the richness of butterfly species in Okinawa, many of them are now endangered. The Red Data Book issued by The Japan Ministry of the Environment lists the Asahina's skipper* and the dark grass blue (*Zizeeria karsandra*) as "vulnerable"; and the great Nawab (*Polyura eudamippus weismanni*) (Fig. 7), the orange oakleaf (*Kallima inachus eucerca*), the bamboo tree brown (*Lethe Europa pavida*), the Masaki's three-ring*, the Ryukyu three-ring*, the Yaeyama four-ring*, the green flash (*Artipe eryx okinawana*), and the forest quaker (*Pithecops corvus ryukyuensis*) (Fig. 8) as "near threatened".

Survival of these precious species requires the protection of rich natural environments. However, the natural environment of the islands has now been lost over large areas by urban development and by the construction of military bases.

The forest quaker is one of the small butterfly species whose habitat has been destroyed by human activities. Across the Japan, the forest quaker is found only on Iriomote-jima Island and Okinawa-jima Island.

Figure 5. The Asahiha's skipper (*Ochlodes asahinai*) immediately after eclosion. May 2011; Ishigaki-jima Island. Photo credit: Akino Miyagi.

Figure 6. Copulating pair of the Masaki's three-ring (*Ypthima masakii*). October 2010; Ishigaki-jima Island. Photo credit: Akino Miyagi.

Figure 7. The great Nawab (*Polyura eudamippus*). June 2009; Okinawa-jima Island. Photo credit: Akino Miyagi.

Figure 8. The forest quaker (*Pithecops corvus*). October 2011; Takae, Higashi Village. Photo credit: Akino Miyagi.

Its habitat on Okinawa-jima Island is limited to small northern areas. Recently, a relatively large population of the species was discovered in Takae (Higashi Village). Such an abundance is very rare on Okinawa-jima Island, but may not persist because of the destructive effects of military helicopter landing pads for V-22 Osprey aircraft training in Takae. Even worse, additional helipads are under construction. The hot downdraft from the Osprey aircraft dries out forest vegetation and blasts the butterflies from their habitats. Conservation projects have begun to save the forest of Takae, which is home to many important species. However, the general public is largely unaware of the ecological significance of the forest. Readers of this book may be inspired to consider more than just the beauty of butterfly wings and expand their horizons of interest to include the evolutionary history and ecological importance of these insects.

The Ryukyuan people have loved butterflies through the ages. A poet wrote a "*Ryuka*", a traditional short poem, that captures the connection of the people to these beautiful insects: "*Tubitachuru habiru maziyumati thirira wanuya hananumutu shiranu amunu thiriti ujindhi*" ("Wait, that butterfly taking flight. I do not know where the flower is. Please take me with you."). The poet asks the butterfly to guide him to the flower, a metaphor for his lover. To this day, butterflies might teach us what is important, what to protect, and what to love.

(English names followed by asterisks are new common names coined by the authors through study of existing Japanese names and Latin binomials.)

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2—5. Flora of the subtropical Ryukyu Archipelago

Tetsuo Denda

People are often under the impression that the Ryukyu Archipelago are a southern paradise full of flowers. But which flower is symbolic of Okinawa? Most people would select a garden plant, perhaps *Hibiscus*, *Bougainvillea*, or *Plumeria*. Beautiful garden flowers surely catch the public's eye, but please turn your eyes now to the wild indigenous plants that have grown in the Ryukyu Archipelago for thousands of years. Although wild flowers are often less attractive than garden plants, their uniqueness is sure to arouse your curiosity.

Champuru flora

The islands of the Ryukyu Archipelago are sometimes referred to as "the Galapagos of the East." The unique ecosystems and high animal biodiversity in the archipelago are similar to those of the Galapagos Islands, which are known as the "living laboratory of evolution." In addition to the rich fauna, the Ryukyu Archipelago have a diverse flora. About 1600 land plant species other than bryophytes are distributed from Amami Oshima Island southward. The richness of the flora becomes clear when we calculate the number of plant species per unit area in the Ryukyu Archipelago; the value obtained is approximately 45 times higher than from Kyushu northwards.

The subtropics lie in a transitional region between the tropical and cool temperate zones. Worldwide, arid areas, such as deserts and savannas, dominate most of the subtropical regions. In contrast, the Ryukyu Archipelago, which lies parallel to the eastern margin of the Chinese continent, has a high annual rainfall provided by the monsoons and typhoons that blow over the islands. This humidity, and the warmth brought to the Ryukyu Archipelago by the Kuroshio Current, account for the rich flora in this area. Both tropical and temperate species can be found in the rich flora. In Okinawa Prefecture, there is a popular dish called "Champuru," which means "mixed up" or "scrambled." The flora of the Ryukyu Archipelago can be described as a "Champuru flora," in which tropical and temperate plants are intermingled.

Exotic plants

Many tropical plants have eccentric appearances and/or beautiful coloration that attract human attention. One example is a fig tree, the Chinese banyan (*Ficus microcarpa*). A traditional tale from Okinawa Prefecture tells of a spirit known as "Kijimuna" who lives in an old Chinese banyan tree (Fig. 1). Although this fig tree is familiar to residents of Okinawa, I suspect you are not aware that the Chinese banyan and some other fig species, such as the Japanese sea fig (*F. superba* var. *japonica*) and *F. virgata*, are also called "strangler figs." Birds and fruit bat eat the fruits of strangler figs and distribute their seeds onto the branches and trunks of other trees. The seeds germinate where they are lodged in the host tree bark and develop into epiphytic seedlings that grow multiple aerial roots toward the ground. These fig roots surround the hosts and gradually

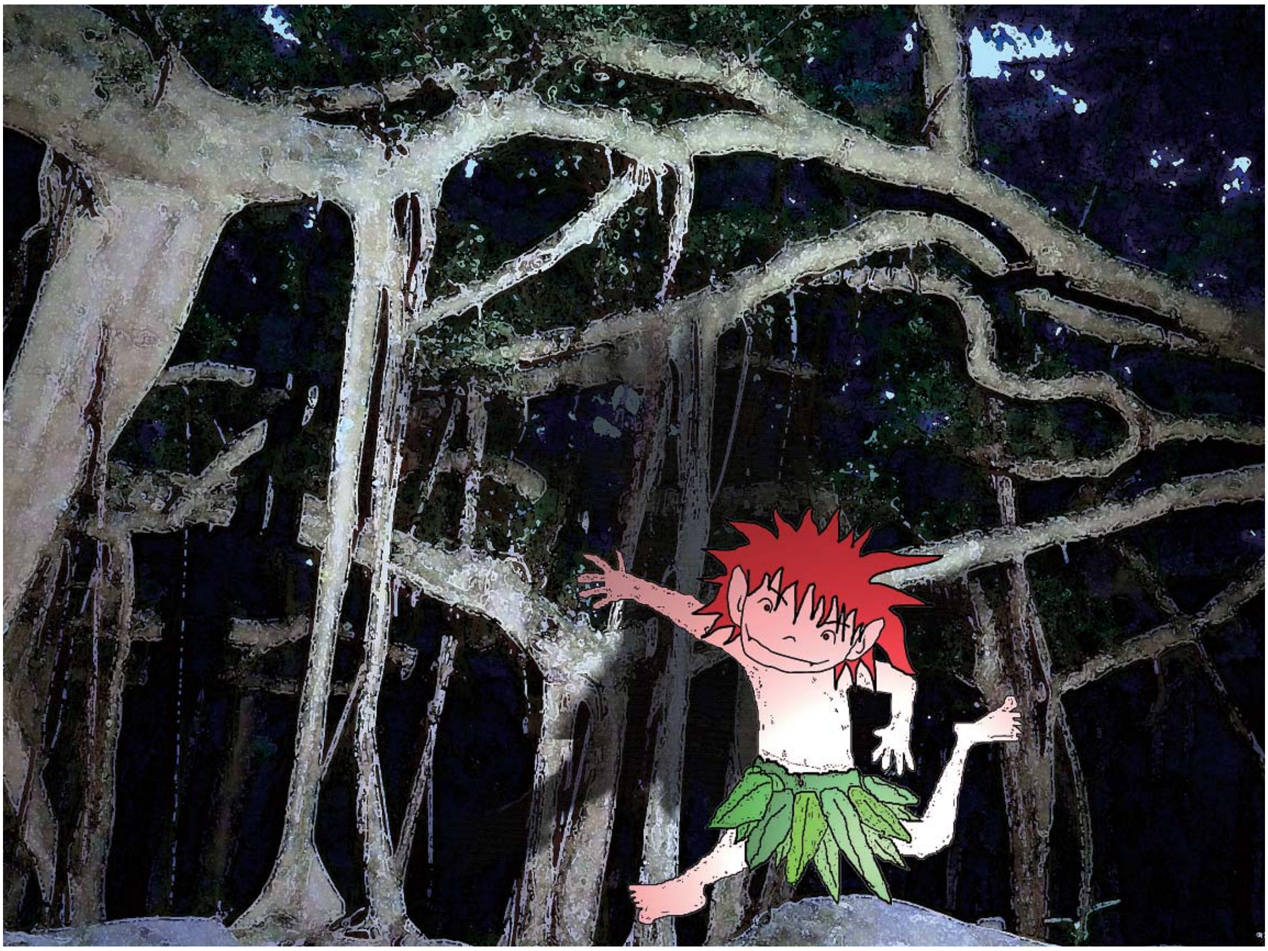

Figure 1. “Kijimuna” is a mischievous spirit who appears in a traditional tale from Okinawa Prefecture. Kijimuna is said to live in old Chinese banyan (*Ficus microcarpa*) trees.

strangle them to death (Fig. 2). This is a gruesome but essential way of life! Epiphytism in the high canopy of host trees is an adaptation for gaining ready access to incoming sunlight, which is rapidly absorbed by the vegetation; the forest floor is in deep shade, even when the sun is highest.

Another fig, the common red-stem fig (*F. variegata*), is widely distributed in tropical regions. Ishigaki-jima Island is at the northern limit of its range. Curiously, fruits of common red-stem fig grow to develop directly on the trunk (Fig. 3), a phenomenon termed cauliflory. Cauliflory is common in tropical trees. People who live in temperate regions may not be aware of this.

Tropical plants in the Ryukyu Archipelago have migrated northward from southern regions in diverse ways. The northward flow of the Kuroshio Current brings both warm water and the seeds of tropical plants to regions north of the Tropic of Cancer. The powder-puff tree (*Barringtonia racemosa*) is a sea-dispersed plant. It is a semi-mangrove (salt-tolerant woody plant growing in swampy habitats in the lee of mangrove forests) species found throughout the tropical regions of Southeast Asia, reaching its northern limit in the central Ryukyu Archipelago. The flowers open on summer nights to reveal a sparkling spectacle of pink, green and white hues (Fig. 4).

Figure 2. A *Ficus virgata* plant wrapped around the trunk of common garcinia (*Garcinia subelliptica*) (upper image). The white portion is the root of the strangler fig. The host tree is eventually strangled to death and rots, leaving an upright strangler fig trunk wrapped around a hollow core. The lower image shows the interior of a hollow trunk seen from below.

Figure 3. Fruits of *Ficus variegata* (upper image) and *F. superba* var. *japonica* (lower image) growing directly on tree trunks (cauliflory).

Plants limited to the Ryukyu Archipelago

A second general feature of the Ryukyu flora is the richness of endemic plants, those that occur within limited geographic regions and nowhere else. Continental islands, which were once connected to neighboring continental landmasses, usually have few endemics. An extreme example is England, which is part of the United Kingdom. This continental island has about the same land area as Japan, but no endemic plants. Although most islands of the Ryukyu Archipelago are continental islands, they are home to more than 130 endemic plant species. These include many temperate plants, some of which have differentiated into endemics by adapting to the subtropical environment of the archipelago.

Solenogyne mikadoi, an endemic belonging to the daisy family (Compositae), is distributed among four major islands in the Ryukyu Archipelago. This endangered species grows on streambed rock surfaces exposed to sunlight. *S. mikadoi* is so small that its flowers are easily overlooked, even in full bloom (Fig. 5).

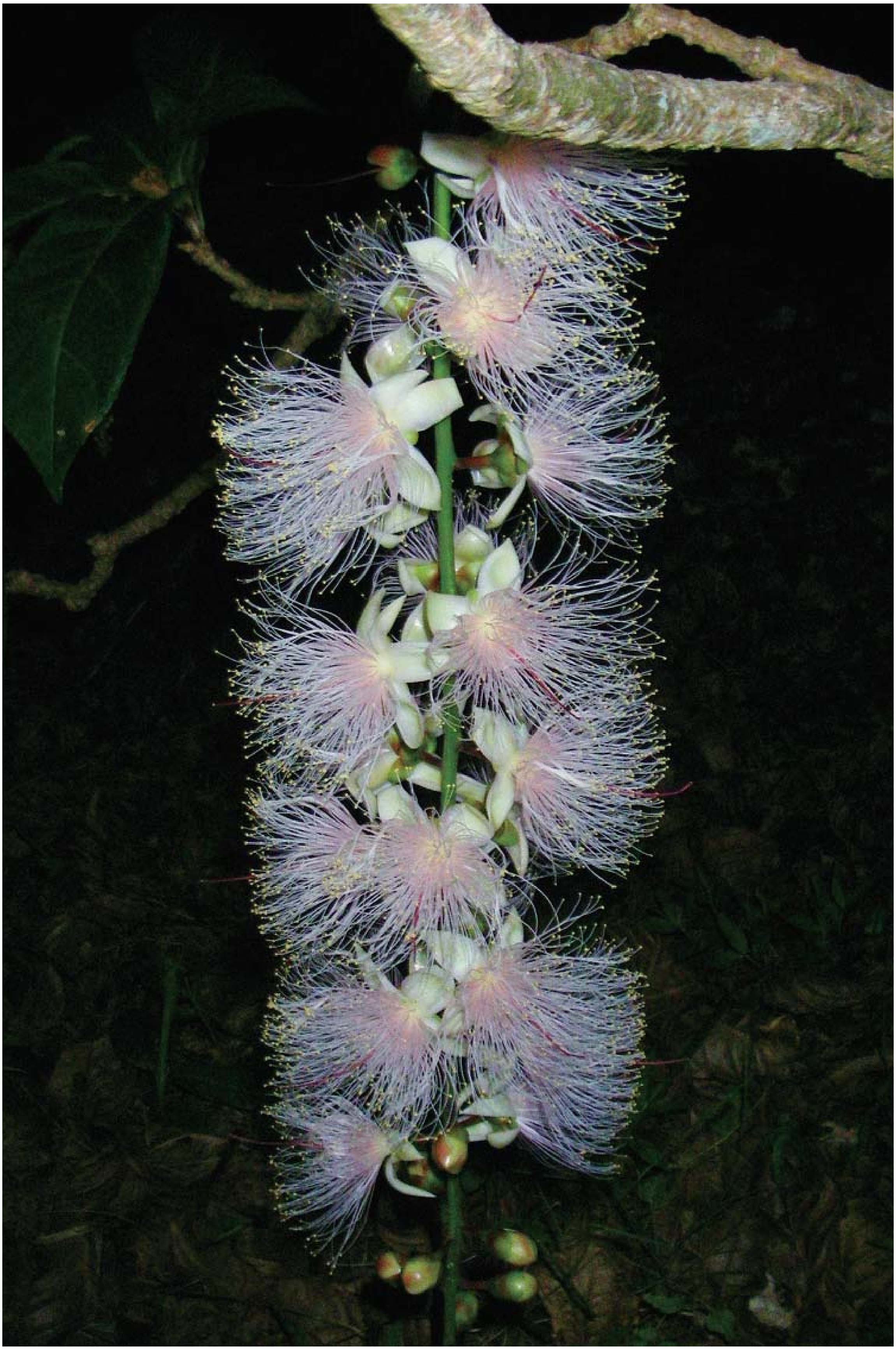

Figure 4. Attractive flowers of the powder-puff tree blooming on a summer night. The Japanese name “Sagari-bana” refers to the flowers, which hang in long racemes. This tree is much loved by the people of Okinawa and often planted in public gardens for ornamental purposes.

Figure 5. Growth of *Solenogyne mikadoi* (upper image). The Japanese name "Koke-Tanpopo" means "dandelion as small as moss"; this plant is very diminutive and unremarkable. Habitat of *S. mikadoi* (lower image). This species is a rheophyte that grows attached to rocks in riverbeds. When the river flows, *S. mikadoi* is exposed to fast-moving currents.

Figure 6. *Ixeris japonica* (upper) and *I. repens* (lower) on sandy beaches in the Ryukyu Archipelago. This meeting of species on the beach was a first step in a speciation mechanism that included hybridization and gene transfer. Although these two species co-occur, there is a fierce, ongoing battle for survival between them.

The species has only three congeners and all are endemic to the temperate region of southeastern Australia. The Australian *Solenogyne* species are larger than *S. mikadoi* and preferentially grow in more open habitats, such as sparse *Eucalyptus* woods, pastures, and park lawns. A recent study has shown that the ancestors of *S. mikadoi* migrated across approximately 5000 km of ocean from Australia to the Ryukyu Archipelago. The warm climate of these subtropical islands of the Ryukyu Archipelago may have exceeded the thermal tolerance of the ancestral form, which found refuge in cool riparian habitats on the islands. However, these habitats are periodically subjected to the physical forces imposed by strongly flowing currents. Adoption of a dwarf form by *S. mikadoi* may have been an adaptation to the forces imposed by flowing waters.

Varied lives of endemic plants

Endemics have diverse origins. Many people enjoy beach parties and/or marine sports on the Ryukyu Archipelago. You may have noticed yellow dandelion-like flowers in the white sand while enjoying your aquatic leisure time. These are the flowers of "weak *Ixeris*" (*Ixeris japonica*). In north from Kyushu, this plant is a common ruderal weed that usually grows on the margins of rice fields or along stream banks. In the Ryukyu Archipelago, *I. japonica* often grows on sandy beaches and produces hybrids with its congener *I. repens* (Fig. 6). The hybrid is recognized as a separate species, *I. nakazonei*, which is thought to be endemic to the Ryukyu Archipelago. It seems *I. japonica* and *I. repens* fell in love on a subtropical beach and produced hybrid babies. This romantic tale has a not-so-romantic ending. *I. japonica* acquires DNA indirectly from *I. repens* through repeated crossing with *I. nakazonei*. In other words, *I. japonica* has adapted to harsh beach environments by robbing *I. repens* (a typical beach plant highly adapted to the maritime environment) of its DNA!

Ongoing evolution in the archipelago

A fierce battle between *I. japonica* and *I. repens* continues at ground level on the sandy beach. Thus plant evolution is not just ancient history, it is an ongoing process in the Ryukyu Archipelago, and it is imperative that we maintain the natural environment of the islands as a stage for such evolutionary developments.

Scutellaria rubropunctata, a herb in the mint family, is endemic to the Ryukyu Archipelago (Fig. 7). This beautiful species is not especially rare. Indeed, it is common in a variety of locations, including the northern part of Okinawa-jima Island. Although the species also grows in the southern part of Okinawa-jima Island, its numbers have declined over the past decade. Some populations have entirely disappeared because of environmental degradation caused by human activities.

Scutellaria rubropunctata has morphological and ecological variations that may reflect adaptation to specific environments within the islands. Many interesting evolutionary phenomena are to be discovered, even in common species like *S. rubropunctata*. Islands are sometimes referred to as the laboratories of evolution. We will continue in our efforts to expand understanding of plant evolution, an ongoing phenomenon in the Ryukyu Archipelago. I sincerely hope that human activities will not bring an end to the ancient and unique evolutionary developments that continue to make these islands a special place on our planet.

Figure 7. *Scutellaria rubropunctata* is endemic to islands in the northern and central Ryukyu Archipelago. Flower color varies among populations. This image shows lilac flowers on Amami Oshima Island.

Column 6.
Diversity of orchids in the Ryukyu Archipelago

Masatsugu Yokota

The orchid family, Orchidaceae, familiar to us for its beautiful flowers, is a member of the monocotyledons and includes as many as about 700 genera and 25,000 species distributed all over the world, excluding desert and glacial areas. Flowering plants (angiosperms) consist of about 700 families and 210,000 species, of which more than one tenth are orchids, being the largest and most diverse family in the plant world.

The Ryukyu Archipelago are located between East Asia and Southeast Asia, and are habitats for both temperate and tropical plants and animals. Where did the orchids of the Ryukyu Archipelago originate?

In Japan, a total of 88 genera and about 300 species of orchids grow in the wild and, of those, 66 genera and about 165 species are hitherto recorded from the Ryukyu Archipelago. As the Ryukyu Archipelago represent only 1% of the area of Japan, many orchid species are concentrated in the Ryukyu Archipelago. Based on calculations of dissimilarity of orchid flora between the island of Kyushu, the 11 large islands of the Ryukyu Archipelago, and Taiwan (Fig. 1), it can be shown that the three islands of the northern Ryukyu Archipelago, i.e., Yakushima, Tanegashima and Nakanoshima, are characterized by many species common to Kyushu Island, while the four islands of the central Ryukyu Archipelago, i.e., Amami Oshima, Tokunoshima, Okinawa-jima and Kume-jima, are more similar to Kyushu and the northern Ryukyu Archipelago than to the southern Ryukyu Archipelago and Taiwan. Finally, the four islands of the southern Ryukyu Archipelago, i.e., Miyako-jima, Ishigaki-jima, Iriomote-jima and Yonaguni-jima, share many orchids with Taiwan. The Tokara Strait, situated between Nakanoshima Island and Amami Oshima Island, is known as the Watase Line, and is the borderline for distributions of many plants and animals between East Asia and Southeast Asia. However, the Watase Line is not important for orchid species of the Ryukyu Archipelago. The Kerama Gap between Okinawa-jima Island and Miyako-jima Island is known as the Hachisuka Line, and is the borderline for distributions of several plants and animals. The Tokara Strait and the Kerama Gap both include deep sea, which may have limited the expansion ranges of plant and animal species that could spread only via a land bridge and not over deep sea areas. However, as orchid seeds are very small and can be dispersed by wind, the deep seas of the Tokara Strait and the Kerama Gap may not have been barriers to the dispersal of orchid seeds across the sea. Thus, the differences in environmental factors, such as temperature, between the northern, central, and southern Ryukyu Archipelago may be more important for the distribution of orchid species.

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The diverse orchid flora of the Ryukyu Archipelago, characterized by both temperate and tropical species (Fig. 2), has been threatened by human activities involving collection and habitat loss. As many as 90% of species of orchids in the Ryukyu Archipelago are endangered by the over-collection of these beautiful flowers. As the islands of the Ryukyu Archipelago are indispensable for humans and wildlife, we must conserve habitats for the survival of orchids and other wildlife.

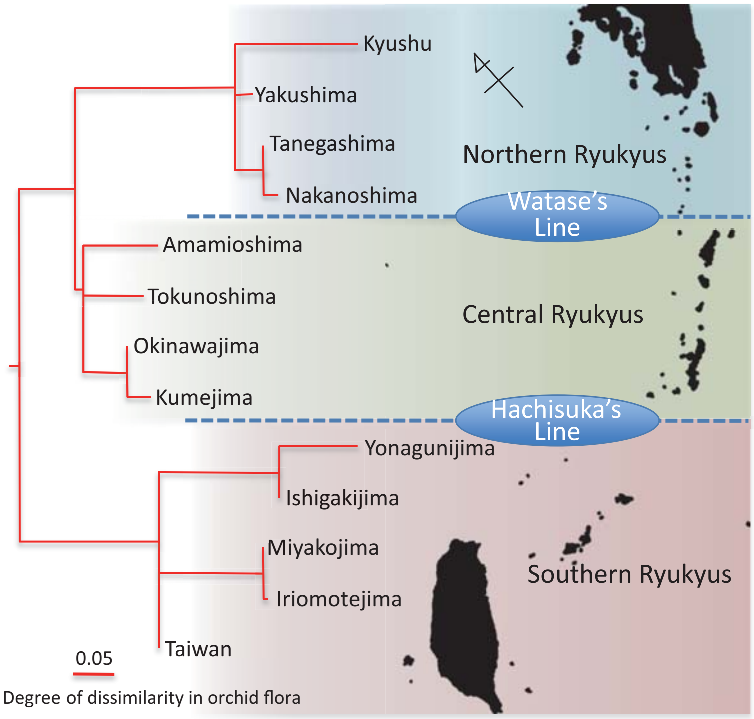

Figure 1. The relationship between 13 islands - Kyushu, the Ryukyu Archipelago, and Taiwan, based on the dissimilarity of orchid flora. Modified from Yokota (2013).

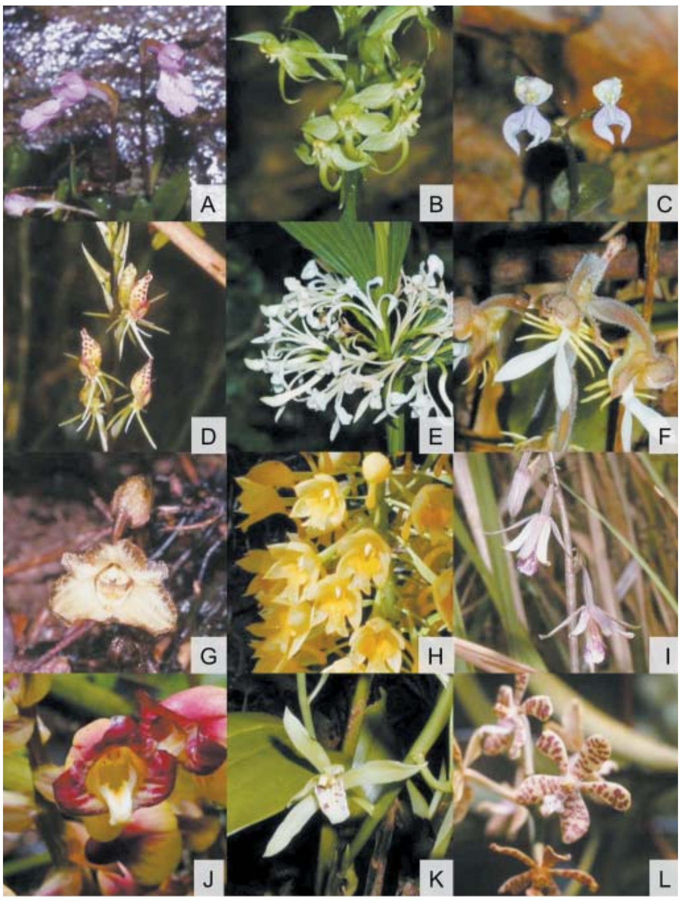

Figure 2. Wild orchids of the central and southern Ryukyu Archipelago. A: *Amitostigma lepidum.* B: *Habenaria stenopetala.* C: *Disperis neilgherrensis.* D: *Cryptostylis taiwaniana.* E: *Corymborkis veratrifolia.* F: *Anoectochilus formosanus.* G: *Gastrodia shimizuana.* H: *Calanthe formosana.* I: *Eulophia taiwanensis.* J: *Acanthephippium pictum.* K: *Cymbidium javanicum* var. *aspidistrifolium.* L: *Staurochilus lutchuensis.*

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2—6. Unique lives of "terrestrial algae"

Shoichiro Suda, Akihiro Oba and Shinpei Sumimoto

Most of the algal biomass in coastal areas is accreted in the thalli of macroscopic seaweeds. Other algae occur in the plankton and in the microbenthos. Freshwaters also harbor large populations of attached and planktonic algae. Here, we focus on terrestrial algae growing on urban walls, tree trunks, rocks and highway guardrails.

What are the conditions of life for terrestrial algae? Table 1 compares terrestrial and aquatic environments. Water supply is limited on land, and mineral nutrients are available to algae only when the cells are immersed in a sufficiently large volume of water. Atmospheric temperature and humidity change frequently. However, CO_2 and light are in abundant supply in subaerial environments, which is not always the case in large water bodies. Terrestrial environments can be severe; e.g., the surface temperature of a highway guardrail habitat often exceeds 50°C (Fig. 1), and can sometimes reach 70°C on summer days. Such conditions prevent algal growth, but the cells persist and begin dividing when temperatures drop and water is made available by precipitation or condensation. Algae are photosynthetic organisms like higher plants; both require light and CO_2, which are abundant in the atmosphere, but water is often scarce in terrestrial habitats. When water is available, terrestrial conditions support higher photosynthetic rates than aquatic environments, although photoinhibition is more prevalent on land. Furthermore, terrestrial organisms are exposed to more damaging ultraviolet (UV) radiation than aquatic forms, and subaerial conditions are more variable than those in marine and freshwater habitats.

The ancestors of terrestrial algae were aquatic. Why did they migrate to a more hostile environment? A possible explanation lies in the enhanced availability of CO_2 in our atmosphere. This gas diffuses ten thousand times faster in air than in water. Plants rely on passive diffusion to supply CO_2 for photosynthesis. Hence, plants living in the atmosphere would have photosynthetic advantages. Fossil records indicate that

Table 1. Differences in algal growth conditions between aquatic and terrestrial environments.

	Aquatic environment	Terrestrial environment
Water	Sufficient	Insufficient (supplied only by dew or rain)
Nutrients	Always available	Only available in aqueous solution
Temperature range	Small	Large
Desiccation	None	Frequent
CO_2 availability	Low	High
Light availability	Low	High

Figure 1. Hot highway guardrail under strong summer solar radiation. The temperature measured on the rail was 52.6°C.

photosynthetic cyanobacteria migrated to terrestrial environments 2.6 billion years ago. These organisms and their algal descendants (cyanobacteria were the ancestors of all algae and higher plant life) are quite cryptic in terrestrial environments, but they can be found even in the most extreme habitats.

Terrestrial cyanobacteria

Cyanobacteria are typical components of the terrestrial algal flora found growing on walls in human urban environments, such as the limestone block walls of Okinawa, which are stained black by cyanobacterial growth (Fig. 2). The black stains are darker and more widely spread in wet sections of limestone than in drier areas. The human populace pays little attention to these stains, which are commonly regarded as deposits from automobile exhaust fumes, colonizing fungi, or simply as dirt. However, cyanobacterial colonies are the major components of the stains. The colonies comprise microscopic filaments with thick sheaths that have brown or reddish hues (Fig. 3). These colored sheaths have a UV-absorbing compound that protects the cells from short-wave solar radiation. When the filaments are cultivated in laboratory with little or no UV radiation, the sheaths are transparent. This UV-absorbing compound is called scytonemin.

Ancestors of terrestrial cyanobacteria migrated from aquatic environments before the development of an atmospheric ozone layer. Without this high-altitude filter, the surface of the land was subjected to much higher levels of UV radiation than those experienced today. UV protection was essential and was provided by a layer of scytonemin in the sheath. This sunscreen is still formed by modern day cyanobacteria growing in terrestrial environments. In addition to sunscreen, these microbes produce several potentially useful anti-cancer agents. Cyanobacteria are much more than just stains on the wall.

Figure 2. A stone monument from which terrestrial cyanobacteria (arrow) were isolated. The black stains yielded diverse forms of terrestrial cyanobacteria.

Figure 3. Cyanobacterial cells found growing in a black stain. Filamentous and unicellular forms are present. The brown and purple colored sheaths provide UV protection to the cytoplasm.

Terrestrial green algae

Green algae are also important components of the terrestrial algal flora. Whereas terrestrial cyanobacteria tend to have blackish hues, green algae are often dull green and mistaken for mosses. They are found in many subaerial habitats. Here we describe those growing on highway guardrails (Fig. 4), which become very hot on summer days. The rails are often in full sunlight and the green algae growing there tend to be colored dark green, orange, dull green or black, and they are encrusted with dust or sand.

Figure 4. Terrestrial green algae growing on the surface of a highway guardrail. The cells form orange and dull green sections.

New guardrails are painted white and their surfaces are smooth. Terrestrial green algae are rarely found on them. The algae are more common on rails that have weathered for least several years in a process that provides rough surfaces for colonization. Even after weathering, surface water retention is minimal. Rain and condensation formed by falling nighttime temperatures provide most of the moisture for the colonies. The algae become dormant to survive desiccating conditions. They revive when rewetted.

Algae on guardrails thrive when wet. We would therefore expect them to grow best in regular aqueous culture medium, but their performance is no better or worse than that of aquatic species. There are two possible explanations for this unexpected outcome. It is possible that the aquatic ancestors of modern terrestrial algae grew more slowly than other species, but were better able to adapt to subaerial conditions. Alternatively, these ancestors may have had high CO_2 requirements for photosynthesis and growth. These considerations are speculative and should be subjected to experimental analyses that also test other potential explanations.

In conclusion, most algae are aquatic, but some occur in terrestrial habitats, where they are often diminutive and misidentified as either stains or other organisms.

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2—7. Solar-powered invertebrates on coral reefs

Euichi Hirose

Plants are able to use light energy to photosynthetically produce energy-rich sugars from inorganic CO_2, but animals cannot. Nevertheless, some animals have symbiotic relationships with photosynthetic algae and cyanobacteria, which transfer some of the products of their metabolism to their partners. Photosynthetic symbionts occur in diverse invertebrates, especially in tropical and subtropical waters. Scleractinian corals and foraminiferans are dealt with in other sections, so this section deals with “photosymbiosis” in some of the other invertebrates commonly found off Okinawa.

Cyanobacteriosponges

Many coral reef sponges have symbiotic relationships with cyanobacteria. *Terpios hoshinota* is a black sponge that appears to smother and kill live corals (Fig. 1). Spherical cyanobacterial cells are crowded in the tissues of this sponge species, which has yielded many bioactive compounds, some of which are probably produced by these symbiotic microbes. Occasional local outbreaks of this sponge seriously damage coral

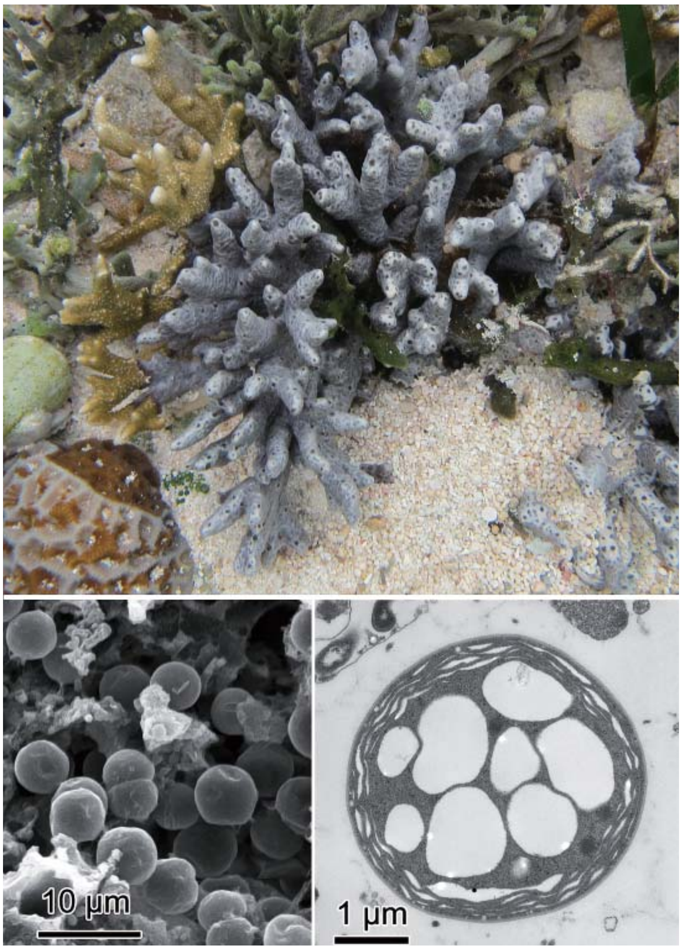

Figure 1. Upper: *Terpios hoshinota* covering coral skeletons (back reef off Bise Point, Okinawa-jima Island). Lower left: a section of *T. hoshinota* (viewed by scanning electron microscopy). The spherical cells are cyanobacterial symbionts. Lower right: cyanobacterial cells in the tissue of *T. hoshinota* (viewed by transmission electron microscopy).

reefs, although the pest disappears several years later. *T. hoshinota* is a considerable threat to coral reefs, but the outbreak dynamics of the species are poorly understood.

Non-coral cnidarians with algal symbionts

Phylum Cnidaria is a large animal group whose members include jellyfish, sea anemones, corals, and hydroids. In addition to corals, many cnidarian species have symbiotic relationships with microalgae. The symbiotic algae are often dinoflagellates of the genus *Symbiodinium*. The algae are colored brown by their photosynthetic pigments. Symbiotic dinoflagellates are usually called zooxanthellae. Tropical sea anemones often have symbiotic relationships with both anemonefishes and *Symbiodinium* (Fig. 2), which gives a brown hue to the cnidarian's tentacles. Some jellyfish cnidarians, such as the spotted jelly and the upside-down jellyfish, also harbor *Symbiodinium*. Fire corals like *Millepora* resemble scleractinian corals, but they are in fact colonial hydroids harboring *Symbiodinium* (Fig. 2). *Millipora* inflicts painful stings on unprotected skin: don't touch with colonies with your bare hands.

Figure 2. Upper: anemonefish in a symbiotic relationship with a sea anemone (off Aragusuku, Miyako-jima Island). Lower left: spotted jelly. Lower right: *Millepora* fire corals (off Aka-jima Island).

Acoelomorpha

Acoels are free-living animals with thin, flat bodies. Many harbor microalgae of diverse taxonomic affiliations. Acoel outbreaks in aquaria are bothersome for both professional and amateur aquarists. *Convolutriloba longifissura* is a red acoel with scattered white spots; it harbors a species of green alga (Fig. 3). This diminutive acoel is rarely seen in the wild, but outbreaks are frequent in an aquarium supplied with running seawater at the Sesoko Marine Station (Tropical Biosphere Research Center, University of the Ryukyus).

Bivalves and sea slugs

Have you ever seen colorful lip-shaped structures while snorkeling over coral reef limestone substrata (Fig. 3)? As you approach, the lips withdraw into the limestone! The lips are the emergent mantle edges of the giant clam *Tridacna crocea*, which has a thick shell and bores into the coral limestone. Thin tubes filled with *Symbiodinium* form a network through the mantle. The clams spread their mantles over the reef surface in order to illuminate the photosymbionts within their tissues. The brilliant colors of the mantle are thought to regulate the quantity and quality of light reaching the algae. All giant clam species harbor *Symbiodinium*. Other bivalves, such as the true heart cockle and strawberry cockle, also harbor *Symbiodinium* in their mantles (Fig. 4). You may not have seen these species on shallow sandy shores because they are partially buried in the sediment.

Sea slugs have diverse diets. Some species feed exclusively on a particular invertebrate or alga, while others have more catholic tastes. Saccoglossan sea slugs pierce the cell walls of macroalgae and suck out the cytoplasm, including the chloroplasts. Some saccoglossans retain intact extracellular chloroplasts in their digestive glands. The tiny organelles continue photosynthesizing and transfer nutrients to the host slugs. This phenomenon is termed “kleptoplasty”; it is not a “symbiosis” because the algae are eaten by the sea slugs. *Plakobranchus ocellatus* is one of the saccoglossans frequently found on the sandy bottoms of back reefs (Fig. 4). This slug is able to survive more than 10 months in an aquarium without a food supply, provided they are illuminated. *P. ocellatus* obtains the nutrients it needs from the chloroplasts retained in the digestive glands. Stable nitrogen isotope analysis indicates that *P. ocellatus* is herbivorous in the wild, but phototrophic when held without food in an aquarium.

The ascidian–*Prochloron* symbiosis

Some colonial ascidians on coral reefs have symbiotic relationships with the cyanobacterium *Prochloron.* About 20 species of ascidians from the Ryukyu Archipelago are known to be photosymbiotic. These are unique relationships among the cyanobacteria for *Prochloron* has both chlorophyll *a* and *b*, like the green algae and land plants. Many bioactive compounds have been isolated from these ascidians; some are synthesized by their photosymbionts.

Dome-shaped colonies of *Didemnum molle* are readily found on the back reefs of Okinawa where they are attached to coral limestone and seagrass leaves (Fig. 4). They are sometimes crowded on the stakes that support algal farm nets. The ascidians take seawater into the colony through small superficial holes and

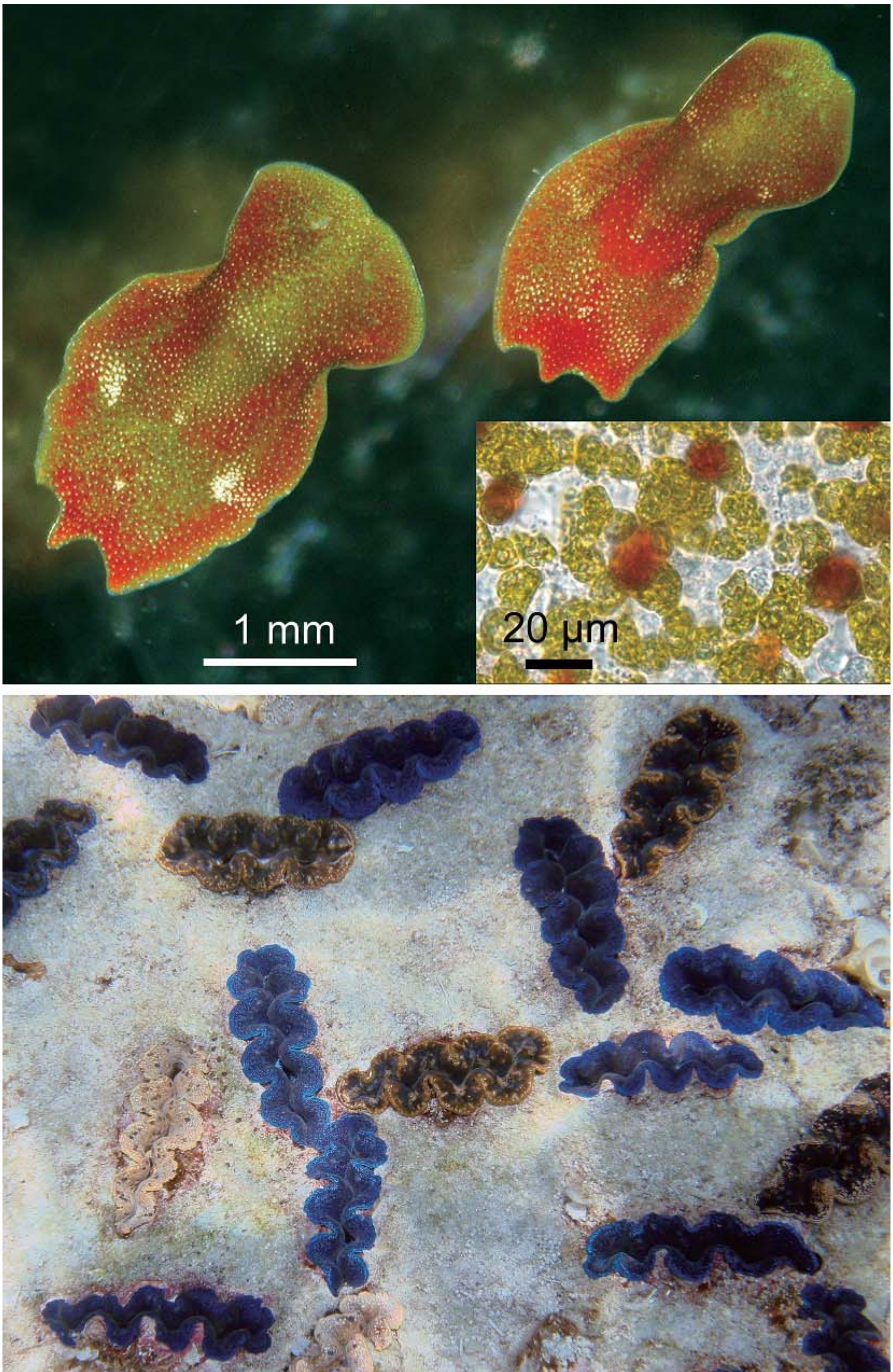

Figure 3. Upper: *Convolutriloba longifissura* with green algae in its tissues (yellow-green cells shown in the inset). Lower: lip-like mantles of *Tridacna crocea* (off Ikei-jima Island).

Figure 4. Upper left: strawberry cockle (off Shinri-hama, Kume-jima Island). Cockles have been partially excavated from the sandy bottom. Upper right: *Plakobranchus ocellatus* (off Teniya, Okinawa-jima Island). Lower: colonies of *Didemnum molle* attached to coral limestone (off Aragusuku, Miyako-jima Island).

discharge it through a large opening on the top of the colony dome. Viewed through the large opening, the internal surface of the colony is seen to be entirely yellow-green (due to chlorophyll *a* and *b* contained in *Prochloron*).

Snorkeling over shallow coral reefs

Diverse invertebrates that are partially fuelled by solar energy live on Okinawan coral reefs. However, many of them normally inhabit shaded habitats, probably because the solar radiation at fully illuminated sites is too strong for their photosymbionts. Strong radiation also contains harmful UV rays. As depth increases, photosymbiotic invertebrates become more rare because seawater strongly attenuates light energy, which rapidly becomes inadequate for photosynthetic production. The deeper waters that are frequently visited by SCUBA often have few solar-powered invertebrates, and I recommend you visit shallow coral reefs with only a mask and a snorkel. Spend time carefully watching a shaded site, like depressions in the limestone or gaps among coral colonies, and you may observe many truly stunning organisms that you have never noticed before.

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2—8. How many species are there in the ocean?

James Davis Reimer

Introduction

How many species are there in the ocean? This question has long fascinated both scientists and the general public. Despite being a simple question, the answer to this question is quite complex, and there is not even a general consensus on rough numbers. Still, scientists keep trying to make more accurate estimates. Why is knowledge of this number so important?

Precise knowledge on marine species numbers would be invaluable for many reasons. First of all, with such knowledge, along with species distributions, scientists could map the biodiversity of marine regions more accurately. This, in turn, would allow countries and interest groups to more accurately manage and protect different areas, and also know where most potential marine resources are. Many groups of marine organisms are important for food, while others are sources of bioactive compounds. In particular, some groups such as sponges (see Column 7 in Chapter 2) are highly targeted by as they contain many useful products, and yet our understanding of their diversity is very poor. Finally, the idea that such a simple question is unanswerable drives us as curious humans to try to find a more exact answer. Thus, it can be said that this simple question, like the ocean itself, holds our imagination.

Species: described and undescribed

In order to answer this question, first we must delineate what we mean by “species”. There are many definitions of species, based on the field of research or the method of scientific investigation. Based on the definition, numbers of species can easily change by large amounts, and even factors of ten.

Traditionally, for counting species, we can use the idea of “taxonomic species”, or put more simply, species with scientific names (the Linnaean system). Taxonomic species have been described, and given a unique name consisting of a genus name and a species name to distinguish it from all other species. Thus, to know the number of marine species, in theory all we have to do is count the number of described species with scientific names from the ocean, and we should arrive at an answer. Researchers have been classifying and naming marine species for a long time, and this process continues today. The most recent estimate of the number of described marine species is 222,000 to 230,000 eukaryotic species.

The problem arises from the fact that there are many species with no names (=undescribed species) (Fig. 1). These undescribed species include species that are known but not yet described, as well as undiscovered species. Whatever the case may be, the number of undescribed species is difficult to estimate, and varies widely from taxonomic group to taxonomic group. Describing these undescribed species takes time and money. Although progress is being made, no one knows when all species will be described, or even if this is possible.

Figure 1. Algae, foraminifers, zoantharians, and ascidians covering the bottom of a coral reef rock. It is possible that among these organisms are species without formal names. Image from Kume-jima Island, Okinawa (Euichi Hirose).

Many different studies have thus based their estimates of the total number of marine species on trying different methods of estimating how many species remain to be described. Estimates vary widely. Low estimates have been generally based on opinions of taxonomic experts, with the total number of marine species ranging from 300,000 to 972,000 species. On the other hand, high numbers are based on examining DNA sequences from relatively understudied taxonomic groups, and extrapolating findings to all marine animals. In such cases, numbers are often huge, and estimates have reached 1,500,000 to >10,000,000 species. As you can see, there is a factor of more than 30 times variability in estimates! Even more surprising, these studies deal only with eukaryotes, and no Eubacteria or Archaea are included in these estimates.

Problems in finding answers

From the numbers above, it is clear that our understanding of total marine species diversity is far from clear. It stands to reason that from concerted research effort we could begin to narrow down the range of species estimates, and slowly arrive at a more accurate number. However, this is not as easy as it would seem.

Humans are terrestrial organisms, and the ocean is not our home. Thus, in order to properly sample diversity, we must enter an alien environment. SCUBA and submarines, as well as more recently remotely operated vehicles (ROVs) and autonomous underwater vehicles (AUVs), can enable us to acquire data from the marine environment, but these require time, effort, and budget at much larger scale than any terrestrial survey, along with required safety measures. Furthermore, the ocean is on average over 4200 m deep, and the total space of the ecosystems contained within the marine environment make up 99% of the space on the planet. From these figures, it is easy to see a huge effort would be needed to make serious progress.

Some marine regions are known to be particularly diverse. One region is the Coral Triangle in the Central West Indo-Pacific, which is theorized to harbor the most species of any marine region. This area includes innumerable diverse coral reefs, and coral reefs are the most diverse marine ecosystem. However, as our understanding of species diversity is far from complete, so is our understanding of diversity patterns. The delineation of the Coral Triangle is based largely on only four taxonomic groups; the hard corals (Scleractinia), tropical fish, molluscs, and lobsters. All of these groups are commercially important. However, for many other taxa, research efforts have been few and far between. For example, even in a report with a conservative estimate of total species, it was calculated only 6% of fungi are known, and only 5 to 9% of copepods. Many recent studies of previously unexamined groups of organisms have demonstrated this problem clearly. For example, the first examination of one family of amphipods (Leucothoidae) from Okinawa found 25 previously unknown species in less than two years (Fig. 2). Similarly, researchers found the second and third species of one group of zoantharians more than 40 years after the first and only report from Madagascar, and these new species were far away on the Great Barrier Reef and in Okinawa (Fig. 3). These results demonstrate that many groups of animals are not rare, but rather that there are not enough specialists able to

Figure 2. 23 species of amphipods (family Leucothoidae) described from Okinawa in less than two years. These species were not rare, but were not known simply that no experts had ever done research on them in Okinawa. These results demonstrate how diverse the oceans can be. Images: Kristine White.

accurately find and describe these species. Therefore, a more complete estimate of numbers of species and their distributions are clearly needed to truly understand where marine biodiversity is highest.

Conclusions

Thus, as you can see, the question "How many species are there in the ocean?" has no simple answer. The best we can do is say between 300,000 to more than 10,000,000. Perhaps a more simple answer would be "many, the ocean harbors much diversity". It is believed many species are becoming extinct every year due to rapid anthropogenic climate change, and undoubtedly they include unnamed and undescribed species. With this in mind, while focusing on research efforts to answer this question, at the same time we should do all that we can to protect the diversity of the ocean, regardless of whether we truly comprehend it or not.

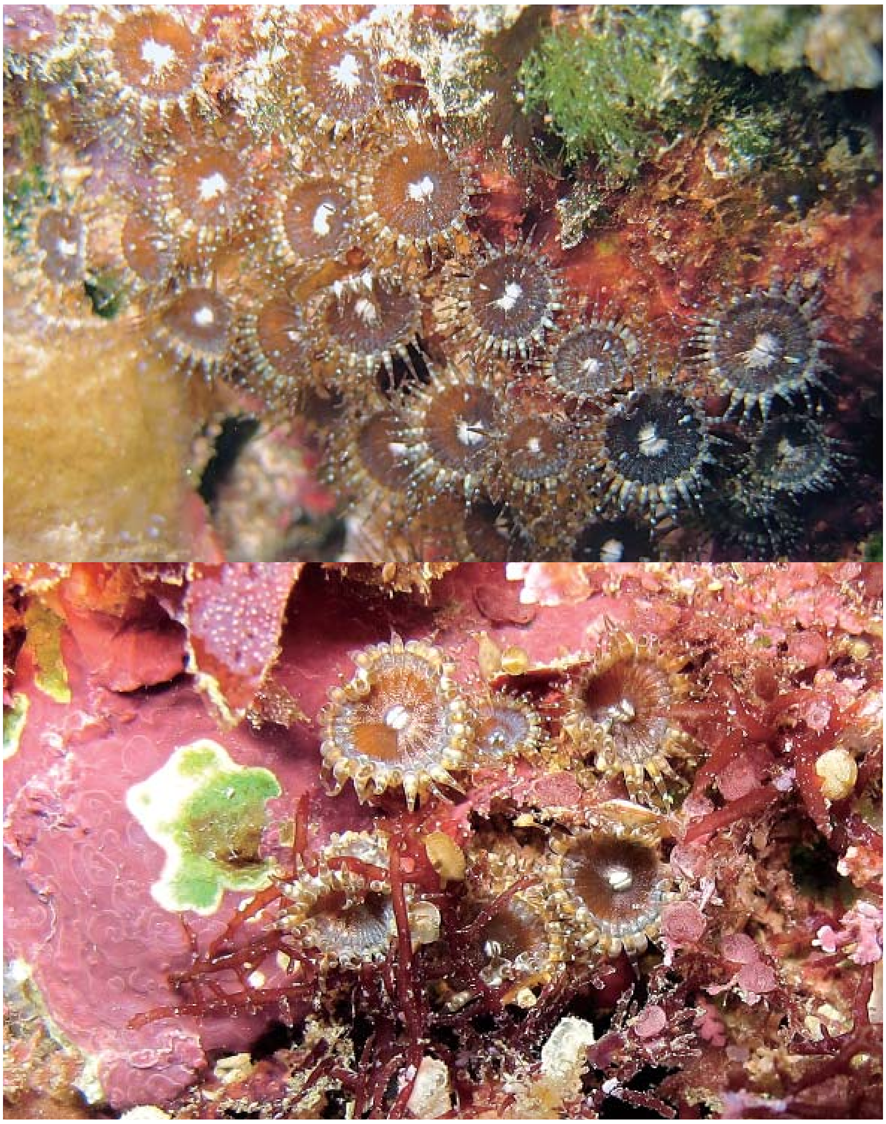

Figure 3. The zoantharian genus *Neozoanthus* only contained one species, but recently two species were found in Okinawa and Australia. Upper image: *Neozoanthus caleyi* from the Great Barrier Reef; Bottom image: *Neozoanthus uchina* at Amami Oshima Island, Kagoshima. These results demonstrate how much more research is needed to truly understand the oceans' biodiversity.

Column 7.
Treasures of the Ryukyu Archipelago—coral reef organisms and biomedical resources

Junichi Tanaka

Numerous therapeutics, including antibiotics and anticancer agents, have been developed from metabolites from terrestrial plants and microorganisms. In the last five decades, marine organisms have also attracted attention as potential biomedical resources, and several are already in clinical use: an analgesic drug from a cone shell, an anticancer agent from a Caribbean tunicate, and a modified sponge metabolite as a drug for use in cases of recurrent breast cancer. As these non-edible source organisms are considered worthless from a fishery viewpoint, most people are unfamiliar with them. However, owing to their possession of lead compounds for medicines and reagents for life science research, marine organisms have been recognized as precious bioresources, resulting in worldwide competition in bioprospective research, particularly in Asian countries.

One of the characteristics of coral reefs, including the Ryukyu Archipelago, is their rich biodiversity. In addition to macroorganisms—sponges, tunicates, bryozoas, and octocorals (Fig. 1)—a huge number of microorganisms—bacteria, fungi, and microalgae—inhabit the macroorganisms, sediments, and water. Furthermore, the distribution of marine organisms is influenced by the underwater environment—geography, season, depth, and other factors. Furthermore, the metabolites of one organism may vary not only with location but also among individuals of that species. Such biodiversity may enhance the chemical diversity of metabolites.

Because no effective drugs are available for many diseases, much collaborative research aims to identify novel chemical entities with activity against infectious diseases and immunity-related conditions by utilizing consituents developed in their long evolution.

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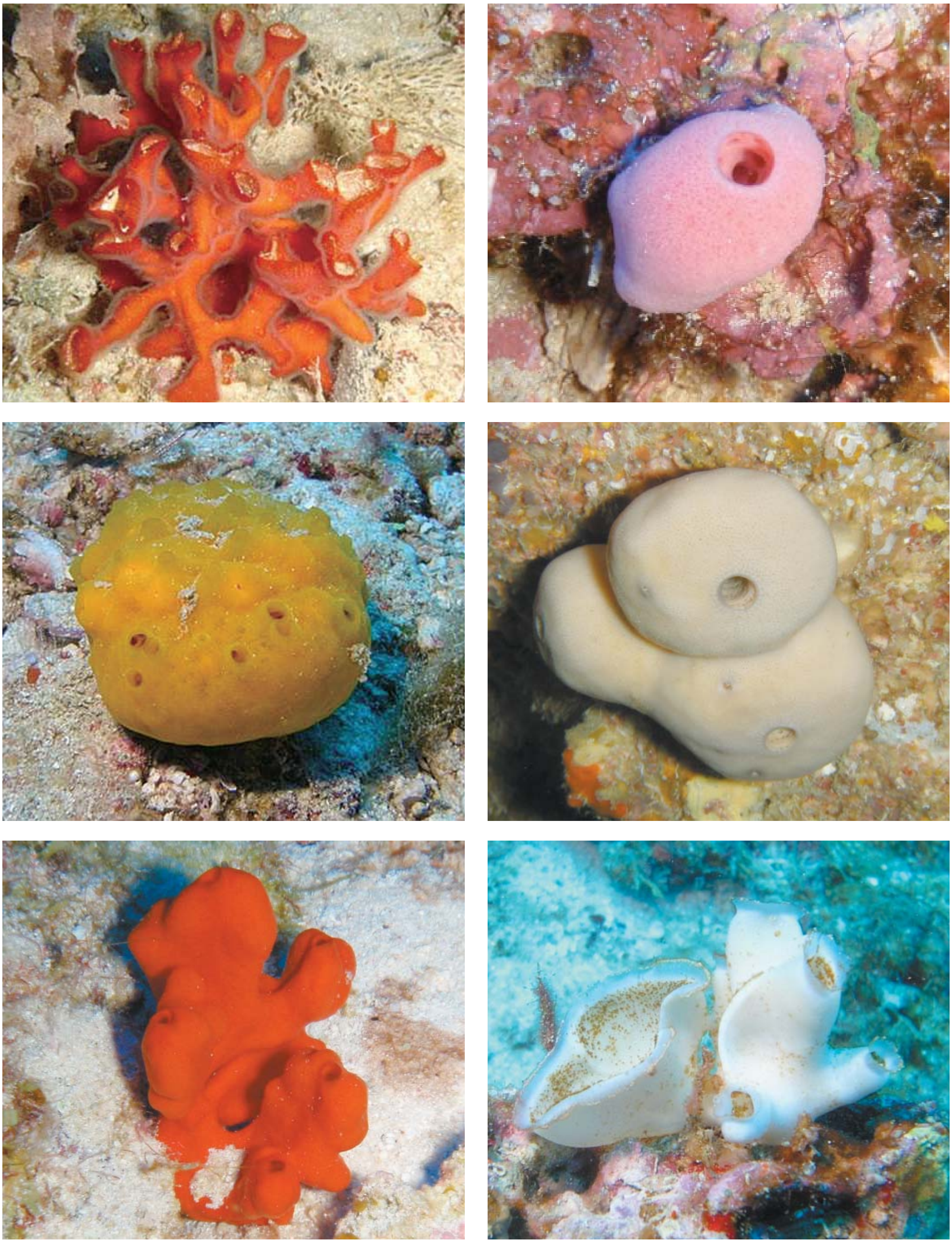
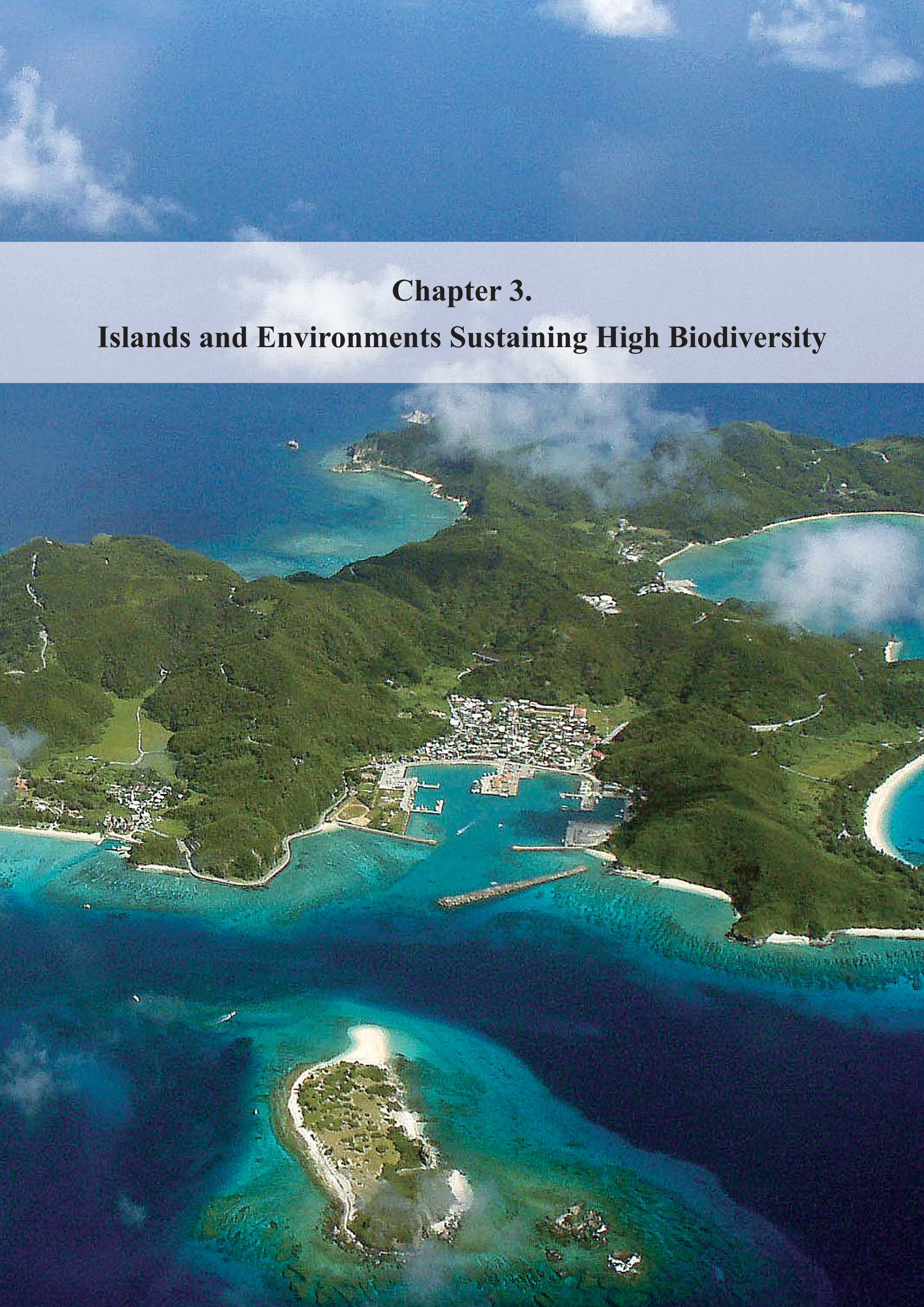


Figure 1. Upper left image: the bryozoa *Calyptotheca* sp. (Seragaki, depth 65 m), Upper right image: the sponge *Leucetta* sp. (Kume, depth 40 m), Middle left image: the sponge *Suberites japonicus* (Manza, depth 50 m), Middle right image: the sponge *Cacospongia mycofijiensis* (Zampa, depth 25 m), Lower left image: the sponge *Negombata* sp. (Kume, depth 45 m), Lower right image: the sponge *Paragrantia* cf. *waguensis* (Manza, depth 40 m)

Chapter 3.
Islands and Environments Sustaining High Biodiversity



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3–1. The geology of Okinawa-jima Island

Ryuichi Shinjo

Structure of the Ryukyu Archipelago

The Ryukyu Archipelago, which form an arc-like structure, extend for approximately 1,200 km from south Kyushu to Taiwan (Fig. 1). Here, the Philippine Sea Plate is subducting in a NW direction beneath the Eurasian Plate along the Nansei-shoto Trench (water depth up to 7,000 m) at a rate of approximately 70 mm/year.

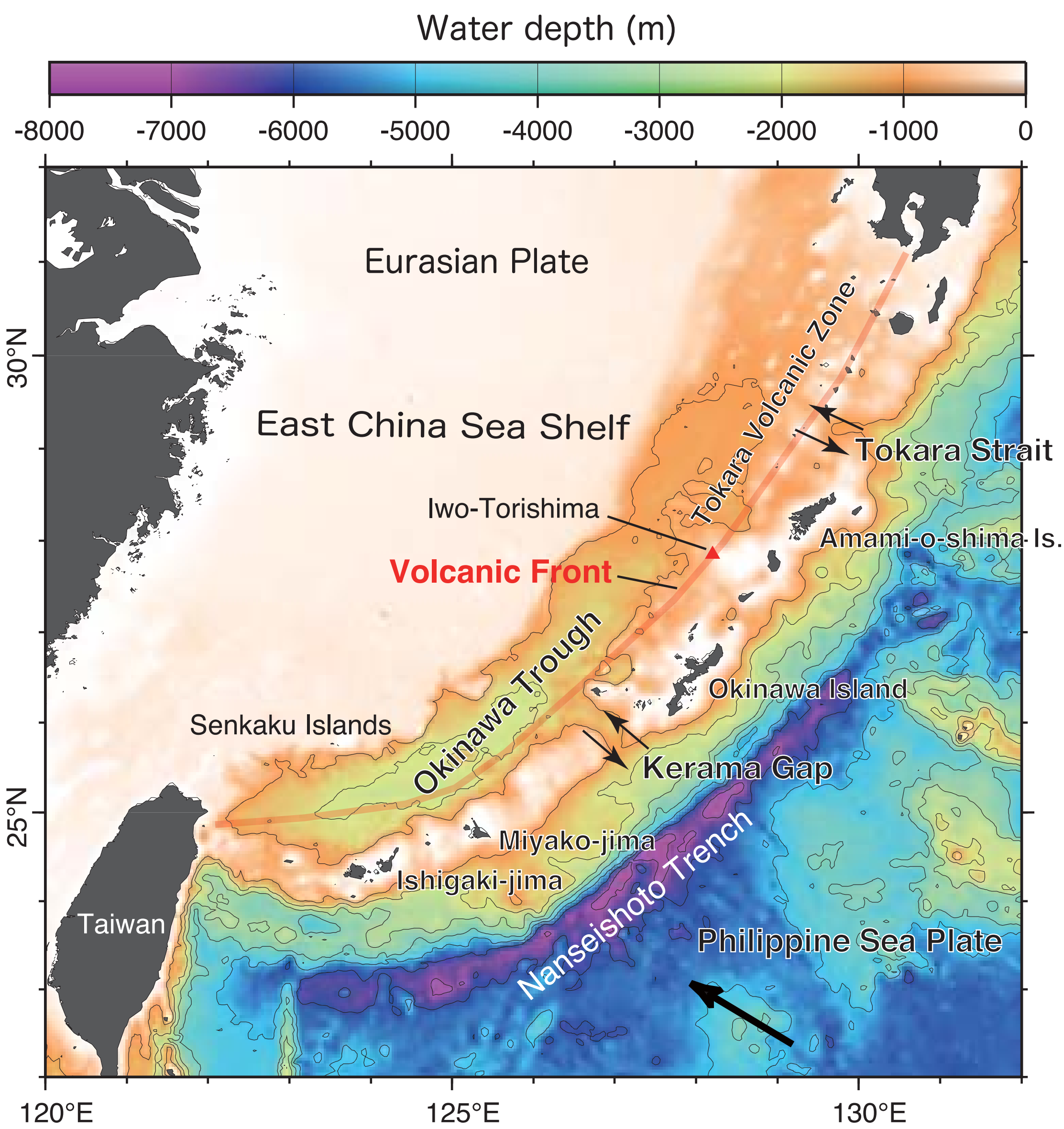

Figure 1. Map showing the geographic and tectonic features of the Ryukyu Archipelago.

The Ryukyu Island Arc is divided into three regions (the North, Central, and South Ryukyu Archipelago) by two deep submarine canyons (the Tokara Strait and Kerama Gap). It is noteworthy that these boundaries correspond to major biogeographical boundaries.

Seismic and volcanic activities are intense at plate subduction zones. An array of volcanoes called the volcanic front (or "Ring of Fire") occurs parallel to the trench. In the northern Ryukyu Archipelago, the Tokara volcanic zone, a chain of active volcanic islands including Kuchinoerabu-jima Island and Suwanose-jima Island, defines the present volcanic front. The southernmost volcano island, located west of Amami Oshima Island, is Iwotorishima Island. Farther to the south, the volcanic front is defined by submarine volcanoes (located near Kume-jima Island, 80 km north of Miyako-jima Island and 60 km north of Ishigaki-jima Island) and extends to Kueishantao Island of northeastern Taiwan.

Okinawa Trough: a young back-arc basin

Behind the Ryukyu Island Arc (*i.e.*, back-arc side), a narrow depression called the Okinawa Trough separates the Ryukyu Arc from the East China Sea Shelf (water depth, 200 m). Subsidence due to rifting and subsequent thinning of the Eurasian continental crust formed the Okinawa Trough. Its depth near the central Ryukyu Archipelago is around 1,000 m, but it exceeds 2,000 m behind the southern Ryukyu Arc. Active submarine magmatic hydrothermal vents and ore deposits have been discovered at the spreading axes of the trough and submarine volcanic front in the southern Ryukyu Arc (see Column 8).

Zonal distribution of older basement rocks

Figure 2 is a geological map showing the distribution of basement rocks in the northern part of Okinawa-jima Island. The geology of this part of the island consists of five units: the Iheya, Nakijin, Motobu, Nago, and Kayo zones from west (older) to east (younger). The older zone is regarded as having been thrust onto the younger zone.

These basement rocks originated in an accretionary wedge, which was formed from marine sediments that were scraped off the subducting oceanic plate and accreted onto the non-subducting plate at a convergent plate boundary.

The most representative rock of the Iheya Zone is chert (flint), a very hard, dense, microcrystalline-to-cryptocrystalline type of quartz. Chert forms by consolidation of the accumulated remains of radiolarian shells. Mount "Tacchu" at Ie-jima Island, which can be viewed from the front gate of the Okinawa Ocean Memorial Park (Fig. 3), is composed of chert of the Iheya Zone. The depositional environment for chert is generally deep-sea, far from land areas.

The typical rock type of the Nakijin Zone is fine-grained gray limestone. This rock was used as wall material for Nakijin Castle. Triassic Ammonoidea (Fig. 3), conodonts (tiny teeth-like fossils), and *Halobia* (a group of bivalves) have been discovered in this limestone. These originated from shallow marine deposits.

The Motobu Zone contains diverse rock types, such as sandstone, limestone (Fig. 3), mudstone, conglomerate, and green rocks (altered volcanic rocks). Permian fossils (*Fusulina*, radiolarians, and conodonts) have

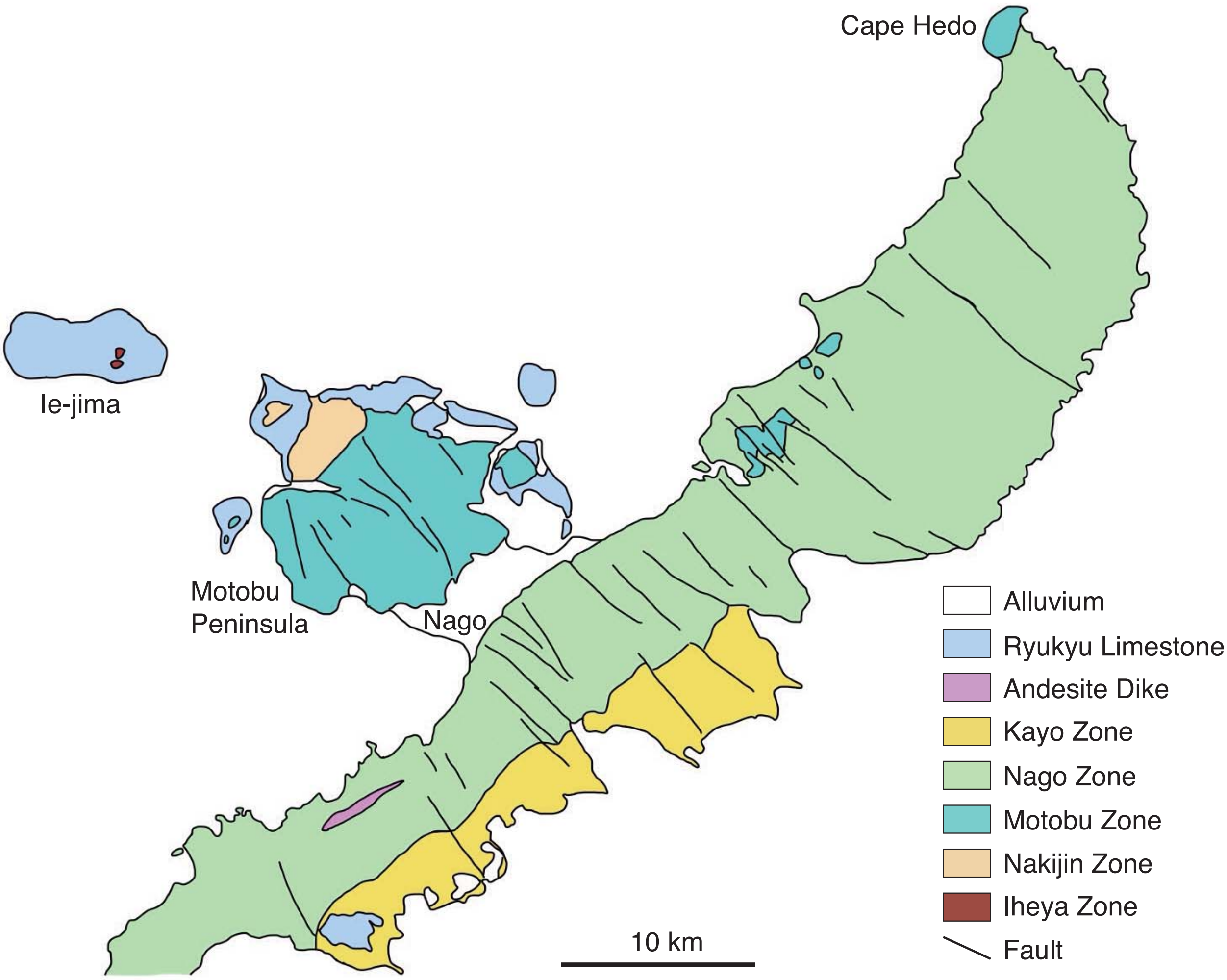

Figure 2. Simplified geological map of the northern part of Okinawa-jima Island.

been discovered together with Triassic fossils in cherts, limestones, and green rocks. These are included in Jurassic to Cretaceous mudstone. Such a mixture is called "mélange" (a French word meaning a mixture of several types of materials). After accretion of the sediments, underlying oceanic crust and limestone developed on seamounts of the subducting plate and several large-scale submarine landslides occurred, which were responsible for the intermingling of the rocks of different ages.

The Nago Zone consists of black mudstone associated with sandstones (Fig. 3) and green rocks. The mudstones are weakly metamorphosed to foliated rocks (black phyllite). The green rocks are mainly volcanic rocks from lava flows. When basaltic lava erupts at the seafloor, the lava is chilled rapidly and forms pillow-like structures (pillow lava). Green rocks in the Nago Zone occasionally preserve a pillow lava structure (Fig. 3). Although no fossils have been found in the Nago Zone, its depositional age has been estimated to

Figure 3. Upper left: View of Mount Tacchu at Ie-jima Island, which belongs to the Iheya Zone. Middle left: Ammonoidea in limestone of the Nakijin Zone. Lower left: Quarry of limestone of the Motobu Zone. Upper right: Black phyllite of the Nago Zone. Middle right: Pillow lavas of green rocks in the Nago Zone (photo: Masaaki Chinen). Lower right: Intensive deformation (folding) of interbedded strata of sandstone and mudstone in the Kayo Zone.

be late Cretaceous (70 to 90 Ma: million years ago). The depositional environment might have been near the trench region as the zone contains abundant sandstone derived from land areas.

The Kayo Zone consists of an alteration of mudstone and sandstone, with sandstone being predominant. The wide exposure of Kayo Zone rocks along the eastern coast at Teniya Village is spectacular, suitable for an earth science field excursion. Depositional structures of submarine landsliding at the trench slope are well preserved. The rock strata are highly deformed and folded (Fig. 3), and outcrops of strata that are up-side-down are observed frequently. These structures were developed in the shallow part of an accretionary wedge. Fossils of large *Nummulites* foraminifera of middle Eocene age (approximately 40 Ma) have been discovered in the Kayo Zone.

"Kucha" and Ryukyu Limestone in southern Okinawa-jima Island

The Shimajiri Group and the Ryukyu Limestone are exposed widely in the southern part of Okinawa-jima Island. These are also distributed in the southern Ryukyu Archipelago (Miyako and Yaeyama Islands).

The typical rock of the Shimajiri Group is loose, gray mudstone (Fig. 4), which is called "Kucha" in Okinawan and has been utilized as a soap and shampoo agent since the Ryukyu Kingdom period. Sediments of the Shimajiri Group are marine deposits of a bathyal environment supplied mainly from the Chinese continent during the late Miocene to Pliocene.

The Ryukyu Limestone overlies the Shimajiri Group with sharp, irregular unconformity (Fig. 4). The Chinen Peninsula is an exceptional locality in the southeastern part of Okinawa-jima Island, where a sandstone bed (Chinen Formation) is present between Shimajiri Group mudstone and Ryukyu Limestone.

Ryukyu Limestone, generally forming a terrace, is distributed at Cape Manzamo (Onna Village) and Cape Zanpa (Yomitan Village) in the west-central part and southern part (Itoman City) of the island. The Ryukyu Limestone consists of Quaternary coral reef and fore-reef deposits and contains abundant fossil coral and calcareous algal (see section 1–4).

Ryukyu Limestone is the most commonly used rock in the Ryukyu Archipelago. The limestone was utilized widely in the stone walls of Shuri Castle and in those of other castles (castles with stone walls are called "Gusuku" in Okinawan), which were registered as World Cultural Heritage Sites in 2000. Additionally, the historic stone-paved road (Ishidatami) at Shuri Kinjo-cho (Fig. 4) is made of Ryukyu Limestone. Therefore, Ryukyu Limestone has been closely related to Okinawan culture and history.

From muddy sea to coral-reef sea: the Shimajiri Event

With an oldest reported age of around 1.6 Ma, deposition of Ryukyu Limestone occurred hundreds of thousands of years ago. The regional distribution of Ryukyu Limestone in the central and southern Ryukyu Island Arc indicates a vast expanse of coral reefs at the time of Ryukyu Limestone deposition.

It is inferred that the marine depositional environment changed drastically from 'muddy sea' during deposition of the Shimajiri Group to 'coral reef sea' during deposition of the Ryukyu Limestone. Thus, this drastic change occurred in the early Pleistocene (approximately 2 Ma), before deposition of the limestone and after

Figure 4. Upper left: Outcrop of mudstone of the Shimajiri Group near the University of the Ryukyus. Middle left: Unconformity between the Shimajiri Group and Ryukyu Limestone. Lower left: Quarry of Ryukyu Limestone near the Peace Memorial Park. Upper right: Cape Manzamo, consisting of Ryukyu Limestone. Middle right: Shuri Castle and Ryutan Pond. Ryukyu Limestone was utilized for the stone wall and as building stone. Lower right: Stone wall and paved road at Kinjo-cho, Shuri. Both are made from Ryukyu Limestone.

deposition of the Shimajiri Group.

For the growth of healthy coral, the massive supply of muddy sediment from the eastern Asian continent to the Ryukyu Arc had to have been reduced significantly. Otherwise, coral would have been suffocated by fine-grained sedimentary particles (see Column 12). The development of the depression at the Okinawa Trough probably trapped a large amount of sediment, resulting in the comfortable conditions for coral growth in the Ryukyu Arc region. At almost the same time, the Ryukyu Arc region may have been uplifted. The submerged part of the Shimajiri Group, which was very soft, was eroded easily, helping to produce a shallow marine environment comfortable for coral growth. This crustal movement is known as the “Shimajiri Event.”

Segmentation of islands: the Uruma Event

A submarine plain called the “500-m-deep Island Shelf” has been found around the southern Ryukyu Arc (Fig. 1). The upper part of the plain consists of reef deposits of Ryukyu Limestone. Because coral reefs generally form in a shallow environment (<100-m water depth), its occurrence at a depth of approximately 500 m implies subsidence of the plain after its formation.

Recent bathymetric surveys have revealed that the plain is cut by several NW–SE-trending faults. Similar faults are also well developed on Miyako-jima Island, where Ryukyu Limestone covers the entire island. These faults, oriented perpendicular to the axis of the Ryukyu Island Arc, are regarded as “across-arc faults.”

The Ryukyu Limestone basement rocks are cut by these across-arc faults, some of which are still active. It is obvious that this crustal movement, called the “Uruma Event,” occurred after the formation of the Ryukyu Limestone and that it promoted segmentation of the Ryukyu Arc region, resulting in the present configuration of the islands.

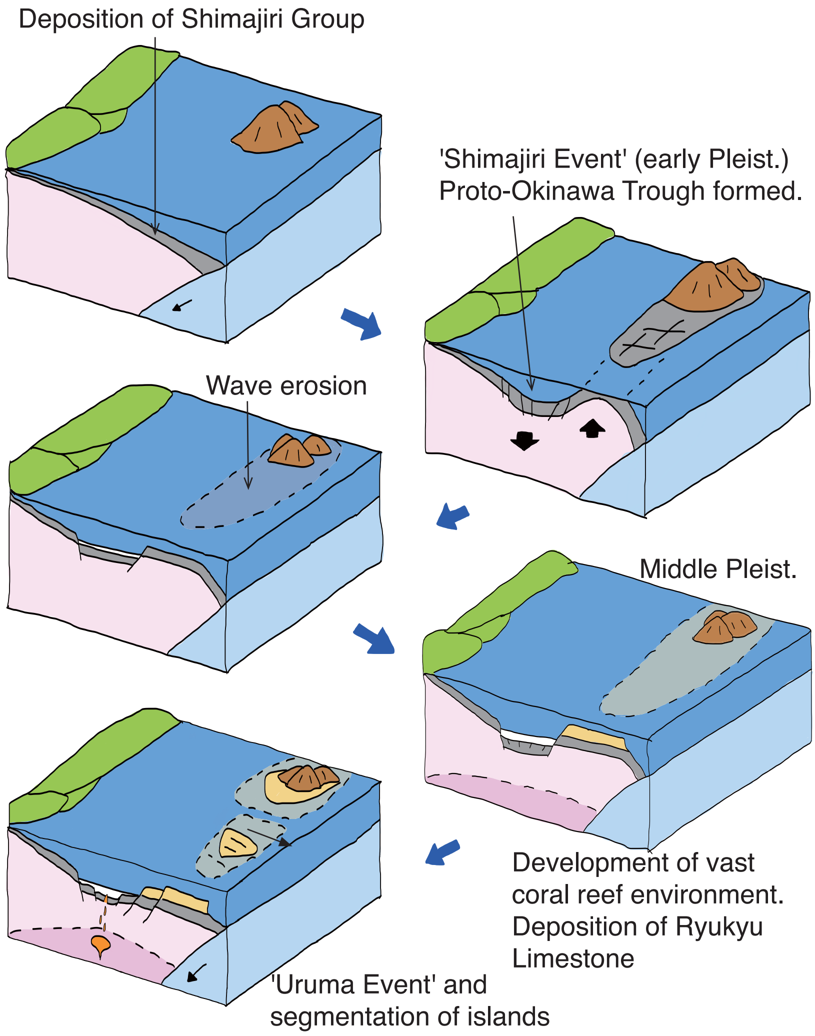

Figure 5. Model of formation of the Ryukyu Archipelago over the last few million years. After deposition of the Shimajiri Group, the Shimajiri Event resulted in subsidence of the Okinawa Trough and uplift of the Ryukyu Arc region, producing a transition from a muddy sea environment to a coral-reef environment. After subsequent deposition of the Ryukyu Limestone, the Uruma Event took place, causing segmentation of the island arc and across-arc faulting.

Column 8.
When do you research hydrothermal systems? Now!

Tomohiro Toki

The seafloor of the East China Sea, located to the west of the Okinawa Islands, is known as the Okinawa Trough, and is a depression with a depth of up to 2000 m. The Okinawa Trough is the first location around Japan at which a hydrothermal system was discovered. At a depth of 2000 m, the water pressure reaches 200-fold normal atmospheric pressure. Such a high pressure allows gas components to dissolve in hydrothermal fluids. Large amounts of methane also dissolve in hydrothermal fluids. Methane is produced by the decomposition of organic matter below the seafloor through processes that involve heat and microbes. Indeed, recent studies have shown that a greater proportion of the methane in hydrothermal fluids from the Okinawa Trough originated from microbial processes than had been supposed by many scientists.

Such hydrothermal systems are now being studied by scientists worldwide. Japan operates a deep-sea drilling vessel, the *Chikyu*, which can drill to a greater depth below the seafloor than any other drilling ship, and a manned submersible *Shinkai 6500* that is capable of diving to the greatest depth of all academic research submersibles. These capabilities reflect the leading role played by Japan in this type of scientific technology. In the future, further research will reveal the roles played by microbes below the seafloor in more detail. Such new scientific findings will appear in school textbooks by the time that current elementary school students become adults.

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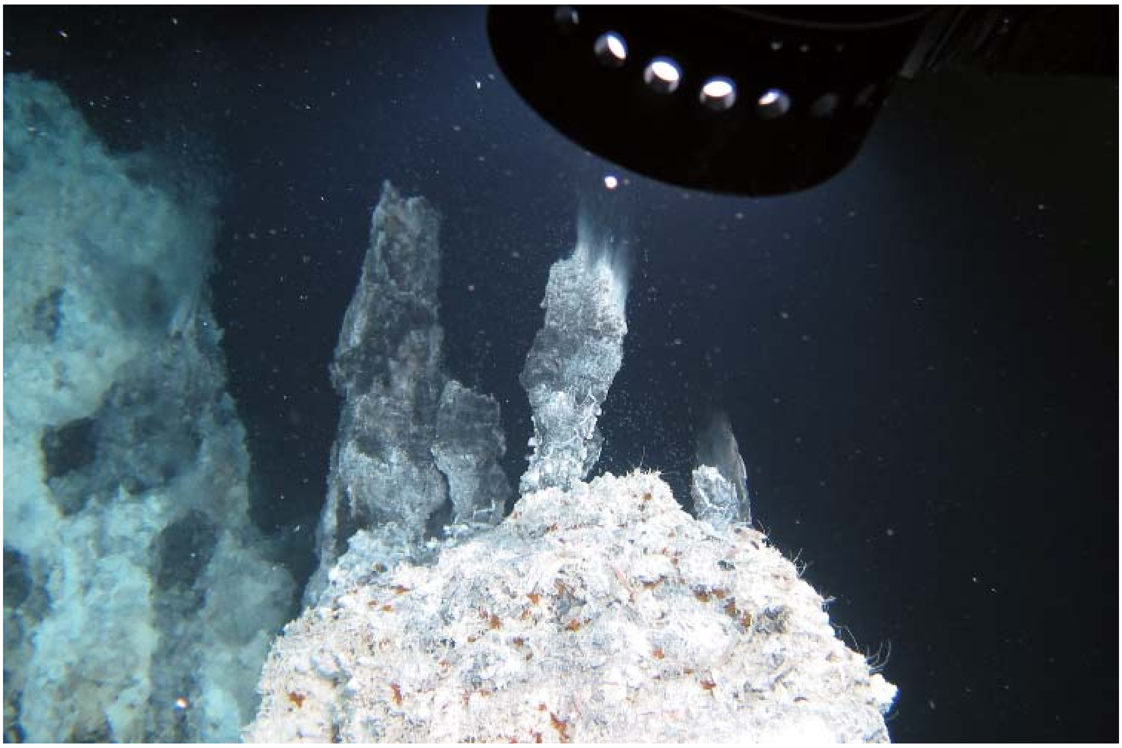

Figure 1. A hydrothermal vent in the Okinawa Trough. The white objects are mostly a type of sandworm. The black material is light from the *Hyper Dolphin* (JAMSTEC). Photography: Hyper Dolphin operation team.

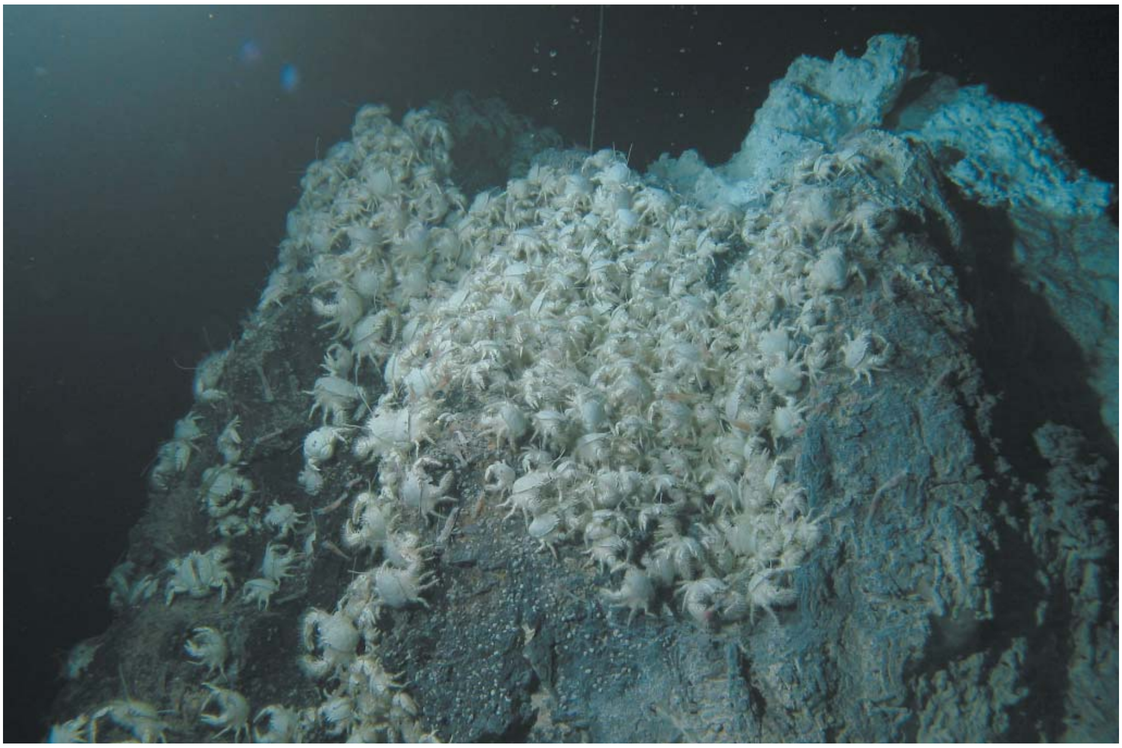

Figure 2. Another hydrothermal vent in the Okinawa Trough. The white objects are *Shinkaia crosnieri*. Photography:Hyper Dolphin operation team.

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3—2. Weather and clouds in the Ryukyu Archipelago

Hiroyuki Yamada

Cumulus clouds in summer

The Ryukyu Archipelago, located in the subtropics, have a climate that differs from that in the mid-latitudes, including other Japanese islands. The subtropical zone refers to an area of high temperature next to the tropical zone. Do you know what other differences distinguish the subtropics from the tropics and mid-latitudes? This question is important for understanding the weather of the Ryukyu Archipelago. In summer, cumulus and cumulonimbus clouds tower up into the sky over the subtropical Ryukyu Archipelago. These clouds may bring local intense rainfall. In the local language, this type of rainfall is referred to as “Kata-bui,” meaning partial heavy rain, and it characterizes the summer weather of the islands. In contrast, such clouds occur throughout the year in the tropics (Fig. 1). Imagine seeing a rain shaft extending from the base of a towering cumulus cloud to the sea, suggesting the occurrence of Kata-bui. From the form of the clouds, there seems to be no difference in clouds between the Ryukyu Archipelago and the tropics. So, what is subtropical weather? This chapter begins by answering this question.

Figure 1. Cumulus clouds growing upward over the tropical ocean.

Summer and winter of the subtropical climate

To reveal the seasonal changes in weather conditions, Figure 2 shows distributions of mean temperature and wind in July and January at 5500 m above sea level. At this level, the influence of topography is small and areal differences can be seen clearly. In July, the temperature at this level over the Ryukyu Archipelago is warmer than −6°C and is almost identical to the temperature in the tropics, including Palau. Winds to the south of the Ryukyu Archipelago are calm or easterly. These conditions indicate that summer weather in the islands is almost identical to that in the tropics. In contrast, the area north of 30°N, including Tokyo, is characterized by westerly winds and decreasing temperature from the south to north, manifestations of the mid-latitude climate.

In January, the prevailing westerlies enhance and cover the Ryukyu Archipelago, where the temperature at 5500 m decreases to approximately −12°C. At this time, there is a temperature difference between the Ryukyu Archipelago and Palau, suggesting that the winter climate of the Ryukyu Archipelago differs from that of the tropics.

Figure 3 shows the seasonal changes in the different regions of surface temperature at Palau, Naha, and Tokyo. Although it is difficult to distinguish the summer season using only temperature, 25°C can serve as a criterion for this separation because this value is used by the Japan Meteorological Agency to identify a “summer day” and “tropical night.” The temperature in Palau is near 28°C throughout the year, indicating perpetual summer. In Naha, the period with temperature greater than 25°C is limited to between the middle of May and early October. Although this summer period is longer than that of Tokyo, it is clear that the climate of Naha consists of summer and another, non-summer season.

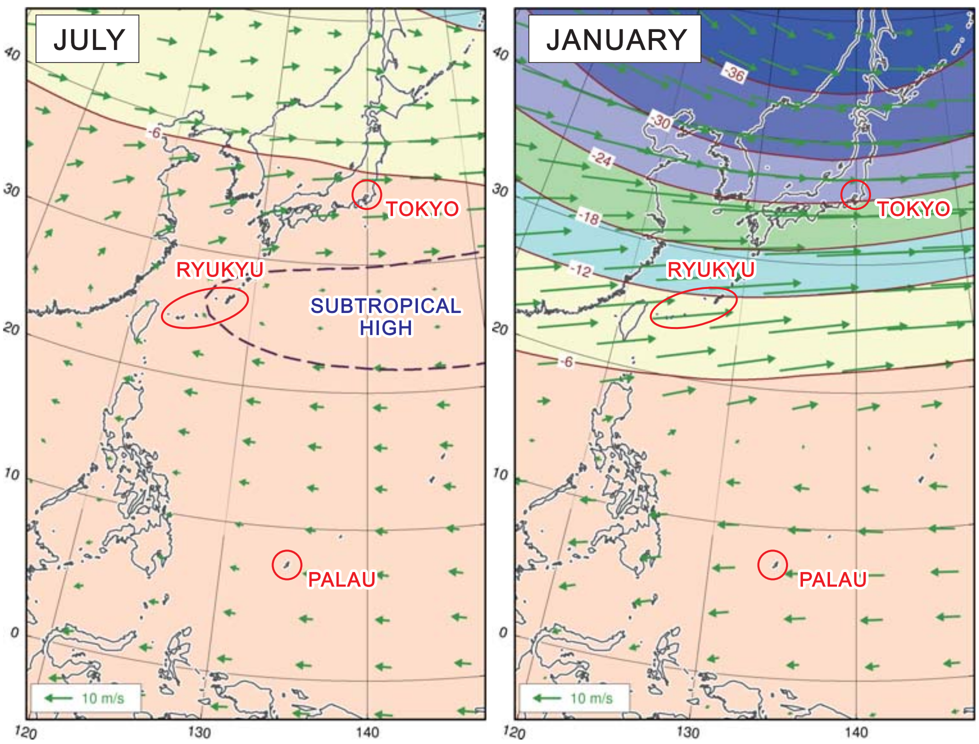

Figure 2. Distributions of monthly mean temperature (solid contours) and wind vectors at 5500 m altitude in July (left) and January (right). The ordinate indicates longitude and the abscissa indicates latitude. These figures are based on 25-year reanalysis data of the Japan Meteorological Agency.

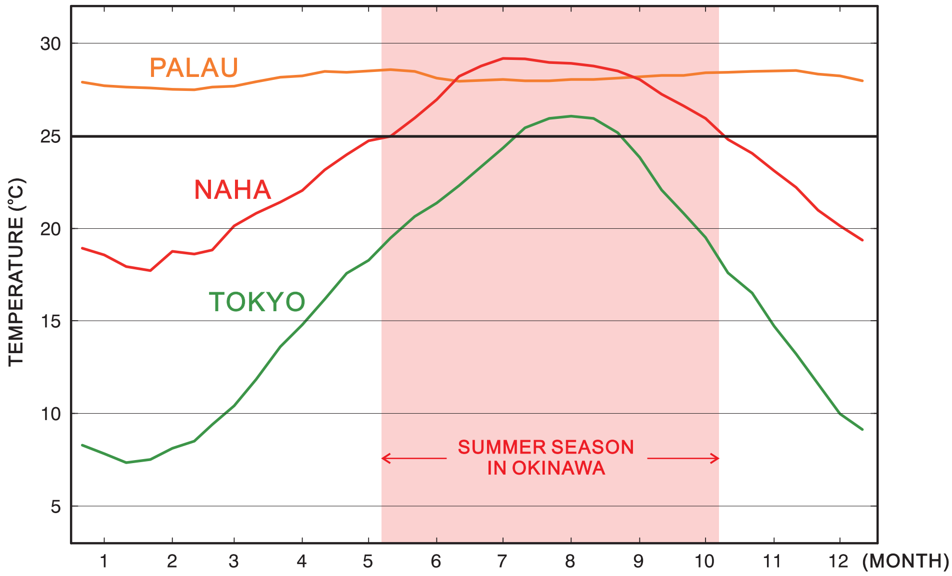

Figure 3. Time series of surface temperature in Palau (tropics), Naha (subtropics), and Tokyo (mid-latitudes).

Differences in cloud evolution between the tropics and the midlatitudes

As described above, there is a period during which the Ryukyu Archipelago experience weather similar to that of the tropics. That is, the subtropical climate consists of tropical weather in summer and a different weather similar to that in the mid-latitudes in winter. Figure 4 summarizes differences in cloud evolution between the Tropics and mid-latitudes. In the mid-latitudes, there is a gradient of temperature in the south–north direction, which causes low-pressure systems with warm and cold fronts. Clouds can develop by upward motion above the fronts. In contrast, in the tropics, there is little gradient in temperature. Tropical clouds can be initiated by heat contrast between warmer sea surface and colder air in the upper troposphere,

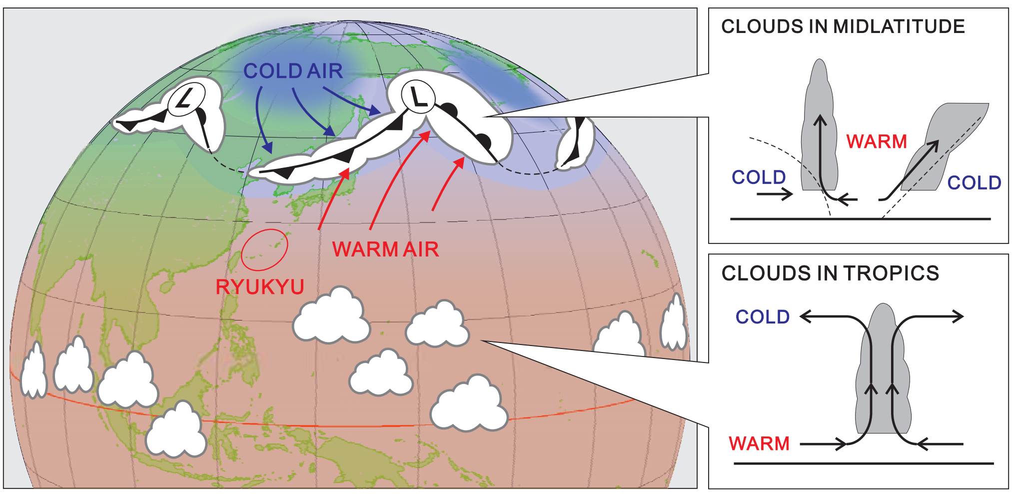

Figure 4. Schematic view of the difference in cloud evolution between the tropics and mid-latitudes. The left panel shows the shape of clouds and wind motions, and the right panels show vertical circulation associated with clouds in the two areas.

which causes upward motion due to buoyancy of the air. The buoyancy may be enhanced by heat released as water vapor condenses to form water droplets. This heat from water is referred to as latent heat, and it is crucial to the development of tropical clouds, including not only cumulus clouds but also tropical cyclones, the most severe weather system in the tropics.

Development of cumulus clouds over the islands

Cumulus clouds usually develop over the islands during daytime on summer days under conditions of low wind speeds. The upper panel of Fig. 5 shows such cumuli over Yanbaru, the northern part of the Okinawa-jima Island. A satellite visible image (lower right panel), acquired at the time this photograph was taken, shows that these clouds develop over the islands and move northwestward in accordance with the southeasterly ambient winds. Showers from such clouds contribute to the maintenance of the ecosystem unique to this area, including the growth of moist forest and presence of rare animals and plants. By the way, do you know why clouds tend to develop over islands rather than ocean? Hereafter, the mechanisms governing cloud evolution over the islands are explained.

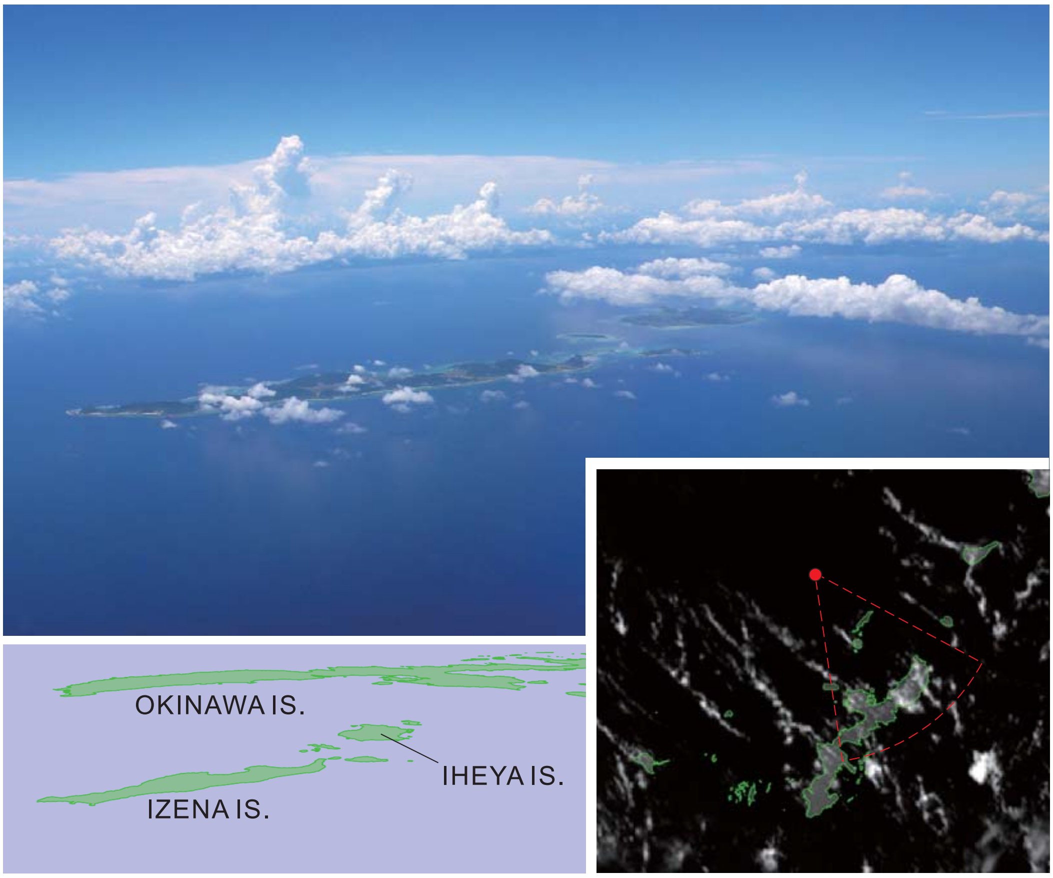

Figure 5. (Top) Photographs of cumuli over the northern part of Okinawa taken from a southbound passenger flight to Naha. (Lower left) The name of each island. (Lower right) A satellite visible image of these clouds. The viewing angle of the photograph is indicated by the broken lines.

Winds induced by heat contrast

The evolution of cumuli over the islands is associated with the heat contrast between land and sea surfaces (Fig. 6). In the daytime, the temperature of the land surface increases due to the absorption of solar radiation. This heat is usually radiated into the atmosphere before it can be conducted deep into the ground. In contrast, in the sea, solar radiation can penetrate to depths of several tens of meters due to the transparency of seawater. The surface temperature of the sea cannot increase higher than that of the land surface, which causes a difference in air temperature between land and sea. As a result, warmer air rises over the land and forms cumulus clouds. The air rising over the land results in localized lower pressure there, which causes a sea breeze to flow from sea to land. At night, circulation in the opposite direction, a land breeze and downdraft over the land, can develop under conditions of a warmer sea surface and cooler land surface. This nighttime circulation occurs because the sea surface cools more slowly compared to the land because of the higher thermal capacity of seawater. We refer to these local circulations with daily variation as sea-breeze and land-breeze circulations. Such circulations tend to develop over tropical islands that experience strong solar radiation.

Water supply system of Okinawa-jima Island using rainwater from Yanbaru

The occurrence of rainfall due to sea-breeze circulation implies that this circulation acts as a water pump, lifting water evaporating from the sea surface to an island. The left panel of Fig. 7 shows the topography

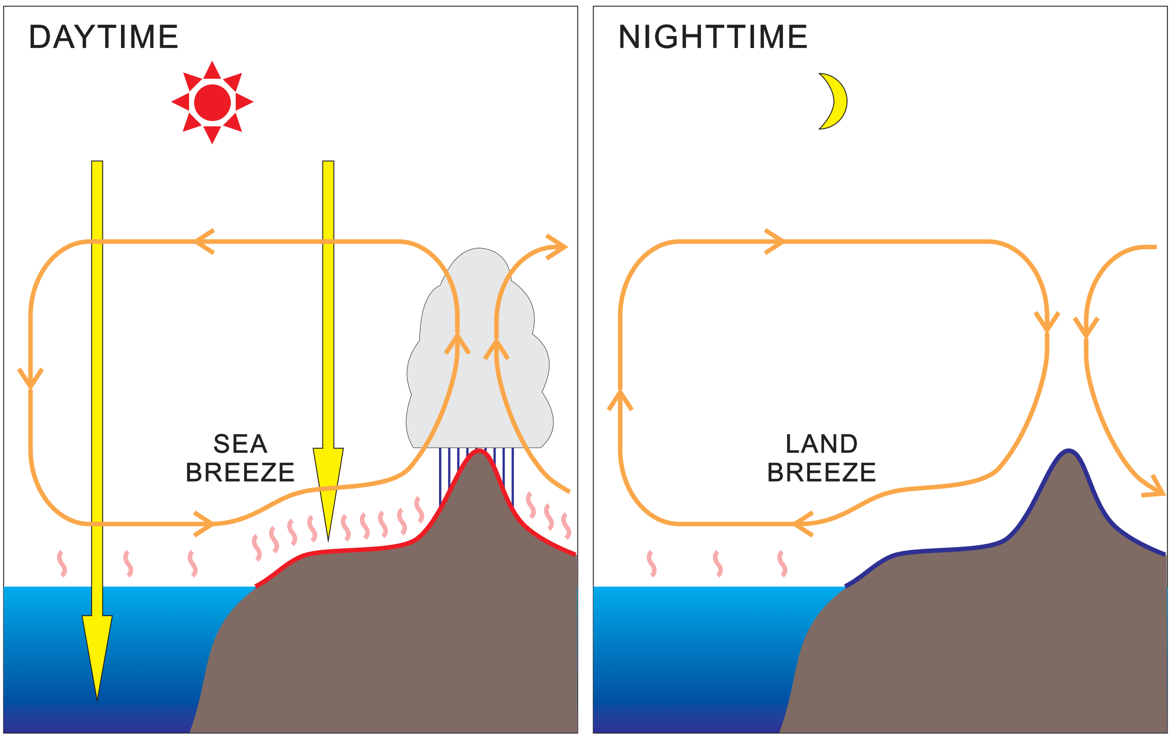

Figure 6. Schematic view of local circulation. The left panel is sea breeze during the day and the right is land breeze during the night.

and annual rainfall distribution in the Okinawa Islands. The amount of rainfall in Yanbaru, the northern part of Okinawa-jima Island, is about 1000 mm greater than that in the southern part of the island. Such contrast of rainfall according to topography is usually obvious on a tropical island. According to a scientific report of the University of Guam, rainfall on Pohnpei Island in Micronesia is distributed with huge variation of up to 4000 mm observed. On Okinawa, the water supply system is built to use rainwater from Yanbaru (Fig. 7, right panel). Many dams are located in the northern part of the island, and major aqueducts and water tunnels transport the water to purification plants in the southern part of the island, where the human population is concentrated. It is certain that rainfall induced by sea-breeze circulation in summer contributes to continued water supply, which benefits the population of the island.

In this chapter, the climatic features of the Ryukyu Archipelago have been described, with a focus on summertime cumulus clouds. Towering cumuli in a bright blue sky characterize tropical weather, and rainfall from these clouds forms a portion of the water used by the populations of these islands. It is interesting to observe cumulus clouds extending upward with varying forms. Any time you look up at the sky, remember that these clouds are a symbol of atmospheric circulation in the tropical climate.

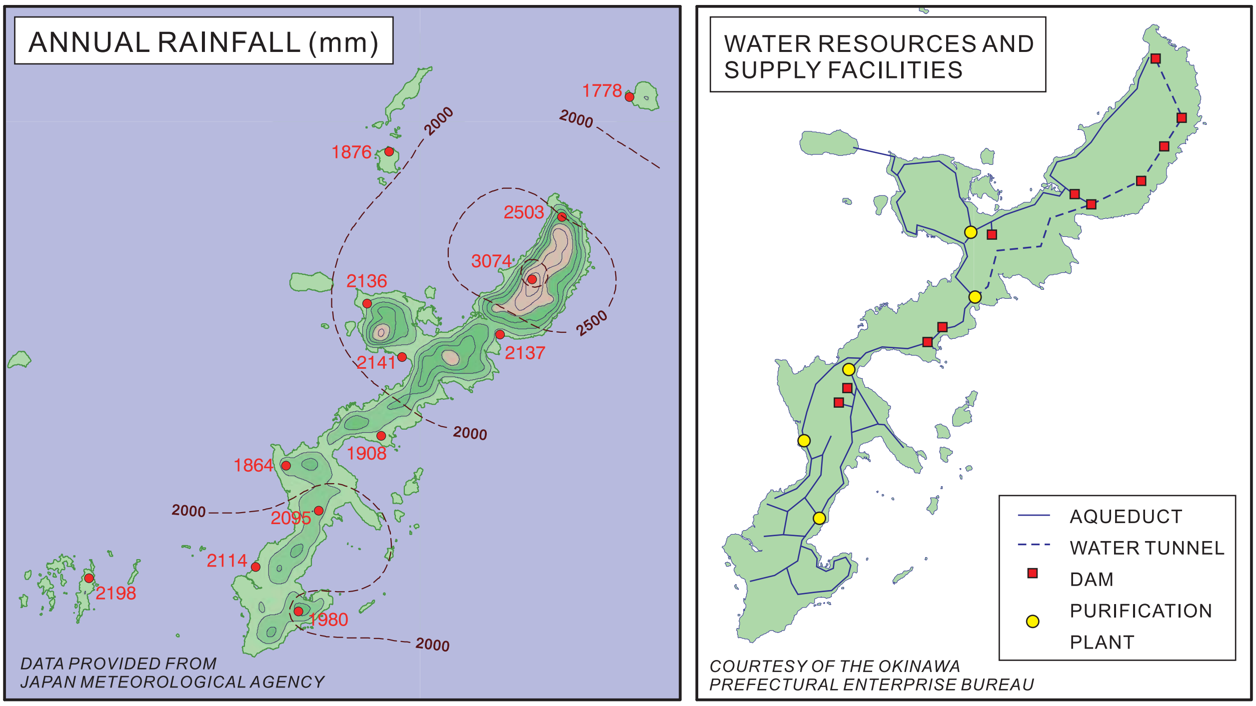

Figure 7. (Left) Distributions of topography and annual rainfall on Okinawa-jima Island and its vicinity. Contours are drawn every 50 m, and areas higher than 200 m are shown in brown. (Right) Distribution of facilities associated with the water supply system on Okinawa-jima Island.

Column 9. The Kuroshio and its bounty

Momoki Koga

The Kuroshio as a part of the subtropical gyre in the North Pacific Ocean

As shown in Figure 1, a large-scale loop current system (subtropical gyre) is present in the low and middle latitudes of the North Pacific Ocean. It is a typical large-scale wind-driven current induced by easterly wind (trade wind) in the low latitudes and westerly wind in the mid-latitudes. The western part of this loop current is swift and narrow because of the effect of the rotation of the earth (westward intensification). This swift and narrow current is named “Kuroshio” in Japanese. The Kuroshio flows northwards along the edge of the continental shelf in the East China Sea near the Ryukyu Archipelago. Its speed is approximately 4 km/h, and its width approximately 100 km. The flow extends to a depth of several hundred meters and transports a large amount of seawater from low latitudes to high latitudes, as if it were a “huge river in the ocean.”

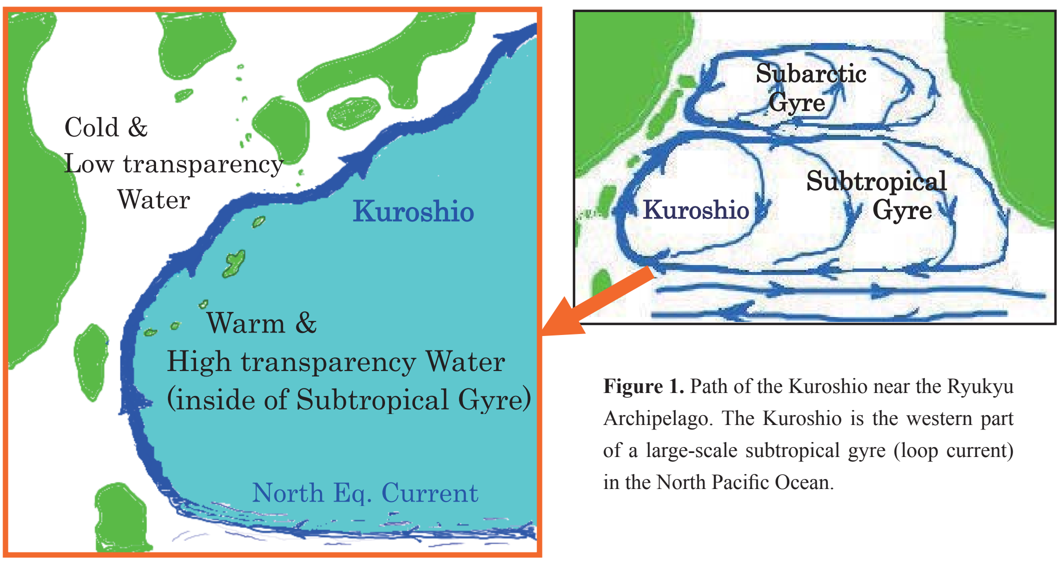

Figure 1. Path of the Kuroshio near the Ryukyu Archipelago. The Kuroshio is the western part of a large-scale subtropical gyre (loop current) in the North Pacific Ocean.

Water temperature and transparency in the Kuroshio region around the Ryukyu Archipelago

Let’s examine the water temperature and transparency in relation to the abovementioned flow of the Kuroshio. Figure 2 shows sea surface temperature (SST) in winter (upper) and summer (lower). Although the seasonal differences of SST are clear between the two seasons, the following fact is important and common to both. To the northwest of the Kuroshio’s path (dashed lines), SST decreases distinctly; but southeast of the path, SST does not decrease as much. This tendency of temperature decrease on the northwest side is clearer in deeper water (*e.g.*, 200 m depth), but the seasonal differences in SST in deeper water is smaller than in more shallow waters. Because the Kuroshio transports warm water from low latitudes, we might expect the water temperature to decrease on both sides of the Kuroshio path. However, the real temperature distribution is not like this. We must consider that the warm water is within a gyre and that the Kuroshio flows at the western edge of this warm water gyre. Although the SST shown in Figure 2 decreases naturally as latitude increases, SST at the same latitude inside the gyre is warmer and rather uniform.

Figure 3 shows the transparency of surface waters. The 25-m transparency contour line in the

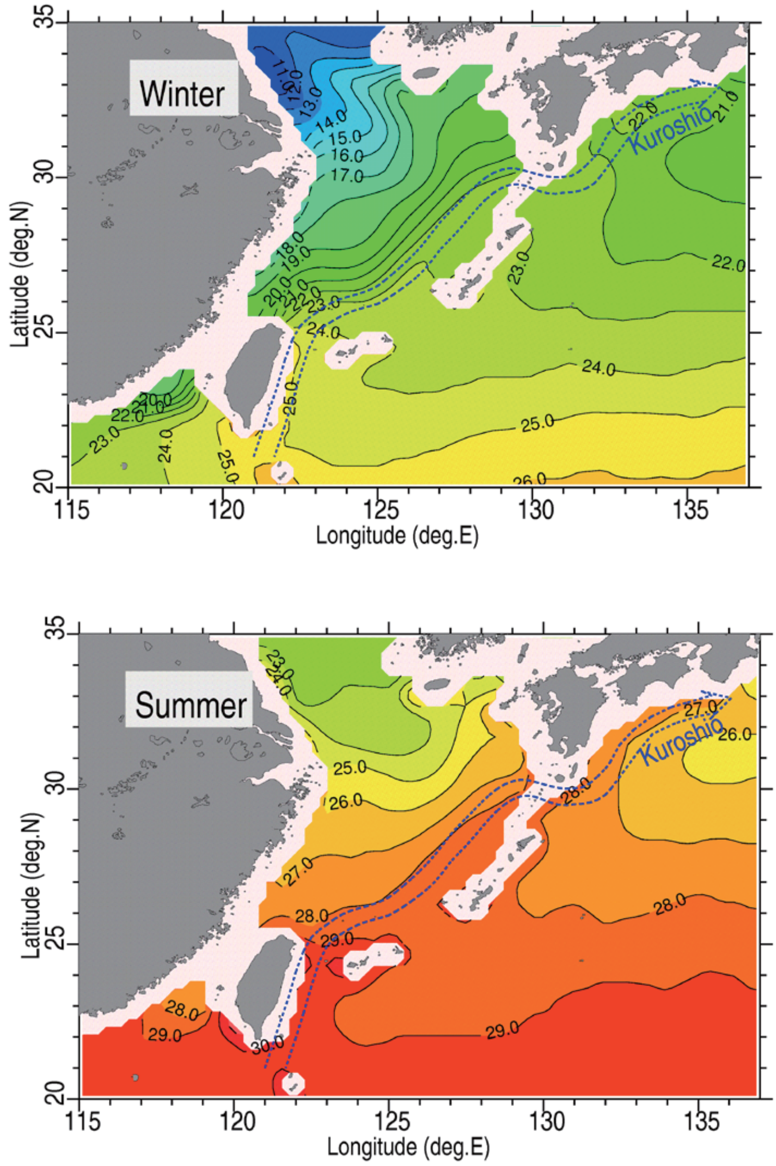

Figure 2. Sea surface temperature (SST; °C) in the Kuroshio region. Upper image: Winter (December, January, and February); Lower image: Summer (June, July, August). Satellite data/RSS-TMI (9 years, 1998–2006) were used.

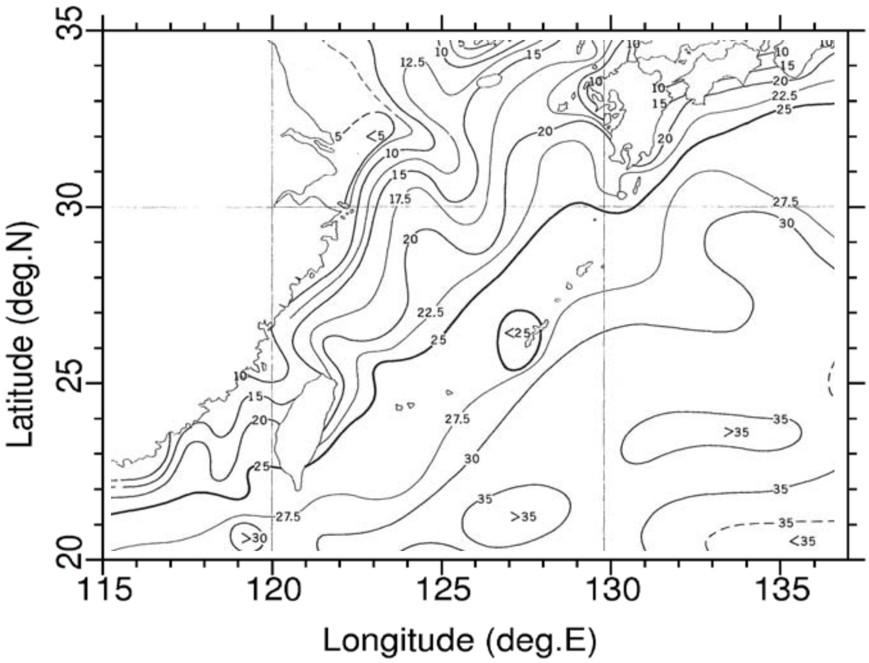

Figure 3. Transparency of surface water in the Kuroshio region. Transparency is measured as the limit of visibility of a Secchi disk (a 30-cm diameter white disk) viewed from the water surface. Inside the gyre (southeast of the Kuroshio), transparency is high at more than 25 m. The contour map is from "Ocean Environmental Map," Japan Hydrographic Association.

figure almost overlaps with the path of the Kuroshio. Inside the gyre (southeast of the path), transparency is high. However, transparency is low outside the gyre. Transparency of more than 25 m indicates very clear water, as the transparency of Lake Mashu, the well-known and clearest lake in Japan, is about 20 m. Hence, we can say that the water within the gyre is relatively warm and very clear (see Fig. 1). In Japanese the word "Kuro-shio," "kuro" means "deep-blue color" (as a result of high transparency) and "shio" means "current".

Bounty from the Kuroshio

The fact that the Ryukyu Archipelago are within the warm and clear subtropical gyre water is important for understanding the natural environmental conditions around the Ryukyu Archipelago. The islands are in a subtropical-oceanic climate under the background of the Kuroshio flowing near the islands. The sea surface temperature (SST) around the islands is more than 22°C, even in winter, as shown in Fig. 2. This strongly contributes the warm winter in the islands, during which the mean air temperature does not drop lower than 15°C. On the other hand, summer is long and muggy with a humidity of approximately 80%, although the mean air temperature during summer is typically below 29°C. Such a unique climate has resulted in the evolution of various unique animals and plants on the islands.

The ocean around the islands is also bountiful, with many tropical and subtropical sea organisms, such as coral, tuna, and many more. Although the clear water indicates less nutrients, the organisms therein compete and cooperate in the warm, light-filled water. In the coastal waters, the marine algae "Mozuku" and "Umi-budo" and the tiger prawn "Kuruma-ebi" are farmed. In the Kuroshio region, various migratory fishes—such as tuna and skipjack—survive by utilizing the Kuroshio. Fishermen set fish-aggregating devices, called "payao," to harvest fishes around the islands (see Figs. 4, 5). Peoples of the region, during their long history, have also contacted each other and traded many goods by utilizing the Kuroshio current. All of these bounties are due to the Kuroshio.

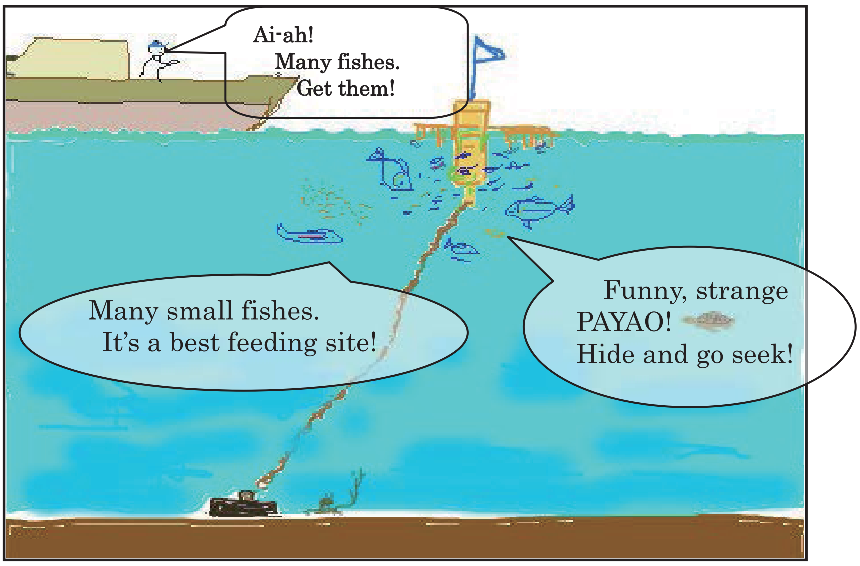

Figure 4. Payao fishery. Fish-aggregating devices, called payao, are used to gather migratory fishes such as tuna, skipjack, etc. The fishing unions of the Ryukyu Archipelago set many payaos of various types in the wafers around the islands.

Figure 5. Tunas and other coastal fishes gathered around payaos. Awase fish market, Okinawa-jima Island.

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3—3. Atmospheric aerosols: connected to the Asian continent

Takemitsu Arakaki

Atmospheric aerosols (or simply "aerosols") are small particles suspended in the air. They consist of both liquid and solid matter. When you open the curtains in the morning, you see small shining particles floating in the air reflecting sunlight—these are aerosols. The size of aerosols ranges from less than one micrometer (1/1000 of 1 mm) to more than tens of micrometers in diameter.

The sources of aerosols in Okinawa include wind-blown seawater (known as "seasalt"), anthropogenic activities such as fossil fuel combustion, and soil dust from the Gobi and Taklimakan deserts, etc. In recent years, increased industrial activity and environmental destruction in Asia have resulted in elevated levels of air pollutants, including aerosols. Aerosols, in particular PM2.5, which refers to aerosols smaller than 2.5 micrometers in diameters, cause health problems. Aerosols originating from the Asian continent can travel as far as the United States and Europe, and they certainly affect Okinawa. In this chapter, we will describe the chemical characteristics of aerosols detected in Okinawa.

Location of Okinawa in Asia

Figure 1 shows the location of Okinawa, which is east of the Asian continent. It is approximately 1800 km from Beijing, China, 1200 km from Seoul, Korea, and 1500 km from Tokyo, Japan. Typically, aerosols

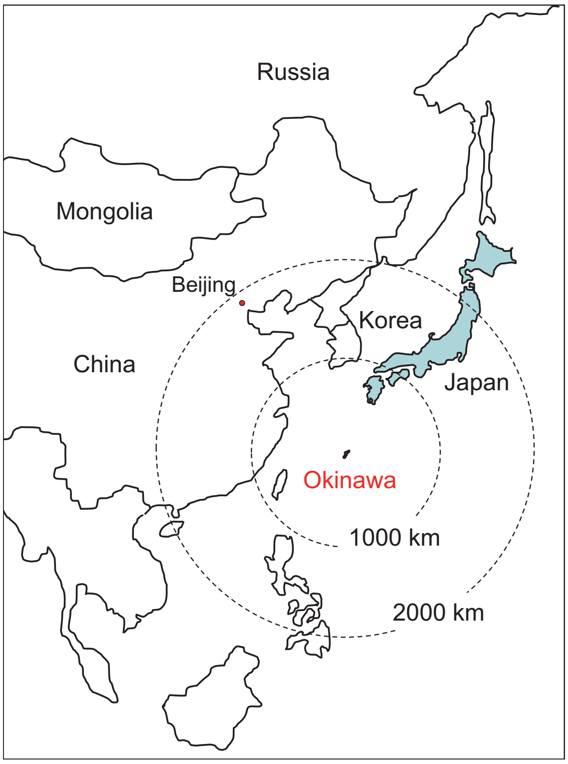

Figure 1. Location of Okinawa in Asia.

travel approximately 400-800 km per day, so aerosols from around Beijing can reach Okinawa in about 3 days. Recent studies have demonstrated that air pollutants emitted from the Asian continent travel across the Northern Hemisphere in 2-3 weeks. Thus, when an air pollution event occurs, pollutants can spread relatively quickly within the hemisphere.

In Okinawa, the wind direction varies greatly with the season. During summer, winds are mainly from east to southeast, whereas they are typically from the northwest during other seasons. Asian dust events (known as "Kosa" in Japan) usually occur during spring, but sometimes also occur in autumn and winter, and these can be observed in Okinawa. Figure 2 compares the haziness observed during a severe "Kosa" event in 2010 with typical clear-sky conditions at the same location in Okinawa. It is clear that air pollutants originating from the Asian continent can reach Okinawa and affect the air quality.

Figure 2. Haziness observed in the central area of Okinawa-jima Island during a severe Kosa event in 2010 (upper photograph) versus typical clear-sky conditions at the same location (lower photograph).

Chemical characteristics of aerosols

Various chemicals are present in aerosols that originate from the combustion of fossil fuels in factories and automobiles, from seawater, and from components of soil during Kosa, etc. These chemicals can mix in various ratios while travelling to Okinawa. By analyzing the chemicals in aerosols during different seasons with different wind directions, information on the sources and extents of pollutants can be obtained.

Figure 3 presents photographs of aerosols collected at Cape Hedo Atmosphere and Aerosol Monitoring Station (CHAAMS) during different seasons. The aerosols in the upper photo, which are yellowish in color, were collected during a Kosa event in spring. Aerosols collected during summer, when the aerosol content of the air is low, are typically a light-gray color (middle photo), while those collected in winter are often a dark color due to the higher content of organics during that season (lower photo). Almost 10 years of observations at CHAAMS have revealed that the concentrations of some major air pollutants in aerosols are about twice as high during spring as in summer. In summer, the dominant wind direction is from east to southeast and clean air from the Pacific Ocean is transported to Okinawa; whereas in spring, with a dominant wind direction of northwest, air from the Asian continent reaches Okinawa. Therefore, the chemicals present in aerosols

Figure 3. Photographs of aerosols collected on quartz filters in Okinawa: a sample collected during an Asian dust event, which is yellowish in color (upper photograph); a typical sample collected during summer, which is a light-gray color due to lower levels of aerosols (middle), and a typical sample collected during winter, which is a blackish color due to higher levels of organic materials (lower photograph).

around Okinawa are greatly influenced by long-range transport of pollutants from the Asian continent.

Chemicals originating from seawater account for about half of the components of aerosols collected in Okinawa, because Okinawa is surrounded by the sea. The proportion is higher during winter when strong northern winds prevail. Still, about half of the chemicals in aerosols originate from human activities and soils, such as Kosa events.

Figure 4 depicts the annual changes in the levels of human-activity-derived nitrate and sulfate in Okinawa during spring when the wind originates mainly from the Asian continent. Both nitrate and sulfate are formed in the atmosphere from by-products of fossil fuel combustion.

Nitrate is derived from the oxidation of nitrogen oxides emitted from automobiles and other combustion processes used at industrial sites, such as power plants. The levels of nitrate have been increasing at an annual rate of 16% since 2006. The level in 2008 was slightly lower due to the stringent traffic control measures enacted for the Beijing Olympic Games. In China, the number of automobiles increased by 2.5-fold between 2006 and 2010. The increase in the number of cars is regarded as a major cause of the increased nitrate levels.

In contrast, levels of sulfate resulting from the oxidation of sulfur in fossil fuels have decreased slightly. The consumption of fossil fuels such as coal increased with rapid economic development in China, which should have increased sulfur dioxide emissions, which become sulfate. However, sulfur dioxide emissions

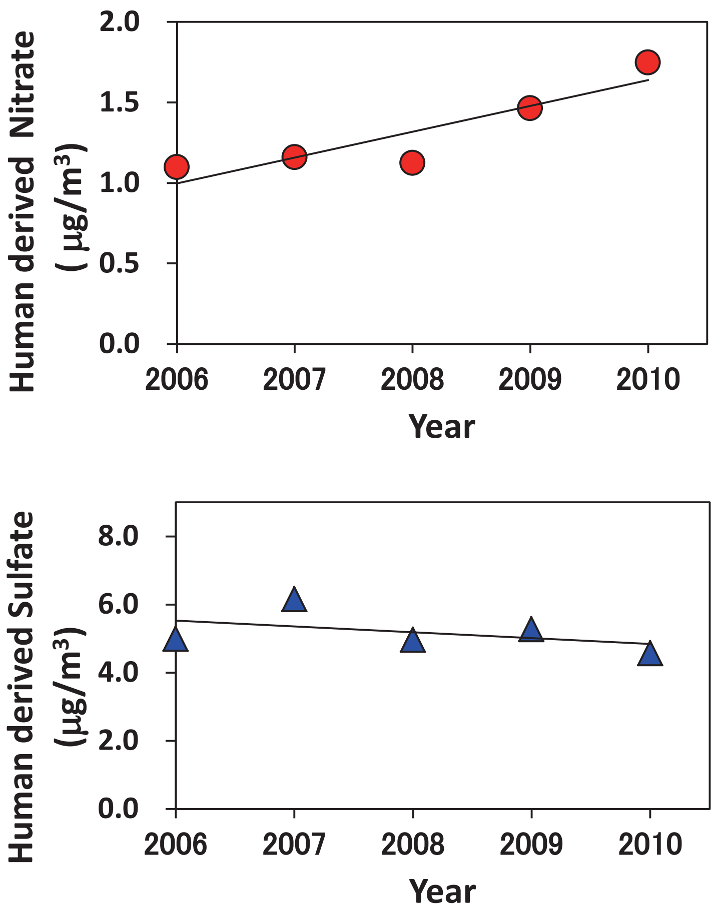

Figure 4. Annual changes in the levels of nitrate and sulfate derived from human activities. The y-axes represent the amounts (1 µg = 10^{-6} g) of nitrate or sulfate per cubic meter. Nitrate levels have increased at an annual rate of 16% since 2006. In contrast, sulfate levels have decreased slightly.

decreased after around 2008, likely due to the widespread use of so-called “desulfurization devices”, which remove sulfur from fossil fuel. Regarding sulfate, it may be said that pollution control is heading in the right direction.

Investigation of aerosols by electron microscopy

Chemical consituents of aerosols are so small that they cannot be seen by the naked eye, but we can take photographs of magnified aerosols by using a scanning electron microscope (SEM) with a magnification of up to 1000×. Figure 5 displays photographs of a filter before and after aerosol collection. Depending on their shapes, aerosol particles can be roughly classified into soil-derived particles with sharp corners or seawater-derived particles with relatively rounded shapes. Typically, seawater-derived particles are so large that they cannot be transported over long distances. Thus, the round particles seen in Fig. 5 are likely to have originated near CHAAMS. Furthermore, SEM allows us to take photographs showing only a specific chemical element. Figure 6 shows photographs of the same particles in Fig. 5, with the left image showing only

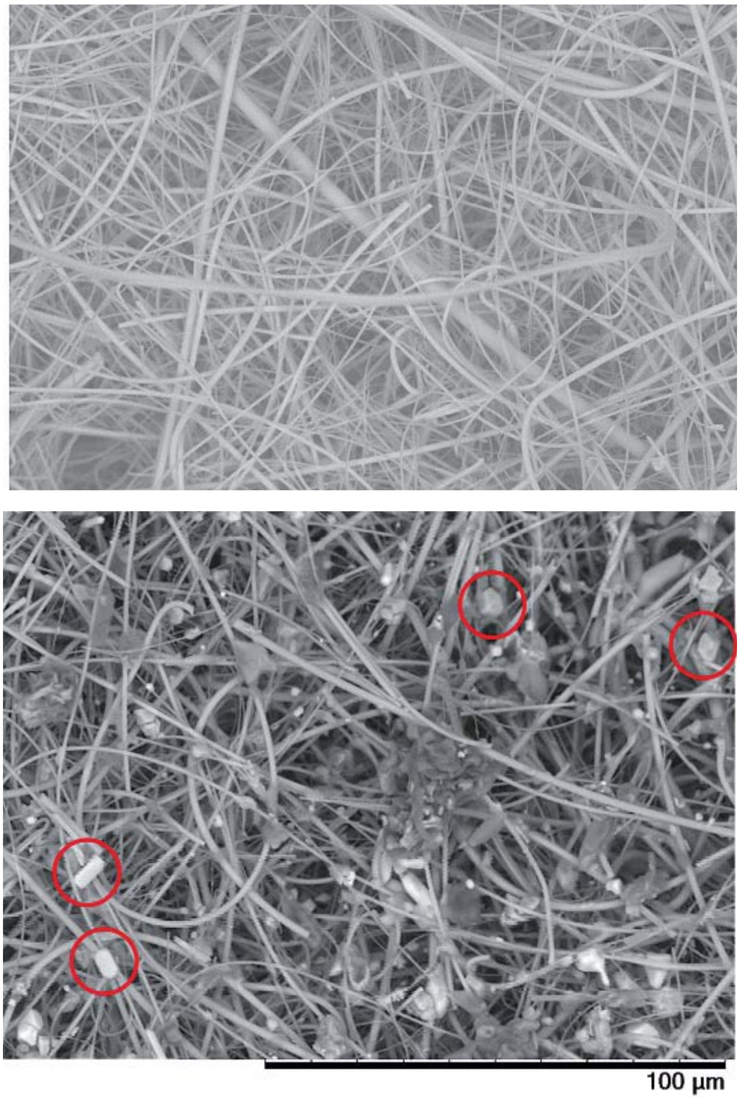

Figure 5. Scanning electron microscope (SEM) images of a filter before (upper photograph) and after (lower) aerosol collection. In the lower photograph, particles indicated by the red circles in the upper-right area have sharp corners, indicating that they were probably derived from crustal materials. Particles identified by the red circles in the lower-left area have relatively rounded shapes, indicating that they probably originated from seawater. Magnification = 1000×.

sodium (colored orange), and the right showing only chlorine (green). Note that the round particles indicated by the red circles in the lower-left area in Fig. 5 are evident in both the sodium and chloride photographs, indicating that they are composed mainly of sodium chloride; *i.e.*, sea salt. Thus, SEM can be used to investigate the chemical composition of aerosols and their sources.

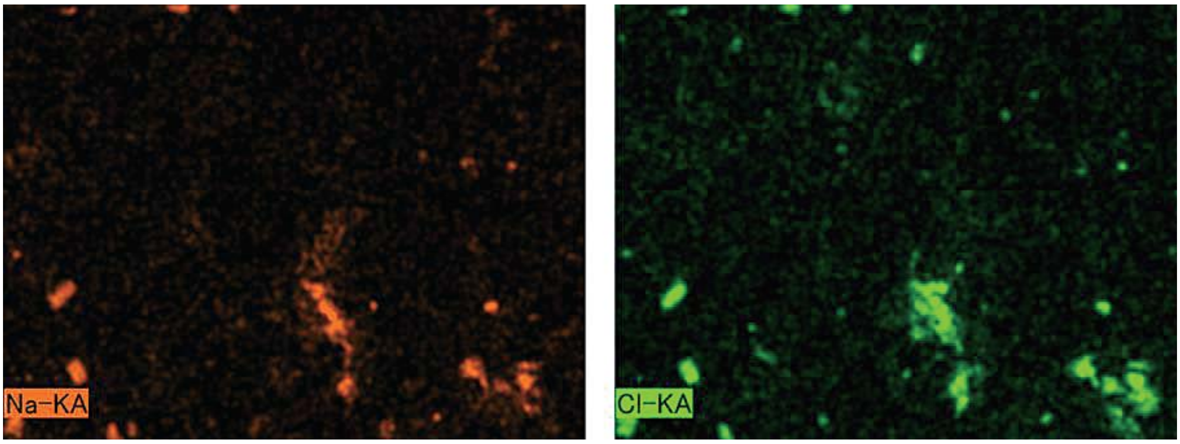

Figure 6. Elemental analyses of the particles shown in Fig. 5. Particles containing sodium appear orange (left photograph), whereas particles containing chlorine appear green (right). Therefore, particles that appear in both photographs are thought to be sodium chloride, which originated from seawater.

Prospect of future aerosol studies in Okinawa

Due to continuing economic development in the Asian continent, air pollution is likely to worsen in the future. The impacts of air pollutants on the ecosystem and biodiversity of Okinawa are poorly understood. For example, as nitrogen oxide emission increases, nitrogen input from the atmosphere into the ocean and soil of Okinawa-jima Island is likely to increase. Nitrate is a nutrient, but it can also cause eutrophication and exert adverse effects on ecosystems (cf. Column 12). In addition to nitrogen oxide, carcinogens and harmful heavy metals are also released from the combustion of fossil fuels. Therefore, it is important that we continue to monitor transboundary air pollutants.

Column 10.
Origin of red soil, Shimajiri-maji

Masahide Furukawa

Red soils are distributed widely over Okinawa, and Shimajiri-maji (Fig. 1) is one of these. Its main material had been considered to be residue from the weathering of Ryukyu Limestone, which is composed mainly of Pleistocene coral reef. However, recent studies strongly suggest that the origin of Shimajiri-maji is eolian dust, or so-called yellow sand, carried by wind from China.

The following three pieces of evidence are considered to support the view of an eolian dust origin.

(1) Ryukyu Limestone is composed mainly of calcium carbonate and contains only approximately 1% mineral particles as a potential base material for the soil. Calcium carbonate dissolves away under weathering (see Section 1-3). Therefore, to make a 1-m thickness of Shimajiri-maji, it would be necessary to weather a 100-m thickness of Ryukyu Limestone. However, large-scale weathering such as this is not known.

(2) The results of various analyses performed on the mineral particles revealed that Shimajiri-maji is similar to soils distributed in the southern part of China, including the Tibetan Plateau.

(3) The concentration of naturally occurring radioactive elements, such as uranium, contained in Shimajiri-maji is comparatively high. Around Okinawa, soils and rocks having a concentration equivalent to that of Shimajiri-maji are distributed widely in only an area of southeastern China that has a high level of natural radiation (Fig. 2).

These pieces of evidence mean that Shimajiri-maji originated from eolian dust blown across the sea from the continent. Additionally, it is estimated that Shimajiri-maji formed during the last ice age, 70,000–10,000 years ago, when the whole surface of the earth was dry and cold. During the ice age, because sea levels were lower than at present, the continental shelf of the East China Sea was dry. In other words, the source area of eolian dust expanded to the region around Okinawa. By this process, it is believed that large amounts of eolian dust were blown to Okinawa, generating Shimajiri-maji on Ryukyu Limestone and also becoming a portion of two other weathered soils of mudstone and sandstone, Jagaru and Kunigami-maji.

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Figure 1. Sugar cane field covered mainly with Shimajiri-maji (red soil) in the southern part of Okinawa-jima Island. In recent years, pebbles of grayish-blue mudstone have been added to the red soil in many fields to increase its moisture-holding capacity.

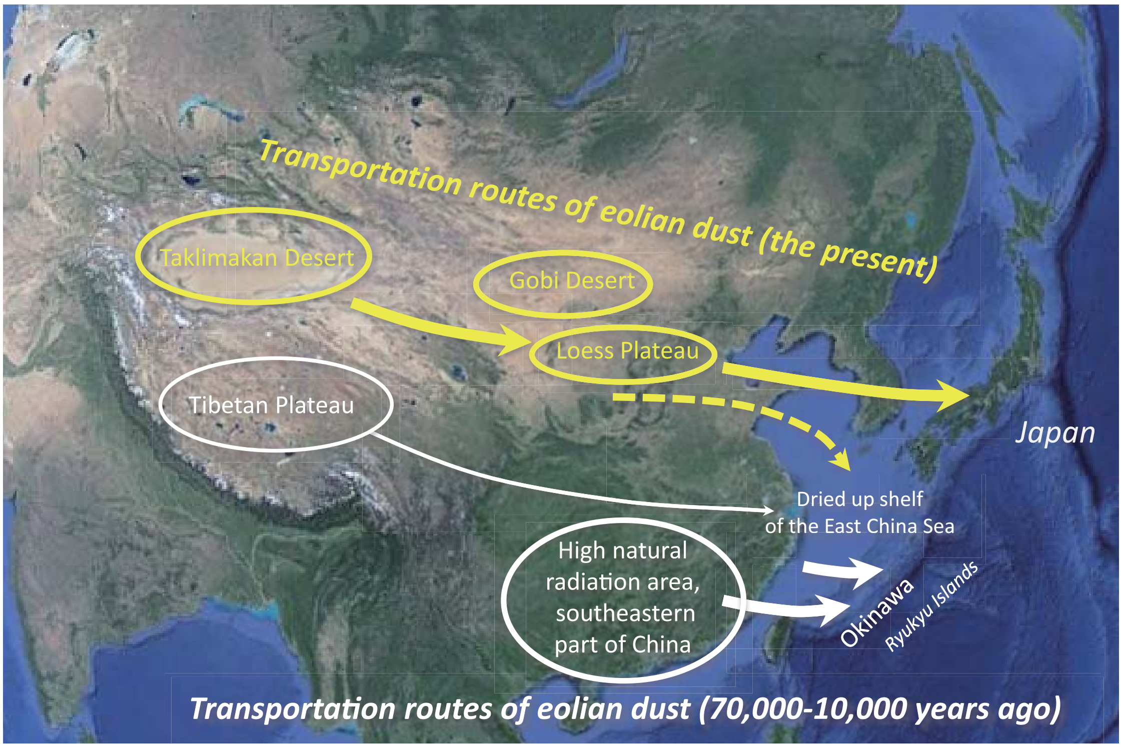

Figure 2. The main sites of origin and transportation routes of eolian dust at present (yellow circles and arrows) and during the last glacial age, 70,000–10,000 years ago (white circles and arrows). During the last glacial age, the emerged continental shelf of the East China Sea is thought to have been the supply area of eolian dust. The map was drawn using Google Earth.

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Chapter 3—4. Inside speleothems

Ryu Uemura

In the Ryukyu Archipelago, there are many limestone caves, which vary in size from small holes to a massive caves with a length of 5000 m. A limestone cave is called "Gama" in the dialect of Okinawa, and is regarded as a sacred place. During World War II, these sacred places became places of death and sorrow because they were used as evacuation shelters, hospital shelters, and for weapons storage (Fig. 1). At present, some historic caves are open to tourists.

Recently, these caves have received worldwide attention as an important place in recording the history of global climate change. The speleothems inside these caves contain hundreds of thousands of years' history of the Earth. Here, we will focus on the inside of various speleothems.

There are many limestone caves in Okinawa, including Gyokusen Cave, a famous cave in the southern part of Okinawa-jima Island. Another large cave, Hoshino Cave, exists on Minami Daito-jima Island, 400 km east of Okinawa-jima Island. Numerous white speleothems with complex and unique shapes made by nature are found in the Hoshino Cave (Fig. 2).

Mechanism of speleothem formation

How do speleothems form? The process is related to the fact that the Ryukyu Archipelago are made mainly of limestone (see section 1-4). Limestone, composed of calcium carbonate, is soluble in rainwater. In particular, it dissolves with the addition of CO_2 emitted from microorganisms and plant roots in soil. Water, containing much calcium, becomes recrystallized in the cave as calcium carbonate (Fig. 3).

Figure 1. Entrance of a cave in the southern part of Okinawa-jima Island.

Figure 2. Hoshino Cave, Minami Daito-jima Island.

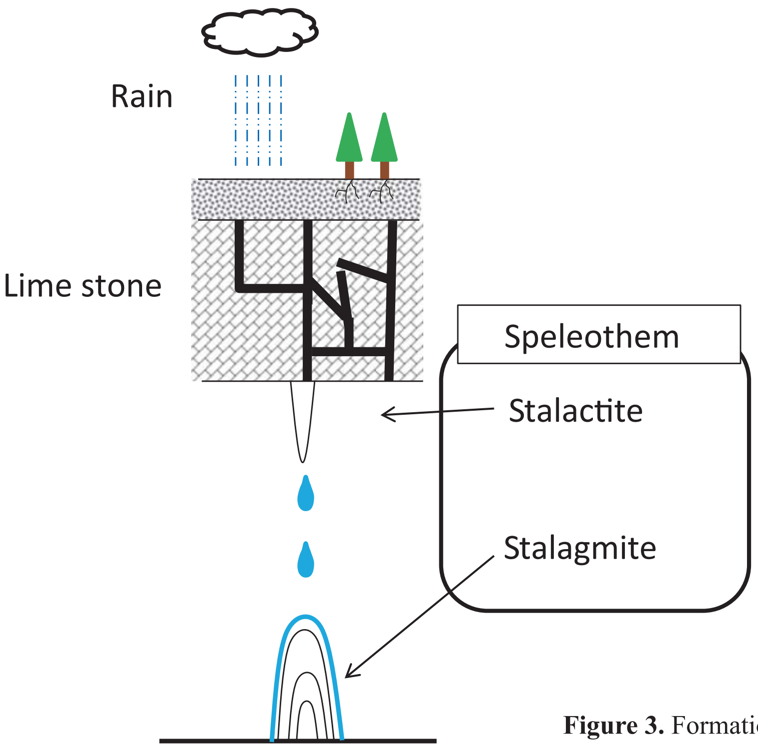

Figure 3. Formation of speleothems.

Speleothems are given various names, depending on their shape and growth location. Those that hang from the ceiling are known as "stalactite", whereas those that grow upward from the floor are called "stalagmites."

The inside of speleothems

Let us look inside speleothems. Because speleothems are a natural rock, breakage is uncommon. The speleothem shown here (Figs. 4, 5 and 8) was cut and damaged during construction of a corridor that was built to enable access by tourists.

The most famous speleothems are stalactites, which hang from the ceiling of the cave. A hollow speleothem can also form from the celling, and is called a “straw.” The stalactite grows along the central axis of this straw; in cross sections, the hollow structure remains in the center. The layers in the vertical direction show that it grew by fattening in the horizontal direction (Fig. 4).

Next, let us look at the cross section of a “stalagmite.” Because of the different growth direction, the layers of a stalagmite are completely different from those of a stalactite. Horizontal layers can be seen in the cross-section of a stalagmite (Fig. 5). Naturally, these grow from the bottom-up.

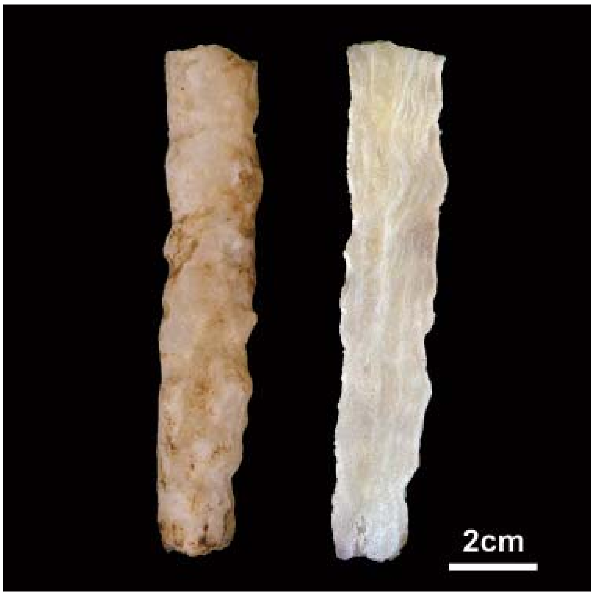

Figure 4. A stalactite (left) and its cross section (right).

Figure 5. A stalagmite (top) and its cross section (bottom).

Figure 6. A helictite (Hoshino Cave, Minami Daito-jima Island).

Figure 7. A stalagmite (Hoshino Cave, Minami Daito-jima Island) and coral skeleton (circle).

Another type of stalactite formation, called a “helictite”, grows in yet another direction. It has branches in the longitudinal and horizontal directions, as if it had grown in the absence of gravity (Fig. 6). In addition, there is a unique stalagmite formation, the surface of which is covered with numerous small balls (Fig. 7). Although crystal growth is an inorganic process, such a speleothem resembles a strange organism. In fact, some coral skeletons in the sea (Fig. 7, circle) appear to be similar in shape.

The past environment is preserved in speleothems

Chemical composition analyses of these mysterious speleothems have revealed much information. Recent advancements in analytical techniques enable us to determine the precise ages of stalagmites by radioisotope analysis. For example, the age of the stalagmite shown in Fig. 8 was estimated to be 14,000 years at the top layer, and 22,000 years at the bottom.

Furthermore, it is possible to estimate the temperature and rainfall amount from the chemical composition of stalagmites because the ratio of stable isotopes of oxygen (which have different weights) changes in response to temperature and precipitation. These data will help us to understand changes in the Earth’s climate. By assessing the chemical composition of stalagmites, climate conditions (such as temperature and precipitation) at that point in time can be determined, providing an accurate history of global climate change over the past several hundred thousand years. Thus, stalagmites represent time capsules that have preserved the climate history of the Earth.

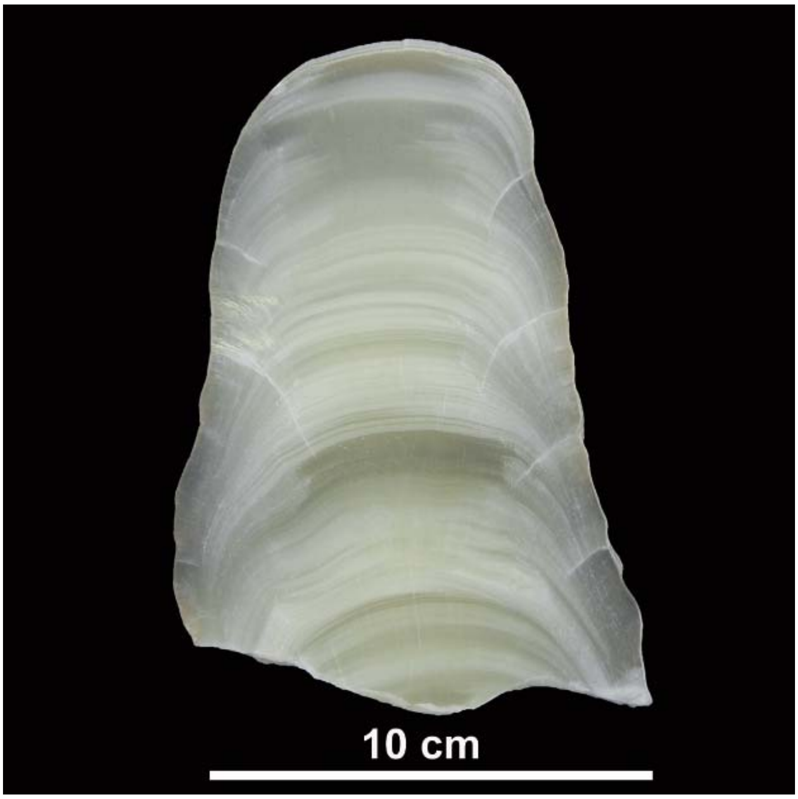

Figure 8. Cross section of a stalagmite (Hoshino Cave, Minami Daito-jima Island).

Column 11.
The growth of speleothems and the cave environment

Akira Tanahara

Many types of speleothem have developed in Hoshino Cave on Minami Daito-jima Island (Fig. 1). How fast do speleothems grow? To determine their grow rate, the quantities of natural radioactive elements in the speleothems are measured precisely. Stalactites grow slowly, at rates ranging from several centimeters to several hundreds of centimeters per 1000 years. One fast-growing type of stalactite is called a "soda straw" stalactite based on its appearance. Most soda straws grow at a rate of several centimeters per 10 years. A large number of soda straws a meter or more in length are found in Hoshino Cave (Fig. 2). Speleothems represent a valuable tourist resource, and therefore we must strive to preserve the cave environment.

Most caves in Okinawa-jima Island have high humidity and little temperature variation in comparison to the outside environment. Because the temperature in the cave is approximately 20°C, persons inside a cave feel cool in summer and warm in winter. This peculiar "microclimate" affects the growth of speleothems and organisms in the cave. The airflow in the cave cannot be felt, but the air circulation is often stronger in one season, usually winter.

High concentrations of a natural radioactive gas called "radon" are present in cave air. Continuous measurement of radon provides information about the air circulation in caves, and can be used to determine the growth rate of soda straws.

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Figure 1. Hoshino Cave on Minami Daito-jima Island. Columns are formed when stalactites and stalagmites meet.

Figure 2. Straw stalactite found in Hoshino Cave. The right-hand photo shows a close up of a straw stalactite.

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Chapter 3—5. The long journey of deep ocean water

Shigeru Ohde and Harutaka Hanada

Seawater deeper than 200 m is generally called deep ocean water (DOW), and sunlight does not reach this depth. Here, we discuss especially DOW at depths greater than 1000 m. DOW is seawater that was originally in the surface layer and was transported to the deep layer by various processes after being kept away from the atmosphere which influences the surface water. Therefore, DOW is much different from surface water in terms of its physical and chemical properties, such as temperature, trace element composition, and so on.

During the 1990s, the practical use of DOW attracted much interest, and in 2000 the Deep Sea Water Research Center was established on Kume-jima Island, Okinawa following the construction of similar facilities in Kochi and Toyama. DOW obtained by land-based apparatus is now used for food processing, agriculture, aquaculture, and so on. In 1995, the Deep Sea Water Development Co-operative Society made a plan to take the seawater from 1400 m depths near the Ryukyu Trench off Itoman, Okinawa. Subsidized by the Okinawa Prefectural Government and using the world's first ocean floating apparatus, Umiyakara 1 (see location in Fig. 1), they succeeded. The following section describes the long history of the 1400 m deep seawater collected by Umiyakara 1.

Chronology of deep seawater

In 2000, radiocarbon (5570-year half-life) in DOW collected by Umiyakara 1 was analyzed for dating, based on the principle that the amount of radiocarbon decreases over time due to radioactive decay. This radiocarbon dating method is often used in archaeology. The measurement showed that the percent of modern carbon (pMC) in DOW was 77.7%, meaning that the quantity of radiocarbon had decreased by 22.3%; this corresponds to a calculated age of 2030 years for DOW at a 1400-m depth in the area. This is a potentially significant finding because an approximate age of 2000 years is almost identical to that of DOW at 2000 to 3000 m deep in the North Pacific Ocean (latitude 30° to 50° north), which has been considered to be the world's oldest DOW. Let us consider the reason that DOW in the North Pacific—including the DOW collected by Umiyakara 1—is about 2000 years old.

Where does deep seawater come from?

In 1958 Henry Stommel, an American physical oceanographer, presented a theoretical ocean global circulation model (OGCM), based upon the properties of seawater including the density, calculation of the Earth's rotation, and the topographies of land and oceans. The model presented the DOW of the world's oceans such as the Pacific, Atlantic and Indian as almost homogeneous, having originated in surface water that sank to great depths in two limited oceanic areas, one area off Greenland and the other in the Antarctic Ocean, and also stated that DOW circulated worldwide in deep currents. The theoretical OGCM by Stommel was shown to be more or less correct through subsequent direct measurements of deep currents and marine observations using tritium (hydrogen isotope) and radiocarbon as tracers.

In 1989 Wallace Broecker, another American marine chemist, demonstrated a very simple and elegant model known as the Ocean Conveyor Belt (Fig. 1) to clarify the OGCM; this was based on measurements of the radioactive isotope levels, temperature, salinity, dissolved oxygen, and chemical compositions of the oceans. Seawater in the surface layer off Greenland sinks into the deep layer, flows southward in the Atlantic Ocean, joins seawater that sunk in the Antarctic Ocean, and travels to the Indian and further to the Pacific Ocean; however, part of this joins DOW flows in the upwelling current in the Indian Ocean while the other part joins the Pacific Ocean. Finally, each water particle returns to the original point off Greenland as surface water (Fig. 1).

Is the Broecker model correct? Tritium (12.3-year half-life) and radiocarbon are both produced as the

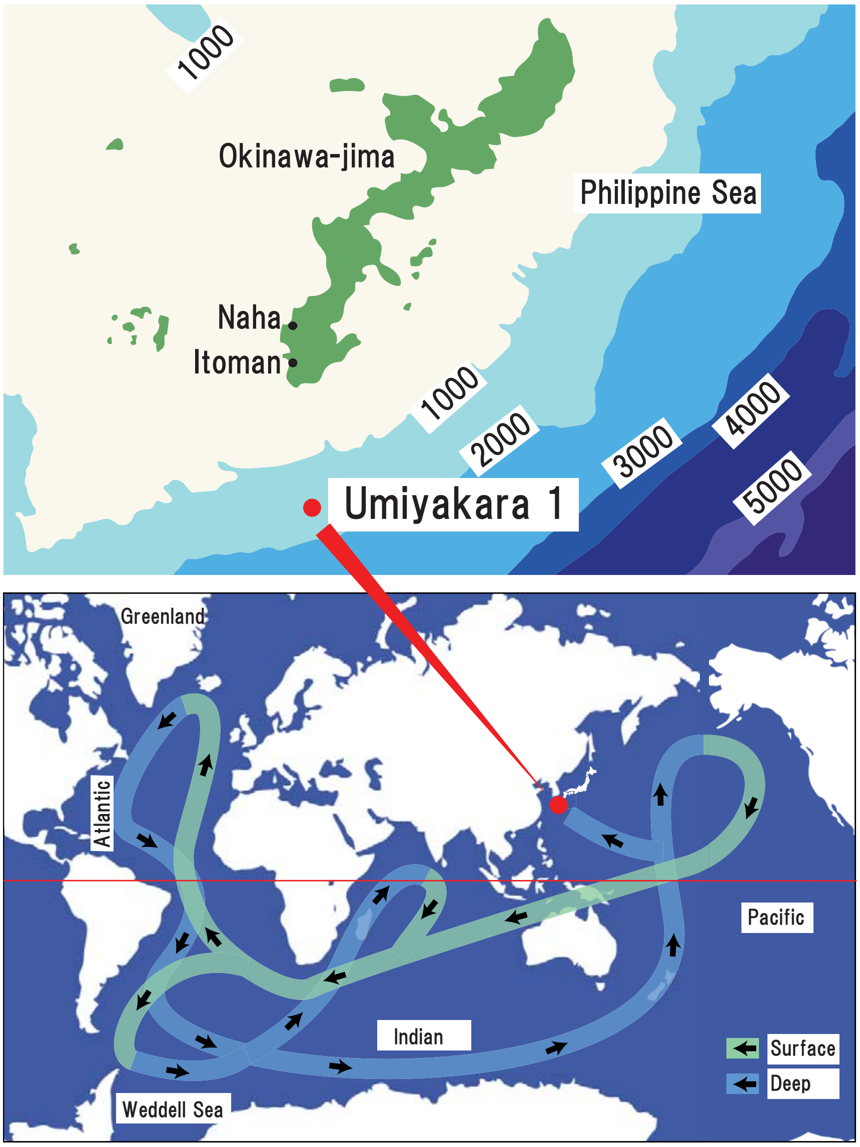

Figure 1. Map showing the location of Umiyakara 1 in the Philippine Sea near Itoman, Okinawa (upper figure). Modified sketch based on the so-called "great ocean conveyor" proposed by Broecker showing the flow of deep seawater (blue ribbon with arrows) originating in the North Atlantic Ocean near Greenland and the Weddell Sea (lower figure).

result of the collision of cosmic rays with the atmosphere, which means that tritium and radiocarbon at the ocean surface comes from the atmosphere. A distribution map of tritium in the Atlantic Ocean was constructed based on measurements of the amount of tritium in the ocean. The tritium map verifies that the surface water off Greenland and in the Antarctic Ocean sinks into the deep layer to a depth of >1,000 m, as a sinking current. Radiocarbon dating of DOW was carried out in the Atlantic, Indian, and Pacific Oceans and revealed that the Atlantic Ocean DOW at 2000 to 3000 m depths on the equator is approximately 500 years old, and that of the Pacific Ocean on the equator is approximately 1800 years old. Considering that the DOW at 2000 to 3000 m depths in the North Pacific Ocean is approximately 2000 years old, investigations using radioisotopes as tracers indicate that the OGCM is by-and-large correct.

Long journey of deep seawater collected by Umiyakara 1

As discussed above, DOW at 1400 m depth near Okinawa in the Philippine Sea is about 2030 years old, which is almost identical to that of the world's oldest North Pacific Ocean DOW at a depth of 2000 to 3000 m. This discovery leads to the conclusion that DOW originating in surface water sunk off Greenland flowed via the global oceanic conveyor through to the Philippine Sea near Okinawa, where Umiyakara 1 is installed, and arrived in the North Pacific Ocean after a long journey (Fig. 1).

To verify this model, we used available radiocarbon data of Philippine Sea DOW. Two samples of DOW from depths of 4814 m (latitude 12° north, longitude 136° east) and 5466 m (latitude 17° north, longitude 133° east) in the Philippine Sea were measured, and revealed ages of 1859 to 1978 years. It is clear that DOW in the Philippine Sea is typically ≤2000 years old. The data strongly indicate that DOW from 1400 to several thousand meters in depth, both in the Pacific Ocean—especially near Japan—and in the Philippine Sea, is approximately 2000 years old. DOW obtained by Umiyakara 1 belongs to the world's oldest water mass. Given that the water mass deeper than 1000 m is physically and chemically homogeneous, and DOW in the Philippine Sea is typically ≤2000 years old, we can recreate the 2000 year history of DOW obtained by Umiyakara 1 at 1400 m depth as follows.

The North Atlantic Ocean DOW originating in surface water that sinks off the coast of Greenland flows southward and in some hundreds to around one thousand years arrives in the Antarctic Ocean; this DOW travels further eastward around the Antarctic. During this time, new seawater that sinks in this area joins the North Atlantic Ocean DOW. Part of this DOW moves into the Pacific Ocean and becomes Pacific Ocean DOW (Fig. 1), which further moves northward to the Tonga Trench, passes the equator, and approaches the Mariana Trench. Part of this DOW moves further northwestward into the Philippine Sea and becomes Philippine Sea DOW; a part of this flows further north through the deep valley of the Kyushu-Palau Ridge to reach the Ryukyu Trench.

The world's oldest seawater (age, approximately 2000 years) accomplishes its long journey as DOW by mixing with seawater shallower than 1000 m off Itoman in the upwelling current. At the final stage of this journey, this nutrient-rich DOW, after mixing with surface water, flows into and enriches coral reefs. This deep seawater might play an important role in maintaining the coral reef ecosystems of Okinawa.


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Column 12.
Benefits and threats of freshwater to coral reefs in coastal areas

Kentaro Tanaka

Seawater of the coral reefs in the Ryukyu Archipelago and Southeast Asia is affected by open-ocean water and fresh water from land, such as rivers and groundwater. Reef-building corals have symbiotic algae in their tissue. Symbiotic algae can photosynthesize and supply nutrients to corals and marine organisms living in coral reefs. Thus, reef-building corals prefer to live in seawater of high transparency, in which the corals can bask in sufficient sunlight. The Ryukyu Archipelago are located along the Kuroshio Current, which is characterized by high transparency (Fig. 1, top). In addition, coastal seawater around the Ryukyu Archipelago is affected by inflows of freshwater from land. Freshwater carries nutrient elements, such as nitrogen, phosphorus and silicon, to coral reefs in the coastal area. Nutrients supplied from land are consumed by primary producers in the marine ecosystem, including the symbiotic algae of corals. In nutrient-rich seawater, symbiotic algae produce much of the organic matter, which promotes growth of the algae. In addition, a proportion of the organic matter is released into the coral reef, and consumed by other marine organisms living there.

However, increases in population and the modernization of agriculture has resulted in pollution of rivers via the discharge of household effluents and chemical fertilizers, the nutrient concentrations of which are very high. The discharge of a large amount of anthropogenic nutrients into coastal seawater via rivers causes reduced transparency of seawater due to the mass blooming of plankton. For example, environments in the Gulf of Thailand are formed by the mixing of fresh water and seawater. During the rainy season, the large discharge of nutrients via rivers causes mass blooming of plankton. This mass blooming event temporally decreases transparency in coral reefs of the gulf (Fig. 1, bottom).

Heavy rain during the rainy season and typhoons leads to erosion of soil in the Ryukyu Archipelago. In addition, bank protection construction erodes soil along rivers. These erosion events temporarily decrease the transparency of seawater in coastal coral reefs, which results in a reduction of the photosynthesis rate of corals' symbiotic algae, and the suffocation of corals.

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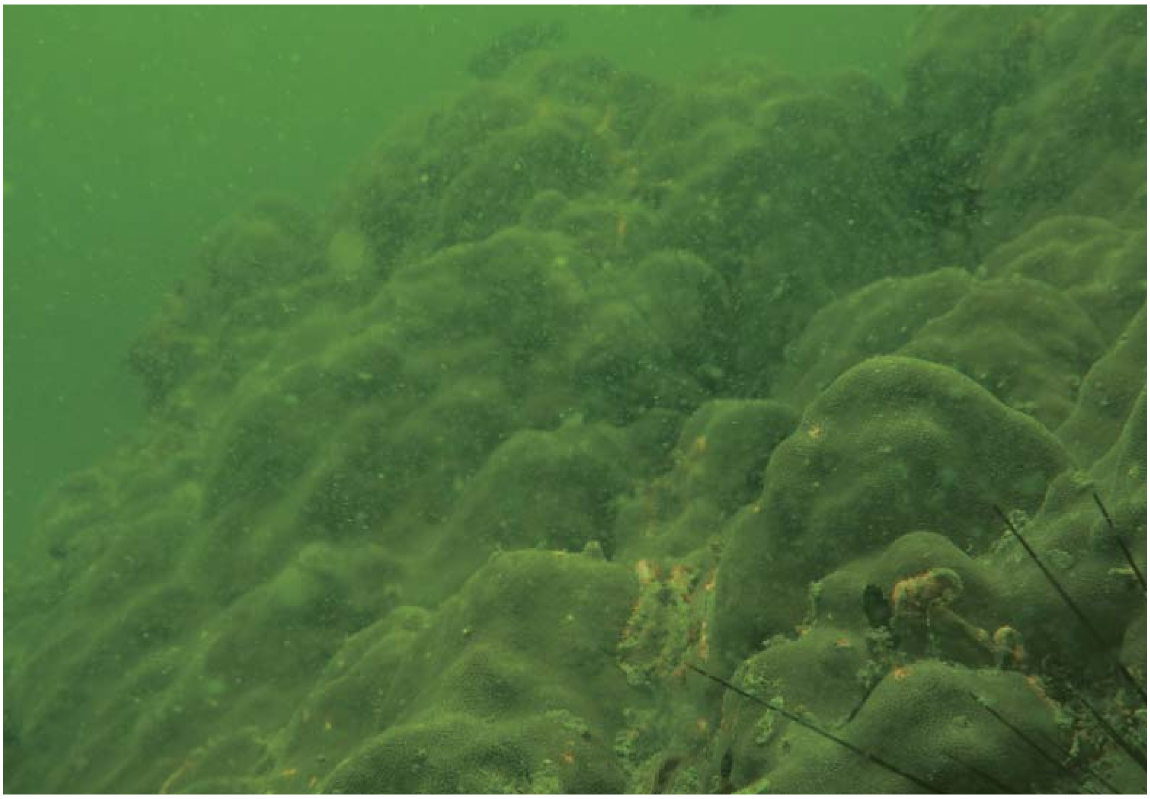

Figure 1. Top: Seawater surrounding coral reefs around the Ryukyu Archipelago (photograph by Chuki Hongo). Transparency is high in the Kuroshio Current due to lower levels of particulate matter and plankton. Bottom: Seawater of a coral reef in the Gulf of Thailand. During the rainy season, transparency is temporarily reduced due to the mass blooming of plankton triggered by large discharges of nutrients via rivers.