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Marine biodiversity research in the Ryukyu Islands, Japan: Current status and trends

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In Japan, the subtropical Ryukyu Archipelago (RYS; also known as the Nansei Islands) with its coral reefs has been shown to harbor very high levels of marine biodiversity. This study provides an overview of the state of marine biodiversity research in the RYS. First, we examined the amount of scientific literature in the Web of Science (WoS; 1995-2017) on six selected representative taxa spanning from protists to vertebrates across six geographic sub-regions in the RYS. Our results show clear taxonomic and sub-region bias, with research on Pisces, Cnidaria, and Crustacea to be much more common than on Dinoflagellata, Echinodermata, and Mollusca. Such research was more commonly conducted in sub-regions with larger human populations (Okinawa, Yaeyama). Additional analyses with the Ocean Biogeographic Information System (OBIS) records show that within sub-regions, records are concentrated in areas directly around marine research stations and institutes (if present), further showing geographical bias within sub-regions.

While not surprising, the results indicate the clear need to study ‘understudied’ taxa in ‘understudied sub-regions’ (Tokara, Miyako, Yakutane, Amami Oshima), and to study ‘understudied areas’ of some sub-regions away from marine research stations. Second, we compared the numbers of scientific papers on eight ecological topics for the RYS with numbers from selected major coral reef regions of the world; the Caribbean (CAB), Great Barrier Reef (GBR), and the Red Sea (RES). Not unexpectedly, the numbers for all topics in the RYS were well below numbers from all other regions, yet within this disparity, research in the RYS on ‘marine protected areas’ and ‘herbivory’ was an order of magnitude lower than numbers in other regions. Additionally, while manuscript numbers on the RYS have increased from 1995 to 2016, the rate of increase (4.0 times) was seen to be lower than those in the CAB, RES, and GBR (4.6 to 8.4 times). As the RYS are considered to contain among the most critically endangered coral reef biodiversity in the world due to high levels of both endemism and anthropogenic threats, much work is urgently needed to address
the areas of relative research weakness identified in this study.
Marine biodiversity research in the Ryukyu Islands, Japan: Current status and trends

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Abstract

In Japan, the subtropical Ryukyu Archipelago (RYS; also known as the Nansei Islands) with its coral reefs has been shown to harbor very high levels of marine biodiversity. This study provides an overview of the state of marine biodiversity research in the RYS. First, we examined the amount of scientific literature in the Web of Science (WoS; 1995-2017) on six selected representative taxa spanning from protists to vertebrates across six geographic sub-regions in the RYS. Our results show clear taxonomic and sub-region bias, with research on Pisces, Cnidaria, and Crustacea to be much more common than on Dinoflagellata, Echinodermata, and Mollusca. Such research was more commonly conducted in sub-regions with larger human populations (Okinawa, Yaeyama). Additional analyses with the Ocean Biogeographic Information System (OBIS) records show that within sub-regions, records are concentrated in areas directly around marine research stations and institutes (if present), further showing geographical bias within sub-regions. While not surprising, the results indicate the clear need to study ‘understudied’ taxa in ‘understudied sub-regions’ (Tokara, Miyako, Yakutane, Amami Oshima), and to study ‘understudied areas’ of some sub-regions away from marine research stations. Second, we compared the numbers of scientific papers on eight ecological topics for the RYS with numbers
from selected major coral reef regions of the world; the Caribbean (CAB), Great Barrier Reef (GBR), and the Red Sea (RES). Not unexpectedly, the numbers for all topics in the RYS were well below numbers from all other regions, yet within this disparity, research in the RYS on ‘marine protected areas’ and ‘herbivory’ was an order of magnitude lower than numbers in other regions. Additionally, while manuscript numbers on the RYS have increased from 1995 to 2016, the rate of increase (4.0 times) was seen to be lower than those in the CAB, RES, and GBR (4.6 to 8.4 times). As the RYS are considered to contain among the most critically endangered coral reef biodiversity in the world due to high levels of both endemism and anthropogenic threats, much work is urgently needed to address the areas of relative research weakness identified in this study.

Introduction

Biodiversity research provides the basis to guide ecosystem management, and consequently, to preserve services and goods that are critical to the economic value of the planet (Costanza et al. 1997; Mace et al. 2012). Moreover, a better knowledge of biodiversity patterns enables the prediction of possible outcomes from ongoing environmental changes (Bellard et al.
2012) and species extinctions (Chapin et al. 2000; Dunne et al. 2002). Analyses of species diversity and distribution also allow the determination of biodiversity hotspots. For example, the ‘Coral Triangle’ hotspot, located in central Indo-Pacific waters, is considered to be the coral reef area with the highest numbers of marine species in the world (Hughes et al. 2002; Toonen et al. 2016). Nevertheless, there is still a lack of diversity information for most marine taxa (Appeltans et al. 2012; Troudet et al. 2017), and this problem is especially prevalent in understudied localities including many in the Indo-Pacific. This data gap hampers our understanding of biodiversity patterns and the conservation of species, and is therefore an obstacle to accurate ecosystem function protection (Cardinale et al. 2012; Costello et al. 2013; Duffy et al. 2017).

The Ryukyu Islands (RYS; also known as the Nansei Islands) comprise the southernmost region of Japan and border the northern edge of the Coral Triangle, spanning 1200 km from Yakushima and Tanegashima Islands (Yakutane sub-region) in the north, across the Tokara, Amami, Okinawa, Miyako sub-regions to the Yaeyama Islands in the south (Figure 1, also Coral Reefs of Japan 2004; Fujita et al. 2015). These waters are all influenced by the warm Kuroshio Current that flows northwards along the west side of the island chain (Andres et al. 2008), and the RYS includes islands of different geological formation, ages, and sizes (Kizaki
Thus, the RYS are a marine region of exceptionally high diversity and endemism of species (Hughes et al. 2002; Cowman et al. 2017). Moreover, it has been calculated that southern Japan and Taiwan rank first in global marine conservation priority when considering high levels of multi-taxon endemism, their high risk of biodiversity loss due to overexploitation and coastal development, and thus need rapid conservation action (Roberts et al. 2002). More than one decade after this initial work, and despite some conservation successes (e.g. Okubo and Onuma 2015; establishment of Keramas National Park in 2016), the RYS are still threatened by rapidly increasing tourism pressure (Dal Kee 2015; Hirano and Kakutani 2015; Tada 2015; Toyoshima and Nadaoka 2015; Okinawa Prefectural Government 2016) and continuous ongoing coastal developmental (Veron 1992; Fujii et al. 2009; Reimer et al. 2015). In fact, the numbers of tourists visiting Okinawa exceeded those of Hawai’i for the first time in 2017 (Ryukyu Shinpo 2018; also FY2017 data on Okinawa Prefecture homepage).

Although the RYS contain high levels marine species diversity, until now there has been no marine biodiversity overview that covers the archipelago in detail (but see Fujikura et al. (2010)’s general overview of marine biodiversity of Japan with a focus on Sagami Bay). Here,
we conduct an extensive data-mining review to provide information on the status of marine biodiversity research within the RYS, with specific information on six sub-regions within the RYS for six important and representative marine taxa. Furthermore, we review and compare data of ecological studies in the RYS to those of other major reef regions (Caribbean, Great Barrier Reef, Red Sea). Finally, we discuss and highlight the trends of biodiversity related research in the RYS, emphasizing the need for continued research as the data gap hampers our understanding of marine biodiversity and conservation efforts in this important coral reef region.

**Materials and Methods**

**The Ryukyu Islands (RYS)**

We divided the RYS into six sub-regions based on geographical, historical, and administrative information (Table 1); the sub-regions generally follow those in Coral Reefs of Japan (2004) and as used by various levels of Japanese government. The sub-regions (south to north) are the island groups of Yaeyama, Miyako, Okinawa, Amami Oshima, Tokara, and Yakutane. The first three sub-regions are within Okinawa Prefecture, while the last three are within Kagoshima Prefecture, and are as follows:

a. Yaeyama Islands: the southernmost group of islands in the RYS, this group experiences
most tropical conditions, has the most well developed coral reefs (Coral Reefs of Japan 2004), including the Sekisei Lagoon, Japan’s largest reef system, and is generally thought to have the highest biodiversity within the entire archipelago (Nishihira and Veron 1995; Roberts et al. 2002; Table 1). This sub-region includes the major islands of Ishigaki and Iriomote as well as several smaller islands.

b. Miyako Islands: includes the large island of Miyako as well as several surrounding smaller islands. This sub-region is notable for having a coral reef system with extensive cave systems and endemic species (e.g. Shimomura et al. 2012).

c. Okinawa Main Island and region: this sub-region is dominated by Okinawa Main Island, the largest and by far the most populous island in the RYS (Table 1). In addition, the island is surrounded by numerous smaller islands notable for their relatively pristine condition and protection within two national parks.

d. Amami Oshima Island and region: Amami Oshima is the second largest island in size and population in the RYS, but this region also includes other major islands such as Yoron, Okinoerabu, and Tokunoshima, as well as many smaller island groups. Notable for endemic terrestrial species, the marine life of this subregion is thought to be understudied when compared
with regions further south (e.g. Fujii 2016; Nakae et al. 2018). The southernmost portion of Kagoshima Prefecture, this area was historically sometimes included within the former Ryukyu Kingdom (current Okinawa Prefecture).

e. Tokara Islands: the smallest and least populated sub-region within the RYS, this group is often considered part of the Yakutane Islands, but differs in several important ways, as it has more developed coral reefs than areas further north in the Yakutane sub-region and south around Amami Oshima (Coral Reefs of Japan 2004), and is heavily influenced by the Kuroshio Current.

Consists of 12 small islands stretched across 160 km, with six islands having well-developed coral reefs (Coral Reefs of Japan 2004). As the least developed sub-region, this area, unlike all other sub-regions, is not easily reachable by major air transport systems, and is considered the least well-studied area in the RYS.

f. Yakutane Islands (also known as the Osumi Islands): consisting of the two major islands of Yakushima and Tanegashima along with neighboring smaller islands, the Kuroshio takes a sudden turn to the east south of Yakushima. This sub-region is considered the northern limit of modern coral reef development in the region (Coral Reefs of Japan 2004) and the northern limit of the subtropical region of Japan.
We searched within the Web of Science (WoS) for papers on six representative marine taxa within the RYS; Pisces, Mollusca, Crustacea, Echinodermata, Cnidaria, and Dinoflagellata, utilizing search strings (Electronic Supplementary Material Table S1). We determined the sub-region location of each paper of these six taxa within the WoS based on the title, key words, and abstract information. When the title and abstract only contained “Okinawa”, “Ryukyu”, or “Nansei”, with no further information, we categorized these papers as “Ryukyu/Nansei unspecified”, as “Okinawa” may refer to the entire Okinawa prefecture, and “Ryukyu” and “Nansei” may refer to anywhere within the RYS island chain. Additionally, deep-sea publications were not included in our examinations. Publication numbers were compiled for 1995-2017 for each taxon for each sub-region to examine what taxa have been investigated in what sub-region. The search was conducted on August/September of 2017.

We searched eight principal topics in ecological studies (apex predators, connectivity, coral bleaching, coral reproduction, herbivory, marine protected areas, Porifera, reef-associated bacteria) with in WoS following the search strings utilized by Berumen et al. (2013) in their
review on biodiversity work in the Red Sea (see also Electronic Supplementary Material Table S1). Subsequently, we filtered and compared the data for four reef regions across the globe. The regions and search strings used to filter the data are the following: RYS (search string was “Ryukyus*” OR “Nansei” OR “Okinawa*”), Caribbean (CAB; search string was “Caribbean”), Great Barrier Reef (GBR; search string was “Great Barrier Reef”), and the Red Sea (RES; search string was “Red Sea”). Publication numbers were compiled annually (1995-2016) and by ecology topic (as above). The search was conducted on September 20, 2017.

Ocean Biogeographic Information System search

As a supplementary examination, we searched the six sub-regions of the RYS within the Ocean Biogeographic Information System (OBIS) for the six representative marine taxa (Cnidaria, Crustacea, Dinoflagellata, Echinodermata, Mollusca, and Pisces) with the aim of examining spatial differences in the research of these taxa within sub-regions. Using the highest grid resolution of OBIS, we examined all square grids that covered the coastline of each island of the RYS and noted the number of records for each quadrat for each taxon. The number of quadrats examined in each sub-region ranged from 11 in Miyako to 50 in Okinawa (Table 1). The search was conducted in August 2017.
Results

Web of Science taxa and sub-regions search

In total, from our WoS searches for papers between 1995-2017, we examined 980 papers, which contained information for 1023 sub-region occurrences (some papers had >1 sub-region in their content). Of these occurrences, 420 were from the Okinawa Main Island sub-region, 307 from an unspecified area in the RYS, 199 from Yaeyama, 48 from Amami Oshima, 29 from Yakutane, 16 from Miyako, and 4 from Tokara (Figure 1).

By taxa, the groups Pisces (n=346), Cnidaria (n=233), and Crustacea (n=225) had the most occurrences, with all other groupings <100 occurrences (Mollusca n=92, Echinodermata n=51, Dinoflagellata n=44; Figure 1). Of note was the fact that ~80% of both Echinodermata and Dinoflagellata papers were from Okinawa (40 of 51 papers, 36 of 44, respectively). Papers dealing with Pisces were most numerous for Yakutane (n=12), Okinawa (n=82), and Yaeyama (n=80), while papers on Cnidaria were most numerous for Amami (n=19) and Okinawa (n=169), and Cnidaria and Crustacea were equally numerous for Tokara (n=2 each) and Miyako (n=6 each). For unspecified sub-regions, Pisces (n=118) and Crustacea (n=108) were the most numerous taxa (Figure 1).
Web of Science ecology search and comparison

Our WoS search results showed that the RYS had less publications overall (n=1288; Figure 2) when compared to the three other coral reef regions examined for the same time period (GBR n=6242, CAB n=6990, RES n=4493). Additionally, RYS publication numbers were lower for all eight ecological topics analyzed (Figure 3). In particular, numbers for RYS were comparatively very low for herbivory and marine protected areas (Figure 3b and 3d, respectively). Temporally, the number of papers published for all regions increased noticeably between 1995 and 2016 (Figure 2), with the number of RYS papers increasing approximately 4.0 times (1995 n=24 publications vs. 2016 n=97), CAB papers increasing 4.6 times (1995 n=100 vs. 2016 n=460), GBR papers increasing approximately 7.6 times (1995 n=66 vs. 2016 n=504), and RES papers increasing approximately 8.4 times (1995 n=47 vs. 2016 n=397).

Ocean Biogeographic Information System results

OBIS results examining the numbers of records of different taxa within the sub-regions showed great variation, with some general trends appearing. In general, the three more northern sub-regions within Kagoshima Prefecture had fewer records than those in Okinawa Prefecture for Cnidaria, Crustacea, Echinodermata, Mollusca, and Pisces. Within Okinawa Prefecture (and
the RYS), Okinawa consistently had the highest numbers of records, with the highest numbers observed around Akajima (Crustacea, n=200-500) and the west coast of Okinawa-jima Island (Cnidaria, Crustacea, Echinodermata, Mollusca, and Pisces). Conversely, even within the Okinawa sub-region, some areas such as the northeast coast of Okinawa-jima Island had none or only few records (Electronic Supplementary Material Figure S1a). Additionally, there was only one record for the entire RYS within OBIS for Dinoflagellata in shallow water (Electronic Supplementary Material Figure S1b).

**Discussion**

From the WoS and OBIS analyses of sub-regions and taxa occurrences it became clear, as in many other marine regions (Hughes *et al*. 2002), that serious taxonomic and geographic bias is present in marine research in the RYS. Some of this taxonomic bias may stem from the commercial importance of Pisces and Crustacea in Japan, which has resulted in many studies on various species’ lifecycles and aquaculture methodologies. Research on these topics, while often conducted somewhere in the RYS, generally did not include field observations or sampling information as the focus was more on *ex situ* analyses and model species, and this was reflected in these two groups’ dominance of the “unspecified RYS sub-region” category (Figure 1).
Overall, most work in the RYS has been conducted on Pisces, Crustacea, and Cnidaria, with the large majority (57.94%, n=135/233) on Scleractinia hard corals, and surprisingly far less work on other commercially important groups such as Echinodermata and Mollusca. While Mollusca research was somewhat evenly spread around the RYS, approximately 80% of Echinodermata research was conducted in the Okinawa sub-region (Figure 1). Due to recent commercial pressure and reported large drops in abundances of some echinoderms (Soliman et al. 2016a, 2016b), it is clear that more research is urgently needed in other sub-regions; this is also the case for Dinoflagellata. Hughes et al. (2002) suggested nearly two decades ago that more work is needed on understudied taxa in understudied locations, and this is clearly still true for the RYS.

From the analyses of records of various taxa in OBIS, research patterns within each sub-region become clear. While generally understudied sub-regions such as Tokara had a lack of research for all taxa across all areas inside the sub-region, in the case of more well-studied sub-regions, these areas were often directly adjacent to marine research stations (e.g. 200-500 Crustacea records on Akajima, containing Akajima Marine Station, active until 2017; Electronic Supplementary Material Figure S1a) and have had much more research conducted than in other
areas. Thus, while Okinawa and Yaeyama can be considered to be comparatively well-studied inside RYS, there are areas within both sub-regions that are almost completely uninvestigated. As conservation studies require data on not only exploited or well-studied areas, but neighboring relatively ‘pristine’ areas as well, research on these uninvestigated areas are an urgent necessity. Additionally, the presence of marine research stations is obviously a driving force for research, and this can be demonstrated by the OBIS records for the Miyako sub-region, which despite a relatively large human population, has no research-focused marine station (Table 1), and a corresponding general lack of scientific publications and data available (e.g. Figure 1).

While the WoS obviously does not include all scientific publications from each region of the world as it does not index all scientific journals, and its coverage in some fields is less complete than in others, the problem is particularly acute when examining marine science publications from Japanese waters. Japan has a long history of marine biodiversity and coral reef science (e.g. Kawaguti 1940), and even today much research is published in Japanese, the large majority of which are in journals that do not appear in the WoS. An exception is Nippon Suisan Gakkaishi, and even though it appears in the WoS, some articles in this journal list title and authors only, with no abstract available in English, and the journal even occasionally contains
articles with no English at all. Such domestic journals are still held in high regard in many scientific fields within Japan, including marine and fisheries sciences, and contain much valuable and important data. Failure to access these journals and their contents undoubtedly results in not gaining a complete picture of marine sciences in Japan, including our examination here of marine biodiversity in the RYS. We suggest that Japanese language science publications make the effort to include translations of the title, authors, and abstract to allow more access from the international science community, as is already performed by such journals as Nippon Suisan Gakkaishi (for most articles, in the WoS) and Fauna Ryukyuana (for all articles, not in the WoS).

Also, for aquaculture or model species studies, listing the exact location from where specimens were collected would be helpful for mapping records and distributions of species in the Oceanographic Biology Information System (OBIS 2018) or other databases.

From the WoS search on ecological topics, the relative and comparative lack of research in the RYS compared to the ‘major’ coral reef areas of CAB, GBR, and the RES is apparent. While our results were not unexpected, particularly given the relatively small size of the RYS (approximately 4642 km$^2$ area and c. 1200 km in length) in comparison to these other regions than GBR, CAB and RES (17,400 km$^2$ area c. 2300 km length; 10,530 km$^2$ area; 8890
km\(^2\) area c. 2000 km\(^2\) length; respectively, data from Berumen et al. (2013)), it should be noted
that in terms of human populations immediately adjacent to reefs, the RYS could be considered
to have higher numbers than those the GBR or even the RES, particularly given that the other
three regions have continental landmasses much larger than those of the RYS islands.

When examining the trends for the different ecological topics, the deficiencies of
research in the RYS become starkly clear, with almost no research conducted on ecosystem
sciences such as herbivory, or on marine protected areas. Historically, Japan and Okinawa have
been somewhat slow to adopt marine conservation measures with legal strength (Reimer et al.
2015) but it also appears that scientists based in the region have been equally slow to adopt
research on these topics, despite a clear public need for such third-party research given the
controversy over continuing coastal development in Okinawa (McCormack 1999; Hook 2010).

Additionally and somewhat surprisingly, there has been little research on apex predators, despite
clear public interest in Japan in this group (e.g. large shark displays at Churaumi Aquarium in
Okinawa). Given the high rates of marine endemism and biodiversity in this region (Roberts et al.
2002), more efforts should be made to conduct research on these topics in the RYS.

Most worryingly, the pace at which scientific research in the RYS has increased has
not kept pace with the other three regions we examined (Figure 2). While the number of
publications from the RYS (and all other regions) is increasing, given the large number of coral
reef, fisheries, and marine science researchers in Japan (e.g. the Japanese Coral Reef Society
created in 1997 has over 600 members [JCRS homepage http://www.jcrs.jp]), we expected the
gap between the RYS and other regions to be smaller. At current rates and based on these data
from the past twenty-one years, compared to other regions the RYS are comparatively less
studied now than in 1995.

In conclusion, marine biodiversity and ecology research in the RYS, while steadily
advancing, lags behind the progress of other major coral reef regions in the world. In particular,
research levels on conservation topics are dramatically lower than in other coral reef regions,
despite the stark need for conservation and protection of these ecosystems. Additionally, despite
the large amount of marine research infrastructure including numerous research facilities and a
large population base, and despite the comparatively small area of the RYS (Table 1), there are
taxa in both sub-regions and smaller areas within sub-regions that are almost completely
unstudied. Moving forward, local, prefectural, and national governments and stakeholders should
focus on addressing the clear gaps in our knowledge base. Such work combined with a more
robust legal framework and the establishment of functioning no-take and marine protected areas should be able to better conserve and protect RYS coral reef ecosystems and their valuable ecosystem services for future generations.

Acknowledgements

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Duffy JE, Godwin CM, Cardinale BJ (2017) Biodiversity effects in the wild are common and as strong as key drivers of productivity. Nature 549:261. doi: 10.1038/nature23886


**Tables**

Table 1 – Information on the six sub-regions investigated in this study in the Ryukyu Islands (RYS).

**Figures**

Figure 1 – Map of the Ryukyu Islands (RYS) with sub-regions used in this study, and total number of publications (1995-2017) in the Web of Science for six different marine taxa.
Figure 2 – (a) Numbers of ecological publications per year, and (b) the total number of publications for the Ryukyus (RYS; blue), Red Sea (RES, red), Great Barrier Reef (GBR, grey), and Caribbean (CAR, yellow) from 1995 to 2016 in the Web of Science.

Figure 3 – Number of ecological publications per year for four regions from 1995 to 2016 in the Web of Science; the Ryukyus (RYS; blue), Red Sea (RES, red), Great Barrier Reef (GBR, grey), and Caribbean (CAR, yellow) by topic. (a) apex predators, (b) herbivory, (c) connectivity, (d) marine protected areas, (e) coral bleaching, (f) Porifera, (g) coral reproduction, and (h) reef-associated bacteria.

Electronic Supplementary Material

Electronic Supplementary Material Table S1 – search terms for Web of Science and numbers of publications per year (1995-2017) for the Ryukyus, Red Sea, Great Barrier Reef, and Caribbean.

Electronic Supplementary Material Figure S1 – Example images of the Okinawa sub-region of the RYS within the Ocean Biogeographic Information System (OBIS) for (a) Crustacea, and (b) Dinoflagellata, showing spatial differences in the records of these taxa. Crustacea have most numerous records (n=200-500) in the square that contains Akajima Marine Station. On the other hand, there are almost no data at all for Dinoflagellata. The search was conducted in August
Table 1 (on next page)

Information on the six sub-regions investigated in this study in the Ryukyu Islands (RYS).
Table 1 – Information on the six sub-regions investigated in this study in the Ryukyu Islands (RYS).

<table>
<thead>
<tr>
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<th>Yakutane</th>
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<th>Amami</th>
<th>Okinawa</th>
<th>Miyako</th>
<th>Yaeyama</th>
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</tr>
</tbody>
</table>

<p>| <strong>Notable marine research stations &amp; institutes</strong> | | | | | | | | |
| | Yakushima Umigane-kan | none | | | | | | Various homepages, pers. comm, with T. Naruse, T. Fujii |
| | Kagoshima University Amami Station, Seikai National Fisheries Research Institute | | Akajima Marine Science Laboratory (closed 2017), | | | | |
| | | | Okinawa Institute of Science and Technology (from 2011), Okinawa National College of Technology, | | | | |
| | | | University of the Ryukyu Iriomote Field Station, | | | | |
| | | | Ishigaki Pref. Exp. Station, Ishigaki MoE Parks Station, | | | | |
| | | | Kuroshima Sea Turtle Station | | | | |</p>
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Coral Reefs of Japan (2004), Ministry of Environment
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Figure 1 (on next page)

Map of the Ryukyu Islands (RYS) with sub-regions used in this study, and total number of publications (1995-2017) in the Web of Science for six different marine taxa.
Figure 2

(a) Numbers of ecological publications per year, and (b) the total number of publications for the Ryukyus (RYS; blue), Red Sea (RES, red), Great Barrier Reef (GBR, grey), and Caribbean (CAR, yellow) from 1995 to 2016 in the Web of Science.
Figure 3

Number of ecological publications per year for four regions from 1995 to 2016 in the Web of Science; the Ryukyus (RYS; blue), Red Sea (RES, red), Great Barrier Reef (GBR, grey), and Caribbean (CAR, yellow) by topic.

(a) apex predators, (b) herbivory, (c) connectivity, (d) marine protected areas, (e) coral bleaching, (f) Porifera, (g) coral reproduction, and (h) reef-associated bacteria.