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.

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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

31 from selected major coral reef regions of the world; the Caribbean (CAB), Great Barrier Reef
32 (GBR), and the Red Sea (RES). Not unexpectedly, the numbers for all topics in the RYS were
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34 'marine protected areas' and 'herbivory' was an order of magnitude lower than numbers in other
35 regions. Additionally, while manuscript numbers on the RYS have increased from 1995 to 2016,
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37 to 8.4 times). As the RYS are considered to contain among the most critically endangered coral
38 reef biodiversity in the world due to high levels of both endemism and anthropogenic threats,
39 much work is urgently needed to address the areas of relative research weakness identified in this
40 study.
41

42 **Introduction**

43 Biodiversity research provides the basis to guide ecosystem management, and
44 consequently, to preserve services and goods that are critical to the economic value of the planet
45 (Costanza *et al*. 1997; Mace *et al*. 2012). Moreover, a better knowledge of biodiversity patterns
46 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, acorss 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

63 1986; Table 1). Thus, the RYS are a marine region of exceptionally high diversity and endemism
64 of species (Hughes *et al*. 2002; Cowman *et al*. 2017). Moreover, it has been calculated that
65 southern Japan and Taiwan rank first in global marine conservation priority when considering
66 high levels of multi-taxon endemism, their high risk of biodiversity loss due to overexploitation
67 and coastal development, and thus need rapid conservation action (Roberts *et al*. 2002). More
68 than one decade after this initial work, and despite some conservation successes (e.g. Okubo and
69 Onuma 2015; establishment of Keramas National Park in 2016), the RYS are still threatened by
70 rapidly increasing tourism pressure (Dal Kee 2015; Hirano and Kakutani 2015; Tada 2015;
71 Toyoshima and Nadaoka 2015; Okinawa Prefectural Government 2016) and continuous ongoing
72 coastal developmental (Veron 1992; Fujii *et al*. 2009; Reimer *et al*. 2015). In fact, the numbers
73 of tourists visiting Okinawa exceeded those of Hawai'i for the first time in 2017 (Ryukyu Shinpo
74 2018; also FY2017 data on Okinawa Prefecture homepage
75 http://www.pref.okinawa.jp/site/bunka-sports/kankoseisaku/h28nendo.html).
76 Although the RYS contain high levels marine species diversity, until now there has
77 been no marine biodiversity overview that covers the archipelago in detail (but see Fujikura *et al*.
78 (2010)'s general overview of marine biodiversity of Japan with a focus on Sagami Bay). Here,

79 we conduct an extensive data-mining review to provide information on the status of marine
80 biodiversity research within the RYS, with specific information on six sub-regions within the
81 RYS for six important and representative marine taxa. Furthermore, we review and compare data
82 of ecological studies in the RYS to those of other major reef regions (Caribbean, Great Barrier
83 Reef, Red Sea). Finally, we discuss and highlight the trends of biodiversity related research in
84 the RYS, emphasizing the need for continued research as the data gap hampers our
85 understanding of marine biodiversity and conservation efforts in this important coral reef region.

86 Materials and Methods

87 The Ryukyu Islands (RYS)

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

94 a. Yaeyama Islands: the southernmost group of islands in the RYS, this group experiences the

95 most tropical conditions, has the most well developed coral reefs (Coral Reefs of Japan 2004),
96 including the Sekisei Lagoon, Japan's largest reef system, and is generally thought to have the
97 highest biodiversity within the entire archipelago (Nishihira and Veron 1995; Roberts *et al*.
98 2002; Table 1). This sub-region includes the major islands of Ishigaki and Iriomote as well as
99 several smaller islands.
100 b. Miyako Islands: includes the large island of Miyako as well as several surrounding smaller
101 islands. This sub-region is notable for having a coral reef system with extensive cave systems
102 and endemic species (e.g. Shimomura *et al*. 2012).
103 c. Okinawa Main Island and region: this sub-region is dominated by Okinawa Main Island, the
104 largest and by far the most populous island in the RYS (Table 1). In addition, the island is
105 surrounded by numerous smaller islands notable for their relatively pristine condition and
106 protection within two national parks.
107 d. Amami Oshima Island and region: Amami Oshima is the second largest island in size and
108 population in the RYS, but this region also includes other major islands such as Yoron,
109 Okinoerabu, and Tokunoshima, as well as many smaller island groups. Notable for endemic
110 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.

127 **Web of Science taxa and sub-regions search**

128 We searched within the Web of Science (WoS) for papers on six representative marine
129 taxa within the RYS; Pisces, Mollusca, Crustacea, Echinodermata, Cnidaria, and Dinoflagellata,
130 utilizing search strings (Electronic Supplementary Material Table S1). We determined the sub-
131 region location of each paper of these six taxa within the WoS based on the title, key words, and
132 abstract information. When the title and abstract only contained "Okinawa", "Ryukyu", or
133 "Nansei", with no further information, we categorized these papers as "Ryukyu/Nansei
134 unspecified", as "Okinawa" may refer to the entire Okinawa prefecture, and "Ryukyu" and
135 "Nansei" may refer to anywhere within the RYS island chain. Additionally, deep-sea
136 publications were not included in our examinations. Publication numbers were compiled for
137 1995-2017 for each taxon for each sub-region to examine what taxa have been investigated in
138 what sub-region. The search was conducted on August/September of 2017.

139 **Web of Science ecology search and comparison**

140 We searched eight principal topics in ecological studies (apex predators, connectivity,
141 coral bleaching, coral reproduction, herbivory, marine protected areas, Porifera, reef-associated
142 bacteria) with in WoS following the search strings utilized by Berumen *et al*. (2013) in their

143 review on biodiversity work in the Red Sea (see also Electronic Supplementary Material Table
144 S1). Subsequently, we filtered and compared the data for four reef regions across the globe. The
145 regions and search strings used to filter the data are the following: RYS (search string was
146 "Ryukyus*" OR "Nansei" OR "Okinawa*"), Caribbean (CAB; search string was "Caribbean"),
147 Great Barrier Reef (GBR; search string was "Great Barrier Reef"), and the Red Sea (RES; search
148 string was "Red Sea"). Publication numbers were compiled annually (1995-2016) and by
149 ecology topic (as above). The search was conducted on September 20, 2017.

150 **Ocean Biogeographic Information System search**

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

175 **Web of Science ecology search and comparison**

176 Our WoS search results showed that the RYS had less publications overall (n=1288;
177 Figure 2) when compared to the three other coral reef regions examined for the same time period
178 (GBR n=6242, CAB n=6990, RES n=4493). Additionally, RYS publication numbers were lower
179 for all eight ecological topics analyzed (Figure 3). In particular, numbers for RYS were
180 comparatively very low for herbivory and marine protected areas (Figure 3b and 3d,
181 respectively). Temporally, the number of papers published for all regions increased noticeably
182 between 1995 and 2016 (Figure 2), with the number of RYS papers increasing approximately 4.0
183 times (1995 n=24 publications vs. 2016 n=97), CAB papers increasing 4.6 times (1995 n=100 vs.
184 2016 n=460), GBR papers increasing approximately 7.6 times (1995 n=66 vs. 2016 n=504), and
185 RES papers increasing approximately 8.4 times (1995 n=47 vs. 2016 n=397).

186 **Ocean Biogeographic Information System results**

187 OBIS results examining the numbers of records of different taxa within the sub-regions
188 showed great variation, with some general trends appearing. In general, the three more northern
189 sub-regions within Kagoshima Prefecture had fewer records than those in Okinawa Prefecture
190 for Cnidaria, Crustacea, Echinodermata, Mollusca, and Pisces. Within Okinawa Prefecture (and

191 the RYS), Okinawa consistently had the highest numbers of records, with the highest numbers
192 observed around Akajima (Crustacea, n=200-500) and the west coast of Okinawa-jima Island
193 (Cnidaria, Crustacea, Echinodermata, Mollusca, and Pisces). Conversely, even within the
194 Okinawa sub-region, some areas such as the northeast coast of Okinawa-jima Island had none or
195 only few records (Electronic Supplementary Material Figure S1a). Additionally, there was only
196 one record for the entire RYS within OBIS for Dinoflagellata in shallow water (Electronic
197 Supplementary Material Figure S1b).

198 **Discussion**

199 From the WoS and OBIS analyses of sub-regions and taxa occurrences it became clear,
200 as in many other marine regions (Hughes *et al*. 2002), that serious taxonomic and geographic
201 bias is present in marine research in the RYS. Some of this taxonomic bias may stem from the
202 commercial importance of Pisces and Crustacea in Japan, which has resulted in many studies on
203 various species' lifecycles and aquaculture methodologies. Research on these topics, while often
204 conducted somewhere in the RYS, generally did not include field observations or sampling
205 information as the focus was more on *ex situ* analyses and model species, and this was reflected
206 in these two groups' dominance of the "unspecified RYS sub-region" category (Figure 1).

207 Overall, most work in the RYS has been conducted on Pisces, Crustacea, and Cnidaria,
208 with the large majority (57.94%, n=135/233) on Scleractinia hard corals, and surprisingly far less
209 work on other commercially important groups such as Echinodermata and Mollusca. While
210 Mollusca research was somewhat evenly spread around the RYS, approximately 80% of
211 Echinodermata research was conducted in the Okinawa sub-region (Figure 1). Due to recent
212 commercial pressure and reported large drops in abundances of some echinoderms (Soliman *et al*.
213 2016a, 2016b), it is clear that more research is urgently needed in other sub-regions; this is also
214 the case for Dinoflagellata. Hughes *et al*. (2002) suggested nearly two decades ago that more
215 work is needed on understudied taxa in understudied locations, and this is clearly still true for the
216 RYS.

217 From the analyses of records of various taxa in OBIS, research patterns within each
218 sub-region become clear. While generally understudied sub-regions such as Tokara had a lack of
219 research for all taxa across all areas inside the sub-region, in the case of more well-studied sub-
220 regions, these areas were often directly adjacent to marine research stations (e.g. 200-500
221 Crustacea records on Akajima, containing Akajima Marine Station, active until 2017; Electronic
222 Supplementary Material Figure S1a) and have had much more research conducted than in other

223 areas. Thus, while Okinawa and Yaeyama can be considered to be comparatively well-studied
224 inside RYS, there are areas within both sub-regions that are almost completely uninvestigated.
225 As conservation studies require data on not only exploited or well-studied areas, but neighboring
226 relatively 'pristine' areas as well, research on these uninvestigated areas are an urgent necessity.
227 Additionally, the presence of marine research stations is obviously a driving force for research,
228 and this can be demonstrated by the OBIS records for the Miyako sub-region, which despite a
229 relatively large human population, has no research-focused marine station (Table 1), and a
230 corresponding general lack of scientific publications and data available (e. g. Figure 1).
231 While the WoS obviously does not include all scientific publications from each region
232 of the world as it does not index all scientific journals, and its coverage in some fields is less
233 complete than in others, the problem is particularly acute when examining marine science
234 publications from Japanese waters. Japan has a long history of marine biodiversity and coral reef
235 science (e.g. Kawaguti 1940), and even today much research is published in Japanese, the large
236 majority of which are in journals that do not appear in the WoS. An exception is Nippon Suisan
237 Gakkaishi, and even though it appears in the WoS, some articles in this journal list title and
238 authors only, with no abstract available in English, and the journal even occasionally contains

239 articles with no English at all. Such domestic journals are still held in high regard in many
240 scientific fields within Japan, including marine and fisheries sciences, and contain much valuable
241 and important data. Failure to access these journals and their contents undoubtedly results in not
242 gaining a complete picture of marine sciences in Japan, including our examination here of
243 marine biodiversity in the RYS. We suggest that Japanese language science publications make
244 the effort to include translations of the title, authors, and abstract to allow more access from the
245 international science community, as is already performed by such journals as Nippon Suisan
246 Gakkaishi (for most articles, in the WoS) and Fauna Ryukyuana (for all articles, not in the WoS).
247 Also, for aquaculture or model species studies, listing the exact location from where specimens
248 were collected would be helpful for mapping records and distributions of species in the
249 Oceanographic Biology Information System (OBIS 2018) or other databases.

250 From the WoS search on ecological topics, the relative and comparative lack of
251 research in the RYS compared to the 'major' coral reef areas of CAB, GBR, and the RES is
252 apparent. While our results were not unexpected, particularly given the relatively small size of
253 the RYS (approximately 4642 km^2 area and c. 1200 km in length) in comparison to these other
254 regions than GBR, CAB and RES (17,400 km^2 area c. 2300 km length; 10,530km^2 area; 8890

255 km^2 area c. 2000 km^2 length; respectively, data from Berumen *et al*. (2013)), it should be noted
256 that in terms of human populations immediately adjacent to reefs, the RYS could be considered
257 to have higher numbers than those the GBR or even the RES, particularly given that the other
258 three regions have continental landmasses much larger than those of the RYS islands.

259 When examining the trends for the different ecological topics, the deficiencies of
260 research in the RYS become starkly clear, with almost no research conducted on ecosystem
261 sciences such as herbivory, or on marine protected areas. Historically, Japan and Okinawa have
262 been somewhat slow to adopt marine conservation measures with legal strength (Reimer *et al*.
263 2015) but it also appears that scientists based in the region have been equally slow to adopt
264 research on these topics, despite a clear public need for such third-party research given the
265 controversy over continuing coastal development in Okinawa (McCormack 1999; Hook 2010).
266 Additionally and somewhat surprisingly, there has been little research on apex predators, despite
267 clear public interest in Japan in this group (e.g. large shark displays at Churaumi Aquarium in
268 Okinawa). Given the high rates of marine endemism and biodiversity in this region (Roberts *et al*.
269 2002), more efforts should be made to conduct research on these topics in the RYS.

270 Most worryingly, the pace at which scientific research in the RYS has increased has

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

278 In conclusion, marine biodiversity and ecology research in the RYS, while steadily
279 advancing, lags behind the progress of other major coral reef regions in the world. In particular,
280 research levels on conservation topics are dramatically lower than in other coral reef regions,
281 despite the stark need for conservation and protection of these ecosystems. Additionally, despite
282 the large amount of marine research infrastructure including numerous research facilities and a
283 large population base, and despite the comparatively small area of the RYS (Table 1), there are
284 taxa in both sub-regions and smaller areas within sub-regions that are almost completely
285 unstudied. Moving forward, local, prefectural, and national governments and stakeholders should
286 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.

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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.

429 Figure 2 – (a) Numbers of ecological publications per year, and (b) the total number of
430 publications for the Ryukyus (RYS; blue), Red Sea (RES, red), Great Barrier Reef (GBR, grey),
431 and Caribbean (CAR, yellow) from 1995 to 2016 in the Web of Science.

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

437 Electronic Supplementary Material

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

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

445 2017.

Table 1 (on next page)

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

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

2

Sub-region	Yakutane	Tokara	Amami	Okinawa	Miyako	Yaeyama	RYS total	Reference(s
Major islands	Yakushima, Tanegashima, Kuchinoerabu, others	Nakanoshima, Suwanose, Kuchinoshima, Taira, Takara, Kodakara, Akuseki, others	Amami-Oshima, Kikai, Tokunoshima, Okinoerabu, Yoron, others	Okinawa Main Island, Kume, Izena, Iheya, Kerama Islands, Ikei Islands, Aguni, Ie, Sesoko, Kouri, others	Miyako, Ikema, Tarama, others	Ishigaki, Iriomote, Taketomi, others	198 islands (not including <0.01 km2)	Wikipedia
Notable marine research stations & institutes	Yakushima Umigane-kan	none	Kagoshima University Amami Station, Seikai National Fisheries Research Institute Amami Station, Kikai Coral Reef Research Institute (from 2014), Kagoshima U. Fac. Fisheries Yoron Station	Akajima Marine Science Laboratory (closed 2017), Okinawa Institute of Science and Technology (from 2011), Okinawa National College of Technology, University of the Ryukyus Tropical Biosphere Research Center Sesoko Station, University of	Miyako City Museum	University of the Ryukyus Iriomote Field Station, Ishigaki Pref. Exp. Station, Ishigaki MoE Parks Station, Kuroshima Sea Turtle Station		Various homepages, pe comm, with T Naruse, T. Fu

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				the Ryukyus Main Campus, Itoman Pref. Exp. Center, Meio University				
OBIS cover (# squares)	27	14	36	50	11	26	164	OBIS
Land area (km2)	1030	101.35	1231.47	1418.59	226.5	587.16	4595.07	Wikipedia
Population	46,500	784	118,773	1,285,003	53,270	53,405	1,557,735	Wikipedia
Population density (/km2)	45.1	7.7	96.4	905.8	235.2	91.0	339.0	Wikipedia
Geological formation	volcanic, sedimentary, granite uplift	volcanic, coral reefs	volcanic, sedimentary, uplift, coral reefs	volcanic, sedimentary, uplift, coral reefs	volcanic, coral reefs	volcanic, sedimentary, uplift, coral reefs	N/A	Coral Reefs o Japan (2004) Fujita et al. (201 Wikipedia
Annual average SST (°C)	24.3		24.5	25.0	25.8	25.2	N/A	Coral Reefs o Japan (2004
Reef perimeter (km)	local coral reef flats only	19	420.3	382.2	121.6	268.4	1211.5	Coral Reefs o Japan (2004
Coral community	118		5951.2	6980	1957.1	19231.5	34237.8	Coral Reefs o

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area (ha)								Japan (2004)
Fishing activities	recreational, commercial	recreational, some commercial	recreational, commercial	recreational, commercial	recreational, commercial	recreational, commercial	N/A	Coral Reefs o Japan (2004)
Agricultural activities	sugarcane, rice, sweet potatoes, vegatables, other fruits, flowers, tobacco, others	minimal	sugarcane, pineapple, potatoes, vegatables, other fruits, flowers, tobacco, others	sugarcane, vegatables, pineapple, other fruits, flowers, tobacco, others	sugarcane, vegatables, other fruits, flowers, tobacco, others	sugarcane, vegatables, pineapple, other fruits, flowers, tobacco, others	N/A	Prefectural homepages
Other activities/issues	local tourism	minimal	local tourism	extensive tourism, red soil runoff, landfill, military bases、local pollution & eutrophication	extensive tourism	extensive tourism, red soil runoff, landfill	N/A	Coral Reefs o Japan 2004, prefectural homepages
COTS outbreaks	none	none	1970s onwards	1970s onwards	1957-59, 1970s-1980s, 2004~	1970s-1980s, 2007~	N/A	Coral Reefs o Japan (2004) Ministry of Environment
Water quality notes	oligotrophic oceanic	oligotrophic oceanic	oligotrophic oceanic with turbid bays	oligotrophic oceanic with turbid bays, local pollution & eutrophication	oligotrophic oceanic with turbid bays	oligotrophic oceanic with turbid bays	N/A	Coral Reefs o Japan (2004)
Recent years of level 2 bleaching	1998, 2001, 2016-7	1998	1998, 2016-7	1998, 2001, 2016-7	1998, 2001, 2016-7	1998, 2001, 2010, 2016-7	N/A	Coral Reefs o Japan (2004)

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events								NOAA, Ministry Environment
National parks	Yakushima	None	Amamigunto	Yanbaru, Keramashoto	None	Iriomote-Ishigaki	5 parks	Coral Reefs o Japan (2004) Ministry of Environment
Number of coral species	151	>151	200	340	302	363	N/A	Nishihira & Ve (1995), Cora Reefs of Japa (2004)

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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.

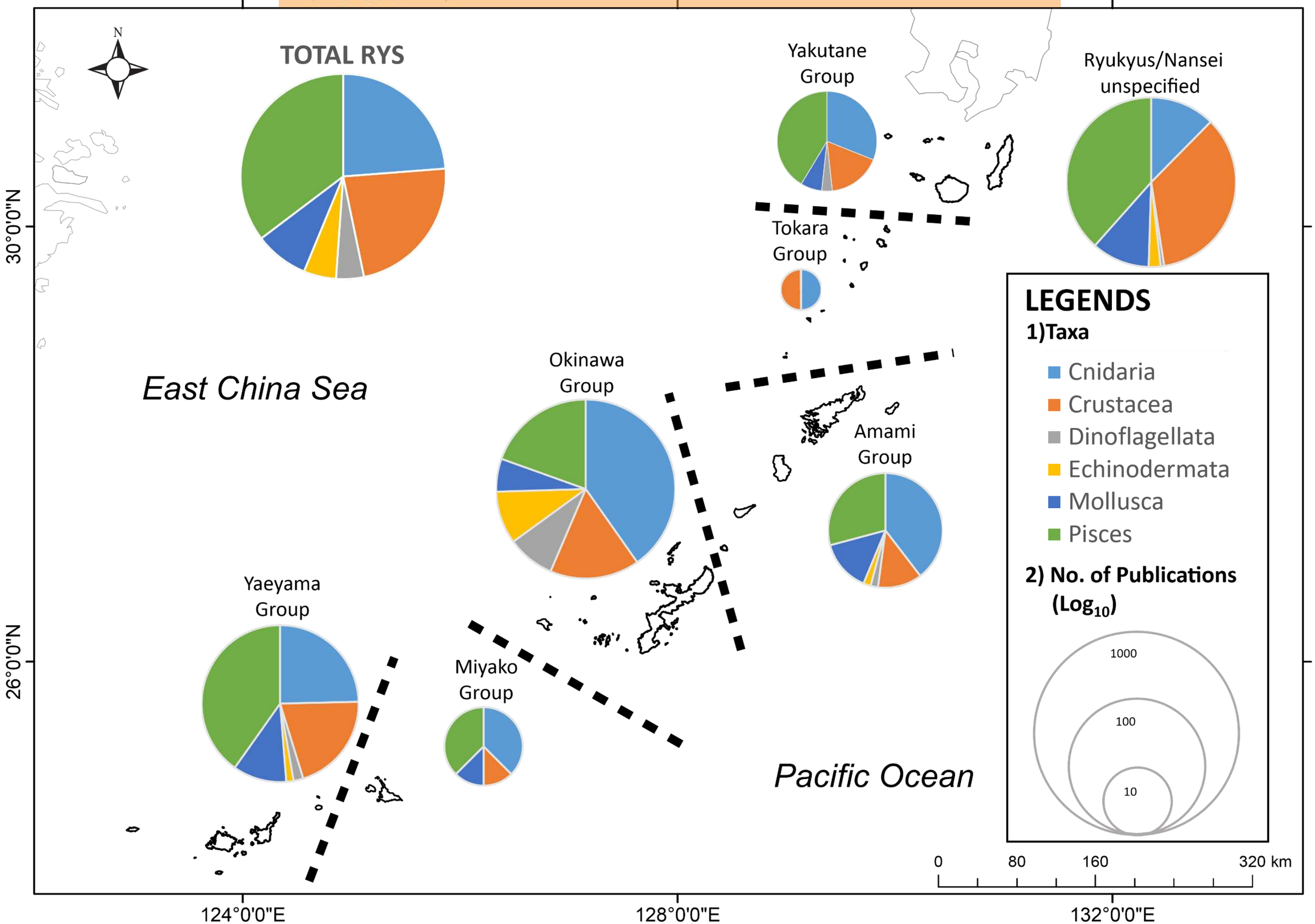

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Figure 2

(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.

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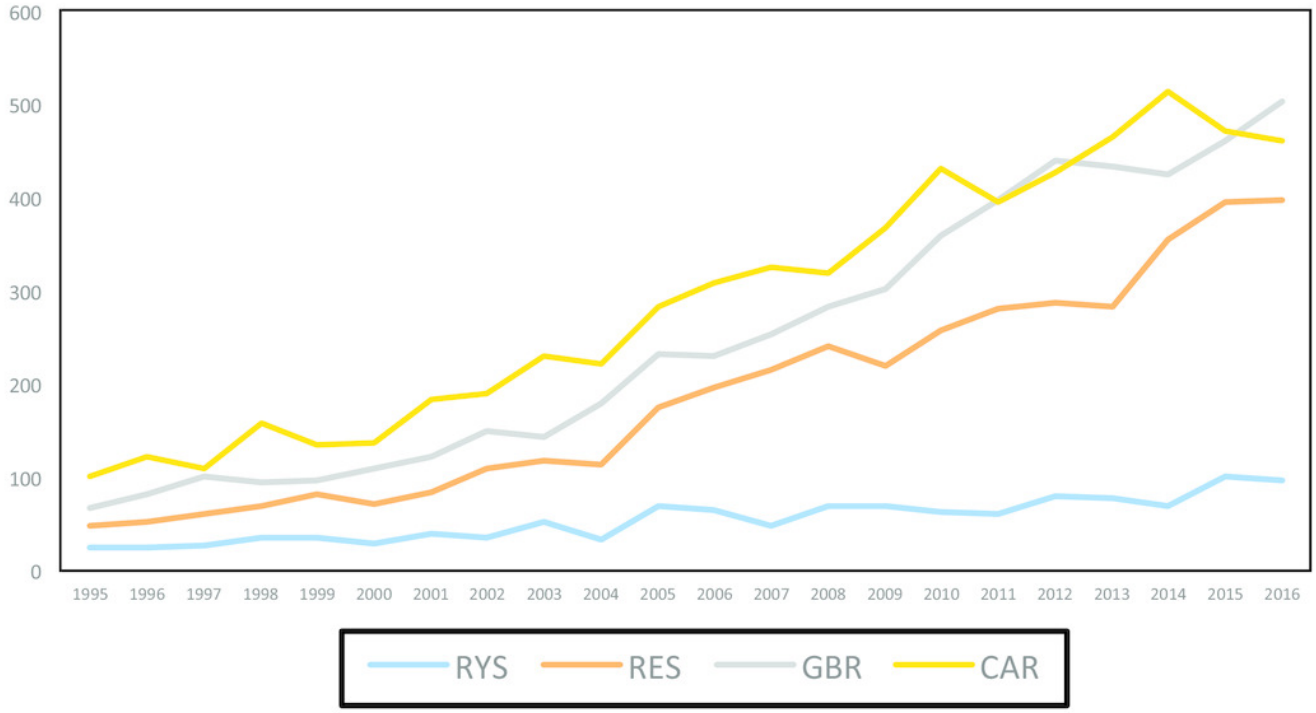
a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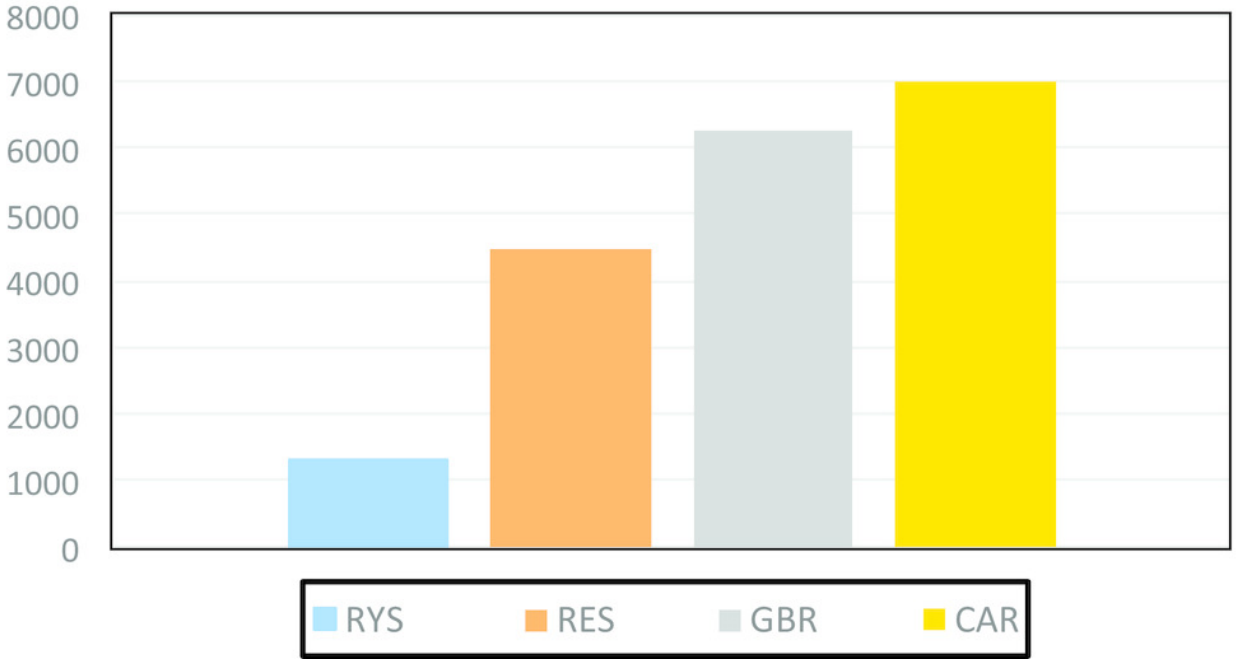
1995 1996 1997 1998 1999 2000 2001 2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015 2016
RYS
RES
GBR
CAR

b


8000
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2000
1000
0
RYS
RES
GBR
CAR

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.

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a
b
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RYS
RES
GBR
CAR