Change in the subtidal reef fish assemblage at Kuchierabu-jima Island, southern Japan, between 1972 and 2005

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Change in the subtidal reef fish assemblage at Kuchierabu-jima Island, southern Japan, between 1972 and 2005

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Abstract

Change in the subtidal reef fish assemblage at Kuchierabu-jima Island, southern Japan, since the 1970s was investigated using an underwater visual census in October 2005. A comparison of this survey to data from 1972 revealed that the frequencies of species that had either increased, remained stable, or declined in abundance were dependent on the geographic range category and the major feeding guild. Temperate herbivorous fishes had noticeably declined in abundance, while subtropical carnivorous species had increased. We discuss causes of the change in the reef fish assemblage from the aspect of water temperature, loss of macroalgal beds, and anthropogenic impacts.

Keywords Climate change, Isoyake, Reef fishes, Range shift, Kuroshio Current

Introduction

Changing species distributions are one of the most pervasive effects of global warming on natural ecosystems (Pecl et al. 2017). The influence of climate warming on the marine ecosystem is relatively well studied for the Pacific and Atlantic oceans, including the North Sea and Mediterranean Sea (e.g. Barry et al. 1995; Holbrook et al. 1997; Perry et al. 2005; Fodrie et al. 2010; Vergés et al. 2014). Recently, warming-associated changes have been identified for various marine taxa, such as corals and seaweeds along the coasts of Japan (e.g. Kurihara et al. 2011; Nagai et al. 2011; Yamano et al. 2011; Tanaka et al. 2012; Vergés et al. 2014; Kumagai et al. 2018). Among subtidal reef fishes, warm-adapted species that were not recorded in the past have been recently detected at various sites in Japan (Nakazono 2002; Nishida et al. 2005; Masuda 2008; Tawa and Takegaki 2009; Sakai et al. 2010). However, previous studies did not evaluate the change quantitatively because almost all the studies lacked comparative historical data on fish species abundance, particularly since the 1960s and 1970s.

One exceptional case in Japanese water is the reefs of Kuchierabu-jima Island, where underwater visual census efforts documented subtidal reef fish assemblages, including not only commercially important fishes, using quantitative data available in the 1970s (Gushima and Murakami 1977, 1978). This oceanic volcanic island in the East China Sea is part of the Osumi Islands and lies approximately 550 km north of the Ryukyu Islands and in close proximity to the Kuroshio Current. Biogeographical classification of the Osumi Islands describes the location as near the boundary between areas of temperate to subtropical waters for shallow rocky-reef fishes and subtropical waters for shallow coral- and rocky-reef fishes (Nakabo 2002, 2013). Over the past 100 years the southern part of the East China Sea, where Kuchierabu-jima Island is located, has shown increases in sea surface temperatures of 1.14°C and 1.45°C for annual and winter temperatures, respectively (Japan Meteorological Agency 2011). In addition, the disappearance or decline of seaweed beds (a phenomenon known as ‘isoyake’), including Sargassaceae species, has been reported in the coastal waters of Kagoshima Prefecture, to which Kuchierabu-jima Island belongs (Tanaka 2011). Seaweeds are an important food resource for some species of reef fish (Gushima 1981; Sano et al. 1984). Therefore, the disappearance of seaweed beds may also affect assemblages of reef fishes—herbivorous species may decline in abundance as compared with carnivorous species, including benthivorous or zooplanktivorous fishes.

To better understand how the subtidal reef fish assemblages at Kuchierabu-jima Island have changed over recent decades, we conducted an underwater visual census in October 2005 and compared our results with a census conducted in October 1972 (Gushima and Murakami 1977, 1978). Specifically, we investigated whether subtropical fishes that are otherwise distributed mainly in southern waters had increased, while temperate species that are otherwise distributed mainly in northern waters had decreased in abundance on the island's reefs. Concurrently, we investigated whether herbivorous species showed a decline in abundance as compared with carnivorous species.

Materials and methods

Underwater visual census. The fish assemblages on reefs at Kuchierabu-jima Island (30°27′N, 130°11′E) were surveyed in October 2005 (Fig. 1), through a visual census on the shallow rocky reefs in Honmura Bay, following the methods of Gushima and Murakami (1977, 1978). A band transect (500 × 6 m) was placed at three different depth intervals, at 1–5 m, 5–10 m, and 10–20 m, in the western part of the bay. The placement of these transects was based on a map provided in the previous censuses by Gushima and Murakami (1977). The substrates in the census area mainly comprised rocks, boulders, and sand. Each band transect was censused three times, between 11:00 and 14:00 h. The identity and abundance of fish species observed within the transects were recorded, with fish identification based on the pictorial keys of Nakabo (2002). The census methods in 2005 differed from those of 1972 in some points. The visual census in the earlier study was conducted by snorkeling (swimming speed ~16.7 m/min: Gushima and Murakami [1977]), whereas the 2005 census used SCUBA (swimming speed ~4.9–6.7 m/min). SCUBA was chosen because snorkeling was not feasible for counting fish along the deep transect line and under conditions of turbidity.

Data analyses. The fish species composition recorded in October 2005 was compared with that reported for October 1972 (Gushima and Murakami 1978). Species reported in the previous study included some that either could not be identified or were possibly misidentified; these species were revised to correspond to the present study where possible (Table S1). Furthermore, bottom-dwelling species (e.g. members of the Serranidae and Synodontidae), strictly sheltered or territorial species (e.g.

Pomacentridae), and nocturnally active species (e.g. Holocentridae, Apogonidae) were excluded from the data collected in 2005 because these fishes were not counted in 1972. In addition, *Halichoeres orientalis* and *Scarus chameleon* were excluded from the 2005 survey data because they had only been taxonomically named since the publication of Gushima and Murakami (1978). Furthermore, pelagic species (e.g. Carangidae, Sphyraenidae) were omitted from both datasets for the analysis (Table 1).

In addition, seaweeds were surveyed by placing 1 x 1 m quadrats every 50 m along each fish survey transect. Each quadrat was photographed and the area of cover of leafy and fleshy algae was then visually estimated from the photographs. The leafy and fleshy algae included large-sized seaweeds and many small-sized seaweeds excluding filamentous algae and coralline algae. We took a total of 33 photos but lost 2 photos because of a camera problem.

The degree of similarity of fish assemblages at each depth interval in 1972 and 2005 was calculated using the Bray–Curtis similarity coefficient based on the number of individuals of each species. We predicted that the abundance of low-latitude species had increased, whereas high-latitude species had decreased in response to general warming trends. To determine whether the direction of change in species abundance is related to geographic range categories, we categorized the observed fish species as temperate (including warm-temperate) or subtropical, based on fish distribution data from Nakabo (2013) and the online resource FishBase (Froese and Pauly 2018). The observed species were further categorized according to one of three major feeding guilds: herbivores (feed mainly on plants or detritus), carnivores (feed mainly on animals), and omnivores, based on Gushima (1981), Tribble (1982), Okamura and Amaoka (1997), and FishBase (Froese and Pauly 2018); this was especially done to evaluate the effect of seaweed forest depletion on the reef fish assemblage. Thus, we defined a total of six categories: temperate herbivore (TH), temperate carnivore (TC), temperate omnivore (TO), subtropical herbivore (SH), subtropical carnivore (SC), and subtropical omnivore (SO). An ‘increased species’ was defined as one that had increased in abundance at least five-fold as compared with its estimated abundance in 1972. A ‘declined species’ was defined as one that had decreased in abundance by at least one-fifth since 1972. All other species were defined as stable.

We compared the frequencies of the increased species/declined species/stable species among the six categories using Fisher’s exact test. The statistical analysis was conducted using R version 3.5.3 (R Core Team 2019).

Results

Our recalculation of data of Gushima and Murakami (1978) revealed that a total of 2,819 individuals, representing 57 fish species from 19 families, had been recorded in October 1972 (Table 1). The 10-most-abundant species (in descending order of abundance) were: *Acanthurus nigrofuscus*, *Calotomus japonicus*, *Naso unicornis*, *Parupeneus spilurus*, *Girella leonina*, *Scarus rivulatus*, *Scarus schlegeli*, *Scarus forsteni*, *Prionurus scalprum*, and *Scarus rubroviolaceus* (Table 1). Of these, four are considered temperate species (*Ca. japonicus*, *Pa. spilurus*, *Gi. leonina*, and *Pr. scalprum*).

In October 2005, a total of 3,292 individuals, representing 110 fish species from 21 families, were observed. The 10-most-abundant species (in descending order of abundance) were: *Ac. nigrofuscus*, *Cirrhilabrus cyanopleura*, *Chaetodon auripes*, *Thalassoma lutescens*, *Zanclus cornutus*, *Sc. forsteni*, *Parupeneus multifasciatus*, *Acanthurus olivaceus*, *Coris gaimard*, and *Co. dorsomacula* (Table 1). All these except for *Ch. auripes* (temperate species) are considered subtropical species. Only two species (*Ac. nigrofuscus* and *Sc. forsteni*) were shared between the 1972 and 2005 records. One wrasse species observed in 2005 (*Ci. cyanopleura*) was not recorded in 1972. The similarities between 1972 and 2005 tended to be smaller with increasing depth (1–5 m: 0.41; 5–10 m: 0.26; 10–20 m: 0.07).

The fish species composition in 1972 mainly consisted of subtropical species but included some temperate species. Of the 57 species observed in October 1972, 6, 9, 1, 19, 19, and 3 species were categorized as TH, TC, TO, SH, SC, and SO, respectively. However, all TH (6 species), 67% of TC (6 species), all TO (1 species), and 47% of SH (9 species) had decreased in abundance, whereas 84% of SC (16 species) and 67% of SO (2 species) had either not increased or changed in abundance (Fig. 2). The ratio was significantly different among these categories (Fisher's exact probability test, $p < 0.01$). Of 26 declined species, 19 species were not even recorded in 2005, which included 4 species among the 10-most-abundant species in 1972: *Ca. japonicus* (TH), *Pa. spilurus* (TC), *Gi. leonina* (TH), and *Pr. scalprum* (TH) (Table 1). In addition, of 110 species observed in 2005, 71 were not recorded in October 1972, and 63 were not recorded in other months of 1972 as well (Table 1). Of the 71 species not recorded in the earlier survey, 55 (77%), 7 (10%), 4 (6%), 4 (6%), and 1 (1%) were categorized as SC, SH, SO, TC, and TO, respectively.

Leafy and fleshy algae were distributed in all three transect lines of October 1972. Mean algal coverage was 26%, 40%, and 38% at depths of 1–5 m, 5–10 m, and 10–20 m, respectively. However, no leafy and fleshy algae were observed in all transect lines in October 2005 (0% coverage).

Discussion

This study shows that the composition of the reef fish assemblage at Honmura Bay, Kuchierabu-jima Island has noticeably changed between 1972 and 2005. Of the 10-most-abundant species in each census, only two species were shared between the 1972 and 2005 records. Furthermore, 71 species were recorded only in 2005. The method of the present study differed in some respects from that of the previous surveys by Gushima and Murakami (1977, 1978). Especially, the underwater visual census was conducted using snorkeling in 1972, while the effort in 2005 used SCUBA. This difference will have affected the detection of some fishes, especially small-sized species (e.g. *Ci. cyanopleura*, *Pseudocheilinus hexataenia*), which are less easily observed by snorkeling than by SCUBA in deeper water. Similarities between 1972 and 2005 tended to be smaller with depth, which indicate that difference in methodology would have affected the results. However, we confirmed that not only some large-sized species (e.g. *Ca. japonicus*, *Na. unicornis*) but also some small-sized species (e.g. *Thalassoma cupido*, *Stethojulis interrupta terina*) showed a decline in abundance (Table 1). Furthermore, even in the shallow lines, where the influence of the method would be small, the similarity between 1972 and 2005 was considerably small. Thus, we consider that the reef fish assemblages have indeed changed at Kuchierabu-jima Island, though the differences in the census methods would also have influenced the findings.

Of the 10-most-abundant species recorded in 1972, four species (*Ca. japonicus*, *Pa. spilurus*, *Gi. leonina*, and *Pr. scalprum*) were not observed in 2005. However, three of these (*Pa. spilurus*, *Gi. leonina*, and *Pr. scalprum*) were confirmed by specimen sampling at Kuchierabu-jima Island in the 2010s (Kimura et al. 2017). In addition, we conducted an investigation of seafood utilization from Kuchierabu-jima Island in 2009 and confirmed that *Pr. scalprum* and *Gi. leonina* were both used as a local food resource (Shimizu et al. unpublished data). Therefore, even though the populations of the three species confirmed in the 2010s seem to have been maintained at the island, the populations have likely declined since the 1970s, at least in Honmura Bay.

In contrast, *Ca. japonicus* was not recorded by sampling in the 2010s (Kimura et al. 2017). In 2005, we observed only three individuals of *Calotomus* sp., which all appeared to be juveniles, thus they could not be confirmed as *Ca. japonicus* or *Ca. carolinus*. Furthermore, we determined that, in 2009, people on Kuchierabu-jima Island generally had little opportunity to consume *Ca. japonicus*, although this fish had been caught and consumed there in the 1970s (Shimizu et al. unpublished data). Therefore, we suppose that *Ca. japonicus* may be at risk of extinction at Kuchierabu-jima Island, which lies near the southern edge of its distribution range in Japan, though the species was observed spawning in 1986 and 1987 (Shibuno et al. 1994). Kumagai et al. (2018) infer a poleward shift in the distribution of *Ca. japonicus* in Japan based on data regarding the deforestation of temperate macroalgal communities as a consequence of overgrazing by this fish.

Overall, the subtropical fish species recorded in 1972 tended to show an increase or no change in abundance, while the temperate species tended to have declined. In addition, 93% of the fishes recorded only in 2005 were subtropical species. Furthermore, all four species that were among the 10-most-abundant in 1972 but were not recorded in 2005 (i.e. *Ca. japonicus*, *Pa. spilurus*, *Gi. leonina*, *Pr. scalprum*), are temperate species. This change corresponds with predictions about the influence of climate warming on species composition in ecosystems. In the southern part of the East China Sea, which includes the location of this island, the average annual and winter sea surface temperatures have increased between 1972 and 2005 (Fig. 3). Rising winter water temperatures correlate to a significant change in fish assemblages in many areas (Masuda 2008; Figueira and Booth 2010). Therefore, ocean warming would be a plausible cause of the shift in the observed reef fish abundance.

We found a notable decrease in the abundance of herbivorous fish species compared with that of carnivorous fish species regardless of their geographic range categories. Gushima and Murakami (1977, 1978) observed luxuriant macroalgal beds composed of species in the family Sargassaceae, between May and August, in the early 1970s (Fig. S1a–d,). However, similar macroalgal beds were not observed in the 2000s (Terada and Suzuki 2011; N. Shimizu, T. Kadota, Y. Sakai, M. Tsuboi, and B. Barros, personal observation) (Fig. S1e–g). The macroalgal beds had apparently already disappeared from the island's reefs by the early 1980s (T. Shibuno, personal communication). Thus, the decline of sargassum beds would have affected the subtidal reef fish assemblage. Evidence supporting this association is that the two species with the greatest decline in abundance (*Ca. japonicus*, *Na. unicornis*) at Kuchierabu-jima Island are reported to feed on macroalgae such as Sargassaceae species (Gushima 1981). Furthermore, we could not confirm the presence of even small-sized leafy and fleshy seaweeds in October 2005, although small-sized seaweeds such as *Asparagopsis taxiformis* were confirmed in the spring of 2009 (Terada and Suzuki 2011). In the 1970s, small-sized seaweeds were reported to remain after autumn (Gushima and Murakami 1977, 1978; Gushima 1981) and to serve as an important feeding site for not only herbivorous fish but also carnivorous fish (Gushima 1981). These included fish species with greatly reduced abundance (herbivores: *Scarus ghobban*, *Sc. schlegeli*, *Sc. rivulatus*, *Pr. scalprum*; carnivores: *Pa. spilurus*, *Th. cupido*, *Stethojulis interrupta terina*). In addition, macroalgal seaweed beds function as nurseries for juveniles in several fish families, such as the labrids, acanthurids, and mullids (Fulton et al. 2020; James and Whitfield 2023). Although few studies have revealed change in a fish assemblage associated with the loss of seaweeds in Japan, great declines in the abundance of *Pr. scalprum* and *Th. cupido* were reported after the loss of macroalgal beds at Tanoura on the south coast of Shikoku Island (Nakamura 2018). The decline of macroalgal beds along the coast of Japan could be related with the increase in coastal water temperatures (Tanaka et al. 2012; Kumagai et al. 2018; Japan Fisheries Agency 2021; Kiyomoto et al. 2021). Thus, marine warming can affect fish assemblages not only directly but also indirectly.

Several alternative hypotheses might explain the change we observed in the subtidal reef fish community between 1972 and 2005. Anthropogenic impacts especially should be considered. The population of Kuchierabu-jima Island has always been relatively small and is declining (427 and 147 inhabitants in the years 1970 and 2002, respectively: Yakushima Town Office at Kuchierabu-jima Island, personal communication); additionally, the island is more than 60 km from the heavily populated Kyushu Island. Therefore, Kuchierabu-jima Island should be less affected by anthropogenic impacts like pollution, eutrophication, and overharvesting. However, the breakwater at Honmura Bay, located inshore from our transects, was extended from 40 m to 250 m in the intervening 33 years between surveys. In addition, a quarry near Honmura Bay has operated for over 20 years. These disturbances could have exerted some influence on the reef fish assemblage via changes in the hydrological effect and turbidity. Furthermore, natural phenomena such as tropical storms also influence subtidal reef fish populations (Lassig 1983). The frequency of typhoons that passed near

Kuchierabu-jima Island was higher in the period 2002–2005 than in 1969–1972 (Japan Meteorological Agency 2019).

Kuchierabu-jima Island is located near a marine biogeographic zone boundary (Nakabo 2002, 2013). Biogeographic transition zones where abiotic and biotic conditions allow for the interactions of organisms from different geographical origins are experiencing rapid changes in the marine realm (Horta e Costa et al. 2014; Troast et al. 2020). In addition, sea surface temperatures are increasing more rapidly in the southern part of the East China Sea (~1.14°C per century) than the global mean of 0.51°C per century (Japan Meteorological Agency 2011). Therefore, the ecological response to rising water temperatures could be relatively evident in the waters around Kuchierabu-jima Island. Recently, Kimura et al. (2014) showed a considerable change in the species composition of a tide pool fish assemblage at Kuchierabu-jima Island, between 1990 and 2011, by specimen sampling. Further studies will reveal the change of reef fish fauna at Kuchierabu-jima Island in more detail.

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Declarations

Conflicts of interest The authors declare that they have no conflict of interest

Ethics approval This study complied with the current laws of Japan and the guidelines of the Ichthyological Society of Japan.

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Figure legends

Fig. 1 Map of Japan and adjacent waters showing the location of the study site, Honmura Bay on Kuchierabu-jima Island.

Fig. 2 Rates of the declined fish species (*black*), stable species (*gray*), and increased species (*white*) in relation to their geographic ranges and trophic categories.

Fig. 3 Annual and winter water temperatures in the northern part of the East China Sea, from 1972 to 2005, based on 3-year running averages (*closed squares*). Redrawn from data provided by the Japan Meteorological Agency (2011).

Fig. 4 Underwater photographs taken around Kuchierabu-jima Island in the 1970s and 2000s, at: (**a**) Honmura Bay, on the southern coast of the island, in May 1971, and (**b**) in August 1971; (**c**) Nishiura Bay, on the northern coast of the island, in August 1972; (**d**) Nishiura Bay in October 1972, and (**e**) Honmura Bay in May 2012; (**f**) Nishiura Bay in May 2006, and (**g**) in September 2005; and (**h**) Honmura Bay in October 2004. Dense seaweed beds were observed from spring to summer (**a**–**c**) but were not in autumn in the early 1970s (**d**). On the other hand, no dense seaweed beds were observed in 2000s. Allows in photograph **d** indicate stems of Sargassaceae species.

Table 1 List of reef fish species and their abundance in the 1972 survey of Gushima and Murakami (1978) and the 2005 survey (present study) at Kuchierabu-jima Island, southern Japan

Scientific name	**Japanese name**	**Abundance**		**Relative change in abundance between 1972 and 2005**	**Geographic range and trophic groups category**	**Reason**
		Oct. 1972	**Oct. 2005**			
Dasyatidae						
*Neotygon kuhlii**	Yakko-ei		2			1
Muraenidae						
*Echidna nebulosa**	Kumo-ustubo		1			1
Synodontidae						
Synodus sp.*			29			1
Holocentridae						
Myripristis sp.*			9			1
*Neoniphon sammara**	Ukeguchi-ittoudai		2			1
*Sargocentron melanospilos**	Sumitsuki-kanoko		10			1
Holocentridae spp.*			43			1
Aulostomidae						
Aulostomus chinensis	Hera-yagara	0	3	Not recorded in 1972[a]	SC	
Fistulariidae						
Fistularia commersonii	Ao-yagara	5	6	1.20	TC	
Serranidae						
*Belonoperca chabanaudi**	Yami-suzuki		1			1
*Cephalopholis miniata**	Yukata-hata		12			1
*Cephalopholis urodeta**	Niji-hata		5			1
*Epinephelus fasciatus**	Aka-hata		6			1
*Epinephelus merra**	Kanmon-hata		5			1
*Grammistes sexlineatus**	Nunosarashi		2			1
*Plectropomus laevis**	Kokuhan-ara		1			1
*Plectropomus leopardus**	Suji-ara		1			1
*Pseudanthias pascalus**	Hanagoi		124			1
*Variola albimarginata**	Ojiro-bara-hata		4			1
*Variola louti**	Bara-hata		7			1
Pseudochromidae						
*Labracinus cyclophthalmus**	Megisu		54			1
Apogonidae						
*Apogon aureus**	Aosuji-tenjikudai		31			1
*Cheilodipterus macrodon**	Ryūkyū-yarai-ishimochi		27			1
*Cheilodipterus quinquelineatus**	Yarai-ishimochi		5			1
Malacanthidae						
Malacanthus latovittatus	Kitsune-amadai	0	1	Not recorded in 1972[a]	SC	
Carangidae						
*Seriola dumerili**	Kanpachi		1			3
Carangidae spp.*			51			3

Lutjanidae						
Lutjanus gibbus	Hime-fuedai	1	1	1.00	SC	
Lutjanidae sp.		1	0	Not recorded in 2005	SC	
Macolor niger	Madara-tarumi	0	2	Not recorded in 1972[a]	SC	
Haemulidae						
Plectorhinchus picus	Ajia-koshōdai	0	2	Not recorded in 1972[a]	SC	
Plectorhinchus vittatus	Musuji-koshōdai	0	3	Not recorded in 1972[a]	SC	
Nemipteridae						
Scolopsis bilineata	Futasuji-tamagashira	0	13	Not recorded in 1972[a]	SC	
Lethrinidae						
Gymnocranius sp.	Tama-meichi	0	2	Not recorded in 1972[a]	SC	
Lethrinus nebulosus	Hama-fuefuki	18	0	Not recorded in 2005	TC	
Monotaxis grandoculis	Yokoshima-kurodai	0	3	Not recorded in 1972[a]	SC	
Mullidae						
Mulloidichthys vanicolensis	Akahimeji	0	1	Not recorded in 1972[a]	SC	
Parupeneus crassilabris	Futasuji-himeji	1	0	Not recorded in 2005	SC	
Parupeneus ciliatus	Hōrai-himeji	0	12	Not recorded in 1972[a]	TC	
Parupeneus cyclostomus	Marukuchi-himeji	0	6	Not recorded in 1972[a]	SC	
Parupeneus indicus	Koban-himeji	9	12	1.33	SC	
Parupeneus multifasciatus	Ojisan	76	**150**	1.97	SC	
Parupeneus pleurostigma	Ryūkyū-himeji	0	6	Not recorded in 1972[a]	SC	
Parupeneus spilurus	Okina-himeji	**186**	0	Not recorded in 2005	TC	
Mullidae spp.		6	1	0.17		
Pempheridae						
Pempheris sp.*	Ryūkyū-hatanpo		5			1
Chaetodontidae						
Chaetodon argentatus	Kagami-chōchōuo	0	14	Not recorded in 1972	SO	
Chaetodon auriga	Toge-chōchōuo	18	5	0.28	SC	
Chaetodon auripes	Chōchōuo	27	**225**	8.33	TC	
Chaetodon kleinii	Mizore-chōchōuo	0	28	Not recorded in 1972[a]	TO	
Chaetodon lineolatus	Nise-fūrai-chōchōuo	1	0	Not recorded in 2005	SC	
Chaetodon lunula	Chōhan	0	6	Not recorded in 1972[a]	SC	
Chaetodon melannotus	Akebono-chōchōuo	0	9	Not recorded in 1972[a]	SC	
Chaetodon plebeius	Sumitsuki-tonosamadai	0	1	Not recorded in 1972[a]	SC	
Chaetodon speculum	Tonosamadai	0	2	Not recorded in 1972[a]	SC	
Chaetodon trifascialis	Yarikatagi	0	1	Not recorded in 1972[a]	SC	
Chaetodon unimaculatus	Itten-chōchōuo	0	3	Not recorded in 1972[a]	SC	
Chaetodon vagabundus	Fūrai-chōchōuo	0	14	Not recorded in 1972	SC	
Forcipiger flavissimus	Fue-yakkodai	0	4	Not recorded in 1972[a]	SC	

Heniochus chrysostomus	Minami -hatatatedai	0	2	Not recorded in 1972[a]	SC	
Heniochus varius	Tsuno -hatatatedai	0	5	Not recorded in 1972[a]	SC	
Pomacanthidae						
Apolemichthys trimaculatus	Shiten-yakko	0	10	Not recorded in 1972	SC	
*Centropyge bispinosa**	Ruri-yakko		2			1
*Centropyge ferrugata**	Akahara-yakko		21			1
*Centropyge tibicen**	Abura-yakko		21			1
*Centropyge vrolikii**	Namera-yakko		192			1
*Paracentropyge venusta**	Sumire-yakko		1			1
Pomacanthus imperator	Tatejima -kinchakudai	0	26	Not recorded in 1972[a]	SC	
Pomacanthus semicirculatus	Sazanami-yakko	2	28	14.00	SO	
Pygoplites diacanthus	Nishiki-yakko	0	4	Not recorded in 1972[a]	SC	
Cirrhitidae						
*Paracirrhites forsteri**	Hoshi-gonbe		3			1
Pomacentridae						
*Abudefduf notatus**	Iso-suzumedai		1			1
*Abudefduf sexfasciatus**	Rokusen-suzumedai		8			1
*Abudefduf vaigiensis**	Oyabiccha		202			1
*Amphiprion clarkii**	Kumanomi		139			1
*Chromis chrysurus**	Amami-suzumedai		397			1
*Chromis margaritifer**	Shikoku-suzumedai		81			1
*Chromis weberi**	Takasago-suzumedai		61			1
*Chromis xanthurus**	Mon-suzumedai		5			1
*Chrysiptera cyanea**	Ruri-suzumedai		1			1
*Chrysiptera rex**	Remon-suzumedai		2			1
*Chrysiptera starcki**	Senaki-ruri-suzumedai		2			1
*Dascyllus reticulatus**	Futasuji-ryūkyū-suzumedai		14			1
*Dascyllus trimaculatus**	Mitsuboshi-kuro-suzumedai		141			1
*Neoglyphidodon nigroris**	Hirenaga-suzumedai		994			1
*Plectroglyphidodon dickii**	Ishigaki-suzumedai		3			1
*Plectroglyphidodon lacrymatus**	Rurihoshi-suzumedai		159			1
*Pomacentrus bankanensis**	Megane-suzumedai		59			1
*Pomacentrus coelestis**	Sora-suzumedai		276			1
*Pomacentrus lepidogenys**	Asado-suzumedai		6			1
*Pomacentrus nagasakiensis**	Nagasaki-suzumedai		3			1
*Pomacentrus vaiuli**	Kuro-megane-suzumedai		36			1
Stegastes spp.*			122			1
Pomacentridae sp.*			1			1
Kyphosidae						
Kyphosus vaigiensis	Isuzumi	37	3	0.08	TH	
Microcanthidae						
Microcanthus	Kagokakidai	4	0	Not recorded in 2005	TC	

strigatus						
Girellidae						
Girella leonina	Kuro-mejina	**178**	0	Not recorded in 2005	TH	
Labridae						
Anampses caeruleopunctatus	Buchi-susuki-bera	13	37	2.85	SC	
Anampses geographicus	Mushi-bera	2	25	12.50	SC	
Anampses meleagrides	Hokuto-bera	0	14	Not recorded in 1972[a]	SC	
Anampses twistii	Hoshi-susuki-bera	0	3	Not recorded in 1972[a]	SC	
Bodianus axillaris	Sumitsuki-bera	0	3	Not recorded in 1972[a]	SC	
Bodianus mesothorax	Kesagake-bera	0	8	Not recorded in 1972[a]	SC	
Cheilinus chlorourus	Akaten -mochinouo	0	6	Not recorded in 1972[a]	SC	
Cheilinus trilobatus	Mitsuba -mochinouo	0	3	Not recorded in 1972[a]	SC	
Choerodon azurio	Ira	1	0	Not recorded in 2005	TC	
Cirrhilabrus cyanopleura	Kuroheri-itohiki -bera	0	**261**	Not recorded in 1972[a]	SC	
Cirrhilabrus temminckii	Itohiki-bera	0	84	Not recorded in 1972[a]	TC	
Coris aygula	Kanmuri-bera	2	6	3.00	SC	
Coris dorsomacula	Suji-bera	0	85	Not recorded in 1972[a]	SC	
Coris gaimard	Tsuyu-bera	15	**103**	6.87	SC	
Epibulus insidiator	Gichi-bera	0	2	Not recorded in 1972[a]	SC	
Gomphosus varius	Kugi-bera	0	31	Not recorded in 1972[a]	SC	
Halichoeres biocellatus	Nishiki-kyūsen	0	5	Not recorded in 1972[a]	SC	
Halichoeres hortulanus	Tokara-bera	0	12	Not recorded in 1972	SC	
Halichoeres marginatus	Kanoko-bera	0	7	Not recorded in 1972[a]	SC	
Halichoeres melanochir	Munaten-bera	0	44	Not recorded in 1972[a]	SC	
Halichoeres nebulosus	Inazuma-bera	0	14	Not recorded in 1972[a]	SC	
*Halichoeres orientalis**	Tsuki-bera		8			2
Hemigymnus fasciatus	Shima -tarekuchi-bera	0	8	Not recorded in 1972[a]	SC	
Hologymnosus annulatus	Namera-bera	14	6	0.43	SC	
Hologymnosus doliatus	Shiro-tasuki-bera	0	22	Not recorded in 1972[a]	SC	
Labroides bicolor	Somewake-bera	0	5	Not recorded in 1972[a]	SC	
Labroides dimidiatus	Hon-somewake -bera	2	36	18.00	SC	
Macropharyngodon meleagris	Nodoguro-bera	1	48	48.00	SC	
Macropharyngodon negrosensis	Sejiro-nodoguro -bera	0	12	Not recorded in 1972[a]	SC	
Oxycheilinus bimaculatus	Tako-bera	0	1	Not recorded in 1972[a]	SC	
Oxycheilinus digramma	Hohosuji -mochinouo	0	1	Not recorded in 1972[a]	SC	
Pseudocheilinus hexataenia	Nise-mochinouo	0	3	Not recorded in 1972[a]	SC	
Stethojulis bandanensis	Akaobi-bera	39	67	1.72	SC	
Stethojulis interrupta terina	Kaminari-bera	21	4	0.19	TC	
Stethojulis strigiventer	Harasuji-bera	1	5	5.00	SC	
Stethojulis trilineata	Oni-bera	2	22	11.00	SC	
Thalassoma cupido	Nishiki-bera	77	3	0.04	TC	
Thalassoma	Senasuji-bera	0	22	Not recorded in 1972[a]	SC	

hardwicke						
Thalassoma lunare	Otome-bera	0	8	Not recorded in 1972	SC	
Thalassoma lutescens	Yamabuki-bera	11	**200**	18.18	SC	
Labridae spp.		10	33	3.30		
Scaridae						
Calotomus japonicus	Budai	**265**	0	Not recorded in 2005	TH	
Calotomus sp.		0	3	Not recorded in 1972[a]		
Chlorurus bowersi	Ōmon-hage-budai	0	1	Not recorded in 1972[a]	SH	
Chlorurus microrhinos	Nan'yō-budai	5	11	2.20	SH	
Chlorurus oedema	Kobu-budai	1	0	Not recorded in 2005	SH	
Chlorurus sordidus	Hage-budai	4	6	1.50	SH	
*Scarus chameleon**	Kamereon-budai		6			2
Scarus festivus	Tsukinowa-budai	12	1	0.08	SH	
Scarus forsteni	Ichimonji-budai	**119**	**151**	1.27	SH	
Scarus frenatus	Amime-budai	5	7	1.40	SH	
Scarus ghobban	Hi-budai	40	0	Not recorded in 2005	TH	
Scarus hypselopterus	Kibire-budai	0	15	Not recorded in 1972[a]	SH	
Scarus niger	Buchi-budai	0	5	Not recorded in 1972	SH	
Scarus ovifrons	Ao-budai	12	0	Not recorded in 2005	TH	
Scarus prasiognathos	Nishiki-budai	1	0	Not recorded in 2005	SH	
Scarus rivulatus	Suji-budai	**158**	8	0.05	SH	
Scarus rubroviolaceus	Naga-budai	**88**	45	0.51	SH	
Scarus schlegeli	Obi-budai	**140**	4	0.03	SH	
Scaridae spp.		153	152	0.99		
Pinguipedidae						
*Parapercis millepunctata**	Wanuke-toragisu		15			1
*Parapercis pacifica**	Oguro-toragisu		11			1
Ephippidae						
Platax orbicularis	Nan’yō-tsubameuo	1	0	Not recorded in 2005	SO	
Siganidae						
Siganus spinus	Ami-aigo	56	0	Not recorded in 2005	SH	
Siganus spp.		22	21	0.95		
Zanclidae						
Zanclus cornutus	Tsunodashi	5	**158**	31.60	SO	
Acanthuridae						
Acanthurus dussumieri	Nise-kanranhagi	67	39	0.58	SH	
Acanthurus lineatus	Nijihagi	5	2	0.40	SH	
Acanthurus mata	Hira-niza	12	0	Not recorded in 2005	SH	
Acanthurus nigricans	Megane-kurohagi	8	0	Not recorded in 2005	SH	
Acanthurus nigrofuscus	Naga-niza	**451**	**361**	0.80	SH	
Acanthurus olivaceus	Montsukihagi	29	**109**	3.76	SH	
Acanthurus pyroferus	Kuroguchi-niza	0	2	Not recorded in 1972[a]	SH	
Acanthurus xanthopterus	Kurohagi	0	3	Not recorded in 1972[a]	SO	
Ctenochaetus striatus	Sazanamihagi	0	12	Not recorded in 1972	SH	
Naso hexacanthus	Tenguhagi-modoki	0	26	Not recorded in 1972[a]	SC	
Naso lituratus	Miyako-tenguhagi	0	16	Not recorded in 1972	SH	
Naso unicornis	Tenguhagi	**259**	34	0.13	SH	
Prionurus scalprum	Nizadai	**111**	0	Not recorded in 2005	TH	
Zebrasoma scopas	Gomahagi	0	1	Not recorded in 1972[a]	SH	

Zebrasoma veliferum	Hirenagahagi	2	17	8.50	SH	
Sphyraenidae						
*Sphyraena obtusata**	Taiwan-kamasu		20			3
Balistidae						
Balistoides conspicillum	Mongara -kawahagi	1	3	3.00	SC	
Odonus niger	Aka-mongara	0	1	Not recorded in 1972[a]	SC	
Sufflamen bursa	Musume-hagi	0	19	Not recorded in 1972[a]	SC	
Sufflamen chrysopterum	Tsumajiro -mongara	0	63	Not recorded in 1972[a]	SC	
Monacanthidae						
Cantherhines dumerilii	Hakusei-hagi	0	8	Not recorded in 1972[a]	SC	
Paraluteres prionurus	Nokogiri-hagi	0	5	Not recorded in 1972[a]	SO	
Ostraciidae						
Ostracion cubicum	Minami -hakofugu	1	4	4.00	TC	
Ostracion immaculatus	Hakofugu	0	1	Not recorded in 1972[a]	TC	
Tetraodontidae						
Arothron nigropunctatus	Kokuten-fugu	0	13	Not recorded in 1972[a]	SC	
Canthigaster axiologa	Hana -kinchakufugu	0	32	Not recorded in 1972[a]	SC	
Canthigaster rivulata	Kitamakura	3	0	Not recorded in 2005	TO	
Canthigaster valentini	Shima -kinchakufugu	0	55	Not recorded in 1972[a]	SO	
Diodontidae						
Diodon holocanthus	Harisenbon	0	5	Not recorded in 1972[a]	TC	
Diodon hystrix	Nezumifugu	2	0	Not recorded in 2005	SC	

Species names follow Nakabo (2013)

Bold letters in abundance indicate the 10-most-abundant species

Asterisks indicate species eliminated from the Results (see *Data analysis* section)

Reason for its elimination from the Results: 1, species which would not have been counted in the precious census in 1972; 2, newly described species; 3, pelagic species

The main geographic distribution and trophic groups of each species were categorized as: SC: subtropical carnivore, SH: subtropical herbivore, SO: subtropical omnivore, TC: temperate carnivore, TH: temperate herbivore, TO: temperate omnivore.

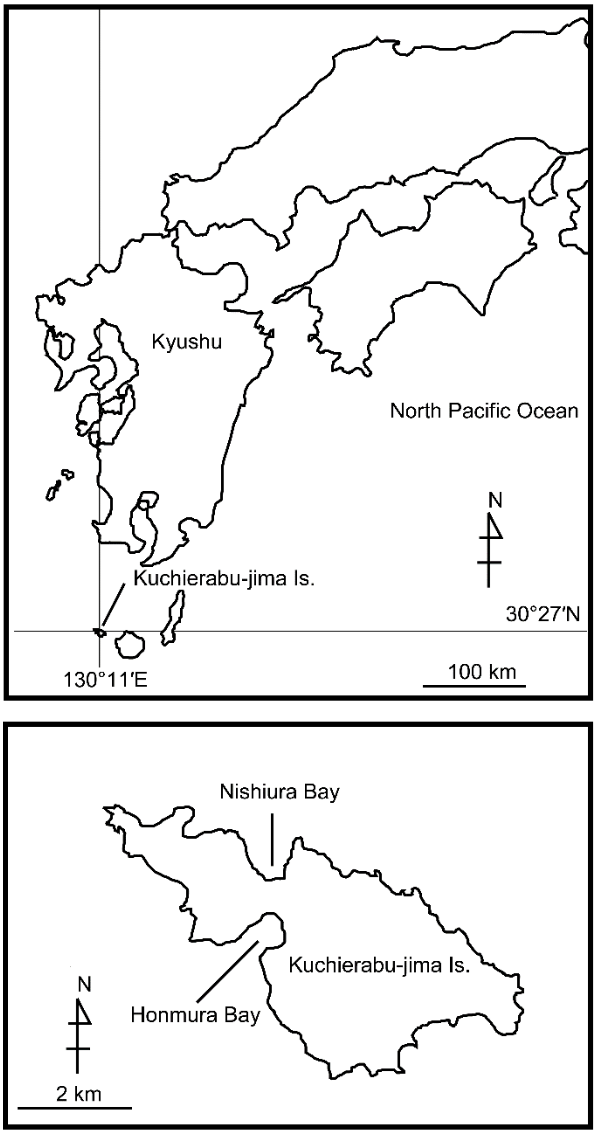
Kyushu
North Pacific Ocean
N
Kuchierabu-jima Is.
30°27′N
130°11′E
100 km
Nishiura Bay
Kuchierabu-jima Is.
N
Honmura Bay
2 km

Fig. 1

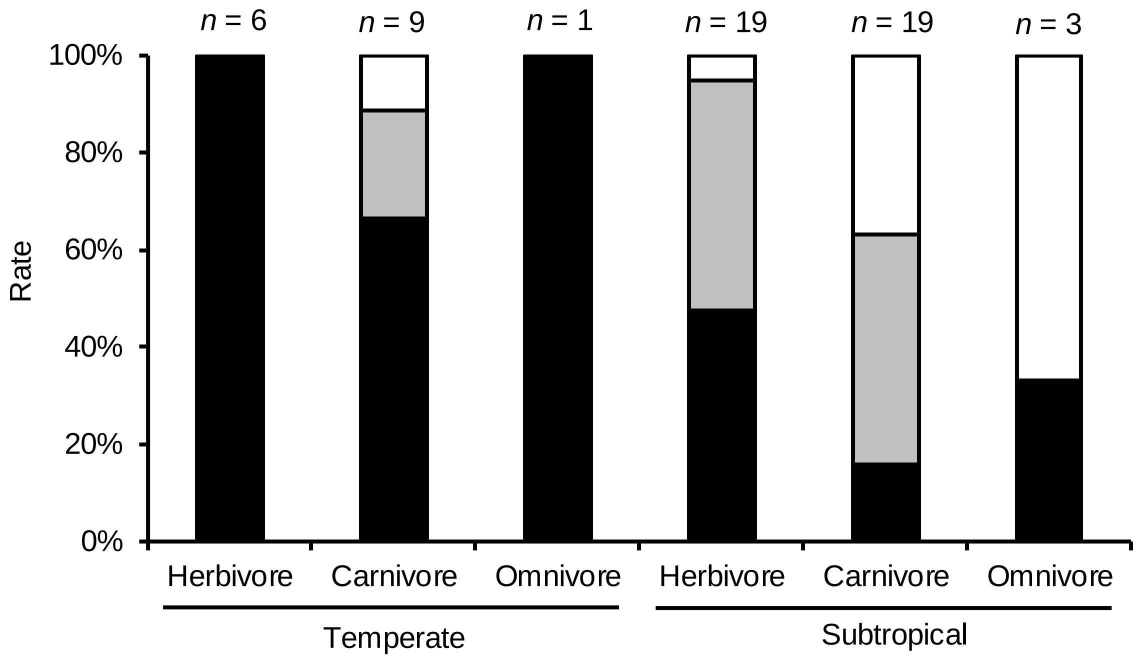
n = 6
n = 9
n = 1
n = 19
n = 19
n = 3
100%
80%
60%
40%
20%
0%
Rate
Herbivore
Carnivore
Omnivore
Herbivore
Carnivore
Omnivore
Temperate
Subtropical

Fig. 2

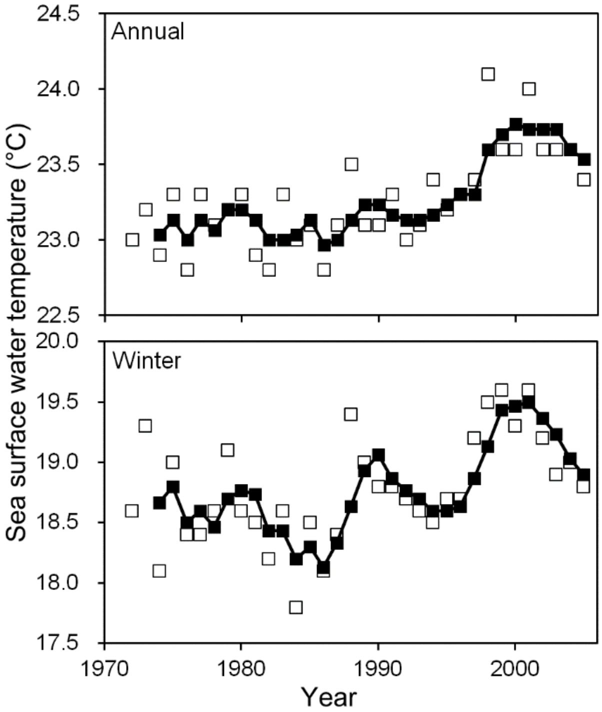
Annual
Winter
Sea surface water temperature (°C)
24.5
24.0
23.5
23.0
22.5
20.0
19.5
19.0
18.5
18.0
17.5
1970
1980
1990
2000
Year

Fig. 3

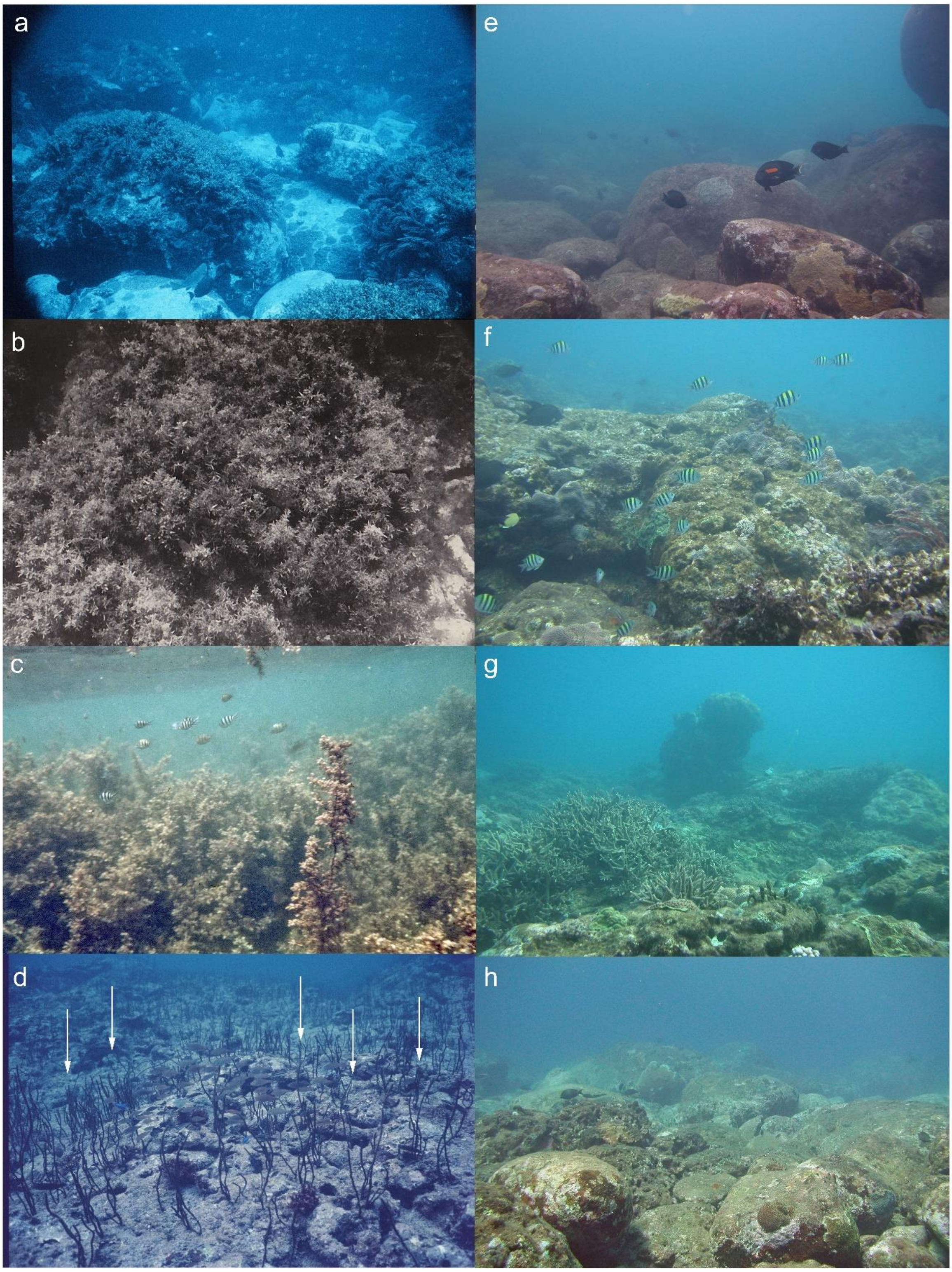

Fig. 4