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TIME SUBMITTED	05-FEB-2021 07:45PM (UTC+0700)	CHARACTER COUNT	32395
SUBMISSION ID	1502280987		

Introduction of Geospatial Perspective to the Ecology of Fish-Habitat Relationships in Indonesian Coral Reefs: A Remote Sensing Approach

Shuhei Sawayama^{1,2*}, Nurjannah Nurdin³, Muhammad Akbar AS⁴, Shingo X Sakamoto¹, and Teruhisa Komatsu^{1,5}

¹Atmosphere and Ocean Research Institute, The University of Tokyo, Chiba 277-8564, Japan

²Japan Society for the Promotion of Science, Tokyo 102-0083, Japan

³Marine Science Department, Hasanuddin University, Makassar 95245, Indonesia

⁴Master of Science in Information Technology for NRM, SEAMEO BIOTROP, Bogor 16134, Indonesia

⁵Japan Science and Technology Agency, CREST, Saitama 332-0012, Japan

Received 30 May 2014; Revised 3 December 2014; Accepted 17 January 2015
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Abstract – Coral reef ecosystems worldwide are now being harmed by various stresses accompanying the degradation of fish habitats and thus knowledge of fish-habitat relationships is urgently required. Because conventional research methods were not practical for this purpose due to the lack of a geospatial perspective, we attempted to develop a research method integrating visual fish observation with a seabed habitat map and to expand knowledge to a two-dimensional scale. WorldView-2 satellite imagery of Spermonde Archipelago, Indonesia obtained in September 2012 was analyzed and classified into four typical substrates: live coral, dead coral, seagrass and sand. Overall classification accuracy of this map was 81.3% and considered precise enough for subsequent analyses. Three sub-areas (CC: continuous coral reef, BC: boundary of coral reef and FC: few live coral zone) around reef slopes were extracted from the map. Visual transect surveys for several fish species were conducted within each sub-area in June 2013. As a result, Mean density (Ind. / 300 m²) of *Chaetodon octofasciatus*, known as an obligate feeder of corals, was significantly higher at BC than at the others ($p < 0.05$), implying that this species' density is strongly influenced by spatial configuration of its habitat, like the "edge effect." This indicates that future conservation procedures for coral reef fishes should consider not only coral cover but also its spatial configuration. The present study also indicates that the introduction of a geospatial perspective derived from remote sensing has great potential to progress conventional ecological studies on coral reef fishes.

Key words – coral reef, fish-habitat, remote sensing, Spermonde Archipelago

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*Corresponding author. E-mail: sawayama@aori.u-tokyo.ac.jp

1. Introduction

Coral reef ecosystems are known to play an indispensable role in providing various ecological goods and services for human beings (Moberg and Folke 1999). However, coral reefs are declining in many regions of the world. For example, Wilkinson (2008) reported that 19% of the world's original coral reefs have been already lost and additional 35% are now endangered. This serious situation with regard to coral reefs is partly due to the multiple stresses generated by human activities such as the release of pollutants, eutrophication and destructive fishing practices (e.g. Mumby 2002; Pet-Soede and Erdman 1988). The increase in the frequency of coral bleaching events and outbreaks of crown-of-thorn starfish (*Acanthaster planci*) are also thought to be the cause of the deterioration of corals (Hughes et al. 2003; Lourey et al. 2000).

Because some coral reef fishes rely heavily on live corals for their shelters and feeding grounds, any degradation in the health of corals directly affects the fish community (e.g. Sano et al. 1987; Jones et al. 2004; Munday 2004; Graham et al. 2006). For the effective conservation or sustainable use of fishes in coral reefs, detailed information on "fish-habitat relationships" is urgently required. Although there have been a lot of previous studies concerning fish-habitat relationships, most of those only dealt with small-scale habitat information such as coral cover, coral species richness or substrate rugosity

within quadrats or transects (e.g. Luckhurst and Luckhurst 1978; Roberts and Ormond 1987). Bell and Galzin (1984) visually assessed the percentage of coral cover throughout a large lagoon (approximately 20 km²) but this method was not quantitative, as they themselves noted. In short, due to the lack of large scale and quantitative techniques for measuring habitats, existing observations of fish-habitat relationship are not practical for the monitoring and conservation of coral reef fish. For instance, when we try to estimate the fish population within a certain area of the reef, a geospatial perspective on two-dimensional (horizontal) expanse of habitats is essential.

In general, changes in species' distributions near habitat edges (edge effects) are among the most extensively studied phenomena in recent ecological studies (Ries and Sisk 2004). It can be expected that the boundaries of coral reefs may possess higher density for some species, just like the edge effect of seagrass beds with regard to fish density reported by some studies (e.g. Gullström et al. 2005; Smith et al. 2008). To verify this hypothesis in coral reefs, there is a need to objectively and quantitatively delimit the boundaries of coral reefs on a horizontal plane. For this purpose, Fortin et al. (2000) proposed that remote sensing is one of the tools that could yield a map which permits us to detect the boundaries of habitats. Especially, Multispectral satellite remote sensing

is suitable for mapping shallow coastal ecosystems (e.g. Komatsu et al. 2012).

Satellite remote sensing can observe large and two-dimensional habitat distribution in shallow coastal areas efficiently and cost-effectively (Mumby et al. 1999). According to some previous studies (e.g. Mumby et al. 1998; Call et al. 2003; Sawayama and Komatsu 2010), coral reefs are suitable sites for habitat mapping with multispectral satellite sensors mainly because of their shallow distributions and high water clarity. Although benthic habitat information derived from remote sensing would be very valuable for fish studies, it has not been sufficiently utilized for studies on fish habitats (Mellin et al. 2009). Thus, it is very meaningful to develop research on fish habitats in coral reefs with remote sensing.

Spermonde Archipelago is located off the west coast of South Sulawesi and consists of numerous coral islands on the continental shelf (Fig. 1(a)). This region is included in a southwestern part of the "coral triangle" where the biodiversity of coral reef fish is considered to be the highest in the world (Roberts et al. 2002; Mora et al. 2003; Bellwood and Meyer 2009). However, there is great concern about the degradation of the coral reef ecosystems of these islands due to the increase in pollution accompanying with the rapid population growth and modernization in nearby cities in recent decades. Destructive fishing activities such as dynamite blast fishing

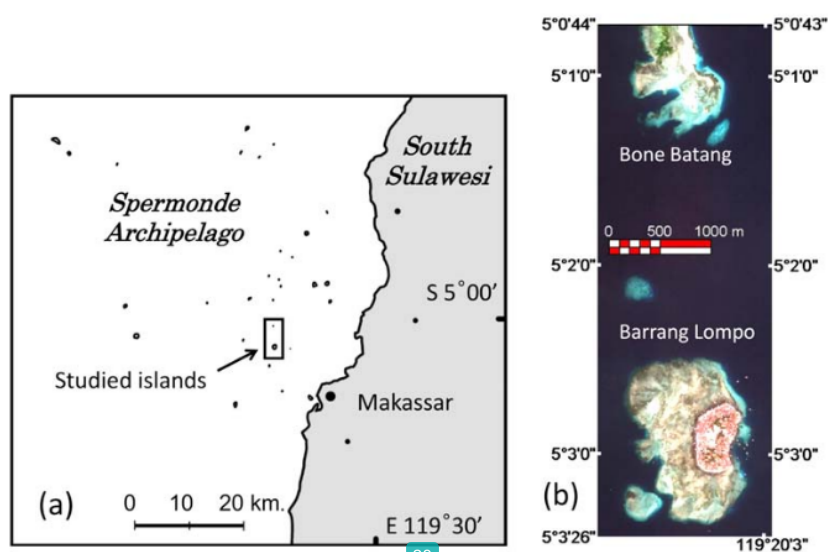


Fig. 1. Location of Spermonde Archipelago and two studied islands: Barrang Lompo and Bone Batang. Map of Spermonde Archipelago (a) and WorldView-2 image of two islands taken on 16 September 2012 shown by RGB true color with stretched histogram (b)

and cyanide fishing are also serious problems that cause coral reef degradation in this area (Edinger et al. 1998). These activities are still routinely engaged in by local fishermen despite prohibitions being issued (Pet-Soede and Erdman 1998; Mous et al. 2000). Considering these problems, it is important to study fish-habitat relationships in this region.

The objective of this study is to develop a method to study fish in coral reefs and expand the knowledge of fish-habitat relationships onto a large horizontal scale by applying remote sensing. Specifically, we focused on the edge effects of coral reef with regard to fish densities. The present study aims to present practical information for fish conservation planning in coral reefs.

2. Materials and Methods

Study site

Two islands in Spermonde Archipelago, Barang Lompo and Bone Batang, were selected as study sites (Fig. 1(b)). Barrang Lompo is a vegetated island possessing a large land area and population, while Bone Batang is a very small uninhabited sand cay without vegetation. There are well developed wide reef flats and long fore reefs at the west side of both lands. This pattern of the reef configuration can be seen typically in many islands of Spermonde archipelago (Moll 1983). The reef flat areas are commonly shallower than 1.0 m depth (intertidal or shallow subtidal) and often covered by seagrasses (Pogoreutz et al. 2012). There are many reef-building corals and rocky substrate around the west slopes, while the east slopes mainly consist of carbonate sand (Renema and Troelstra 2001). Outside the end of the west flats, there are zones of relatively gentle slopes to bottom depths of roughly 10 m and steep slopes from those to more than 20 m. All transect surveys on fish were conducted at the west side of the reefs, where there are relatively gentle slopes between depths of 1.0 m and 8.0 m.

In this region, the period from May to October is the dry season due to the Southern Monsoon wind. Therefore, the sea water in this term is generally clearer than that in the wet season. It was reported that water clarity around Barrang Lompo reef in May–August was relatively high, estimated about 17 m using secchi disk extinction measurements (Edinger et al. 1998; Renema and Troelstra 2001). Water visibility around Bone Batang reef is considered to be at the same level as (or higher than) that around other reefs because nutrient load due to human activity is less in Bone Batang.

Satellite imagery analysis

The satellite imagery obtained by WorldView-2 (WV-2) sensor in September 16, 2012 (ID: 103001001A1C1D00) (Fig. 1(b)) was selected from its archives due to the high water clarity and low cloud cover. The WV-2 image possesses six visible bands (band-1 to 6) and two near infrared bands (band-7 and 8). Spatial resolution of the sensor is 27 m and regarded to be adequate for habitat mapping in coral reefs (Mumby and Edwards 2002).

The flow chart of image processing is shown in Fig. 2. All of these processes were done using GIS software, TNTmips Pro ver. 2010 (MicroImages Inc.). Raw data of each band was transformed from digital number (DN) to radiance value. Electric noise was removed by a 3×3 square kernel median filter. The masks of land and deep sea areas were produced from certain threshold values of bands and modified by manual operation occasionally. The unmasked area of each image was divided into two zones of bottom depths: shallow (inner reef) and deep (outer reef) zones, using a threshold value of band-6 and manual operation. This process, we termed “zonal masking,” was expected to reduce the effect of water column attenuation and improve accuracy, similar to Pasqualini et al. (1997) and Sagawa et al. (2008).

Ground truth surveys were conducted around the two islands during May 27 and June 2, 2011. In situ bottom substrate data were recorded by an underwater video camera (FM-4100,

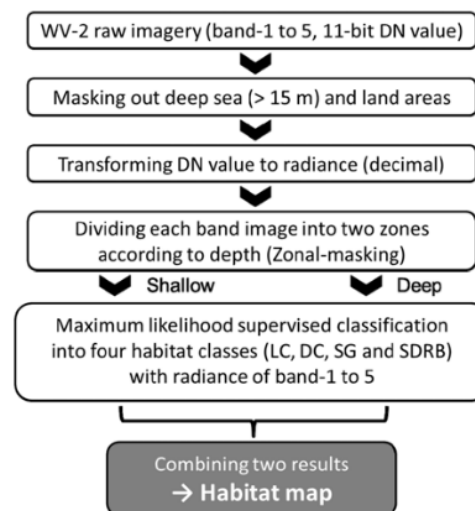


Fig. 2. Flow chart of image processing from raw imagery to habitat map. LC, DC, SG and SDRB indicate live coral, dead coral, seagrass and sand with rubble, respectively

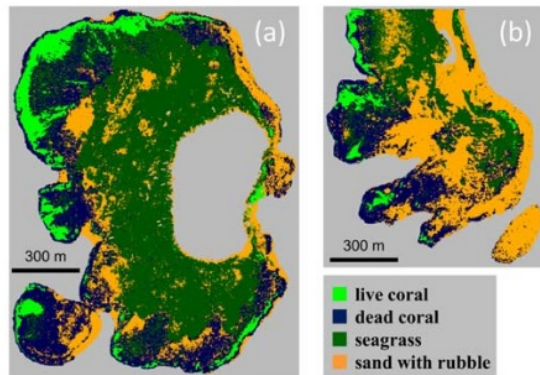


Fig. 3. The substrates map derived from maximum likelihood supervised classification with zonal masking. Barrang Lompo (a) and Bone Batang (b)

QI Inc.) towed from a boat. Coordinates of the boat positions were recorded by a differential GPS logger (m-241, HOLUX 2c). Four classes of the most typical habitat in these sites: live coral, dead coral, seagrass and sand with rubble were defined and extracted from the video records. 4781 points of ground truth data were used as training data for supervised classification (2618 and 2163 points in inner and outer reef, respectively), while another 445 points were randomly selected and used as reference data for accuracy analysis.

Using the training data, maximum likelihood classification was conducted for the two zonal images and all the pixels were classified into four habitats. Then two zonal maps were integrated into one, referred to as “the habitat map” or “the map” in this article. To examine the reliability of the habitat map, user’s accuracy, overall accuracy and Tau coefficient (Ma and Redmond 1995) were calculated for the habitat map using reference data.

In order to focus on fish fauna in reef slopes, shallow areas were excluded from the map. The slopes were classified into three “sub-areas” defined on a basis of habitat distributions: continuous coral reefs (CC), boundary of coral reefs (BC) and few coral reefs (FC). FC was defined as a sub-area in which the neighborhood (inside the 11×11 square kernel) includes 12 or fewer pixels of live coral (below 10% of 121 pixels). BC was defined as a sub-area of coral reefs except FC within a distance of 40 m from large patches of sand with rubble (patch size > 10 pixels). A sub-area, excluding FC and BC, was defined as CC. Although both CC and BC are the reefs surrounded by many live corals, BC can be regarded as the “edge” of coral-rich areas.

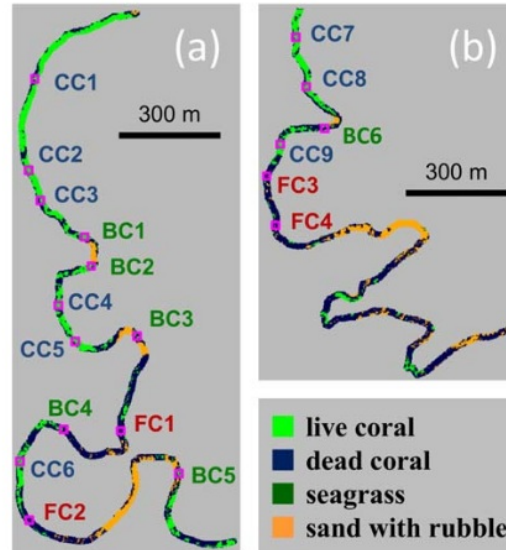


Fig. 4. Target areas (west reef slopes) of Barrang Lompo (a) and Bone Batang (b) extracted from Fig. 3. Small squares with labels indicate the locations of fish survey sites (20 m \times 20 m) of continuous coral reefs (CC), boundary of coral reefs (BC) and few coral reefs (FC)

Fish survey and data analysis

Underwater visual fish observations were conducted at a total of 19 survey sites located at the reef slopes of the two islands (see Fig. 4) from 19 to 28 June 2013. These were conducted at nine, six and four sites in CC, BC and FC, respectively. Each survey site was 20 m \times 20 m square including three 20 m length transect lines (field tape measures) laid parallel at intervals of 7.5 m. All transect lines were placed approximately parallel to the reef slope (perpendicular to the reef crest). Transect width was 2.5 m for both left and right sides of the line so that one transect covers an area of 100 m² (5 m \times 20 m).

Seven target species (see Table 1) were selected on the basis of several ecological and methodological limitations (i.e. commonness, mobility, countability and detectability). The number of each target species that appeared along three transects (100 m² \times 3) was counted by a SCUBA diver (Sawayama S) and summed up as “density” (D) of that site (Ind. / 300 m²). Time taken for one transect survey from the start to the end of the 20 m line was always around 12 minutes so that swimming speed of the observer was almost the same among all surveys. After the diver settled the 20 m field tape measure on the site, the diver stayed outside of the transect

Table 1. List of seven studied fish species with known ecological characters. Dietary information is referenced from Nakamura et al. (2003), Westneat (1994), Mazlan et al. (2006), Pratchett (2013), Russel (2001), Gushima et al. (1994) and Randall (2001). Habitats are informed from Allen et al. (2003), slightly modified. Abbreviations of diet: BI = benthic invertebrate, HC = hard coral polyps and SF = small fish

Family	Species	Diet	Habitat
Labridae	<i>Cheilinus chlorourus</i>	BI	Mixed sand, rubble and coral reefs
	<i>C. fasciatus</i>	BI	Mixed sand, rubble and coral reefs
Chaetodontidae	<i>Chaetodon octofasciatus</i>	HC	Shallow lagoons Inner reefs with good coral cover
Nemipteridae	<i>Pentapodus trivittatus</i>	SF, BI	Coastal reefs
	<i>Scolopsis margaritifera</i>	SF, BI	Sand and rubble fringe of reefs
Pseudochromidae	<i>Labracinus cyclophthalma</i>	BI, SF	Coastal and outer reefs
Pinguipedidae	<i>Paraperis cylindrica</i>	BI, SF	Sand, rubble and weedy bottoms

area during 5 minutes before starting observation to avoid creating any bias caused from fish evasion responses, as outlined by Fowler (1987). After a fish observation for each transect, a video of the bottom surface along it was taken by a diver using an underwater camera.

To investigate the edge effect of live coral reefs on fish density, correlation analysis and multiple comparison tests were conducted. For 15 sites in BC and CC (N = 6 and 9, respectively), Spearman's rank correlation coefficients were calculated between density (D) of each species and the one-line distance (m) from the nearest large patch of sand with rubble (size > 10 pixels by four-cell rule).

For parametric analysis, D data were square root transformed by the equation (1).

$$D' = \sqrt{D+0.5} \quad (1)$$

After the transformation, Tukey-Kramer post hoc test was conducted to examine the difference of mean D' among three sub-areas (CC, BC and FC) at the 95% and 99% confidence level.

The local status of corals might be another factor affecting fish density in addition to the edge effect of live coral reefs. Considering that, Spearman's rank correlation coefficient was calculated between D and four indicators concerning the local status of corals: total cover, *Acropora* cover, branching-

shape cover and proportion of live corals against dead corals (LC/DC) in each site. The former three indicators were estimated from the video movie taken by a diver using the line intercept transect method (Canfield 1941). Branching-shape corals (especially *Acropora* corals) are known to be preferred by many fishes which rely on live corals for food or shelter (e.g. Pratchett 2013). Only the LC/DC index was obtained from the habitat map. The proportion was calculated inside each fish survey site (20 m × 20 m), which was regarded as an indicator of relative coral health near the site.

3. Results

Habitat map

Fig. 3 shows the habitat map after the integration of the two zonal habitat maps.

Calculated overall accuracy and Tau coefficient were 81.3% and 0.76, respectively. A Tau coefficient value of 0.76 indicates that 76% more pixels are correctly classified than would be expected by chance (Ma and Redmond 1995). User's accuracy of live coral reached 99%, indicating that the distribution of live coral in the map was quite reliable. According to these accuracy levels, this map was considered accurate enough for the analyses quantifying live corals and defining coral reef boundaries.

Table 2. Data of mean density (D) with \pm SD of seven species obtained from visual transect surveys within three sub-areas

Species	BC (N = 6)	CC (N = 9)	FC (N = 4)
<i>Cheilinus chlorourus</i>	3.5 \pm 3.0	1.3 \pm 1.7	1.3 \pm 1.0
<i>C. fasciatus</i>	2.5 \pm 2.1	2.3 \pm 1.2	0.3 \pm 0.5
<i>Chaetodon octofasciatus</i>	20.5 \pm 12.8	6.0 \pm 4.2	6.5 \pm 4.2
<i>Pentapodus trivittatus</i>	5.3 \pm 2.8	6.9 \pm 5.8	4.3 \pm 3.3
<i>Scolopsis margaritifera</i>	4.3 \pm 1.4	2.1 \pm 2.5	3.3 \pm 0.5
<i>Labracinus cyclophthalma</i>	5.3 \pm 5.8	5.4 \pm 4.1	5.0 \pm 3.6
<i>Paraperis cylindrica</i>	0.7 \pm 1.6	1.1 \pm 1.3	5.0 \pm 2.2

Table 3. Spearman's rank correlation coefficients between D of seven species and the distance from large sandy bottom (patch size > 10 pixels by four-cell rule). Asterisks indicate significant correlations ($p < 0.05$). Shaded cells indicate negative correlations

Species	coefficient	p
<i>Cheilinus chlorourus</i>	-0.15	0.59
<i>C. fasciatus</i>	0.28	0.31
<i>Chaetodon octofasciatus</i>	-0.57	0.03 *
<i>Pentapodus trivittatus</i>	-0.19	0.49
<i>Scolopsis margaritifera</i>	-0.55	0.03 *
<i>Labracinus cyclophthalma</i>	0.23	0.41
<i>Parapercis cylindrica</i>	0.33	0.23

Fig. 4 shows the target areas for fish analysis (west reef slopes of two islands) extracted from Fig. 3. Boundaries of coral reefs (BC) were distributed nearby the large sandy areas interrupting continuous coral reefs (CC).

Fish survey and analyses

Mean densities (D) of seven fish species obtained from visual transect surveys are listed on Table 2.

Spearman's rank correlation analysis between D of seven species and the distance from large sandy bottoms indicated that only two species (*C. octofasciatus* and *Scolopsis margaritifera*) performed significant negative correlation ($p < 0.05$) (Table 3). There were no species which showed significant positive correlation in this analysis.

Tukey-Kramer multiple comparison tests among three sub-areas showed that Mean D' of *C. octofasciatus* was significantly higher in BC than in CC ($p < 0.05$) while mean D' of *S. margaritifera* showed no significant difference among them (Table 4). Mean D' of *Parapercis cylindrica* was significantly

Table 4. The results of Tukey-Kramer multiple comparison tests for seven species' D' among three sub-areas. Asterisks indicate significant difference (* = $p < 0.05$ and ** = $p < 0.01$). ">" or "<" means that D' is large/small between two sub-areas and "diff" is the absolute difference of them

Species		CC-BC	CC-FC	BC-FC
		<	<	>
<i>Cheilinus chlorourus</i>	diff	0.60	0.03	0.58
	p	0.20	1.00	0.35
		>	>	>
<i>C. fasciatus</i>	diff	0.02	0.81	0.80
	p	1.00	0.02 *	0.03 *
		<	<	>
<i>Chaetodon octofasciatus</i>	diff	1.94	0.09	1.85
	p	0.01 *	0.99	0.05 *
		>	>	>
<i>Pentapodus trivittatus</i>	diff	0.20	0.45	0.25
	p	0.90	0.68	0.90
		<	<	>
<i>Scolopsis margaritifera</i>	diff	0.75	0.50	0.25
	p	0.07	0.36	0.79
		>	>	<
<i>Labracinus cyclophthalma</i>	diff	0.09	0.01	0.07
	p	0.99	1.00	0.99
		>	<	<
<i>Parapercis cylindrica</i>	diff	0.24	1.14	1.37
	p	0.67	0.01 **	0.00 **

higher in FC than in CC and BC ($p < 0.01$) while D' of *Cheilinus fasciatus* showed a counter result ($p < 0.05$). *C. chlorourus*, belonging to the same genus as *C. fasciatus*, performed no significant difference among sub-areas. Fig. 5 exhibits the mean D' in three sub-areas, only for species which showed at least one significant difference between any combinations

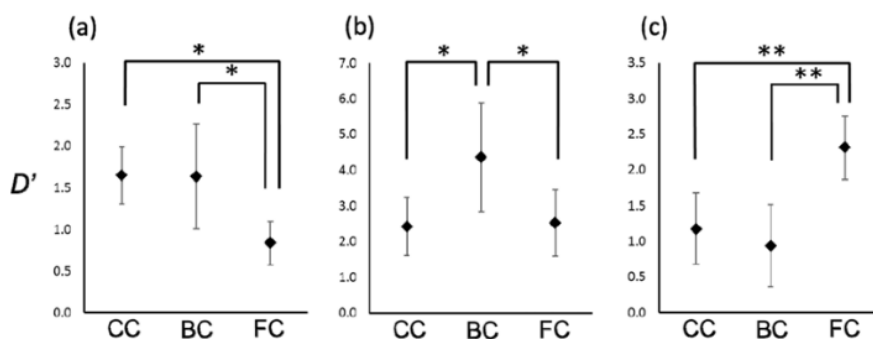


Fig. 5. Mean D' of three target species, *Cheilinus fasciatus* (a), *Chaetodon octofasciatus* (b) and *Parapercis cylindrica* (c) at continuous coral reefs (CC), boundary of coral reefs (BC) and few coral reefs (FC). Error bars are \pm SD. Asterisks indicate significant difference by Tukey-Kramer multiple comparison tests (* = $p < 0.05$ and ** = $p < 0.01$). See Table 5 for more details

Table 5. Spearman's rank correlation coefficients between *D* and four indicators of coral status: Total = total coral cover, Ac = *Acropora* coral cover, br = branching-shape coral cover and LC/DC = proportion of live coral to dead coral. Asterisks indicate significant correlations (* = $p < 0.05$ and ** = $p < 0.01$). Shaded patterns indicate negative correlations

Species	Total		Ac		br		LC/DC
<i>Cheilinus chlorourus</i>	0.28		0.01		0.36		-0.20
<i>C. fasciatus</i>	0.51	*	-0.01		0.46	*	0.48
<i>Chaetodon octofasciatus</i>	0.10		0.26		0.52	*	-0.14
<i>Pentapodus trivittatus</i>	0.16		0.20		0.16		0.18
<i>Scolopsis margaritifera</i>	0.31		0.16		0.09		-0.22
<i>Labracinus cyclophthalma</i>	-0.01		-0.34		-0.36		0.02
<i>Parapercis cylindrica</i>	-0.62	**	0.19		-0.49	*	-0.52

of sub-areas.

Table 5 shows the results of Spearman's rank correlation analysis between *D* of seven fish species and four indicators of the coral conditions. There were significant positive correlations ($p < 0.05$) between *D* of *C. fasciatus* and three indicators (Total cover, branching-shape cover and LC/DC) while there were significant negative correlations ($p < 0.01$ or 0.05) between *D* of *P. cylindrica* and them. *C. octofasciatus* showed a significant positive correlation only with branching-shape cover ($p < 0.05$). *S. margaritifera* had no correlation with any indicators.

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4. Discussion

In the present study, some fish species performed interesting responses to the relative geospatial arrangement of habitats (coral-rich reefs) and non-habitats (sand patches). The negative correlation, obtained between the density of *S. margaritifera* and the distance from the nearest sand patch, might be due to its habitat use. In fact, *S. margaritifera* is known to use fringing of sandy bottoms as main feeding grounds (Russel 2001; Allen et al. 2003). Thus, the reefs close to a large sandy patch might be suitable for the feeding activities of this species. Given the fact that the density of this species revealed no difference between BC and CC, this habitat preference is not so steep response as edge effects.

The highest density of *P. cylindrica* in FC might be because the species prefers sand and rubble bottoms as habitats rather than coral-rich areas, as mentioned in Randall (2001) and Allen et al. (2003). On the other hand, the density of *C. fasciatus* was smaller in FC than in the other sub-areas. However, there was no difference between density in CC and that in BC. This result indicates that this species selectively uses coral-rich reefs as habitats but there is little or no edge effect on its density. These outcomes agree with the results

of the correlation analysis.

The density of *C. octofasciatus* was the highest in BC among the three sub-areas, which indicates that this species shows the strongest preference for the edge of coral-rich reefs among the seven species. This result is consistent with the negative correlation obtained between density and distance from the nearest patch of sand with rubble. This species, "eight-banded butterflyfish" in English common name, is known to be an obligate feeder of hard coral polyps (Pratchett 2013). Pratchett et al. (2006) and Cole et al. (2008) pointed out that obligate coral feeders' densities were influenced by local conditions of corals. However, they did never refer to the idea of arrangement of corals in space. The present study discovered that the density of a coral feeding fish could be strongly affected by the relative geospatial arrangement of coral-rich reefs.

The result that the mean density of *C. octofasciatus* in FC and that in CC showed almost the same level was unexpected because the areas with poor corals seemed to be unsuitable for its habitats. This might be because there are small and sparse live coral patches that cannot be detected by the spatial resolution of the satellite (2.0 m).

The density of *C. octofasciatus* showed positive rank correlation with branching-shape corals. These corals included the genera *Acropora*, *Pocillopora*, *Montipora* and *Porites*, which are considered as the main preys of coral feeding butterflyfishes (Pratchett 2013). In addition, juveniles of this species are known to use the branching corals for shelter (Myers and Pratchett 2010). Indeed, branching corals were distributed relatively abundant at BC. This is considered to be one of the reasons for the positive edge effect. Because *C. octofasciatus* is known to prefer protected lagoons (Myers and Pratchett 2010), current might be another factor with regard to its habitat preference. However, continual current statuses in coral reefs are spatially heterogeneous and hard to observe and comprehend. Therefore, the present approach,

which includes the factors of both coral richness and relative geospatial arrangement through the application of satellite remote sensing, is suggested as a practical way to overview the distribution and abundance of *C. octofasciatus*. On IUCN red list 2013, *C. octofasciatus* is categorized as “least concern” but it is pointed out that this species may decline in abundance following coral depletion induced by climate change (Myers and Pratchett 2010). Moreover, obligate coral feeders have quite important roles in coral reef ecosystems (Cole et al. 2008). Thus, the importance of monitoring the abundance of this species should be high in Spermonde Archipelago because there is growing concern about the degradation of coral reefs (Edinger et al. 1998).

5. Conclusion

The present study revealed that density of *C. octofasciatus*, a coral feeding species, was strongly influenced by the “edge effects” of live coral reefs. Conventional ecological studies and conservation planning of coral reef fishes have overemphasized the importance of live coral cover. However, our results show that densities of fish species, especially those relying heavily on corals, might be affected by not only live coral richness but also its relative arrangement in space. Therefore, future conservation procedures for coral reef fish communities must include the idea of spatial planning of habitats and non-habitats.

Additionally, the present study confirms that the introduction of a geospatial perspective derived from remote sensing has great potential to progress ecological studies on coral reef fishes. Because most of the conventional descriptions about the habitat uses of coral reef fishes were originated from empirical knowledge, it would be desirable to acquire the new information based on quantitative and objective criteria. Thus, the remote sensing approach proposed here can provide a progressive way to obtain beneficial knowledge on the habitat preference of coral reef fishes. Also, it might be possible to estimate the populations of fishes by combining fish-habitat relationships with geospatial and quantitative information on habitats. In other words, remote sensing can play an important role in bridging the gap between knowledge on various fish-habitat relationships and practical conservation planning.

Acknowledgements

This work was supported by Japanese Society for the

Promotion of Science (JSPS) KAKENHI Grant Number 25-6727 and Grant-in-Aid for JSPS fellows. This study represents a component of the research conducted under the Environment Research and Technology Development Fund (S-9) of the Ministry of the Environment in Japan, and from the Japan Science and Technology Agency (JST/CREST). We also gratefully acknowledge the sponsors of this study which was conducted under the network of the Asian CORE Program of the Japan Society for the promotion of Science, “Establishment of research and education network on coastal marine science in Southeast Asia”, and the Ocean Remote Sensing Project for Integrated Coastal Area Management (WESTPAC-ORSP: PAMPEC) of Intergovernmental Oceanographic Commission Sub-Commission for the Western Pacific supported by Japanese Funds-in-Trust provided by the Ministry of Education, Culture, Sports, Science and Technology in Japan.

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