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The Pattern of Herbivorous Fish Assemblages in The Western and Eastern Outermost Island Indonesia

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ABSTRACT

The herbivorous fishes have been considered as a critical functional group and have capability maintaining coral reef resilience and avoiding coral-algal phase-shifts. The present condition shown, almost in tropical reef location, alga has dominated coral, even in the small outer island. The requirement to conduct comprehensive basic research in studying the patterns and composition of herbivorous fish, especially on the small outer islands. Twelve coral reef sites in eastern Indonesia (Liki Islands) and western Indonesia (Natuna Island) used as a research location for comparing the structure patterns of herbivorous fish communities (diversity, density, and body size) using the Underwater Visual Census (UVC) method. There was different pattern of herbivorous fishes families in Liki Island and Natuna Islands, where Acanthuridae is dominant in eastern Indonesia (Liki Islands), including *Ctenochaetus striatus* (41,00 ± 11,72 se) individuals/350m^2, *A. maculiceps* (23,33 ± 13,61 se) individuals/350m^2, *Naso hexacanthus* (18,67 ± 6,34 se) individuals/350m^2 while Scaridae is dominant in western Indonesia (Natuna island), including *Scarus rivulatus* (31,67 ± 10,61 se) individuals/350m^2, *Chlorurus sordidus* (30,00 ± 8,52 se) individuals/350m^2 and *Scarus quoyi* (19,00 ± 9,73 se) individuals/350m^2. Based on herbivore fishes composition Liki Island has a higher density and biomass compared to Natuna Island.

Keywords: herbivore, fish, coral, small outer island, Indonesia

ABSTRAK

Ikan herbivora telah dianggap sebagai kelompok fungsional penting dan memiliki kemampuan dalam mempertahankan ketahanan terumbu karang serta menghindari pergeseran dari fase karang-alga. Kondisi saat ini menunjukkan, hampir di sebagian besar lokasi ekosistem terumbu karang tropis, pertumbuhan alga telah mendominasi karang, bahkan di lokasi pulau-pulau kecil terluar. Pentingnya kebutuhan untuk melaksanakan penelitian dasar yang komprehensif dalam mempelajari pola dan komposisi ikan herbivora, terutama di pulau-pulau kecil terluar. Dua belas lokasi stasiun terumbu karang yang berada di kawasan timur Indonesia (Pulau Liki) dan wilayah barat Indonesia (Pulau Natuna) dijadikan sebagai stasiun penelitian untuk membandingkan pola struktur komunitas ikan herbivora (keanekaragaman, kepadatan, dan ukuran tubuh) dengan menggunakan metode Underwater Visual Census (UVC). Pola keluarga ikan herbivora di Pulau Liki dan Kepulauan Natuna, menunjukan bahwa famili ikan Acanthuridae dominan di wilayah Kepulauan Liki, termasuk diantaranya beberapa spesies ikan seperti *Ctenochaetus striatus* (41,00 ± 11,72 se) individu/350m^2, *A. maculiceps* (23,33 ± 13,61 se) individu/350m^2, *Naso hexacanthus* (18,67 ± 6,34 se) individu/350m^2, sedangkan famili Scaridae dominan di wilayah pulau Natuna, termasuk diantaranya spesies ikan dari *Scarus rivulatus* (31,67 ± 10,61 se) individu/350m2, *Chlorurus sordidus* (30,00±8,52 se) individu/350m^2 dan *Scarus quoyi* (19,00 ± 9,73 se) individu/350m^2. Berdasarkan komposisi ikan herbivora Kepulauan Liki memiliki kepadatan dan biomassa yang lebih tinggi, dibandingkan dengan Pulau Natuna.

Kata kunci: herbivore, fish, coral, small outer island, Indonesia

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1. Introduction

Herbivorous fishes have a significant role in reducing algal standing stock in the coral ecosystem (McManus & Polsenberg, 2004), and the population of herbivorous fishes consequence of influence in algal cover after the loss of corals (Rongo & van Woesik, 2013; Sheppard, Ateweberhan, Bowen, *et al.*, 2012; Wilson, Graham, Pratchett, *et al.*, 2006). There is an interesting hypothesis in interaction from coral, algae, and herbivorous fishes. After the loss of coral cover, the densities of herbivores increased significantly (Ruppert, Travers, Smith, *et al.*, 2013). The increase of herbivorous fish can be related to higher food availability (Adam, Schmitt, Holbrook, *et al.*, 2011; Fong, Frias, Goody, *et al.*, 2018) and might be expected the abundance of algae trigger herbivorous fishes to grow following an extensive coral loss (Jayewardene, 2009). The hypothesis confirms the role and importance of herbivorous reef fishes in maintaining coral reef resilience and avoiding coral-algal phase-shifts (Bellwood, Hughes, Folke, *et al.*, 2004; Hughes, Baird, Bellwood, *et al.*, 2003; Hughes, Rodrigues, Bellwood, *et al.*, 2007). The shifting coral to algal indicates reef in a condition not healthy due to the intensive of anthropological pressure and natural disturbance. Without the capacity to support herbivores, these reefs are likely to be vulnerable to algal overgrowth and potential long-term phase shifts (Rogers, Blanchard, Newman, *et al.*, 2018).

Understanding algal succession and the influence of herbivorous fishes is central to the development of knowledge about how coral reef ecosystems may respond to and recover from increasing anthropogenic pressures (Burkepile & Hay, 2010; Ceccarelli, Jones & McCook, 2011). The herbivorous fishes have been considered as a critical functional group and have capability maintaining coral reef resilience and avoiding coral-algal phase-shifts (Bellwood *et al.*, 2004; Dromard, Bouchon-Navaro, Harmelin-Vivien, *et al.*, 2015; Fong *et al.*, 2018; Hughes *et al.*, 2003, 2007). The strong functional group of herbivorous fish may maintain the coral reef and remove algal states (Fong *et al.*, 2018), with consuming primary benthic algae and regulate competition between algae and reef-building corals (Edwards, Friedlander, Green, *et al.*, 2013; Wilson, Bellwood, Choat, *et al.*, 2003). The present condition shown, almost in tropical reef location, alga has dominated coral, even in the small outer island and several oceanic islands in pacific.

There are only a few small studies on the small outer islands that discuss the ecological function of coral reefs. Some obstructions become significant problems in researching the small outer islands, including high costs, difficult access, limited transportation and accommodation, limited research equipment, and several islands that are uninhabited and far from the mainland. Therefore, knowledge to understand the ecological conditions of ecosystems in the small outer islands still needs to be explored further. Decades have shown that most ecosystems are subject to massive pressure and degradation caused by anthropological factors (Brown, Bender-Champ, Kubicek, *et al.*, 2018; Ferrigno, Bianchi, Lasagna, *et al.*, 2016; Quimbayo, Dias, Kulbicki, *et al.*, 2019) and natural disturbance (Guest,

Table 1. Location and direction of the study sites

Sites .id	Latitude	Longitude	Location
LIKC.01	1^o 37' 34.255 S	138^o 43' 43.411 E	Liki Island
LIKC.02	1^o 38' 43.451 S	138^o 46' 47.402 E	Liki Island
LIKC.03	1^o 37' 42.305 S	138^o 44' 42.862 E	Liki Island
LIKC.04	1^o 36' 52.902 S	138^o 42' 49.052 E	Liki Island
LIKC.05	1^o 35' 32.028 S	138^o 43' 56.024 E	Liki Island
LIKC.06	1^o 37' 12.299 S	138^o 44' 54.210 E	Liki Island
NTNC.01	4^o 02' 28.716 N	108^o 20' 12.119 E	Natuna Island
NTNC.02	4^o 08' 20.004 N	108^o 06' 55.439 E	Natuna Island
NTNC.03	4^o 12' 33.336 N	108^o 10' 53.075 E	Natuna Island
NTNC.04	3^o 41' 15.360 N	108^o 04' 23.627 E	Natuna Island
NTNC.05	3^o 34' 43.644 N	108^o 04' 45.804 E	Natuna Island
NTNC.06	3^o 59' 30.156 N	108^o 22' 32.160 E	Natuna Island

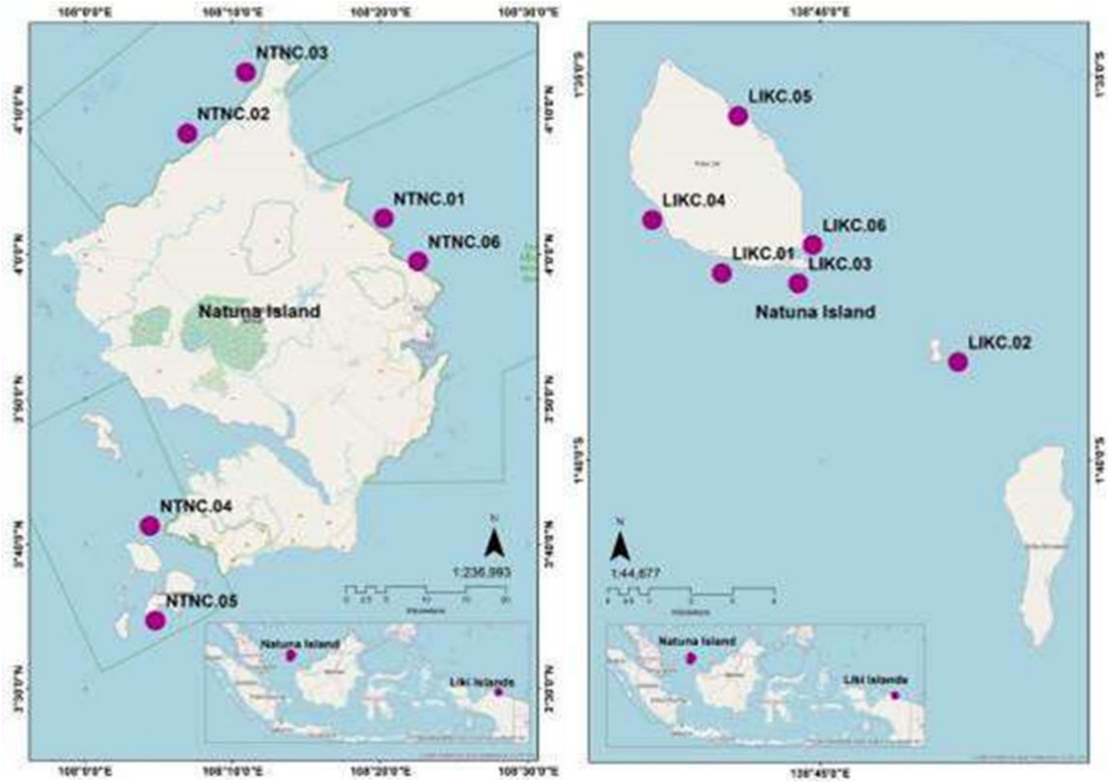

Figure 1. Map of the study area and sampling sites

Vergés, Bauman, *et al.*, 2016; Mcleod, Anthony, Mumby, *et al.*, 2019; Souter & Lindén, 2000).

The research studies from the impact on acute threat and chronic stress from coral reef ecosystem which happened in the last few decades in the small outer islands were still limited, including the rising sea surface temperatures that cause coral bleaching (Pratchett, Bridge, Brodie, *et al.*, 2019; Wild, Hoegh-Guldberg, Naumann, *et al.*, 2011), nutrification (Leão, Kikuchi & Oliveira, 2019), destructive fishing (Edinger, Jompa, Limmon, *et al.*, 1998; Kunzmann & Samsuardi, 2017), and over-exploitation (Martin, Momtaz, Jordan, *et al.*, 2016; Rogers *et al.*, 2018) in the small outer island. All of this disturbance are the major problems being faced by coral reef ecosystems in the small outer island with causes phase-shifts in coral dominated to algal dominated, and the level of anthropogenic activities was very different in the western and eastern regions of Indonesia. In the long term, the pressure will have a significant impact on coral mortality (Jompa & McCook, 2002). The herbivore fishes had an essential role in maintaining the changing phase-shift coral-algal dominated, and the pattern of herbivore fishes composition play an important role in the process of coral reef recovery in the small outer island. They understand the shifting phase from coral to algae dominated, and the pattern of herbivore fishes composition help to prevent massive coral mortality and the needs required for comprehensive basic research to study the pattern and composition of herbivorous fish, especially in small outer islands.

2. Materials and Methods

2.1. Study site

Measurements of the herbivorous fish community were conducted in two locations of Small Outer Island in the Eastern Indonesia Region (Liki Island) and Western Indonesia Region (Natuna Island) (Figure 1). Both islands have six sites points for sampling and enumerated herbivorous fish (Table 1) and distributed evenly across the Island to represent the overall condition of both islands. Natuna and Liki have inhabited islands with a higher population intensity and human activities (including fishing, tourism, and boat anchoring) occurring on Natuna.

Liki Island is the outermost island of Indonesia, located north of the island of Papua, and faced the Pacific Ocean. Liki Island is also the easternmost island of the Republic of Indonesia and bordered by the country of Papua New Guinea. Most of Liki local community activities are fishermen and selling marine resources, including tuna, red snapper, and mackerel, and sold directly to the market in Sarmi Regency. The local community in Liki island has local wisdom in protecting the local marine ecosystem and resources called "*Sasi*" which is temporarily closed for all fishing activities in a specific area to aim to condition and protecting marine resources in Liki Island. The main goal of *Sasi* is to give time for marine biota to grow and raise. The condition of marine ecosystems on Liki Island consisted of coral reefs with good condition and had Live coral cover reaching 60%. The growth form mostly branching, *Porites* spp., *Pocillopora spp*., and *Acropora spp*. were the dominant species and followed by *Acropora tabulate*, *Pavona spp*., *Lobophyllia spp*., and also some sponges, and the coral on Liki Island can be found up to a depth of 20 meters.

Natuna is one of the outer islands in Indonesia and faces the Natuna Sea. Natuna Regency, Riau Islands Province, is one area that has a high marine resource potential, with live coral cover reaching 24.53% and included in the medium coral cover category. The growth form of coral mostly massive, encrusting, and branching. *Porites lutea*, *Porites cylindrical*, *Porites* rus very common species. The coral still found to a depth of 10 m. Most of the local people in Natuna are fishermen, and their lives depend on marine resources. The northern of the Natuna Islands had overexploitation fishing activities. Based on information from the local government, most areas in Natuna,

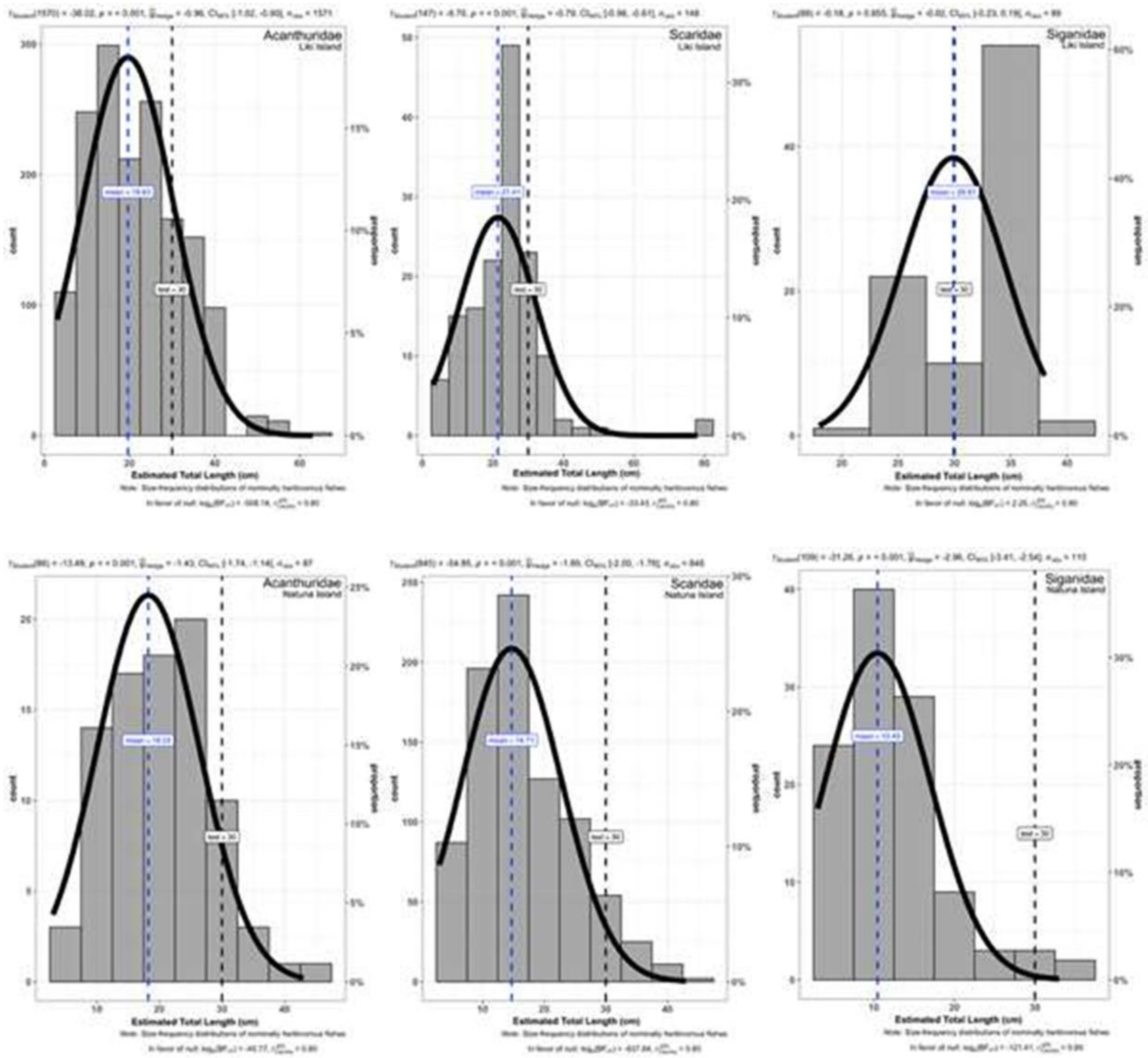

Figure 2. Size-frequency distributions of nominally several herbivorous fishes families (Acanthuridae, Scaridae, Siganidae) at Eastern Indonesia - Liki Island (top) and Western Indonesia - Natuna Island (bottom).

experienced destructive fishing activities, including bombing and potassium poison.

2.2. Survey Methods

To quantify herbivorous fishes community structure (diversity, density, and length of body size) was recorded using SCUBA diving equipment with Underwater Visual Census (UVC). The UVC method is the most common method for non-destructively surveying community dynamics (Davis & Smith, 2017; Figueroa-Pico, Carpio & Tortosa, 2020), superior to collection techniques for the marine organism, especially in sensitive areas (Pinault,

Table 2. List of Herbivore Fishes Species and density (mean ± standard deviation) individuals/350m^2 in Liki Island and Natuna Island

Herbivore Fish Species	IUCN	Liki (n_{sites} = 6)	Natuna (n_{sites} = 6)
Family: Acanthuridae			
Acanthurus albipectoralis Allen & Ayling, 1987	LC	7,50 ± 7,11	0.00 ± 0.00
A. auranticavus, Randall 1956	LC	8,17 ± 1,08	0,83 ± 0,83
A. blochii, Valenciennes 1835	LC	5,00 ± 1,71	0.00 ± 0.00
A. fowleri de Beaufort, 1951	LC	0,67 ± 0,67	0.00 ± 0.00
A. grammoptilus Richardson, 1843	LC	1,50 ± 1,50	1,00 ± 0,68
A. leucocheilus Herre, 1927	LC	4,33 ± 4,33	0.00 ± 0.00
A. lineatus Linnaeus, 1758	LC	5,17 ± 0,98	5,00 ± 2,76
A. maculiceps Ahl, 1923	LC	23,33 ± 13,61	0.00 ± 0.00
A. mata Cuvier, 1829	LC	6,33 ± 2,44	0.00 ± 0.00
A. nigricans Linnaeus, 1758	LC	9,17 ± 1,11	0.00 ± 0.00
A. nigricauda Duncker & Mohr, 1929	LC	2,50 ± 1,12	0.00 ± 0.00
A. nigrofuscus Forsskål, 1775	LC	1,33 ± 1,33	0.00 ± 0.00
A. nubilus Fowler & Bean, 1929	LC	5,50 ± 5,50	0.00 ± 0.00
A. olivaceus Bloch & Schneider, 1801	LC	5,83 ± 3,54	0.00 ± 0.00
A. pyroferus Kittlitz, 1834	LC	12,00 ± 2,59	0.00 ± 0.00
A. thompsoni Fowler, 1923	LC	12,67 ± 3,96	0.00 ± 0.00
A. triostegus Linnaeus, 1758	LC	0.00 ± 0.00	1,33 ± 0,88
A. xanthopterus Valenciennes, 1835	LC	15,67 ± 11,55	0.00 ± 0.00
Ctenochaetus binotatus Randall, 1955	LC	13,67 ± 1,09	0.00 ± 0.00
C. cyanocheilus Randall & Clements, 2001	LC	7,33 ± 1,36	0.00 ± 0.00
C. striatus Quoy & Gaimard, 1825	LC	41,00 ± 11,72	1,17 ± 1,17
C. tominiensis Randall, 1955	LC	5,50 ± 2,70	0.00 ± 0.00
Naso brachycentron Valenciennes, 1835	LC	3,33 ± 2,17	0,33 ± 0,33
N. brevirostris Cuvier, 1829	LC	2,00 ± 1,37	0.00 ± 0.00
N. hexacanthus Bleeker, 1855	LC	18,67 ± 6,34	0.00 ± 0.00
N. lituratus Forster, 1801	LC	3,50 ± 0,96	2,00 ± 0,93
N. lopezi Herre, 1927	LC	7,17 ± 4,09	0.00 ± 0.00
N. thynnoides Cuvier, 1829	LC	1,33 ± 1,33	0.00 ± 0.00
N. vlamingii Valenciennes, 1835	LC	10,17 ± 4,61	0.00 ± 0.00
Paracanthurus hepatus Linnaeus, 1766	LC	4,00 ± 1,91	0.00 ± 0.00
Zebrasoma scopas Cuvier, 1829	LC	17,33 ± 1,56	1,00 ± 1,00
Z. veliferum Bloch, 1795	LC	0,83 ± 0,54	1,83 ± 1,33
Family: Scaridae			
Bolbometopon muricatum Valenciennes, 1840	VU	0,50 ± 0,34	1,67 ± 1,67
Calotomus carolinus Valenciennes, 1840	LC	0,17 ± 0,17	0.00 ± 0.00
Cetoscarus ocellatus Valenciennes, 1840	LC	1,50 ± 0,67	0,33 ± 0,33
Chlorurus bleekeri de Beaufort, 1940	LC	5,50 ± 0,56	7,17 ± 1,22
C. bowersi Snyder, 1909	NT	0,17 ± 0,17	3,33 ± 0,76
Chlorurus capistratoides Bleeker, 1847	LC	0,17 ± 0,17	2,67 ± 1,45
Chlorurus frontalis Valenciennes, 1840	LC	0,50 ± 0,50	0.00 ± 0.00
C. japanensis Bloch, 1789	LC	2,67 ± 1,36	0.00 ± 0.00
C. microrhinos Bleeker, 1854	LC	0,83 ± 0,31	2,50 ± 0,96
C. sordidus Forsskål, 1775	LC	14,17 ± 3,48	30,00 ± 8,52
C. spilurus Valenciennes, 1840	LC	0.00 ± 0.00	2,00 ± 1,44
Hipposcarus longiceps Valenciennes, 1840	LC	0,83 ± 0,83	0,50 ± 0,50
Leptoscarus vaigiensis Quoy & Gaimard, 1824	LC	0,00 ± 0,00	0.00 ± 0.00

Table 2. (continued)

Scarus chameleon Choat & Randall, 1986	LC	1,67 ± 0,92	0,33 ± 0,33
S. dimidiatus Bleeker, 1859	LC	12,83 ± 1,96	2,17 ± 1,08
S. flavipectoralis Schultz, 1958	LC	1,50 ± 0,96	0.00 ± 0.00
S. forsteni Bleeker, 1861	LC	2,00 ± 0,93	3,17 ± 1,05
S. frenatus Lacepède, 1802	LC	0,50 ± 0,50	2,00 ± 1,10
S. ghobban Forsskål, 1775	LC	1,83 ± 0,83	5,33 ± 3,24
S. *globiceps* Valenciennes, 1840	LC	0.00 ± 0.00	2,83 ± 1,60
S. hypselopterus Bleeker, 1853	LC	0,00 ± 0,00	7,83 ± 3,98
S. niger Forsskål, 1775	LC	19,33 ± 3,02	5,50 ± 1,43
S. oviceps Valenciennes, 1840	LC	2,17 ± 1,05	3,50 ± 2,01
S. prasiognathos Valenciennes, 1840	LC	0.00 ± 0.00	1,67 ± 0,80
S. psittacus Forsskål, 1775	LC	0,33 ± 0,33	0,83 ± 0,83
S. quoyi Valenciennes, 1840	LC	2,17 ± 0,54	19,00 ± 9,73
S. rivulatus Valenciennes, 1840	LC	0,50 ± 0,50	31,67 ± 10,61
S. rubroviolaceus Bleeker, 1847	LC	4,83 ± 2,18	0,83 ± 0,83
S. schlegeli Bleeker, 1861	LC	1,00 ± 0,68	0,50 ± 0,50
S. spinus Kner, 1868	LC	3,33 ± 0,71	4,00 ± 1,77
S. tricolor Bleeker, 1847	LC	14,17 ± 5,15	0.00 ± 0.00
Family: Siganidae			
Siganus canaliculatus Park, 1797	LC	5,00 ± 3,20	0,17 ± 0,17
S. corallinus Valenciennes, 1835	LC	0.00 ± 0.00	0,83 ± 0,40
S. doliatus Guérin-Méneville, 1829-38	LC	2,17 ± 2,17	0.00 ± 0.00
S. fuscescens Houttuyn, 1782	LC	0.00 ± 0.00	0.00 ± 0.00
S. guttatus Bloch, 1787	LC	2,33 ± 2,33	1,17 ± 1,17
S. lineatus Valenciennes, 1835	LC	1,33 ± 0,84	0.00 ± 0.00
S. puellus Schlegel, 1852	LC	1,17 ± 0,75	0,33 ± 0,33
S. punctatus Schneider & Forster, 1801	LC	0.00 ± 0.00	1,17 ± 0,60
S. spinus Linnaeus, 1758	LC	0.00 ± 0.00	3,15 ± 2,20
S. stellatus Forsskål, 1775	LC	1,00 ± 1,00	0.00 ± 0.00
S. vermiculatus Valenciennes, 1835	LC	1,17 ± 0,75	0.00 ± 0.00
S. virgatus Valenciennes, 1835	LC	0.00 ± 0.00	8,67 ± 3,90
S. vulpinus Schlegel & Müller, 1845	LC	0,67 ± 0,67	3,17 ± 1,17

Bissery, Gassiole, *et al.*, 2014), and the method was sufficient to long term monitoring program (Kulbicki, Cornuet, Vigliola, *et al.*, 2010). The UVC method is the most common technique used in fishes census (Ricart, Sanmartí, Pérez, *et al.*, 2018). Most of the fish researcher was applied this method to records reef fishes, invertebrates and benthic substrate (Dwirama Putra, Suryanti, Kurniawan, *et al.*, 2018; Figueroa-Pico *et al.*, 2020; Jones, Davidson, Gardner, *et al.*, 2015; Pereira, Moraes, dos Santos, *et al.*, 2014; Robinson, Baum & Giacomini, 2016; Rongo & van Woesik, 2013). The study uses UVC methods to record each observed herbivore fish species along modification line transects based on (Lewis & Wainwright, 1985; Rotjan & Lewis, 2006; Wen, Chen, Hsieh, *et al.*, 2013) with 70 m long at 5 - 10 m depth and the observer within 5 m on either side of the transect was identified herbivore fishes.

The UVC performed in diurnal times due to the increase in temperature during diurnal due to heating causes an increase in dissolved oxygen from photosynthesis results on the reef, where these environmental variables in diurnal conditions correlate with eating patterns and abundance of herbivorous fish; thus it can maximally to observe herbivorous fish in the reef area (Polunin & Klumpp, 1989). Three families of major herbivore fish identified by underwater visual census methods (Acanthuridae, Scaridae and Siganidae) (Chabanet, Bigot, Nicet, *et al.*, 2016; Lewis & Wainwright, 1985; Williams, 1991).

2.3. Data Analysis

Three main herbivorous fishes families (Acanthuridae, Scaridae, and Siganidae) were identified by Underwater Visual Census (UVC) methods were registered according to the lowest species of the taxon. The study focuses on herbivorous fish composition with diversity (number of species), abundance (number of individuals) and biomass per transect, was calculated using the length-weight relationship by (Chabanet *et al.*, 2016; Putra, Afatta, Wilson, *et al.*, 2015) with equation W = a.LTb. Where W is the weight (g), LT the fork length of herbivore

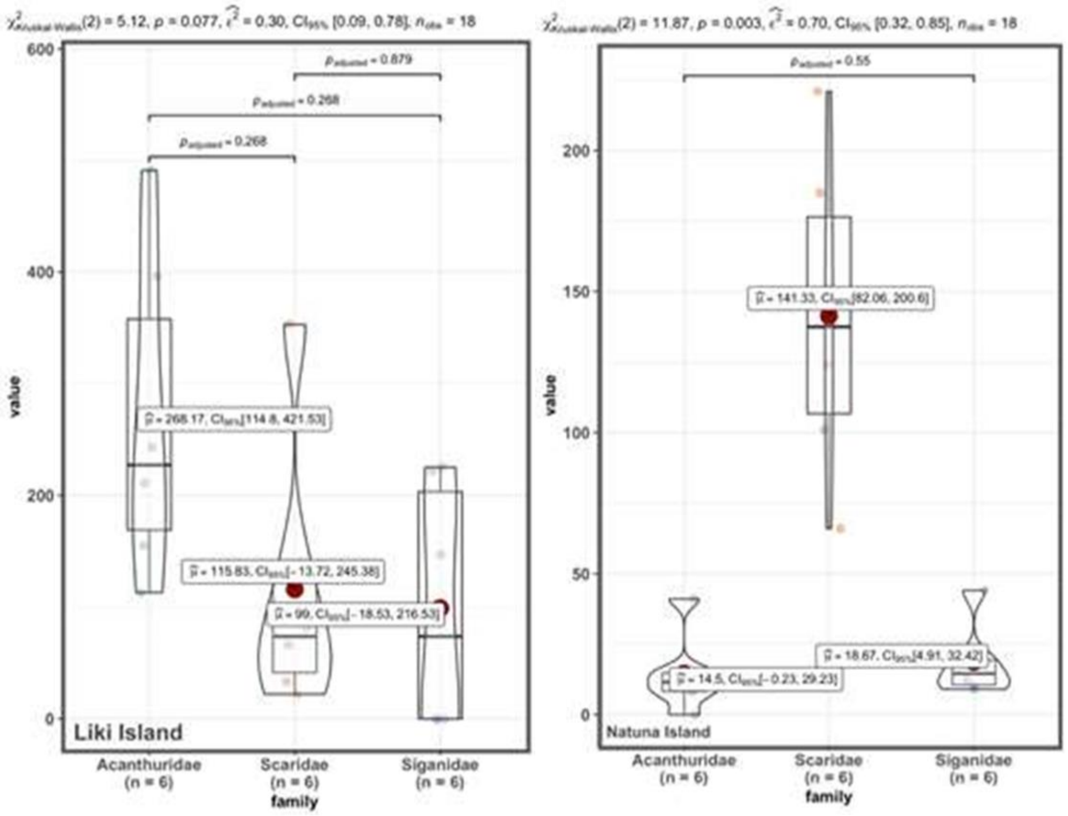

Figure 3. Mean density (ind./350m^2) of herbivorous fishes families (Acanthuridae, Scaridae, and Siganidae in Eastern SOI Indonesia (Liki) and Western SOI Indonesia (Natuna) with Kruskal Wallis test and 95% confidence interval (CI).

fish (cm), and a and b are coefficients specific to each species from FishBase data (Froese and Pauly, 2003). The total biomass for each station corresponds to the total weight of all fish per unit area (g/m2). The research concentrates on the main herbivorous fishes by analyzing mean density with standard error (se) herbivore fishes (Acanthuridae, Scaridae, and Siganidae) in Liki Island and Natuna Island. The nominally of size-frequency distribution analyses using "ggstatsplot" packages (Patil, 2018) implemented in the R Statistical Software Analysis. Subsequently, a non-parametric Kruskal-Wallis was performed also using "ggstatsplot" packages (Patil, 2018) to compare density from three herbivorous families (Acanthuridae, Scaridae, and Siganidae). For a more comprehensive analysis, the mean density of herbivore fishes was compared in every herbivore family in each location with a pairwise Wilcoxon test with a significant difference, p-value < 0.05 (Booth & Beretta, 2002). The relationship between density and biomass in each herbivorous fishes families was analyzed using a biplot density-biomass distribution regression linear analysis with dominant species, where the axis variable (*x*) is herbivore fishes density and ordinate (*y*) is the herbivore fishes biomass.

3. Results and Discussion

3.1. Size frequency distribution

The standard length-frequency distributions of these individuals were summarized in Figure 2. The total herbivorous fishes counted was 1808 individuals in Liki Island (Eastern Indonesia) from 3 reef fishes families, including Acanthuridae (n = 1571), Scaridae (n = 148), and Siganidae (n = 89).

Table 3. Table showing parameter values for Turbidity in Liki Island and Natuna Island

Turbidity (NTU) in six sites location sampling						
Liki Island (eastern)	0.25	0.16	0.29	0.22	0.24	0.15
Natuna Island (western)	0.9	0.44	0.32	0.31	0.54	0.32

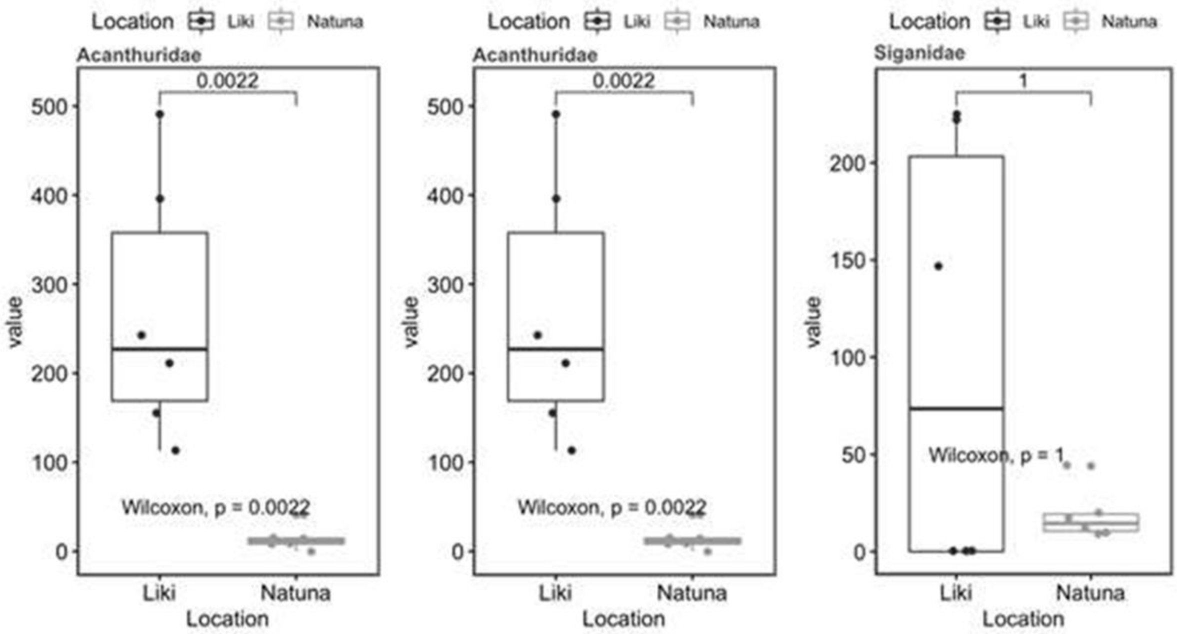

Figure 4. Comparison mean density of herbivorous fishes families in each family of herbivorous fishes with Wilcoxon test.

Acanthuridae fishes in Liki Islands ranged to 60.0 cm, with a mean standard length of 19.63 cm ($t = -38.02$; $g_{hedge} = -0.96$, $CI_{95\%}$ [-1.02, -0.90]), Scaridae ranged to 80 cm, with a mean standard length of 21.41 cm ($t = -9.70$; $g_{hedge} = -0.79$, $CI_{95\%}$ [-0.98, -0.61]), and Siganidae ranged from 20 cm to 40.0 cm ($t = -0.18$; $g_{hedge} = -0.02$, $CI_{95\%}$ [-0.23, -0.19]). There were some differences in the length−frequency distributions for Natuna Islands (Western Indonesia) herbivorous fishes composition counted with total of 1043 individuals of herbivorous fishes from 3 reef fishes families, including Acanthuridae (n = 87), Scaridae (n = 846), and Siganidae (n = 110). Acanthuridae fishes in Natuna Islands ranged to 40.0 cm, with a mean standard length of 18.23 cm ($t = -13.49$; $g_{hedge} = -1.43$, $CI_{95\%}$ [-1.74, -1.14]), Scaridae ranged to 40 cm, with a mean standard length of 14.71 cm ($t = -54.95$; $g_{hedge} = -1.89$, $CI_{95\%}$ [-2.00, -1.78]), and Siganidae ranged to 35.0 cm ($t = -31.26$; $g_{hedge} = -2.96$, $CI_{95\%}$ [-3.41, -2.54]). The highest number of individuals fishes per family was obtain from the Acanthuridae family with the total number of individuals fishes of both locations was (n = 1658) individuals, followed by Scaridae family (n = 994) individuals, and Siganidae family (n = 199) individuals. There was a clear trend in herbivorous fishes population in small outer islands for Acanthuridae families more abundant in Liki island, while the Scaridae family was more dominant in Natuna Islands. From both location, the Siganidae families had the lowest number of individual and smallest mean body size.

Our result showed the size-frequency distributions of nominally in each herbivorous fishes family was dominant in the eastern region (Liki Islands) than the western region (Natuna Island). Even the population of Acanthuridae families in Liki more sufficient ten times than the Natuna (Figure 2). The size distribution pattern also is shown herbivorous fishes in Liki bigger than Natuna, and it indicates the coral ecosystem in Natuna Island had more pressure than the Liki Island. In addition, the presence of the Scaridae family in the high population in Natuna has a positive impact on the coral ecosystem for the recovery process (Figure 2). Coral reefs rely on a range of ecological functions to maintain their resistance to disturbance. Many factors can disrupt the composition of coral reefs, and herbivorous fish, including several significant factors, are sedimentation, coral bleaching, nutrification, and destructive fishing. Apart from the factors that construct the composition of herbivorous fish, the level of disturbance suffered by a certain region in terms of herbivorous grazing activity can also affect the algal succession pathway in coral ecosystems (Fox & Bellwood, 2007). The continuous disruption will lose the resilience of coral reef ecosystems and cause obstruction of coral regrowth and recolonization; consequently, the condition of coral reefs has shifted from a state of coral domination to algal dominance (Nystrom, Folke & Moberg, 2000). The result

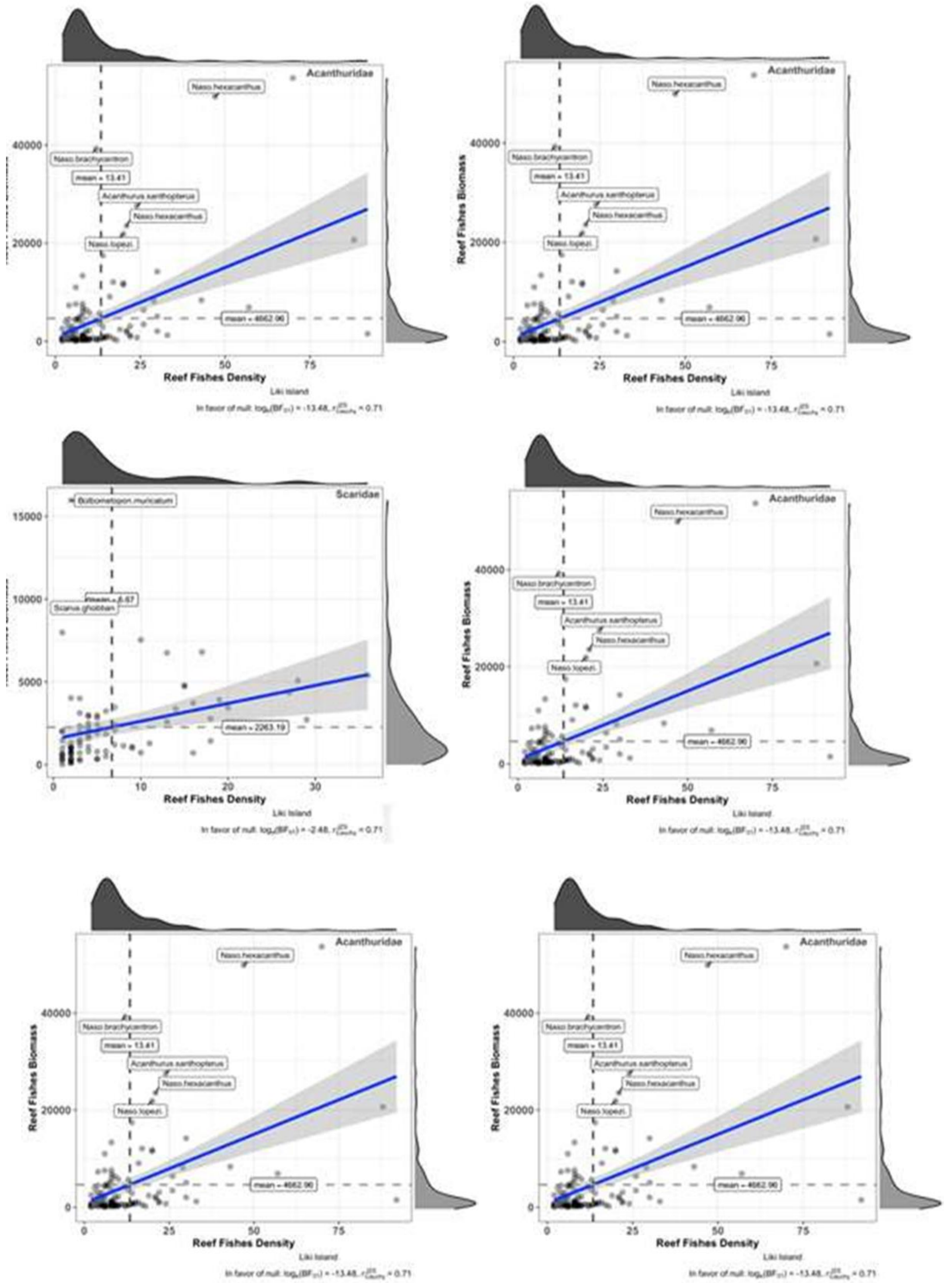

Figure 5. The relationship between density and biomass in each herbivorous fishes families (Acanthuridae, Scaridae, and Siganidae) with dominant appearance species in Eastern SOI Indonesia (Liki) and Western SOI Indonesia (Natuna)

from rapid process changes in coral-algal interactions also depends on specific coral and algal taxa, and several principle factors such as herbivorous fish composition, habitat complexity, water quality, and type of disturbance (Jompa & McCook, 2002). Several coral reef ecologists believe, depending on the level of herbivores and other disturbances to algae, nutrification reefs will be dominated by reef algae that will eventually grow too fast and kill corals (McClanahan, 2002). However, research from (Graham, Wilson, Jennings, *et al.*, 2007) shows that when the disturbance is extensive and occurs on a large spatial scale, it can lead to an increase in the number of large herbivores with a faster growth rate. Eventually, herbivorous fish are the primary ecological process on coral reefs that support complex food webs and significantly contribute to the resilience of this system, particularly their had ability to reorganize and maintain ecosystem functions after disturbance (Vergés, Bennett & Bellwood, 2012).

Another factor causing the herbivorous fish composition is due to the influence of the bleaching phenomenon that occurred in Natuna during 2016 thermal heat stress. Based on studies from (Putra, Suhana, Kurniawn, *et al.*, 2019), the majority reef location in Riau Island in 2016 had an impact on bleaching coral, including Natuna Island during the extreme events of El-Nino Southern-Oscillation (ENSO). Several studies have shown bleaching event result of gradual increases in stress due to loss of herbivory and increases in nutrient levels and cause the coral-algal phase-shift phenomenon (McManus & Polsenberg, 2004). Bleaching events decrease not only live coral cover but also provide large areas for macroalgal colonization to prevent corals from recovery and restoring if herbivores fishes are not present in sufficient numbers to suppress macroalgal colonization and growth (Burkepile & Hay, 2018). Finally, the numbers of herbivorous fishes positively associated with the increasing algal cover that replaced corals in consequence of bleaching events (Ruppert *et al.*, 2013; Sheppard, Spalding, Bradshaw, *et al.*, 2002; Wismer, Tebbett, Streit, *et al.*, 2019).

3.2. The density of Herbivorous Fishes families

A total of 77 species (3520 individuals) of herbivore fishes was recorded in Liki Island (2361 individuals) and Natuna Island (1159 individuals). *Ctenochaetus striatus* was the highest density of herbivore fish in the Liki Island with mean density (41,00 ± 11,72 se) individuals/350m^2 where *Scarus rivulatus* was the highest density of herbivore fish in Natuna Island (31,67 ± 10,61 se) individuals/350m^2 (Table 2). Based on herbivore fishes categories, the most dominant herbivore fishes for Acanthuridae family was *Ctenochaetus striatus*, where another dominant species in Liki Island for Scaridae and Siganidae were *Scarus niger* (19,33 ± 3,02 se) individuals/350m^2 and *Siganus canaliculatus* (5,00 ± 3,20 se). The different condition herbivorous fishes density based families group shown in Natuna Island, the dominant Acanthuridae species in Natuna Island was *A. lineatus* (5,00 ± 2,76 se), where for Scaridae and Siganidae family were *Scarus rivulatus* (31,67 ± 10,61 se) and *Siganus vulpinus* (3,17 ± 1,17 se).

The highest individuals of herbivore fishes was recorded in Liki Island from Acanthuridae family, with mean density per sites location (n = 6) was (μ = 268,17 individuals/350 m^2, $CI_{95\%}$ [114.80, 421.53]), followed by Scaridae family (μ = 115,83 individuals/350 m^2, $CI_{95\%}$ [-13.72, 245.38]), and Siganidae family (μ = 99,00 individuals/350 m^2, $CI_{95\%}$ [-18.53, 216.53]). There was no significant differences were recorded between the herbivorous fishes families in Liki Islands (Kruskal-Wallis = 5.12, p_{-value} = 0.077, $CI_{95\%}$ [0.09, 0.78], n_{obs} = 18) (Figure 3a). There was different pattern of herbivorous fishes families in Natuna Islands. The highest individuals of herbivorous fishes was recorded in Natuna Islands from Scaridae family, with mean density per sites location (n=6) was (μ = 141.33 individuals/350 m^2, $CI_{95\%}$ [82.06, 200.60]), followed by Siganidae family (μ = 18.67 individuals/350 m^2, $CI_{95\%}$ [4.91, 32.42]), and Acanthuridae (μ = 14.5 individuals/350 m^2, $CI_{95\%}$ [-0.23, 29.23]). The significant differences were recorded only Scaridae family in Natuna Island (Kruskal-Wallis = 11.87, p_{-value} = 0.003, $CI_{95\%}$ [0.32, 0.85], n_{obs} = 18) (Figure 3b).

Based on several water quality parameters data from our research, including temperature, salinity, and pH did not provide a significant difference for Liki and Natuna Island. Our research shows that the water turbidity between Liki and Natuna provides a high interval difference in each research sites location (Table 3). The differences in water turbidity intervals indicate a high sedimentation process and affect herbivorous fish populations on Natuna Island, especially in the Acanthuridae family. The low Acanthuridae population in the Natuna Islands due to its location has higher sedimentation than Liki Island (Figure 3; Table

2). The sedimentation affects the composition of herbivorous fish (Fabricius, De'ath, McCook, *et al.*, 2005), where herbivorous coral reef fishes are highly sensitive to changing benthic sediment load (Goatley & Bellwood, 2012), especially roving herbivores (surgeonfishes and parrotfishes) that resourcefully discover and feed on algal turfs.

In contrast, territorial herbivores (damselfishes) may be more resistant due to a mechanism for capability removing sediment (Wenger, Fabricius, Jones, *et al.*, 2015). The sedimentation load provides turf elongation; this may inhibit reef resilience by direct and indirect harmful effects on coral (Clausing, Annunziata, Baker, *et al.*, 2014). The sediment load had the capability in the mechanisms to increase algae growth with sediments blanket algal turf tissue and resulted in block herbivore access and enhancing the risk of increased turf height (Clausing *et al.*, 2014). If sediment does block herbivory access from coral-rich epilithic algal turfs will reduce roving herbivory (Bellwood, Fulton & Fulton, 2012). The mechanism of sedimentation influence in alga turf due to the benthic sediment load and algal turf length increase simultaneously (Bellwood *et al.*, 2012; Goatley & Bellwood, 2012; Goatley, Bonaldo, Fox, *et al.*, 2016).

Previous studies from (Wenger *et al.*, 2015) shown with sediment removal resulting in a more than 200% increase in roving herbivory fishes species. The reduction of the overlaying sediment load in coral-rich epilithic algal turfs resulted in a quick and intense increase in grazing rates by herbivorous fishes (Bellwood *et al.*, 2012). The several present species in Scaridae family (parrotfishes) will help to reduce sediment loads, particularly from Scarus genus likely removes algae and sediment by close cropping (Bellwood *et al.*, 2004; Roth, Saalmann, Thomson, *et al.*, 2018). The parrotfishes can reduce sediment loads and increasing the potential for coral recruitment and survival, indirectly provide the probability of further herbivorous fishes.

The comparison of herbivorous fishes families based on location for each family shown in Figure 5. There was a highly significant difference in the number of individual herbivorous fish of Acanthuridae family in the Liki Islands (μ = 268,17 individuals/350 m^2) when comparing from Natuna Islands (μ = 14.5 individuals/350 m^2) with Wilcoxon rank test (p_{-value} = 0.0022), where the mean density of Acanthuridae family in Liki Island higher than Liki Island. The mean density of the Scaridae family in Liki Island was lower than Natuna Island. A comparison of the number of individual herbivorous fish of Scaridae family between Liki Island (μ = 115,83 individuals/350 m^2) and Natuna Island (μ = 141.33 individuals/350 m^2) shows the non-significant difference in the number of individual herbivore fishes with Wilcoxon rank test (p_{-value} = 0.26). The relatively uncommon pattern of Siganidae families was shown in the comparison location in Liki island (μ = 99,00 individuals/350 m^2) and Natuna Islands (μ = 18.67 individuals/350 m^2) in the non-significant difference of number individual herbivore fishes with Wilcoxon rank test (p_{-value} = 1.00). The Acanthuridae family has shown 42.99% density composition of herbivorous fishes, followed by Scaridae (39.11%), and Siganidae (17.90%).

The increasing population and the presence of migrants to Natuna have a negative influence on coral reef ecosystems. Intensive development in coastal areas and the increasing destructive behavior of local communities have caused the coral reef ecosystem in Natuna to be depressed. The increased land activities and destructive fishing behavior will reduce coral reef resilience with exacerbate the increase in algal abundance (Burkepile, Allgeier, Shantz, *et al.*, 2013; Burkepile & Hay, 2008) and elevate nutrients concentrations via sewage (Littler, Littler & Brooks, 2006). All of these factors indicate that nutrient enrichment can influence coral reef community development and reduced herbivorous fishes (Harvey, Nash, Blanchard, *et al.*, 2018; Roth, Stuhldreier, Sánchez-Noguera, *et al.*, 2015). Previous studies from (Jayewardene, 2009) highlight the main factor of promoting the proliferation of algae on coral reefs, including increased nutrient availability due to eutrophication, and reduced grazing resulting from fishery depletion of herbivorous fishes, so the increasing nutrient concentration could be decreased with reduced destructive fishing activities (Burkepile *et al.*, 2013). It is strongly advocated that the maintenance or restoration of herbivore populations within reef areas should be part of management, in addition to controlling nutrient pollution (Dubinsky, 2013).

Natuna has a very high fishing activity and includes in overexploitation both from the local community and foreign vessels that come to Natuna. In addition, several destructive fishing activities found in Natuna, information from the local government in Natuna, and some of the local fishers still use bombing and poisons in fishing practices. Different conditions from Natuna, Liki apply the Sasi system in fishing practice, where the system serves to protect the diversity and population of marine organisms in Liki. Our results indicate that locations with are high fishing grounds are more likely to have lower herbivorous fish compositions (Figure 4). Previous studies shown high fishing impacts strongly decrease herbivory performance on a coral reef (Kubicek & Reuter, 2016) and reduce on the abundance, biomass and community composition of these fishes (Edwards *et al.*, 2013). The studies from (McClanahan, 2014) also shown the fishing impact influence the larger diversity of herbivores fishes, especially in over-fishing practice in the coral region. Overfishing occurs on virtually every reef, including in small outer islands and impact to larger economic fishes group (grouper, snapper, sweetlips), even herbivorous fish are much reduced (Burke, Reytar, Spalding, *et al.*, 2011). The historical shown overfishing practice not only reduces important economic fishes, but several piscivores, corallivorous, endangered species, and herbivorous fishes decrease significantly (Hopley, 2011). In recent decades roving herbivorous fishes have been identified as critical elements of coral reef communities, and overfishing of these fishes is considered a significant factor contributing to global reef degradation (Vergés *et al.*, 2012).

3.3. The relationship between density and biomass

Both of research location (Liki and Natuna) showed the relationship biomass, and density was positively linear correlated in each family herbivorous fish (Acanthuridae, Scaridae, and Siganidae). The growth in density and biomass of herbivorous fish shows a positive balanced proportion, which indicates herbivore fishes can still grow in the coral reef ecosystem of both islands. If the correlation between growth in density and biomass herbivorous fishes shown the constant linear trend or towards a negatively linear relationship, this indicates extremely high pressure on the herbivorous fish group impartially. Although the relationship of density and biomass of herbivorous fish shows a positive linear relationship, the comprehensive analyzed show the density and biomass distribution of herbivorous fish for each family (Acanthuridae, Scaridae, and Siganidae) on Natuna Island is lower than in Liki Island which biomass can reach two times bigger for the Scaridae fish family group and six times greater for the Siganidae group in Liki Island, and this indicates that there is pressure on the coral reef ecosystem on Natuna Island

From the result, the correlation from distribution grand mean biomass-density of the Acanthuridae family in the Liki Island was (μ_b = 4662.96 gram/350 m^2 ; μ_d = 13.41 individuals/350 m^2) for each site's location with several dominant of species including *Naso hexacanthus, N. brachycentron, N. lopezi,* and *Acanthurus xanthopterus*. The correlation distribution from grand mean biomass-density of Scaridae family in the Liki Island for the six sites location was lower than Acanthuridae family with (μ_b = 2263.19 gram/350 m^2 ; μ_d = 6.67 individuals/350 m^2) for each sites location and *Bolbometopon muricatum* was dominant species from Scaridae family in Liki Island. the lowest correlation distribution from grand mean biomass-density in Liki Island from Siganidae family with (μ_b = 2263.19 gram/350 m^2 ; μ_d = 6.67 individuals/350 m^2) for each sites location.

Natuna Islands had different patterns of distribution grand mean biomass-density compare with Liki Island. Scaridae was the highest grand mean biomass-density in the Liki Island (μ_b = 1191.14 gram/350 m^2 ; μ_d = 9.98 individuals/350 m^2) for each site's location with several dominant species, including *B. muricatum*, *Chlorurus microrhinos, C.* bleekeri, *C.* sordidus, Scarus *quoyi*, *S. niger*, and *S. rubroviolaceus.* The correlation from distribution grand mean biomass-density of Acanthuridae family in the Natuna Islands was lower compared to Scaridae with (μ_b = 945.50 gram/350 m^2 ; μ_d = 5.44 individuals/350 m^2) and only dominant species was *N. brachycentron*. From 3 herbivorous family fishes, the Siganidae has shown the lowest grand mean biomass-density in the Natuna Islands (μ_b = 207.93 gram/350 m^2 ; μ_d = 5.60 individuals/350 m^2) with several dominant species, including *Siganus punctatus*, *S. virgatus,* and *S. vulpinus.*

Although from our studies, we found the pressure to herbivorous fishes family in Natuna island, the lack of monitoring and controlling in the long-term period in the small outer island will increase the overfishing and destructive fishing activities, especially in reducing herbivore fishes. The impact of reducing herbivory through overfishing on a reef in the long-term period with high productivity contribute an increase in macro-algae density, and the long term provides persistence to algal dominance (Hughes, Graham, Jackson, *et al.*, 2010; Littler *et al.*, 2006; Marshell & Mumby, 2012; McClanahan, 2002; McManus & Polsenberg, 2004; Teixeira-Neves, Neves &

Araújo, 2016). Another previous research from (Burkepile & Hay, 2018) shown the removed herbivorous fish in the coral ecosystem from overfishing cause the macroalgal to replace the coral and biogenic structure of the reef will degrade. Other evidence that can indicate overexploitation of coral reef ecosystems is the lack of presence of large excavator, including *Bolbometopon muricatum* and *Cetoscarus ocellatus* from Scaridae family, due to a large-bodied excavator are usually among the first to disappear on an overfished reef (Grimsditch, Tamelander, Mwaura, *et al.*, 2009). From our result, we found several sites presence of very low large excavators in the Natuna Islands, including *B. muricatum* and *C. ocellatus* from the Scaridae family. The low presence of large excavator herbivorous fishes in Natuna Island was a dominant influence by the benthic community (Dwirama Putra *et al.*, 2018) (Figure 5; Table 4).

Our study shows exciting results in herbivorous fishes assemblages, where the eastern region (Liki Island) is dominated by Acanthuridae while in the western region (Natuna Island) is dominated by Scaridae. Both of fishes families is a part of Roving herbivorous and identified as the key functional group performing the significant ecological role concerning the dynamics of benthic communities (Dromard *et al.*, 2015; Hoey & Bellwood, 2008; Mumby, Dahlgren, Harborne, *et al.*, 2006). Several studies also have shown the main herbivorous fishes on coral reefs are generally surgeonfishes (Acanthuridae), parrotfishes (Scaridae) with rabbitfishes (Siganidae), and several territorial herbivorous fishes from damselfishes (Pomacentridae) also responsible for considerable herbivory in specific locations (Burkepile & Hay, 2018; Dubinsky, 2013; Jompa & McCook, 2002). In several reef sites location, both fishes have a dominant population with the most abundant of herbivorous fishes (Grimsditch *et al.*, 2009; Pereira *et al.*, 2014).

As a part of roving herbivorous fishes, Scaridae and Acanthuridae have special functions in the coral reef ecosystem, the surgeonfishes (Acanthuridae) has dominant play a role in keeping EAM (Marshell & Mumby, 2012), while Parrotfishes (Scaridae) are essential as grazers and bioeroders on coral reefs (Bellwood, Hoey & Choat, 2003; Comeros-Raynal, Choat, Polidoro, *et al.*, 2012; Rice, Ezzat & Burkepile, 2019). Based on previous studies from (Fox & Bellwood, 2007; Marshell & Mumby, 2012) shown the surgeonfishes represented 74% of the herbivorous fish biomass in feed Epilithic algal matrix (EAM) and responsibility removed 73% of daily EAM productivity in the shallow zone. The differences and the existence of populations of these two fish can explain the condition and status of coral reef ecosystems. Previous studies shown the population from roving herbivores are more abundant in unprotected reef sites. In contrast, the piscivores, carnivores, mobile invertebrate feeders, and territorial herbivores all were significantly more abundant in protected sites (Floeter, Halpern & Ferreira, 2006). The differences in population reef fishes caused by the characteristics of some types of fish in response to anthropogenic pressure.

The biggest challenge at SOI is to protect the area from anthropogenic pressure, including overexploitation and destructive fishing practice. High over exploitation will reduce rapidly of carnivorous fishes as important economic fishes, so the only a small population is found in the unprotected area, whereas if carnivorous fish populations increase (e.g., grouper, snapper, sweetlips) resulted in increased predation rates on small herbivorous as parrotfishes (Burkepile & Hay, 2018) and cause the herbivorous population fishes is low. The opposite even will also happen if following the decline in cover of live coral, the herbivore assemblage on the forereef became increasingly dominated by parrotfish (Adam *et al.*, 2011). After the larger carnivorous animals are depleted, fisheries switch to smaller predators such as groupers and then increase the population of herbivorous fish such as parrotfishes (Burkepile & Hay, 2018). However, the presence of herbivorous fish has indirect positive effects on corals. (Rotjan & Lewis, 2006). The main problem is that the capacity of herbivorous fish that plays a role as coral reef resilience is also limited if anthropogenic pressure or natural disturbance is increasing. Several small outer islands or oceanic islands as Most Caribbean reefs today are also algal-dominated, because of overfishing of herbivorous fishes and the continuing low densities (Hughes *et al.*, 2010). This has become a global problem because reductions in herbivore diversity and abundance via

Table 4. The Percentage of Hard Coral and Dead Coral Algae in Natuna Island

	NTNC.01	NTNC.02	NTNC.03	NTNC.04	NTNC.05	NTNC.06
HC (%)	36.87	33.27	14.33	30.93	23.73	19.73
DCA (%)	58.93	48.87	48.07	56.47	51.27	63.53

overfishing may harm corals directly and may indirectly increase coral susceptibility to other disturbances (Burkepile & Hay, 2010; Hughes *et al.*, 2007).

For herbivorous fishes, besides the several standard protocols has used to measures density, richness, and diversity per family, the measurements of size an essential consideration for (Leão *et al.*, 2019) to determine if the biomass as ecological functions condition. The measurement of biomass, diversity, and abundance of herbivorous fishes that perform these critical functions is becoming a key role in the evaluation of coral reef resilience (Goatley *et al.*, 2016). Large populations of herbivorous fish that have high biomass indicate an ecosystem that protects herbivorous fish. In addition, the ecosystem protection increase size of herbivorous fishes, and the effect of several species of megaherbivorous fishes as *B. muricatum* and *C. ocellatus* can increase growth in maximum size (Johnson, 2009). Our result has shown consistency with previous research from (Beita-Jiménez, Alvarado, Mena, *et al.*, 2019) with the biomass of predators, carnivores, and herbivores were greater in areas with protection. Another consistency of herbivorous pattern in our result shown in the protection area has a significantly higher coral cover, and less fleshy algae cover compared to fished reefs area (Ford, Eich, McAndrews, *et al.*, 2018). Other benefits of several large herbivorous fish species with high biomass allow for more bites per individual fish (Burkepile & Hay, 2018) and responsible for reducing algal biomass (Ceccarelli *et al.*, 2011; Paddack, Cowen & Sponaugle, 2006) for help in resilience reef ecosystems rapidly.

In addition, the presence of large herbivorous fishes attracts some top-level predators and helps in restoring ecosystem balance. The high predation mortality of herbivorous fish will increase predator biomass (Rogers *et al.*, 2018). Previous studies from (Floeter *et al.*, 2006) shown roving herbivores showed an overall negative response to more excellent protection, where fish species from higher trophic levels (e.g., piscivores) were among the more positive impact in protection area with growth optimally. Our last result consistent with the high abundance and biomass of herbivores in marine ecosystems may indicate a sign of degradation due to the higher biomass of algae (Medeiros & Grempel, 2007). Our result show, all of the family group herbivorous fishes with small to medium biomass and the mean of length of herbivorous fish under 30 cm of body size. Previous studies shown on Pacific reefs and several reef sites in Great Barrier Reefs, herbivore biomass is dominated by smaller-bodied fishes including acanthurids and smaller parrotfishes (Bellwood *et al.*, 2004; Rogers *et al.*, 2018; Russ, 2003); thus, the presence of several sizeable herbivorous fish species signifies a healthy coral reef ecosystem. Studies from (Wilson, Graham, Fisher, *et al.*, 2012) confirm the good coral ecosystem in the protected area had higher biomass of herbivorous than fishes area.

4. Conclusion

Herbivorous fish biomass patterns are very helpful in understanding the condition of coral reef ecosystems comprehensively. There is a unique pattern of herbivorous fish distribution, where Acanthuridae is dominant in eastern Indonesia (Liki Islands) while Scaridae is dominant in western Indonesia (Natuna island). The eastern part of Indonesia has a higher herbivorous fish composition, both in density and biomass, compared to the western part of Indonesia. Our result in two locations small outer island Indonesia concludes with the consistency of previous studies shown increased herbivore richness, density, and biomass strongly reduced the cover, biomass, and diversity of fleshy algae (Burkepile & Hay, 2008; Cowburn, Samoilys, Osuka, *et al.*, 2019; Newman, Paredes, Sala, *et al.*, 2006; Sandin, Sampayo & Vermeij, 2008).

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