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Primary research paper

Assessment of spatio-temporal variations of macroalgal canopies and fish schools before and after coastal desertification using acoustic methods

H. Shao[1, *], S. Kiyomoto[1], T. Kadota[1], M. Nakagawa[2], H. Yamanaka[3], Y. Kawauchi[4], K. Minami[5], K. Miyashita[6]

[1] Fisheries Technology Institute, Japan Fisheries Research and Education Agency, 1551-8 Taira-machi, Nagasaki, Nagasaki 851-2213, Japan
[2] Fisheries Technology Institute, Japan Fisheries Research and Education Agency, 148 Fukai-ota, Ishigaki, Okinawa 907-0451, Japan
[3] Iki Sea Farming Center, 1168 Oshima, Gonoura-cho, Iki, Nagasaki 811-5161, Japan
[4] Fisheries Resources Institute, Japan Fisheries Research and Education Agency, 2-12-4 Fukuura, Kanazawa, Yokohama, Kanagawa 236-8648, Japan
[5] Estuary Research Center, Shimane University, 1060 Nishikawatsu-cho, Matsue-shi, Shimane 690-8504, Japan
[6] Field Science Center for Northern Biosphere, Hokkaido University, 20-5 Benten-cho, Hakodate, Hokkaido 040-0051, Japan

***** Correspondence: shao_huamei06@fra.go.jp

Abstract: Macroalgal canopies, which provide nutrients and habitat for many invertebrates and fishes in coastal waters, are disappearing worldwide. The simultaneous assessment of changes in macroalgae and fish distribution before and after coastal desertification, including deeper coastal waters where beyond macroalgae growth need attention. Therefore, we investigated their spatial distribution in the coastal waters off southwestern Japan in late autumn and winter using the acoustic method combined with visual observation. The number of fish schools was higher in late autumn than in winter, while they had similar acoustic backscattering strength (Sv) and school size, tended to be distributed in shallower waters. The number was lower after the macroalgae disappeared in both seasons, while the average Sv was higher, and the size was larger. They were distributed in similar water depths during the winter season. Fewer fish schools and higher Sv were observed in deeper waters after the macroalgae disappeared. We concluded that more fishes moved to shallower waters in the autumn than in the winter because of higher water temperatures. Macroalgae benefited small juvenile fishes in both shallow and deep coastal waters. Further studies on the distribution of specific species are expected for the assessment and restoration of the macroalgal ecosystem.

Keywords: Acoustic; Coastal desertification; Fish school; Macroalgae; Spatial distribution

Introduction

Macroalgal canopies have high productivity, probably comparable to that of tropical rainforests (Mann, 1973). They also provide nutrients and habitat for many invertebrates and fishes, and thus play an important ecological role in many coastal water ecosystems (Mann, 1973; Steneck et al., 2002). In recent years, macroalgal populations have been declining and disappearing in the coastal waters worldwide, because of rising water temperatures, herbivory, and overharvesting (Mann, 1982; Watanabe and Harrold, 1991; Fujita, 2010; Jueterbock et al., 2013; Vergés et al., 2016; Wernberg et al., 2016). Particularly in Japan, the decline or disappearance of macroalgal canopies, apart from seasonal and slight annual fluctuations, was reported more than 100 years ago, and the affected area has been expanding ever since then (Yendo, 1903; Fujita, 2010). Declines in large canopy-forming macroalgae, such as *Ecklonia* spp. and *Sargassum* spp., have been observed in the coastal waters of southwestern Japan (Serisawa et al., 2004; Yatsuya et al., 2014a; Kiyomoto et al., 2018). In particular, the presence of macroalgae throughout the year gradually disappeared in the coastal waters of Iki Island off the southwestern mainland Kyushu (Yatsuya et al., 2014a; Kiyomoto et al., 2021), and macroalgal canopies could only be observed in the southeastern coastal site of Iki Island in 2017. The coastal waters of Iki Island are influenced by the Tsushima Warm Current, which is a branch of the Kuroshio Current, and more warm water flows into the western coastal waters than into the eastern coastal waters. The sea surface temperature of the southeastern coastal waters is lower than that of the western area (Fig. 1; Fukuoka Regional Headquarters, Japan Meteorological Agency (FRH, JMA), 2022). Desertification occurred in almost all of the western coastal waters before 2017 due to the several ocean warmings since 1998, macroalgal canopies remaining in the southeastern area seems to have benefited from the lower temperature than that of the western area.

However, as the condition of macroalgal canopies deteriorates each year, excessive grazing pressure from fish is considered a concurrent cause, along with ocean warming of the macroalgal decline since 1998, wherein water temperature was lower than the limit of survival temperature (28 °C) (Murase 2010) in autumn (Kiriyama et al., 1999; Yatsuya et al., 2014a; Kiyomoto et al., 2021). In addition to direct damage from high temperatures, threats to macroalgae by herbivorous fishes have also been reported in other temperate seas due to global ocean warming (Verges et al., 2014; Wernberg et al., 2016; Gianni et al., 2017). As macroalgae declined in other coastal waters surrounding the island, herbivorous fishes may have migrated to this area for grazing. Although the remaining macroalgae survived after several times of ocean warming, the macroalgae growing around the survey area disappeared in previous years due to higher water temperature in the summer and the excessive grazing pressure from herbivorous fishes in the autumn (Yatsuya et al., 2014a; Kiyomoto et al., 2021). Some herbivorous fishes, especially *Kyphosus bigibbus* Lacepède, 1801, which could move in a wide area, have also been reported (Yamaguchi et al., 2006), which were caught by the fishermen on the study island. Thus, herbivorous fishes are likely to move and graze on the nearby remnant macroalgae as the loss of food source, we hypothesize that the remnant macroalgae canopies would subsequently disappear even though the water temperature is below the limit growth temperature as the excessive grazing pressure. Whether the remnant macroalgal canopies could survive continuously in the future and whether the distribution patterns of fish schools would change needs attention. Not only the macroalgae themselves, but also the simultaneous assessment of the spatial distribution of the interacting species is necessary to further understand and conserve the coastal macroalgae ecosystem.

Some studies verified the correlation between macroalgal canopies and fish assemblages in coastal waters and reported that macroalgal canopies are important habitats for juvenile fishes in some temperate reef and tropical coastal waters (Levin and Hay, 1996; Tano et al., 2017; Hinz et al., 2019). Fish assemblages have also been studied around various vegetation types and barren beds in some temperate coastal regions of southwestern Japan by direct observation and seine survey, and various macroalgae types were found to be important for some fish assemblages (Kamimura and Shoji, 2009; Terazono et al., 2012; Kadota et al., 2017b; Nakamura et al., 2018). Both fish species richness and abundance decreased significantly after the disappearance of the large sized macroalgae *Ecklonia cava* Kjellman, 1885 in temperate coastal waters of Japan (Nakamura et al., 2018). However, the simultaneous assessment of the changes in the spatial distribution patterns of fish schools in coastal waters before and after the macroalgae disappearance of macroalgae is limited. In addition, several studies have investigated the influence ray of artificial reefs, which can be defined as the distance from the reef where fish density significantly decreases. Since the influence ray of a reef for fishes can be up to 300 m or more (Soldal et al., 2002; Kang et al., 2011), the fish assemblages that exceed the macroalgal canopies within this distance are likely to have changed after the disappearance of macroalgae due to the loss of suitable habitats. Thus, the distribution patterns of macroalgal canopies and fish assemblages in a wider and deeper waters, beyond the macroalgal growth areas is need attention.

Direct observation by divers is a conventional method used for monitoring macroalgal canopies (Pehlke and Bartsch, 2008; Yatsuya et al., 2014a; Kiyomoto et al., 2018) and it is suitable for small-scale surveys. In recent years, hydroacoustic methods, such as the use of scientific echosounders and side-scan sonars, have been developed to survey macroalgae and seagrass canopies (Sabol et al., 2002; Minami et al., 2010; Paul et al., 2011), as well as fish distribution and biomass (Simmonds & MacLennan, 2005; Boswell et al., 2007; Kang et al., 2011) and seafloor classification (Anderson et al., 2008; Brown et al., 2011; Mehler et al., 2018). Previous studies have suggested that echosounder surveys are useful tools for estimating the canopy height and the spatial distribution of canopies formed by macroalgae and seagrass (Sabol et al. 2002; Minami et al., 2010; Sonoki et al., 2016; Shao et al., 2017). Some studies have also reported the influence of bottom structure, artificial reef, marine environment, and blue-green algae on fish abundance using acoustic methods (Tanoue et al., 2008; Kang et al., 2011; Godlewska et al., 2016). Although fish species discrimination solely based on the acoustic methods alone is difficult, similar patterns of fish density have been reported across independent sampling units using the acoustic and diving methods (Zenonea et al., 2017). The change in patterns of fish schools and macroalgal canopies could be detected over a larger area in a shorter time using the acoustic method compared to visual observations by diving.

Therefore, we aimed to estimate the spatial distribution of macroalgal canopies simultaneously with that of fish schools in the vicinity, using the acoustic method combined with visual observation in the coastal waters where sea desertification occurred. First, we tested whether macroalgae would subsequently disappear with excessive grazing pressure, even if the temperature remained suitable for macroalgal growth. Then, we hypothesized that the distribution patterns of fish schools would change after the disappearance of macroalgae due to the loss of suitable habitats; the number of fish schools would decrease in the nearby deeper waters in addition to the shallower waters where macroalgae grow.

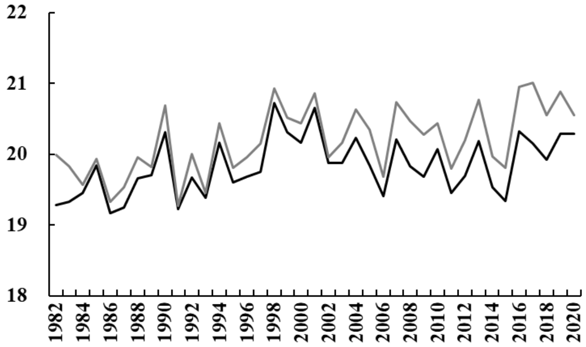

Fig. 1 Annual mean sea surface temperature of the southeastern and western coastal waters of the Iki Island from years from 1982 to 2020. The black and gray lines indicate the southeastern and western coastal waters, respectively (Fukuoka Regional Headquarters, Japan Meteorological Agency, 2022). The horizontal axis shows the year, and the vertical axis shows the water temperature in degrees.

Materials and Methods

Data collection

Surveys were conducted at the southern coastal site of Iki Island, Nagasaki, Kyushu, the southwestern mainland of Japan (Fig. 2a), where large macroalgal canopies were observed before the first survey. We conducted four surveys: November 24, 2017 (late autumn), January 29, 2018 (winter), and November 27, 2018 (late autumn), February 20, 2019 (winter). We conducted the acoustic survey during the daytime from 10 am to 2 pm, which was at least two hours after the sunrise and before the sunset to avoid the transition periods of most fish. During the surveys, we first set a transect line for visual observation on the seafloor using a 100 m long tape measure to identify benthic aquatic biota. The maximum depth of the survey lines was less than 15 m, which is suitable for the habitat of most macroalgae in the area and for the safety of the divers. Then, we measured the maximum height of the macroalgae and took photographs in each 1 m^2 quadrant at each meter mark along the transect lines, to record information on the vegetation and topography. Visual observation surveys along the transect line were omitted in November 2018 due to the disappearance of large macroalgae, which were recorded by divers prior to conducting acoustic surveys. Subsequently, we collected acoustic data three times along the line using a portable scientific echosounder (DT-X extreme, BioSonics Inc., Seattle, WA, USA) at a frequency of 200 kHz with an internal differential global positioning system on a boat (3.4 t). The transducer was attached to the end of a stainless steel pole fixed to the side gunwale of the boat, and positioned 0.5 m below the sea surface (Fig. 2b). Specifications for data collection from the echosounder during the surveys are given in Table 1. Acoustic data, along with the latitude and longitude information, were recorded on a laptop computer (Toughbook CF-31, Panasonic Co., Kadoma, Osaka, Japan) connected to the echosounder. The speed of the survey boat was approximately 3 knots (1.54 m/s) to reduce the formation of air bubbles in the seawater. Following the acoustic survey for the visual observation lines, we collected acoustic data along the transect lines, which were set approximately perpendicular to the shoreline with horizontal distance intervals of 100-200 m except for the first survey in autumn 2017 (Fig. 2 a). The portable scientific echosounder was calibrated before or after the surveys using a 38.1 mm diameter tungsten carbide calibration sphere (Demer et al., 2015).

In addition, we set a water temperature logger (TidbiT V2, Onset Computer Co., Bourne, MA, USA) on the seafloor (approximately 10 m water depth) near the study area and recorded the data at 30-min intervals from 26 September, 2017 to 13 March, 2019.

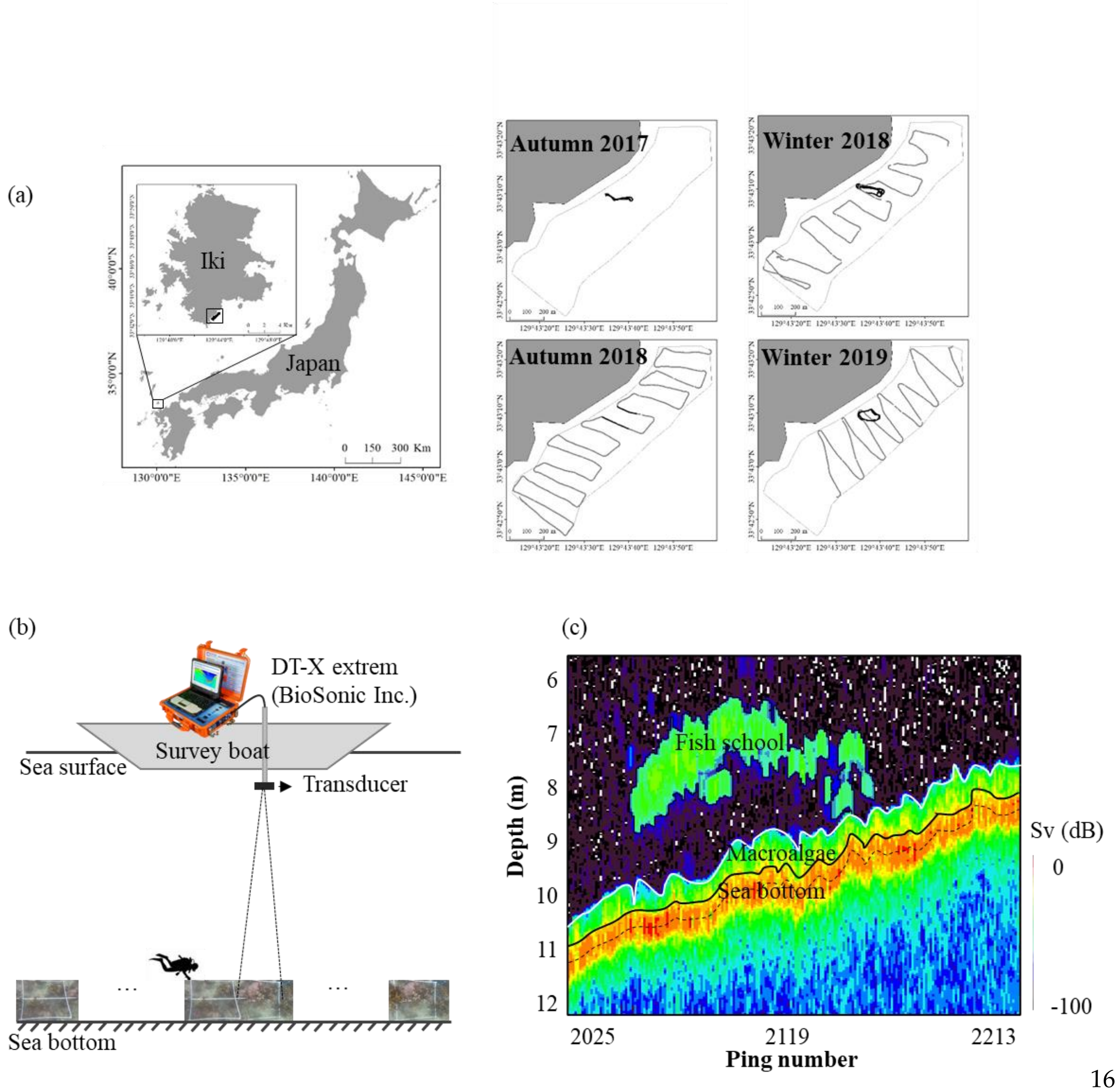

Fig. 2. (a) Survey area and transect lines in the coastal waters of Iki Island, Nagasaki, southwestern Japan. The gray lines in the four maps on the right represent the transect lines of the acoustic method; the shorter black lines represent transect lines of both visual and acoustic methods. (b) Conceptual diagram of direct

and acoustic observations along survey lines. Divers observed the macroalgae along the visual transect lines set on the seafloor using 1 m^2 quadrat, the images above the seafloor line show the macroalgae photographed by divers. (c) An example echogram of the seafloor, macroalgae, and fish schools. The horizontal axis indicates the number of pings collected by the echosounder, and the vertical axis indicates the water depth. The dashed line indicates the strongest backscattering strength, and the black solid line indicates half the pulse length distance above the dashed line, which was used as the boundary between the seafloor and the macroalgae, and the white solid line indicates the boundary between the macroalgae and the seawater. The distance between the white and black solid lines indicates the height of the macroalgal canopy. The green polygons indicate fish schools detected by the acoustic method.

Table 1. Specifications of the scientific echosounder used in the surveys.

Specification	
Beam type	Split
Frequency (kHz)	200
Power (W)	1000
Pulse length (ms)	0.5
Ping interval (s)	0.2
−3 dB beam width (degree)	6.8
2-way beam angle (dB)	−20.97
Digital sampling frequency (kHz)	75
Radius of transducer (m)	0.09
System noise (dB)	−140

Data analysis

Visual observation data collected by divers were classified as macroalgal canopy or bare ground based on macroalgal cover and maximum height. We classified a macroalgal assemblage as a canopy if the maximum height was >0.2 m as the large sized macroalgae *Ecklonia* spp. and *Sargassum macrocarpum* C. Agardh 1820 dominated in this area. The mean height and the occurrence rate of macroalgal canopies >0.2 m in height along the visual observation transect line was calculated during each survey, except for the one in November 2018 survey when the macroalgae disappeared.

With respect to the collected acoustic data, the recorded volume backscattering strength (Sv) data were exported according to each resolution pixel along the transect lines using Echoview (Ver. 5.3, Echoview Software Pty Ltd. Hobart, Tasmania, Australia). Because echoes from seawater are significantly weaker than those from the seafloor or seaweed due to the absence of hard objects (Horne, 2000), the seafloor was set as the strongest value, and the maximum difference value (ΔSv) of two adjacent pixels above the seafloor was set as the boundary of the seawater. To obtain the Sv value of macroalgal meadows in survey areas, we calculated the average value of 30 pings where macroalgae were observed by direct observation. The threshold between seawater and macroalgae was -71.63 dB, and the strongest value considered as the seafloor was -9.40 dB. In addition, since the dead zone near the seafloor is usually defined as half the pulse length (Ona and Mitson, 1996), we excluded the 37.5 cm distance in the surveys calculated based on the 0.5 ms pulse length. Thus, the line 37.5 cm above the strongest value line was considered the bottom line of the macroalgal meadow. The lines were identified using Echoview software (Fig. 2(c)). Finally, the height of the macroalgal canopy (H) was defined as the distance between the seafloor minus half of the pulse length distance and the seawater. In addition, the near-field zone of the transducer near the surface was excluded from the analysis because the acoustic pressure was unstable. The distance threshold (rend, m) for an accurate measurement was calculated using the following formula (Medwin and Clay, 1998):

$$\mathrm{rend} = \pi R^2/\lambda \quad (1)$$

where R is the radius of the transducer (0.09 m), λ is the wavelength (approximately 0.01 m); thus, rend was calculated to be approximately 3.3 m. In addition, we summed up 0.5 m for the transducer depth and 0.375 m for the pulse resolution; thus, we excluded the collected acoustic data in water depth less than 4.2 m before the analyses. Then, the water depth during each survey was calibrated by the tide level to low tide; it was from 2.5 m when we excluded the acoustic data less than 4.2 m. Subsequently, the start and end ping numbers were exported to each 1 m grid along the transect lines, and the mean values of H were calculated for each 1 m of the horizontal distance. Because high-relief rocks (≥0.20 m) were rarely observed in the surveys, if H was greater than 0.2 m, we defined it as macroalgae, otherwise it was classified as barren seafloor. We only analyzed macroalgae larger than 0.2 m because our focus was on the change pattern of large macroalgae; however, other methods are available for the accurate analysis to accurately analyze macroalgae smaller than 0.2 m (Shao et al., 2021).

The school detection feature of Echoview was used to detect fish schools. First, we set the minimum length and height of the candidate size in Echoview, and Echoview detected the minimum size of an echo as a candidate for a school, excluding those smaller than this value from detection. We then set the maximum vertical and horizontal link distance to decide the neighboring school as a single school if two echoes were closer than the predetermined distance. Echoview detected a school from the remaining candidate echoes by size by setting the minimum total school length. Our goal was also to identify small schools during the surveys, so parameters with small values were selected, as shown in Table 2.

To clarify the changes in the fish schools from the autumn of 2017 to the winter of 2019 in the shallow coastal waters, the average number of fish schools was calculated along the visual transect lines at every 1 km distance. In addition, the number of fish schools (schools/km) was also calculated along the entire acoustic transect lines from winter 2018 to winter 2019 to clarify the changes in the study area. The numbers along each transect line were also extracted and we performed the non-parametric Steel-Dwass test using R (Ver. 3.6.3, R Core Team, 2020) to check and discuss the differences between the different surveys. In addition, the characteristics of the schools detected in all the surveys were exported in the comma-separated value file format. Fish school characteristics were categorized into energetic, morphological, and positional types, as the classification descriptor has been previously reported to be influential (Reid et al., 2000; Charef et al., 2010; Kang et al., 2011). Energetic characteristics included mean Sv. Positional characteristics included water depth and school depth. Morphological characteristics included corrected length, height, perimeter, and area. To understand the relation distance between fish schools and macroalgae, we used ArcGIS software to calculate the closest distance of fish schools from all surveys to the macroalgae observed in winter 2018. Additionally, we performed the nonparametric Steel-Dwass test between surveys using the free R software between surveys to estimate annual and seasonal changes in terms of the presence and absence of macroalgal canopies.

In addition, to show the distribution pattern along different bottom depths, the proportion of macroalgal canopies present, density, Sv, and perimeter of fish schools were calculated for each 5 m water depth range of each survey. Because we excluded acoustic data near the sea surface, the depth range below 5 m in this study was 2.5-5 m.

The average water temperature of each day during the recording period was calculated. In addition, we used the sea surface temperature (SST) data from 1982 to 2020 of Iki Channel, the eastern coastal waters of Iki Island from FRH, JMA, 2022, and calculated the annual average SST anomaly with respect to the average temperature.

Table 2. Parameters for fish school extracted from acoustic data in Echoview software.

Parameter	
Minimum data threshold (dB)	−65
Minimum total school length (m)	3
Minimum total school height (m)	1
Minimum candidate length (m)	2
Minimum candidate height (m)	1
Maximum vertical linking distance (m)	1
Maximum horizontal linking distance (m)	2

Results

Macroalgal canopies along visual observation lines

Illustrative images of the macroalgal conditions visually observed during the four surveys are shown in Fig. 3. Large macroalgae (*Ecklonia* spp. and *S. macrocarpum*) dominated the study area, forming dense macroalgal canopies in the autumn of 2017 and in the winter of 2018 (Fig. 3). Mean heights of macroalgal canopies along the visual observation transect lines were 0.37 and 0.39 m in the autumn of 2017, and 0.54 and 0.48 m in the winter of 2018, by visual observation and acoustic method, respectively (Fig. 4a). Only a few stems were observed in the autumn 2018 survey, and fish bite marks were observed by divers. In the winter of 2019, a few small-sized juveniles were observed, while no large-sized adult macroalgal individuals > 0.2 m in height were observed (Fig. 3). These observations indicated the disappearance of large macroalgae. The mean height of large-sized macroalgae estimated by the acoustic method was 0.25

m in the autumn of 2018, which was less than that in the autumn of 2017, and 0.24 m in the winter of 2019, which was less than that in the winter of 2018.

The presence rate of macroalgal canopies was 99% in the autumn of 2017 and 96% in the winter of 2018 by visual observation, which is similar to the presence rate observed by the acoustic method along the visual transect lines in both the surveys (99%). The presence rate of macroalgal canopies estimated acoustically was 3% in the autumn of 2018 and 5% in the winter of 2019 (Fig. 4).

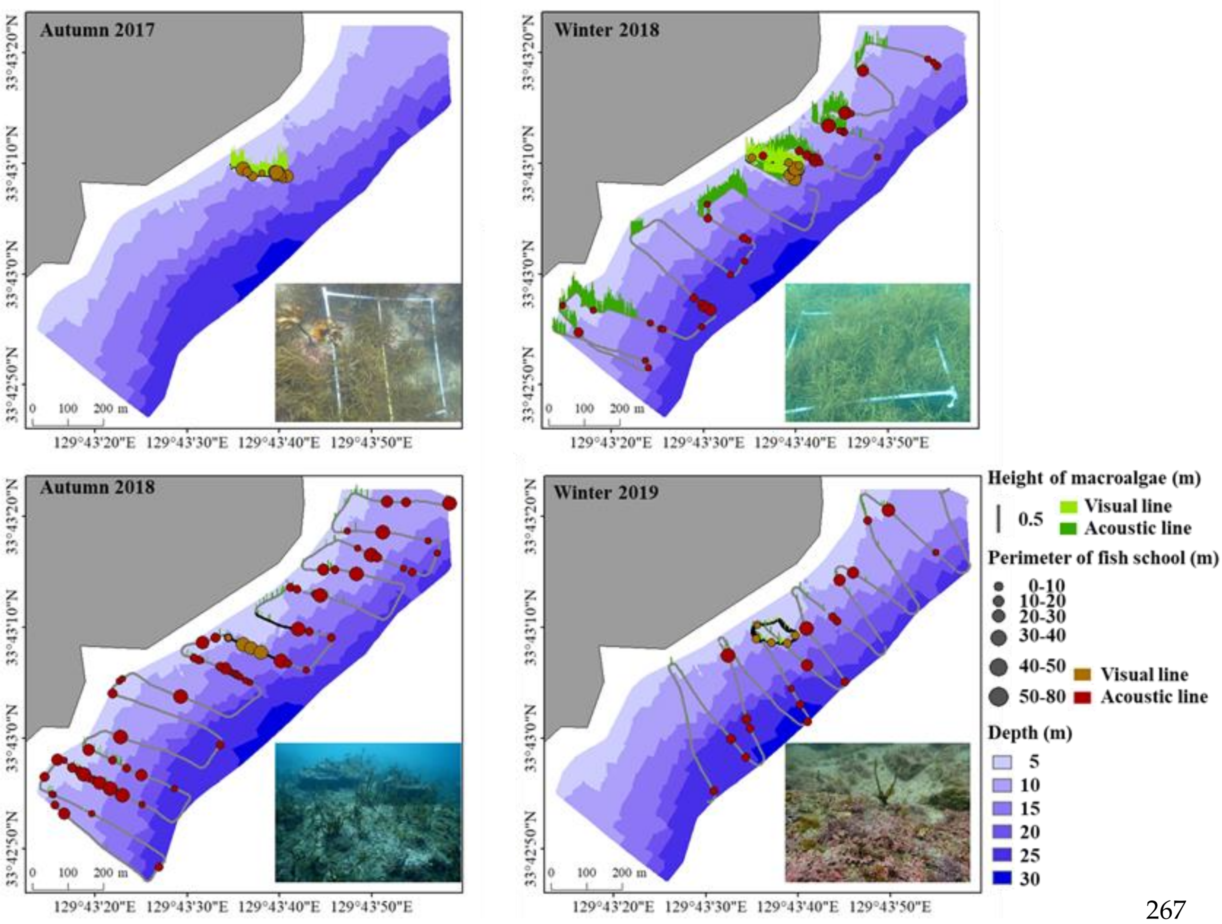

Fig. 3. Distribution of macroalgae and fish schools along transect lines during the four surveys conducted from 2017 to 2019. Gradient blue color indicates water depth of the survey area, light green bars indicate the height of macroalgae along visual lines, and dark green indicates the height along acoustic lines. Closed circles in orange color indicate perimeter size of fish schools along visual lines, and closed circles in red indicate the size along acoustic lines. Photos on the right side of the maps show the condition of the macroalgae of each survey by visual observation.

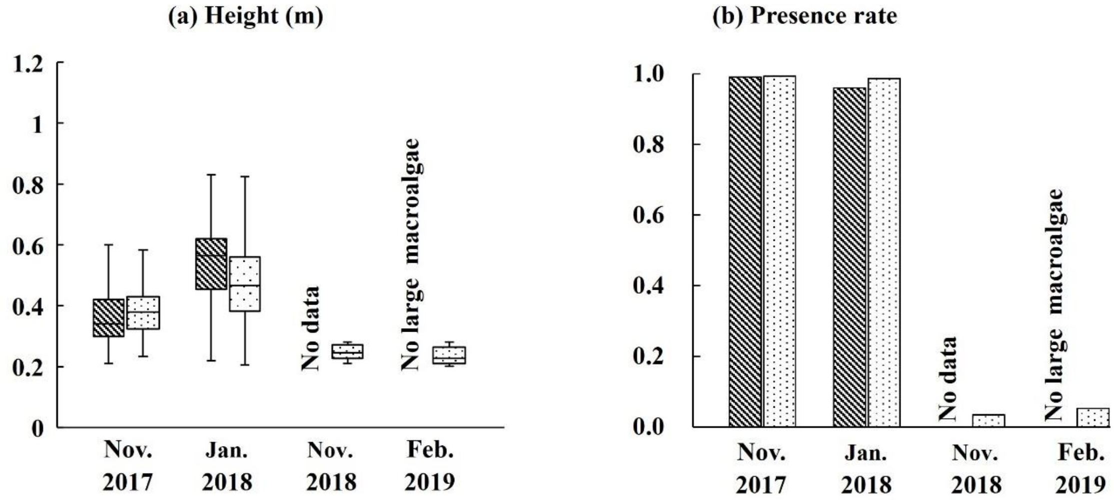

Fig. 4. (a) Height and (b) presence rate of macroalgae along visual observation lines by visual observation and the acoustic method. (a) Heights of each 1 m^2 are shown by the box plot, the box is drawn from Q1 to Q3 with a horizontal line indicating the median. (b) Presence rates along the survey lines are shown by the vertical bars. Shaded areas filled with lines represent results obtained by visual observation, and areas filled with dots represent results obtained by the acoustic method.

Presence of macroalgal canopies and fish schools

The spatial distribution of macroalgal canopies and fish schools along the visual and acoustic transect lines is shown in Fig. 3. The presence rate of macroalgal canopies and the number of fish schools detected by the acoustic method along the visual observation transect lines are shown in Fig. 5a and along the total transect lines throughout the study area are shown in Fig. 5b. The total distance of acoustic transect lines in the study area was 4.13 km in January 2018, 5.69 km in November 2018, and 3.62 km in February 2019. The number of fish schools was the highest in the autumn of 2017 and the lowest in the winter of 2019. The number of fish schools in the autumn was higher than that in the winter of the following year during the study period. The number of fish schools in the winter of 2018, when macroalgae were observed, was higher than that in the winter of 2019, when sea desertification occurred (Fig. 5a). The same trend was also observed in the late autumn: more fish schools were observed when macroalgae occurred than when sea desertification occurred (Fig. 5a). The number of fish schools in the autumn of 2018 was higher than in the winter of the following year, when the presence rate of macroalgal canopies was both < 5% (Fig. 5b), and a significant difference was found between the two surveys (Steel-Dwass test, $p < 0.001$). In addition, the number of fish schools in the winter of 2018, when macroalgae were observed, was higher than that in 2019, when coastal desertification occurred, and a significant difference was found between the two surveys (Steel-Dwass test, $p < 0.05$).

The main species of fish schools observed along the transect lines during visual observation by diving were *Halichoeres tenuispinis* (Günther, 1862), and small sized undetermined species of Clupeidae in January 2018, and *Girella punctata* Gray,1835, *Siganus fuscescens* (Houttuyn, 1782), *H. tenuispinis* in November 2018.

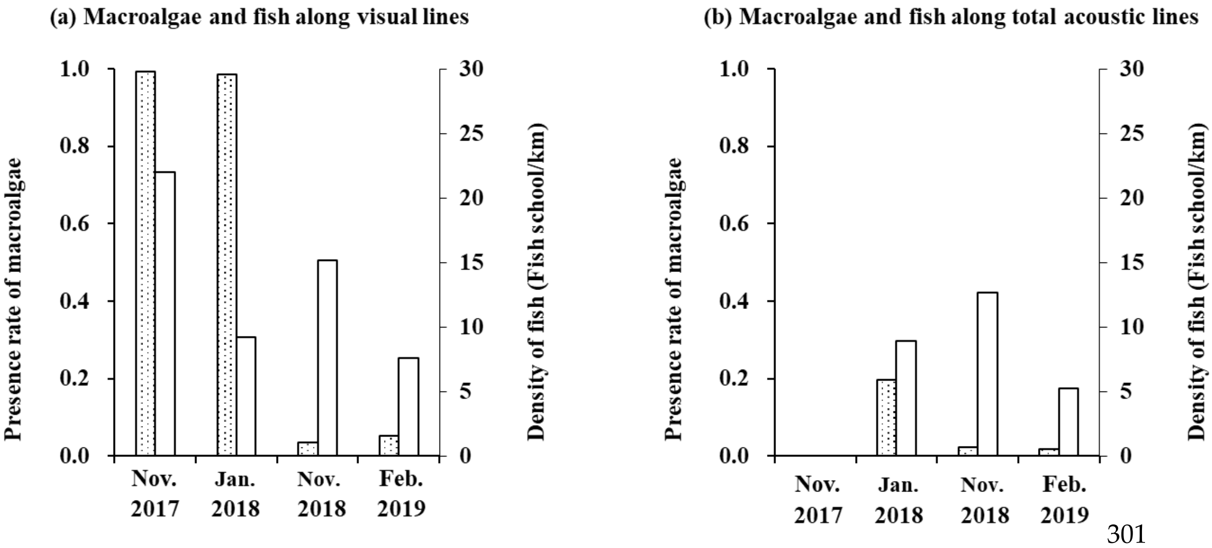

Fig. 5. Presence rate of macroalgae and density of fish schools using the acoustic method along (a) the visual observation line and (b) the entire transect line. Shaded bars filled with dots represent the presence rate of macroalgae (left vertical axis) and the white bars represent fish density (number of fish schools per km, right vertical axis).

Characteristics of fish schools

Fish school characteristics along the entire survey line are shown in Fig. 6. The mean Sv of the winter 2018, when macroalgae were observed, had a value of −51.1 dB, which was lower than that of autumn 2018 (-47.3 dB, Steel-Dwass test, $p < 0.001$) and lower than that of winter 2019 (-42.8 dB, Steel-Dwass test, $p < 0.001$), when sea desertification occurred. No significant difference was observed between the autumn of 2018 and the winter of 2019 after sea desertification.

For both water depth and fish school depth, the observed values in the late autumn of 2018 were less than those in the winter of 2019 (Steel-Dwass test, $p < 0.01$) after the macroalgae disappeared. While the water depth of fish schools in the autumn of 2018 was less than that in the winter of 2018 ($p < 0.05$), no significant difference in water depth was observed between them. The closest distance to the macroalgal canopies was less than 262 m and had the same trend as the water depth. Significant differences in morphological parameters of fish schools were observed between winter and autumn 2018, autumn 2018 and winter 2019 (Steel-Dwass test, $p < 0.05$), except for the height between the winter of 2018 and 2019. No significant differences in morphological parameters were observed between autumn 2018 and winter 2019, after the disappearance of macroalgae.

The presence rate of macroalgal canopies and the number of fish schools based on water depth at 5 m intervals are shown in the upper part of Fig. 7. The presence rate of macroalgae decreased with increasing water depth in all surveys. The number of fish schools was highest in the 15-20 m water depth range in winter 2018, and in the 25-30 m water depth range in 2019. The number of fish schools decreased in all water depth ranges after the macroalgae disappeared in winter. More than 90% of the fish schools detected in late autumn were distributed in water depths less than 20 m, and they tend to be distributed in shallower coastal waters in late autumn than in winter, as described above. The mean Sv of fish schools at 5 m water depth intervals are shown in the middle part of Fig. 7. The mean Sv of fish schools was the highest for water depth intervals of 5-10 m, and it was similar for water depth intervals of > 10 m in the winter of 2018. The mean Sv was similar for water depth intervals of < 15 m, and it was higher for water depth intervals of > 15 m in autumn 2018. The Sv value was similar for water depth intervals of 5-25 m, and it was higher than the left range in winter 2019. The perimeter of fish schools at 5 m water depth intervals is shown in the lower part of Fig. 7. The perimeter size of fish schools < 15 m was larger than > 15 m in the winter of 2018, which is a trend that is similar to the mean Sv. The perimeter size was the largest at 10-15 m water depth in the autumn of 2018 and the winter of 2019 after the disappearance of macroalgae.

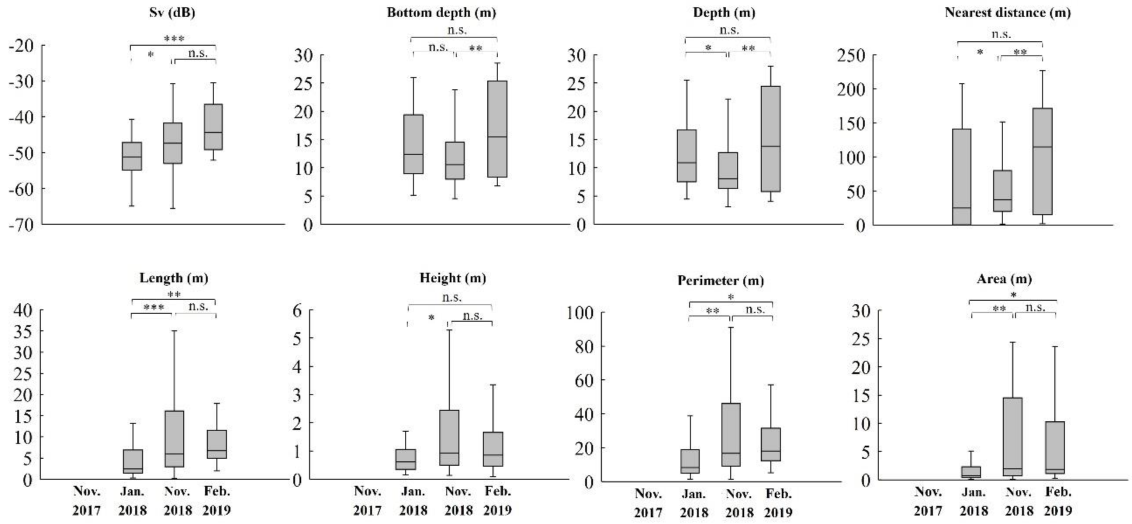

Fig. 6. Box plots of various acoustic characteristics of fish schools. Fifty percent of the samples (box) and the first and third quartiles (bars) are shown. The horizontal line in the box indicates the median value. The horizontal axis shows the survey times and the vertical axis show Sv, bottom depth, fish school depth, closest distance to the macroalgae, length, thickness, perimeter, and area of fish schools respectively. * (asterisk) indicates a statistically significant difference; n.s. indicates a statistically insignificant difference.

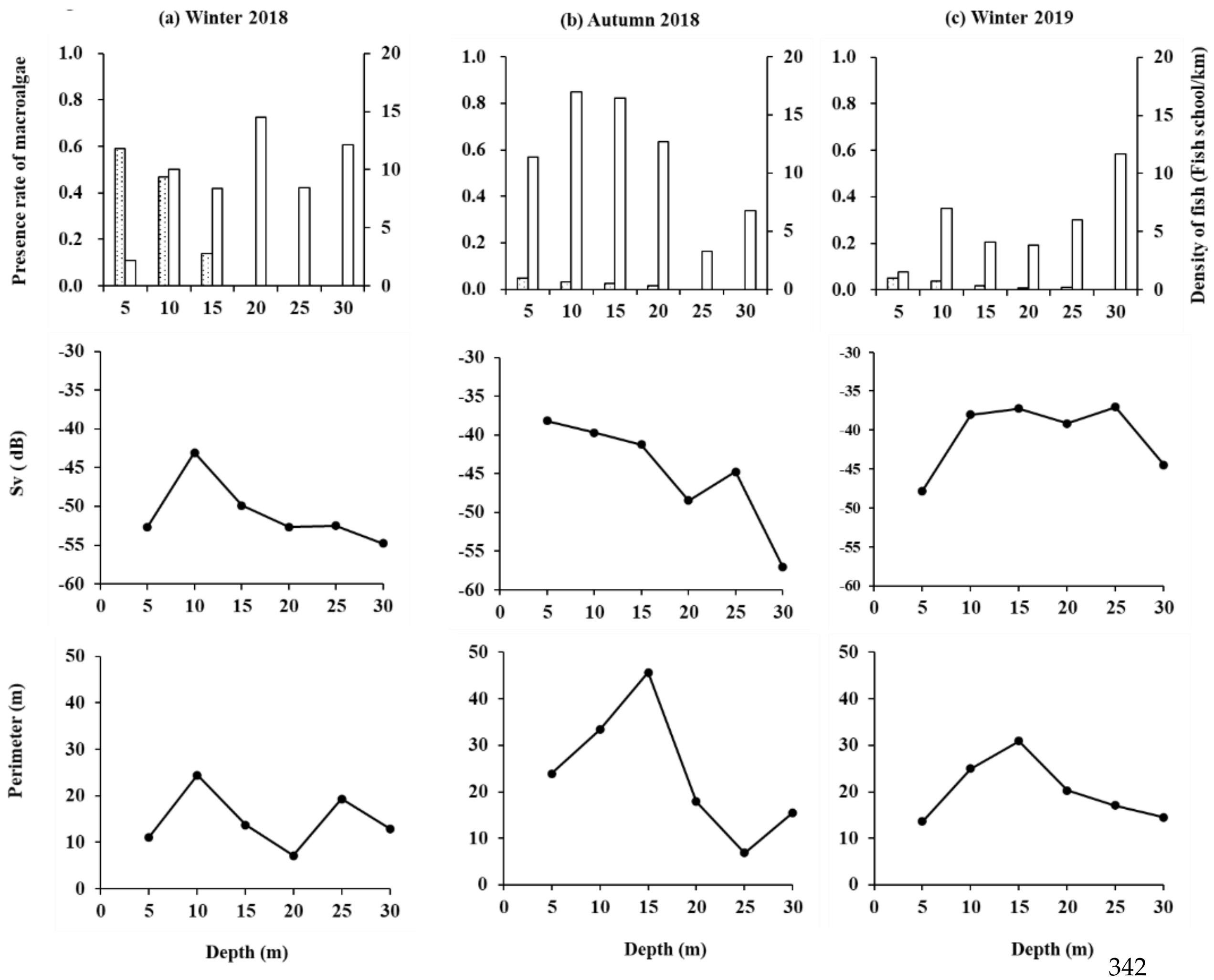

Fig. 7. Macroalgae and fish schools based on a water depth of 5 m intervals observed during the surveys in (a) winter 2018, (b) autumn 2018, and (c) winter 2019. Presence rate of macroalgae (dotted bars) and number of fish schools (empty bars) in the top panels, Sv in the middle panels, and perimeter in the bottom panels. The horizontal axis indicates water depth, the left vertical axis indicates the presence rate of macroalgae, and the right vertical axis indicates the density of fish schools in the top panels.

Water temperature

The mean water temperature recorded daily during the study period, as shown in Fig. 8 (a), was 19.5 and 19.9 °C during the autumn surveys in 2017 and 2018, respectively, while it was 14.1 and 14.8 °C during the winter surveys in 2018 and 2019, respectively. The highest mean water temperature recorded on a daily basis was 26.9 °C, and the highest temperature recorded on a 30-minute basis was 27.9 °C. The annual mean SST anomaly with respect to the mean temperature from 1982 to 2020 is shown in Fig. 8 (b); the mean sea surface temperature in 2017 was higher than that in 2018; the highest temperature was observed in 1998, and since then, generally high temperatures have been observed frequently.

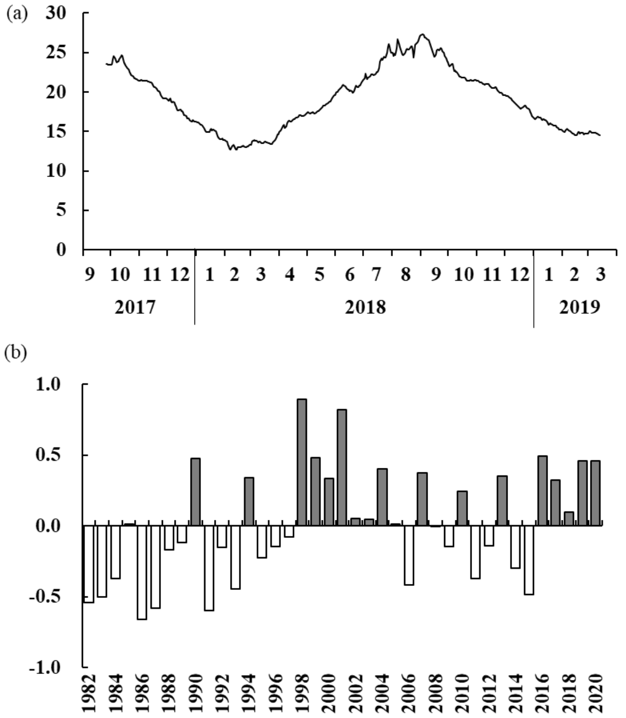

Fig. 8. (a) Mean daily water temperature from September 2017 to March 2019. Horizontal axis indicates the study period (year and month), vertical axis indicates the temperature. (b) Annual mean sea surface temperature anomaly value with respect to the mean temperature from 1982 to 2020 (original data are cited from Fukuoka Regional Headquarters, Japan Meteorological Agency, 2022). The gray bars above the horizontal axis indicate the water temperature higher than the mean value, and the white bars indicate the temperature lower than the mean value. The vertical and horizontal axes indicate the deviation in temperature and years, respectively.

Discussion

The mean height and presence rate of macroalgae observed using the acoustic method along the visual transect line were similar to those obtained by visual observation. This simple method of extracting the height of macroalgae using the acoustic method showed the changing trend of large macroalgae over the study area. The presence rate was approximately 100% and the height of macroalgae increased along the visual observation transect lines from late autumn 2017 to winter 2018. The main species observed were *S. macrocarpum* and *Ecklonia* spp. They are reported to be perennial species that grow in the winter around the study area (Murase, 2001; Yatsuya et al., 2014b); therefore, the presence rates were similar, and the height was higher in January 2018 than that in November 2017, reflecting their life cycle under the suitable conditions. In contrast, only a few stems of macroalgae were visually observed in the late autumn of 2018, indicating excessive natural degradation. The highest temperature recorded by the data logger near the survey area in 2018 was 27.9 °C, which was lower than the growth limiting temperature of *Ecklonia* spp. and *S. macrocarpum* (28 °C and 30 °C, respectively; Murase, 2001 and 2010). In the summer 2013, there were 20 days with water temperatures above 28 °C, and the average temperature was about 2 °C higher than that recorded from 2006 to 2012. Therefore, it was speculated that the higher temperature was the main reason for the decline of macroalgae near the study area around Iki Island in summer 2013, as reported by Yatsuya et al., (2014a). However, since the highest temperature in 2018 was similar to the recorded mean temperature, i.e., < 28 °C, which was also lower than several extreme marine heat incidents events that occurred in the years since1998, we consider that the water temperature was not the direct reason for the sudden decline of the macroalgae.

Fish bite marks were observed on macroalgae during visual observations in autumn 2018. *Kyphosus* spp., *Siganus* spp. and *Calotomus japonicus* (Valenciennes, 1840) have been reported as the main species responsible for the overgrazing of macroalgae in Japan (Vergés et. al., 2014). Among them, the herbivorous fish *S. fuscescens*, which feeds on macroalgae, was observed during our surveys. *K. bigibbus* was observed in some fishing ports of Iki Island, and seasonal variations in its school were revealed (Kadota et al., 2017a), they may migrate in some seasons. Excessive grazing pressure from fish has also been suggested as a cause of macroalgal decline in coastal waters in near the study area in the late autumn of 2013, when marine heat occurred in summer and water temperature decreased to a suitable level for macroalgal recovery in autumn (Yatsuya et al., 2014a; Kiyomoto et al., 2021). The hypothesis that macroalgae would subsequently disappear even if temperatures remained suitable for macroalgal growth throughout the year was confirmed by their disappearance before autumn 2018. Herbivorous fishes may have migrated to this area for grazing as the macroalgae declined in other coastal waters surrounding the island. Further studies on the migration of herbivorous fishes and the clarification of the population distribution, with the knowledge of the surrounding environment are also needed, especially since the water temperature of Japanese coastal waters has increased by about 1.19 °C over the past 100 years with the annual fluctuations (JMA, 2022).

Regarding the distribution characteristics of fish schools over the area, although detected numbers of fishes presented within the macroalgal canopies may have been underestimated by the acoustic method, more fish schools were detected in the presence of macroalgae than in their absence. Therefore, we considered that the total number of fish schools decreased with the disappearance of macroalgae. This observation was similar to the results of visual observations, which suggested that the number of fish was higher in macroalgal canopies than in a barren area in the northern coastal waters of Japan (Nakamura, 2018; Kadota et al., 2017b). The main observed species that declined after macroalgae disappeared over the year were *G. punctata*, *Prionurus scalprum* Valenciennes, 1835, and *Thalassoma cupido* (Temminck & Schlegel, 1845) (Nakamura, 2018); *G. punctata* was observed during visual observation surveys, and all three species were observed and reported in Iki coastal waters (Dotsu, 1977). Macroalgae were important for some reef fishes in other temperate and tropical coastal waters (Levin & Hay, 1996; Fulton et al., 2019; Hinz et al., 2019). Therefore, we consider that fish schools formed by certain fishes around macroalgal canopies decreased soon after macroalgae declined during winter in this coastal water. In contrast, lower mean Sv values and smaller fish school sizes were observed in the presence of macroalgae compared to the absence of macroalgae. Mean Sv value could reflects fish biomass (Simmonds & MacLennan, 2005), so we considered that the proportion of fish schools with low biomass decreased. Macroalgal canopies are more important for juvenile fishes in some coastal waters (Cheminée et al., 2017; Hinz et al., 2019); therefore, more fish schools with low biomass formed by juvenile fishes with small size were likely detected by the echosounder near macroalgal canopies. We considered that juvenile fishes forming small schools had probably moved to other areas due to the loss of feeding and hiding places. The proportion of fish species probably changed after the disappearance of the macroalgae. The small size and low Sv value of fish schools detected by the echosounder could indicate distribution patterns in a larger area of coastal desertification.

The number of fish schools observed in the late autumn was higher than that in the following winter, regardless of the presence or absence of macroalgae along the visual and acoustic observation line. The water temperature near the survey area was approximately 20 °C in the late autumn of 2017 and 2018, and

14 °C in the winter of 2018 and 2019, which is consistent with previous studies: more fishes were observed in the late autumn than in the winter in other temperate coastal waters (Hagan and Able, 2003; Masuda, 2008), and an increase in water temperature was considered a reason for the higher number of fish schools in the autumn than in the winter. While no significant difference in Sv and size was found between the autumn of 2018 and the winter of 2019 after macroalgae disappeared, some schools with larger sizes and biomass compared to macroalgae were probably presented throughout the year. *S. fuscescens* was observed by diving in the shallow waters in autumn 2018, and *S. fuscescens* has been reported not to migrate from the coastal waters of Nomozaki, Nagasaki (Yamaguchi et al., 2006), which is near the study area; therefore, some herbivorous fishes with higher biomass were probably resident in the barren area during the winter season. Similar patterns of fish density across independent sampling units using acoustic and diving methods have been reported (Zenonea et al., 2017), and the acoustic method revealed a seasonal variation pattern in which macroalgae were irregularly present or absent in this study.

Fish schools were distributed in shallower water in autumn than in winter, and mean Sv was larger in shallower water, indicating that more fish schools with higher biomass were distributed in shallower water in autumn. *S. fuscescens* and *G. punctata* schools were observed by diving in the shallow water in autumn 2018. *S. fuscescens* tended to move to shallower water more frequently when the water temperature was above 20 °C, as revealed by a biotelemetry method off the nearby coastal waters of Nagasaki (Yamaguchi et al., 2006), and *G. punctata* at about 17 °C in southern Japan (Saburomaru et al. 1984). More fishes tend to move to shallow waters in the autumn than in the winter as the higher temperature in the survey area. *Siganus* spp. has been reported as the species that overgraze macroalgae in Japan (Vergés et al., 2014), and the mean Sv value may could also represent the density of macroalgae-feeding fish schools around the macroalgal canopies combined with the direct observation, the further quantitative estimation is expected based on the target strength by species.

The number of fish schools decreased in all water depth ranges after the disappearance of macroalgae, we considered fish schools in deeper waters in addition to shallower waters where macroalgae growth also benefits from macroalgal canopies. As some fish species including macroalga-feeding ones tend to be distributed in deeper water during winter as discussed above; thus, the decline in macroalgae is likely to have affected fish schools in deeper waters. In addition, several studies have investigated the influence ray of artificial reefs, the influence ray of a reef on fishes can be 300 m or more (Soldal et al., 2002; Kang et al., 2011), which is larger than the value of the largest nearest distance (262 m) in this study. Further studies of the influence ray of macroalgae over a larger area and a wider range of water depths are expected. The Sv values and perimeter of fish schools at 5-10 m water depth were the largest in winter 2018, larger values < 15 m in autumn 2018, suggesting that the biomass of each school was the largest in this range, and this water depth range has the potential for the removal of macroalgae-feeding fishes, including commercially important fish catches combined with species discrimination. Unfortunately, the acoustic data below 2.5 m water depth were limited, and the information on very shallow water was insufficient, it could only represent results deeper than 2.5 m. Further studies on fishes distributed shallower than 2.5 m water depth range are expected.

In conclusion, macroalgae were observed in the study area until the spring of 2018, while they disappeared before the autumn, even the water temperature was more suitable for macroalgal growth than several extreme marine heat events that occurred in previous years when they were in growth. This was considered as attributed to the excessive grazing by herbivorous fishes following the disappearance of macroalgal canopies in other nearby coastal areas. The fish schools observed by diving in shallow water and the acoustic characteristics of fish schools over the study area changed after the disappearance of the macroalgae; therefore, the distribution patterns and even the species proportions surrounding the macroalgal canopies, including deeper waters, could be altered with long-term ocean warming, with the shift proceeding to a distant area, although annual temperature fluctuations were observed. In addition, we obtained the distribution and school characteristics along with the various water depths, which could lead to more effective conservation plans for coastal macroalgal ecosystems. Further studies on changes in the distribution of certain species are also expected for the assessment and the recovery of coastal macroalgal canopies. In recent years, certain subtropical macroalgal species have been observed only in the spring season, in contrast to other native species have been observed throughout the year in some temperate coastal waters due to ocean warming. Thus, assessing the changing patterns of fish schools by species, in relation to the distribution of various types of macroalgal canopies over larger study areas, is expected to improve the sustainability of the coastal resources and ecosystems with the ocean warming.

Author Contributions

Conceptualization, H.S.; methodology, H.S.; software, H.S.; validation, H.S. and S.K.; formal analysis, H.S.; investigation, H.S., S.K., T.K. M.N. and H.Y.; resources, H.S., S.K., T.K. and H.Y.; data curation, H.S.; writing—original draft preparation, H.S.; writing—review and editing, S.K., Y.K., T.K., K.M. and K.M.; visualization, H.S.; supervision, S.K., K.M. and K.M.; project administration, S.K., M.N and H.S.; funding acquisition, H.S. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement

Not applicable.

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Conflicts of Interest

Not applicable.

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