Spawning aggregation of blacktail snapper (Lutjanus fulvus) in an Okinawan coral reef: lunar-phase periodicity of aggregation formation, seasonal consistency in fish spatial distribution, and fish size and age frequency in the aggregation site

Spawning aggregation of blacktail snapper (*Lutjanus fulvus*) in an Okinawan coral reef: lunar-phase periodicity of aggregation formation, seasonal consistency in fish spatial distribution, and fish size and age frequency in the aggregation site

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Abstract Snappers (family Lutjanidae) are main fishery target species and some fish species in this family form spawning aggregations on coral reefs. This study aimed to clarify the ecological characteristics of fish aggregation of *Lutjanus fulvus*: 1) lunar-phase periodicity of aggregation formation, 2) seasonal consistency of the aggregation site, 3) differences in fish density between inside and outside the aggregation site, 4) gonad development of fish individuals inside the aggregation site, 5) frequency distribution of size and age of fish individuals at the aggregation site, and 6) to determine if the aggregation is a spawning aggregation. Time-lapse still photography and data plotted with a correlogram revealed that fish aggregations were observed only around the 20th day of the moon. Underwater observations revealed greater fish density (42 - 2042 individuals per 600 m × 5 m) between April and September. Plotting fine-scale fish spatial distributions revealed consistent spatial patterns from May to September. The fish density inside the aggregation site was about 7960.5-fold greater than that outside the aggregation site. Most females inside the aggregation site had hydrated eggs. The average fork length and age of fish individuals inside the aggregation site were 241.8 mm and 12.2 years for males and 247.8 mm and 13.4 years for females, respectively. This study revealed that the aggregation of *L. fulvus* on an Okinawan coral reef could be regarded as spawning aggregation. The results can provide insights into the precise setting position of marine protected area to effectively protect the spawning ground of *L. fulvus*.

Keywords Spawning aggregation • Snapper • *Lutjanus fulvus* • Marine protected area •

Okinawan coral reef

Statements and Declarations

Competing interests The author declares that there are no competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Introduction

Fish exhibit diverse reproductive behaviors in coral reefs (Thresher 1984) and some species form aggregations with greater densities during specific seasons and lunar phases at particular sites (Nemeth 2009). These are known as spawning aggregations (Sadovy de Mitcheson and Colin 2012). Spawning aggregations are defined as the gathering of conspecific individuals at specific sites during a specific period (Domeier 2012). Spawning aggregations have two types: resident and transient spawning aggregations (Domeier and Colin 1997; Claydon 2004). Resident spawning aggregations predominantly consist of smaller-sized species (e.g., parrotfishes, surgeonfishes and wrasses) that form daily aggregations with shorter migration distances (within a few kilometers) and shorter durations of the spawning event (several hours). By contrast, transient spawning aggregations consist of larger-sized species and some fishery target species (e.g., emperorfishes, groupers and snappers) that form monthly or annual aggregations with longer migration distances (several to several-hundreds of kilometers) and longer durations of the spawning event (several days to several weeks) (Nemeth 2009; Sadovy de Mitcheson and Colin 2012).

These fish species that form transient spawning aggregations are top predators, and control the population size of marine organisms at lower trophic levels (Graham et al. 2003). Considering that the patterns of transient spawning aggregation formation are spatially and temporally predictable, such spawning aggregations have a great possibility of over exploitation (Samoilys 1997; Rhodes and Tupper 2008; Sadovy de Mitcheson et al. 2008; Sadovy de Mitcheson and Erisman 2012). Thus, the spawning aggregations of these fishery target species should be protected (Beets and Friedlander 1999; Linderman et al. 2000; Sala et al. 2001; Nemeth 2005; Sadovy and Domeier 2005; Russell et al. 2012).

Snappers (family Lutjanidae) are primary fishery target species and are top predators on coral reefs (Allen 1985; Polovina and Ralston 1987; Nanami and Shimose 2013; Taylor et al. 2018). Some snapper species form transient spawning aggregations (Sadovy de Mitcheson and Colin 2012; Nanami 2023). In previous studies, ecological aspects of the spawning aggregations of snappers, such as temporal periodicity of spawning aggregation formation (Kadison et al. 2006; Biggs and Nemeth 2014, 2016; Cimino et al. 2018; Nanami, 2023), location of aggregation site (Claro and Lindeman 2003; Heyman and Kjerfve 2008; Malafaia et al. 2021), spawning migration movements (Farmer and Ault 2011; Feeley et al. 2018), and spawning behavior (Carter and Perrine 1994; Heyman et al. 2005; Sadovy de Mitcheson et al.; 2012, Sakaue et al. 2016), have been examined.

The blacktail snapper *Lutjanus fulvus* is a fishery target species on coral reefs (Akita et al. 2016) and a spawning aggregation of this species has been reported from Palau (Sadovy de Mitcheson et al. 2012). In the Okinawan region, the main spawning season of *L. fulvus* occurs between April and October in the Yaeyama Islands (Shimose and Nanami 2014). However, the spawning sites of *L. fulvus* have not yet been found there. Recently, a *L. fulvus* aggregation was found on an Okinawan coral reef (Fig. 1, Video S1) suggesting that this aggregation may be a transient spawning aggregation. If so, this fish aggregation should be appropriately protected because this species is a target species in commercial fisheries in Okinawa (Shimose and Nanami 2014). Thus, the precise ecological characteristics of the aggregation of this species should be identified so that effective, science-based management can occur.

This study aimed to examine the ecological characteristics of this *L. fulvus* aggregation. In particular, this study aimed to clarify: 1) lunar-phase periodicity of fish aggregation formation, 2) spatial consistency of the location of fish aggregation at the aggregation site, 3) difference in fish density between inside and outside the aggregation site, 4) gonad development of fish individuals inside the aggregation site, 5) size and age frequency distribution of fish at the aggregation site, as well as 6) to determine whether the aggregation of this species was spawning aggregation. This study is the first to examine the aggregation of this species on an Okinawan coral reef, thus providing a more comprehensive understanding of the spawning aggregation behavior of snappers.

Materials and Methods

Study site

This study was conducted at the Sekisei Lagoon in the Yaeyama Islands, Okinawa, Japan (Figs. 1a, 1b). An aggregation of *L. fulvus* was recently found in the study area (Fig. 1c). At present, the study site is not protected during the spawning periods of the species (Shimose and Nanami, 2014). Thus, the precise location is not shown because showing the precise location might cause over-exploitation of this aggregation.

Time-lapse still photography

To examine lunar-related periodicity in aggregation formation, stationary cameras (Pentax WG-1 and WG-10) in waterproof cases, set to record images during 1-h intervals, were deployed on the sea floor within the aggregation site.

In a preliminary survey, one camera was deployed within the aggregation site between August and September 2021 (August 9 - 16, August 24 - 30 and September 20 - 25) to roughly obtain the location of the fish aggregation and the lunar-phase periodicity of aggregation formation (Table S1). After the preliminary survey, one camera was deployed for 93 days (first survey, between June 23 and September 23, 2023; Table S2) and again for 73 days (second survey, between April 25 and July 6; Tables S3). The duration of the camera's battery was about 3 weeks. Thus, one camera was initially set to run for about 3 weeks and then replaced with another camera as the first camera's battery expired. This procedure was continued during the study period. After collecting the camera, the presence or absence of fish aggregation on still images was recorded in the laboratory. In this procedure, fish images were categorized into four types: (1) no individuals, (2) single individual, (3) multiple individuals (2 - 5 individuals) and (4) aggregation (≥ 6 individuals). A total of 24 still images were taken per day. These images recorded the presence of variable numbers of fish because of fish movement around the camera each day. Thus, the still image that showed the largest number of fish was used to indicate total abundance for a focal day.

A correlogram was applied to examine the statistical significance in the periodicity of fish aggregation formation. The first (93 days between June 23 and September 23, 2023) and the second (73 days between April 25 and July 6, 2024) surveys were analyzed separately. In the analysis, the aforementioned three types of fish images (no individuals, single individual, and multiple individuals) and another type of fish image (aggregation) were assigned 0 and 1, respectively. Then, a correlogram was produced using the R statistical computing package (function “acf”: R core team, 2023). The statistical significance of the auto-correlation coefficient was examined by using a 95% confidence interval (CI), which is calculated as follows:

$$95\%\ \mathrm{CI} = 1.96 / \sqrt{(T)}$$

where T is the number of observations.

Significance of the auto-correlation coefficient was determined by the equation:

$$|p_k| > 95\%\ \mathrm{CI} = 1.96 / \sqrt{(T)}$$

where p_k is the value of the auto-correlation coefficient at the kth time lag, and $|p_k|$ is the absolute value of p_k. If $|p_k|$ is greater than the 95% CI, then the auto-correlation at the kth time lag was significant. The T value was 93 and 73 for the first and second surveys, respectively. Thus, the 95% CI was calculated as $1.96 / \sqrt{(93)} = 0.203$ and $1.96 / \sqrt{(73)} = 0.23$ for the first and second surveys, respectively.

Monthly variations in the fish density at the aggregation site

Daytime underwater observations using SCUBA were conducted to clarify the monthly variation in the fish density at the aggregation site. As the main spawning season of the species was between April and October (Shimose and Nanami, 2014), a line transect (600 m × 5 m) was set to cover the main aggregation site between March 2022 (one month before the expected spawning period) and November 2022 (one month after the expected spawning period). Time-lapse camera photography revealed that the peak fish density was found around the 20th day of the moon (see Results). Thus, the observation days were adjusted to be carried out around the 20th day of the moon (Table S4).

The number of individuals on the 600 m × 5 m line transect was counted every 1 minute. During the observations, a portable GPS receiver (GARMIN GPSMAP 64csx) in a waterproof case was attached to a buoy, and the buoy was towed. In addition, a water-proof watch was carried to record the observation time. The time displayed on the watch was synchronized with the time on the GPS receiver. Thus, the course and distance of the tracks were obtained. The fish count data was one per minute at the end of the minute. The water depth range at which the underwater observations were conducted was approximately 10 - 15 m.

Spatial consistency of the location of fish aggregation

To examine the spatial consistency of location of fish aggregation, the 600 m × 5 m line transect was divided into 1-min sub-transects (average distance ± standard deviation = 21.5 ± 3.5m). After obtaining the number of fish individuals and the distance for the 1-min sub-transect, the number of individuals was converted to density (20 m × 5 m) for each 1-min sub-transect. The fish density on the 1-min sub-transect was individually plotted by a bubble plot along the entire line transect.

Monthly fish aggregations were observed between April and September (see Results). For each month, the fine-scale spatial variation in fish density was shown as frequency data (histogram). The probability densities of the histograms were analyzed with the R statistical computing package (function “density”: R core team, 2023). In addition, the Kolmogorov-Smirnov test was applied to test the significant difference in fine-scale spatial variation in fish density among the six months. For multiple comparisons among 15 pairs, the Bonferroni correction was applied (p = 0.05/15 = 0.0033).

Histological observation of ovarian development

The presence of females bearing mature, hydrated eggs while at the aggregation site provides evidence of spawning aggregation formation at that site (Domeier 2012; Sadovy de Mitcheson and Colin 2012). To examine the occurrence of female fish with matured eggs, individual fish were speared at the conclusion of daily observations. The fork length (FL), whole body weight and gonad weight were measured in the laboratory. The gonadosomatic index (GSI) was calculated as follows:

$$GSI = \text{gonad weight (g)} / [\text{whole body weight (g)} - \text{gonad weight (g)}] \times 100$$

For each individual, a small piece of gonad (about 1 cm length × 1 cm width × 1 cm height) was preserved in 20% buffered formalin over 48 h and then kept in 70% ethanol baths (50 ml per one sample). Embedded pieces of gonads were sectioned and stained with Mayer’s hematoxylin–eosin prior to histological observations. The developmental stages of the ovaries were observed under a microscope and categorized following Ohta and Ebisawa (2015) and Ohta et al. (2017). Oocytes showing the migration nuclear stage, pre-maturation stage, and maturation stage were defined as hydrated in accordance with the categorizations.

Fish density comparison between outside and inside the aggregation site

Spawning aggregation is defined as the fish aggregation with at least fourfold greater density at the aggregation site than that outside the aggregation site (Domeier 2012). To verify that the aggregation under study fitted this definition, the number of fish individuals was counted at 69 study sites outside the aggregation site between June and December 2016 (Fig. S1). A 20-min underwater survey with a portable GPS receiver was conducted at each site (for details of the method, see Nanami 2020). By using the 20-min fish count data and measured distance, fish density per 600 m × 5 m was estimated. The estimated fish densities among the 69 sites were averaged and regarded as the average fish density outside the aggregation site. Then, the fish density outside the aggregation site was compared with that inside aggregation site between April and September, during which fish aggregations were observed.

Fish length and age frequency distributions

Histograms of the FL frequency were plotted for each sampling month. To clarify the age frequency distribution of fish at the aggregation site, the ages of the fish sampled were examined by analysis of sagittal otoliths (for details of the method, see Nanami 2023). In short, one otolith was embedded in epoxy resin and transversely sectioned into 0.5-mm-thick sections. The sectioned otoliths on a glass slide were observed under a microscope with 4× magnification, and the number of opaque rings on each otolith was counted. The number of opaque rings can be considered as age (year) as Shimose and Nanami (2014) revealed that each opaque ring was formed annually.

The probability densities of the FL and age frequencies of males and females were analyzed with the R statistical package (function “density”: R core team, 2023). Significant differences in the FL and age between males and females were examined by using the Mann-Whitney U-test.

Results

Time-lapse still photography

The first survey (93-day observation) revealed that fish aggregations were found consecutively over a period of 4 or 5 days between the 17th and 23rd days of the moon (Fig 2a). The correlogram revealed significantly positive auto-correlation coefficients when time lags were 28 - 33 days and 60 - 62 days (Fig. 3a). The second survey (73-days observation) revealed that fish aggregations were found consecutively 6 days between the 16th and 22nd days of the moon (Fig 2b). The correlogram revealed significantly positive auto-correlation coefficients when time lags were 27 - 32 days and 58 - 59 days (Fig. 3b). Overall, the fish aggregations were found during several consecutive days between the 16th and 23rd days of the moon, and the fish aggregation formations were observed about every 30 days.

Seasonal variations in the number of individuals and reproductive activity

On the 600 m × 5 m transect, one individual was found in March, and 42 individuals was found in April. Over 1500 individuals were found between May and September when the water temperature exceeded 26°C (Fig. 4a). The number of individuals ranged from 1576 (July) to 2042 (August). One individual was found in October and November, although the water temperature exceeded 26°C in the two months.

The GSI values of females that were caught at the aggregation site ranged from 1.21 to 15.34 (average ± standard deviation = 5.31 ± 2.42: Fig. 4b). About 68.3% of individuals (28 out of 41) had hydrated stage oocytes (Fig. 4c, Table S5).

Fine-scale spatial variations in fish density at the aggregation site

Fine-scale spatial distributions revealed relatively consistent spatial patterns during the six months (April - September) (Fig. 5a). Although most cases showed that fish densities within the 20 m × 5 m area were generally less than 20 individuals, over 100 individuals (i.e., over one individual per 1 m × 1 m area) were found within some 20 m × 5 m areas from May to September (Fig. 5b). The Kolmogorov-Smirnov test with Bonferroni correction revealed no significant differences in the frequency distribution of fish density among the five months (May-September, $p > 0.05$ for all comparisons). By contrast, the frequency distribution of fish density in April was significantly smaller than the other five months ($p < 0.0033$ for all comparisons).

Fish density outside and inside the aggregation site

The fish density per 600 m × 5 m area outside the aggregation sites ranged from 0 to 3.81 individuals. The fish density inside the aggregation site was 221.1 to 10747.4-fold (average = 7960.5-fold) greater than that outside the aggregation site (Table 1).

Fork length and age of fish individuals inside aggregation site

The FL of most individuals ranged from 220.0 to 269.5 mm for both males and females (Figs. 6a, 6b). Although the average size of males (average FL ± standard deviation = 241.8 ± 13.1 mm) was slightly smaller than that of females (247.8 ± 13.7 mm), no significant difference in FL composition was found between males and females (Mann-Whitney U-test, $p > 0.05$).

Although the average age of males (average age ± standard deviation =12.2 ± 4.7 years) was slightly younger than females (13.4 ± 5.0 years) (Figs. 6c, 6d), no significant difference in age composition was found between males and females (Mann-Whitney U-test, $p > 0.05$).

Discussion

Verification of the spawning aggregation of *Lutjanus fulvus*

Although a spawning aggregation of *L. fulvus* has already been reported from Palau (Sadovy de Mitcheson et al. 2012; Cimino et al. 2018), a spawning aggregation of this species has not been reported from Okinawan coral reefs, Japan. Thus, this study was the first attempt to examine whether fish aggregations of the species in an Okinawan coral reef can be regarded as spawning aggregation. This study demonstrated that: (1) repeated aggregation formation is spatially and temporally predictable (particular site and days of the moon), (2) the fish density inside the aggregation site was over fourfold greater than that outside the aggregation site, and (3) most females inside the aggregation site had hydrated eggs, indicating that the aggregation formation is for reproduction. Thus, the aggregation of *L. fulvus* can be regarded as spawning aggregation based on the definition of Domeier (2012).

In Palau, Cimino et al. (2018) reported that the aggregation of *L. fulvus* at daytime may be pre-spawning aggregation, although the aggregation was formed for reproduction. Considering that the actual spawning behavior has not been observed yet in daytime observations, the aggregation site in this study site might also be the pre-spawning aggregation site. Another possibility is that spawning occurred at nighttime, since this study revealed the presence of hydrated eggs in females collected from the aggregation site.

Nevertheless, the location and timing the aggregation formation were spatially and temporally predictable, and a number of fish individuals gathered in the site. In particular, over 100 fish individuals per 20 × 5 m area (one individuals per 1 m × 1 m area) were observed at some places within the aggregation site. Thus, the aggregation site should be effectively protected to avoid overexploitation of this species.

Spawning season and spawning day

Based upon data from commercial catches, Shimose and Nanami (2014) estimated that the main spawning season of *L. fulvus* is between April and October with a peak between June and September. By contrast, this study revealed that the main aggregation of the species was observed between May and September, although a small-scale aggregation (42 individuals) was found in April. Only one individual was found in

October, which was consistent with the observations made in non-spawning months (March and November). Most females inside the aggregation site during April and September showed developed or matured oocytes (migration nuclear stage, pre-maturation stage and maturation stage). Therefore, it is suggested that the main spawning season at the aggregation site was between April and September.

Fish aggregations were only found on several consecutive days around the 20th day of the moon. In addition, Shimose and Nanami (2014) have reported that the "spawned phase" of the ovary, which had postovulatory follicles, was observed between 18th and 23rd days of the moon based upon their analysis of data from commercial catch samples. Thus, spawning likely occurs around the 20th day of the moon. By contrast, fish aggregations of the species were found during 1 day before and 4 days after the full moon in Palau (Cimino et al. 2018), which was several days earlier than that in Okinawa. This difference might be a geographical variation in reproductive activity between the two regions.

Water temperature is a primary factor influencing gonad development of marine fishes (Wang et al. 2010). This study revealed that the reproductive activity of *L. fulvus* likely occurs when the water temperature exceeded 26°C. In addition, the decline in temperature at the beginning of September might be a factor reducing ovarian development. This trend is consistent with the cubera snapper (*Lutjanus cyanopterus*) in the Caribbean (Heyman et al. 2005; Motta et al. 2022), as well as the checkered snapper (*L. decussatus*) and the blackspot snapper (*L. fulviflamma*) in Okinawa (Nanami 2023), demonstrating that increased water temperature is a factor controlling the spawning aggregation formation of lutjanid species in coral reefs.

Size and age frequency of fish individuals at the aggregation site

The main FL range of commercial catch individuals was 210-280 mm and 220-290 mm for males and females, respectively (Shimose and Nanami 2014), whereas that of individuals at the aggregation site was 220.0-259.5 mm and 220.0-279.5 mm for males and females, respectively. A similar trend was also found for age frequency. The maximum age of commercial catch individuals was respectively 29 and 34 for males and females, respectively (Shimose and Nanami 2014), whereas that of individuals at the aggregation site was 23 and 24 for male and female, respectively. These results indicate that most individuals forming the spawning aggregation were slightly smaller and younger.

Conclusions

This study revealed that the aggregation of *L. fulvus* on an Okinawan coral reef could be regarded as spawning aggregation. This finding can be explained by the fact that fish aggregation formation with greater density repeatedly occurred, and such formation was spatially and temporally predictable. In addition, the presence of hydrated eggs in females within the aggregation site was confirmed. Although a spawning aggregation of *L. fulvus* has already been reported in Palau, almost no ecological information about a spawning aggregation of this species has been reported in an Okinawan coral reef. Thus, this study is the first to document the existence of a spawning aggregation of *L. fulvus* within the Okinawan region. As this species is a fishery target species in the study region, the results of this study can be applied to determine the precise location for the creation of a marine protected area for the effective protection of the spawning aggregation site and the species that uses it.

Author contribution Atsushi Nanami conceptualized and designed the study and conducted all formal analysis, data curation and writing.

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author upon reasonable request.

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Ethical approval This study was conducted by field observations. Fish were sampled by spearfishing and euthanized immediately to minimize suffering. The Okinawa Prefectural Government fisheries coordination regulation No. 37 approved the sampling procedure, which permits capture the marine fishes on Okinawan coral reefs for scientific purposes.

Field studies All data was obtained only by field observations, which do not require a field permit in Okinawa.

Conflict of interest The author declares no competing interests.

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Figure captions

Fig. 1. Location of the Yaeyama Islands (a), study site (b), and fish aggregations of *Lutjanus fulvus* (c). Aerial photograph in (b) was provided by the International Coral Reef Research and Monitoring Center.

Fig. 2. Daily plotting of the presence/absence fish aggregations recorded by a stationary time-lapse camera during the first survey (a) and second survey (b). Fish images were categorized into four types: (1) no individuals, (2) single individual, (3) multiple individuals (2 - 5 individuals) and (4) aggregation (≥ 6 individuals). Lunar phases are abbreviated as follows: FM, full-moon; LQM, last-quarter moon; NM, new moon; FQM, first-quarter moon. The numbers above the sky-blue dots represent the day of the moon.

Fig. 3. Correlogram showing the auto-correlation coefficient with time lag, which examines the periodicity in fish aggregation formation at a particular time lag for the first survey (a) and second survey (b). Blue horizontal lines represent 95% confidence interval of the auto-correlation coefficient.

Fig. 4. Monthly changes in the number of fish individuals on the 600 m × 5 m line transect (a), gonadosomatic index of female inside the aggregation site (b), and oocyte developmental stage for *Lutjanus fulvus* (c). In (a), daily changes in with seawater temperature were also plotted. In (b), horizontal black bars represent the average values, and the numbers beside the sky-blue dots represent the maximum and minimum values

of gonadosomatic index. In (c), the oocyte developmental stage was abbreviated as follows: TYS, tertiary yolk stage; MN, migration nuclear stage; PMA, pre-maturation stage; MA, maturation. Seawater temperature data in (a) were provided by the Japan Meteorological Agency (https://www/data.jma.go.jp/kaiyou/data/db/kaiyo/series/ emgam/txt/area708.txt).

Fig. 5. Spatial distribution of *Lutjanus fulvus* on the 600 m × 5 m line transect in the aggregation site (a) and frequency of the fine-scale fish density (number of individuals in the 20 m × 5 m area) (b). The 600 m × 5 m line transect was divided into 1-min sub-transects. In (a), fish data are shown as bubble plots and each bubble represents the fine-scale fish density (number of individuals in the 20 m × 5 m area) on each 1-min sub-transect. Cross marks represent the absence of fish individuals in the sub-transect. Red stars represent the deployment location of the stationary camera. In (b), dotted lines represent the probability density function.

Fig. 6. Fork length and age frequency of *Lutjanus fulvus* individuals that were captured at the aggregation site. Dotted lines represent the probability density function. *: among the 32 individuals in (a), the age of one individual could not be measured because of the difficulty in counting the number of opaque rings in the otolith. Thus, the sample size was 31 in (c). **: among the 41 individuals in (b), the age of two individuals could not be measured because of the difficulty in counting the number of opaque rings on otolith. Thus, the sample size was 39 in (d).