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Diel variation in home range size and precise returning ability after spawning migration of coral reef grouper *Epinephelus ongus*: implications for effective marine protected area design

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ABSTRACT: Marine protected areas (MPAs) are considered an effective tool for protecting marine organisms. The precise estimation of home range size, as well as diel differences in home ranges, are essential when considering the appropriate size of an MPA. In addition, behavioral characteristics of spawning migration should also be considered for species that form spawning aggregations. Our aim was to clarify the diel variation in home range size and the degree of precision of the returning ability of white-streaked grouper *Epinephelus onus* by acoustic telemetry. Seventeen individuals were studied, and nighttime home range sizes that were calculated by 50 and 95% kernel utilization distributions were 5.9-fold and 5.5-fold greater, respectively, than the daytime home ranges. The average inter-center distance between home ranges during the 2 time periods ranged from 3.0 to 67.9 m (22.5 m on average), suggesting that the day–night home range shift within the home ground varied individually. Returning ability for 10 individuals that showed clear spawning migration behavior was also analyzed, and the average inter-center distance between home ranges during the periods before and after spawning was 8.1 m. Eight out of these 10 individuals showed precise returning after the spawning migration to the patchy coral substrates that were used before the spawning migration. The present study suggests that appropriate setting position of the home ground can establish long-term protection of the species due to their precise returning ability after the spawning migration.

KEY WORDS: Marine protected area · Home range size · Returning ability · Spawning migration · White-streaked grouper

INTRODUCTION

Marine protected areas (MPAs) are considered an effective tool for the protection of marine organisms. For coral reef fishes, Green et al. (2015) suggested that a precise estimation of the home range size is essential for determining appropriate MPA size. An inappropriate MPA size that was smaller than the

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home range size of the focal species would enhance the risk of vulnerability outside the MPA boundary (Chateau & Wantiez 2008, Di Franco et al. 2018). In addition, since many coastal fishes show species-specific or individual-specific diel differences in activity and space use (e.g. Holland et al. 1993, 1996, Di Lorenzo et al. 2016, Honda et al. 2016), the extent of diel differences in home range size should be considered when evaluating effective MPA size. If diel differences in the home range size for focal species are found, the size of the MPA should be determined by larger home range size among the diel time periods. Furthermore, if the focal species show a day–night habitat shift, both daytime and nighttime home ranges should be incorporated into the MPA. Many studies have estimated the home range size of coastal fishes by direct underwater observations (e.g. Nanami & Yamada 2008, Nanami 2015) and acoustic telemetry (e.g. Afonso et al. 2008, Welsh & Bellwood 2012, Taylor & Mills 2013, Currey et al. 2015, Di Lorenzo et al. 2016, Matley et al. 2016, Davis et al. 2017, Di Franco et al. 2018). Since species diversity of coral reef fishes is remarkably high, diel activity patterns among coral reef fishes are also very diverse (Smith & Tyler 1972, Krumme 2009). However, the extent of diel differences in home range size for numerous coral reef fishes remains unknown.

Di Lorenzo et al. (2014) and Green et al. (2015) have also shown the importance of considering the behavioral characteristics of spawning migrations of coral reef fishes and coastal fishes for establishing MPAs. Some coral reef fish species migrate long distances to spawning grounds (e.g. Nemeth et al. 2007, Rhodes et al. 2012, Nanami et al. 2015). However, the returning ability of coral reef fishes in relation to the spawning migration has not been sufficiently studied. If fish do not return to their initial home ground after the spawning migration, they would potentially have multiple separate home ranges throughout a lifetime. As a result, critical determination of an appropriate location for an MPA at the home ground would not be possible.

Grouper (family Epinephelidae) are important fisheries targets in tropical and sub-tropical waters worldwide (Levin & Grimes 2002, Sadovy de Mitcheson et al. 2008, 2013). Some species of grouper show high site fidelity to their home ground (Zeller 1997, Zeller & Russ 1998, Lembo et al. 2002, Teesdale et al. 2015). Furthermore, some species of groupers show spawning migration behavior from inshore reefs to the coral reef edge, and form large aggregations at particular spawning grounds during the spawning season (Domeier 2012). Based on these ecological aspects, estimation of home range size for the home ground during non-spawning periods, as well as estimation of the precision of the returning ability, should be clarified for effective management of groupers by MPA.

Some previous studies have shown the returning ability of groupers at a landscape-level (i.e. at a scale of several hundreds of meters; Kaunda-Arara & Rose 2004, Rhodes et al. 2012). However, few studies have clarified the precise returning ability (i.e. within several tens of meters) of groupers in coral reefs. Although several previous studies have shown a fine-scale returning or homing ability of marine fishes using artificial displacement experiments (e.g. Lembo et al. 1999, Mitamura et al. 2002, 2005, 2009, Kaunda-Arara & Rose 2004), studies of the fine-scale homing ability after the spawning migration in natural conditions have not been carried out.

White-streaked grouper *Epinephelus ongus* is one of the important fisheries targets around the Okinawan region (Ohta & Ebisawa 2016) and is known to form spawning aggregations in this region (Kawabata et al. 2015, Ohta & Ebisawa 2015, 2017, Nanami et al. 2017). These spawning aggregations are found in April and/or May. Maximum age is 20 yr and females begin maturing at age 4 (Ohta & Ebisawa 2015, 2016). An MPA has been established at the spawning ground in order to protect the spawning aggregation of *E. ongus* (Nanami et al. 2014, 2017). However, although the species shows high site fidelity to their home ground during the non-spawning period (Nanami et al. 2014), neither their home range size nor the diel differences in home range size have been clarified. Furthermore, although Nanami et al. (2014) observed *E. ongus* returning to their home ground after the spawning migration, the extent of the differences between the locations of the home range before and after the spawning migration has not yet been determined. Since the annual total catch of *E. ongus* has been declining and *E. ongus* are primarily targeted in their home ground (Ohta & Ebisawa 2017), the establishment of an appropriate MPA at their home ground would improve their protection. Thus, clarifying the home range size as well as the degree of precision of their returning ability would be useful.

The purpose of the present study is to ascertain the home range size and the degree of precision of the returning ability of *E. ongus* in order to determine the appropriate size of an MPA for *E. ongus* during the non-spawning period. Specifically, the aims were to clarify (1) home range size at the home ground during the non-spawning period; (2) diel differences in home range size at the home ground; and (3) whether *E.*

ongus individuals can return to their initial home ranges after the spawning migration. For this, the precise locations of tagged fishes were detected throughout the study period using acoustic telemetry.

MATERIALS AND METHODS

Study site and arrangement of acoustic receivers

This study was conducted from March to June 2014 at Sekisei Lagoon in the Yaeyama Islands, Okinawa, in the southern part of the East China Sea (Fig. 1). The study area was covered by a sandy sea bottom with patchily distributed coral colonies (mainly massive *Porites*, branching *Porites* and dead massive corals). The sandy sea bottom was almost flat (water depth was 8 m over the whole study area) and no remarkable topographic features (except for the patchy habitats) were found in the study area.

Nanami et al. (2014) and Kawabata et al. (2015) have shown that an area approximately 6 km away from the spawning ground is an appropriate study area for monitoring the home ground in relation to the site fidelity and spawning migration of *Epinephelus ongus*. Thus, in order to estimate home range size at the home ground, 19 automated monitoring acoustic receivers (VR2W, VEMCO) were deployed at the home ground (Fig. 1d). Testing has shown that the detection range for a signal is approximately 50 m (Nanami et al. 2014). Therefore, receivers were placed approximately 80 m apart, resulting in a 400 × 400 m detection area. All receivers were attached with synchronization tags (V16-6H coded transmitter, VEMCO; average signal intervals = 600 s) for the VEMCO Positioning System (VPS; https://vemco.com/products/vps/). The distance between receivers and the seafloor was 1 m.

Each receiver detects the signals from acoustic tags that are attached to fishes. The VPS positioning algorithm is based on the 3-receiver time-difference of arrival from the tags (Espinoza et al. 2011). The precision and accuracy is expected to increase with the number of deployed receivers. Under this situation, the exact time should be collected by each receiver. The synchronized tags are indispensable for time

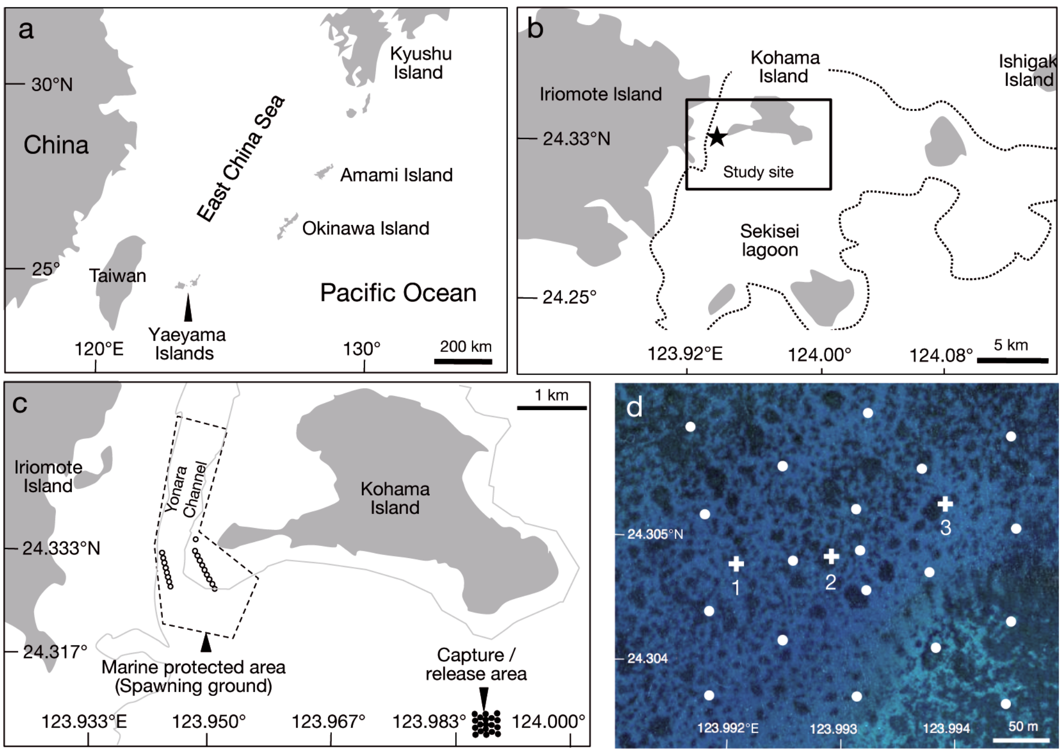

Fig. 1. Study site showing (a) the Yaeyama Islands; (b) Sekisei Lagoon (enclosed by a dotted line) and the Yonara Channel (★), which is the main spawning ground of *Epinephelus ongus* in the Yaeyama Islands (Nanami et al. 2017); (c) the positions of the 19 receivers (●) deployed in the capture/release area and 18 receivers (○) deployed in the spawning ground (the marine protected area in the spawning ground during the spawning period is enclosed by a dashed line); and (d) the detailed positions of the 19 receivers (○) and 3 reference tags (✚) deployed in the capture/release area (*E. ongus* home ground). The dark and light areas in the aerial photograph show hard substrates (coral colonies and dead corals) and sandy sea bottom, respectively. The aerial photograph in (d) was provided by the International Coral Reef Research and Monitoring Center

synchronization among multiple receivers (Espinoza et al. 2011, VEMCO 2013).

The monitoring duration was 107 d (between 5 March and 20 June 2014) and the spawning migration of *E. ongus* was observed around the last quarter of the moon in May 2014 (the date of the last quarter moon was 21 May 2014; Nanami et al. 2017).

Fish tagging

Nine individuals were captured by hook-and-line at coral colonies (branching *Porites* massive *Porites* and dead massive corals) during the daytime (09:00 to 17:00 h) within the 19 receiver arrays using SCUBA equipment in accordance with Nanami et al. (2014). To minimize the effects of pressure change, all captured individuals were taken slowly to the surface using SCUBA equipment, and no adverse effects were observed in any of the captured individuals. The total length of the captured individuals was measured to a 1 mm level. An acoustic coded transmitter (V9-1H, VEMCO; diameter 9 mm × length 24 mm, weight in air = 2.2 g, average signal interval = 300 s, expected battery life = ca. 180 d) was surgically implanted into the abdominal cavity of each fish under anesthesia using 0.1% 2-phenoxyethanol (see Kawabata et al. 2008 for details of the surgical procedure). The ratio between transmitter and fish weight ranged from 0.47 to 0.93%. All tagged individuals were promptly released back to the site of their capture at the respective coral colony.

In addition, 8 individuals that had been tagged and released during previous studies (release dates were April 2012 and April 2013, when 33 and 11 individuals were tagged and released, respectively; see Nanami et al. 2014, Kawabata et al. 2015) were used since these individuals were found within the monitoring site and signals from the transmitters could be detected. Acoustic coded transmitters (V9-2L and V9-2H, VEMCO; diameter 9 mm × length 21 mm, weight in air = 2.9 g, average signal intervals = 240 or 300 s, expected battery life = 934 or 450 d) were tagged for the 8 individuals (Nanami et al. 2014, Kawabata et al. 2015). A preliminary experiment using dummy transmitters showed no effects of the transmitter implantations on survival, growth, and spawning (Nanami et al. 2014). Total length for the 8 individuals was estimated by using the duration between release date and first date of the monitoring for the present study (335 d for 2 individuals, 337 d for 5 individuals and 694 d for 1 individual) and the growth equation determined for specimens in the Yaeyama Islands (Ohta & Ebisawa 2016). Sex could not be identified for these individuals. In total, 17 individuals were used for the present study (Table 1). Animal care and experimental procedures were performed in accordance with the guidelines for animal experimentation of Nagasaki University.

Accuracy and precision of the VPS location detection at the home ground

In order to estimate the accuracy and precision of the VPS location detection at the study site, 3 reference tags (V9-1H, VEMCO) were placed at 3 separate sites (Fig. 1d). Accuracy was defined as the difference in distance between the actual setting position of the reference tag and averaged detected position of the reference tag by VPS. Precision was defined as the standard error of the detected position. Thus, smaller values represent a greater degree of accuracy and precision.

Values of accuracy and precision were obtained for 4 time zones (dawn, daytime, dusk, and nighttime: for definitions, see 'Definition of daytime, nighttime, dawn, and dusk'). The precision and accuracy obtained by the 3 reference tags were averaged.

Home range size estimation

In the present study, home range was defined as the area including locations of the fish during the non-spawning period at their home ground. This includes both the resting site and foraging area. Since *E. ongus* are mainly commercially caught by spear during both the daytime and nighttime in the non-spawning season, the home ranges during both the daytime and nighttime should be included for precise establishment of an MPA to protect the species. VPS detections obtained within 24 h after release were excluded from the analysis in order to remove possible effects of fish tagging. Home range size was estimated using the dataset that was obtained between 6 March (24 h after fish tagging) and 20 June 2014. The positions that were estimated by VPS detections were used for the analysis.

Home range size was estimated for each individual by kernel utilization distributions (KUDs) using the kernelUD function of the adehabitatHR package in R (Calenge 2015, R Core Team 2017). The core home range (50% KUDs) and overall home range (95% KUDs) were estimated. During the estimation procedure, the grid size was manually set as 1000 × 1000 in the adehabitatHR package in accordance with Taylor

Table 1. Summary of 17 tagged *Epinephelus ongus* individuals in the present study. X: individuals that showed sufficient detection after the spawning migration (over 20 detections). These individuals were also confirmed to have undertaken a spawning migration to the spawning ground (Yonara Channel, Fig. 1, Fig. S1 in Supplement 1). Dates are given as dd.mm.yy. All detections performed with VEMCO Positioning System (VPS)

ID	Total length (mm)	Total weight (g)	Initial release date	Start date of VPS detection	Departure date to spawning ground	Returning date to home ground	End date of VPS detection	VPS monitoring duration (d)	Detections for home range estimation (05.03.–20.06.14)	Detections before spawning (22.04.–20.05.14)	Detections at spawning ground	Detections after spawning (22.05.–20.06.14)	Analysis of returning ability
1	278	338	05.03.14	06.03.14	13.05.14	25.05.14	08.05.14[e]	63	2158	559	1	0[e]	
2	261	252	05.03.14	06.03.14	19.05.14	26.05.14	19.06.14	105	1708	581	3	119	X
3	290	354	05.03.14	06.03.14	09.05.14	–	08.05.14	63	2135	859	276	0	
4	293	376	05.03.14	06.03.14	10.05.14	25.05.14	18.06.14	104	3506	1577	1058	224	X
5	302	404	05.03.14	06.03.14	09.05.14	24.05.14	12.06.14	98	2238	1251	1578	90	X
6	279	328	05.03.14	06.03.14	10.05.14	27.05.14	07.06.14	93	1149	252	0	3	
7	245	236	05.03.14	06.03.14	16.05.14	30.05.14	11.05.14[e]	66	401	26	155	0[e]	
8	272	276	05.03.14	06.03.14	16.05.14	24.05.14	08.06.14	94	1384	219	34	34	X
9	310	464	05.03.14	06.03.14	12.05.14	28.05.14	20.06.14	106	3407	1309	7	360	X
10[a]	276[c]	391[d]	04.04.13	05.03.14	10.05.14	26.05.14	05.06.14	92	3530	1277	410	1	
11[a]	260[c]	266[d]	04.04.13	05.03.14	18.05.14	25.05.14	19.06.14	106	340	60	2	32	X
12[a]	233[c]	193[d]	02.04.13	05.03.14	14.05.14	24.05.14	19.06.14	106	718	98	1	25	X
13[a]	304[c]	423[d]	02.04.13	05.03.14	10.05.14	26.05.14	09.05.14[e]	65	1169	52	0	0[e]	
14[a]	253[c]	246[d]	02.04.13	05.03.14	13.05.14	24.05.14	20.06.14	107	4005	1653	13	292	X
15[a]	267[c]	288[d]	02.04.13	05.03.14	10.05.14	25.05.14	08.05.14[e]	64	717	36	110	0[e]	
16[a]	259[c]	263[d]	02.04.13	05.03.14	17.05.14	24.05.14	19.06.14	106	5238	1488	70	148	X
17[b]	271[c]	301[d]	10.04.12	05.03.14	12.05.14	28.05.14	19.06.14	106	1924	507	131	23	X

[a]Individuals that were tagged and released by Kawabata et al. (2015)
[b]Individual that was tagged and released by Nanami et al. (2014)
[c]Estimated total length using initial release date and growth equation (Ohta & Ebisawa 2016)
[d]Estimated whole weight using total length-whole weight relationship (whole weight = 0.00001946 (total length)$^{2.955}$; A. Nanami unpubl. data)
[e]No VPS detections were made although detections were made by VR2W after the spawning migration (see Fig. S1)

& Mills (2013). The smoothing parameter for KUDs estimation was obtained by using the ad hoc method in the adehabitatHR package. Estimated home ranges were overlaid on an aerial photograph that was provided by the International Coral Reef Research and Monitoring Center, Ministry of the Environment, Japan. The aerial photograph showed the spatial distribution of hard substrates (i.e. patchy distributed corals and rocks) and sandy sea bottom.

Definition of daytime, nighttime, dawn, and dusk

The sunrise and sunset times were 07:02 and 18:47 h, respectively, on 5 March 2014 and 05:55 and 19:34 h, respectively, on 20 June 2014. Using the sunrise and sunset times, 4 time periods (daytime, nighttime, dawn, and dusk) were defined. These were (1) daytime: between 08:00 and 17:59 h; (2) nighttime: between 20:00 and 04:59 h; (3) dawn: between 05:00 and 07:59 h; (4) dusk: between 18:00 and 19:59 h.

Before the analysis, the relationship between the number of VPS detections and home range size was studied, and no significant relationship was found for all 4 time periods for both 50% KUDs and 95% KUDs estimations (Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/m606p119_supp1.pdf). Thus, it was concluded that the number of VPS detections had no effect on the home range size estimation. Repeated-measures analysis of variance (RM-ANOVA) was then performed to clarify the home range size differences among the 4 time periods using SPSS software. Prior to the analysis, home range size data were log $(x + 1)$ transformed.

Since home range size is positively correlated with body size for numerous coral reef fish species (reviewed in Nash et al. 2015), a generalized linear model (GLM) was run using R to clarify the relationship between total length and home range size for each time zone (R Core Team 2017). Data were assumed to have a gamma distribution and the log link function was applied for the analysis.

Day–night spatial shift of home range

Since the home range was larger in the nighttime than in the daytime (see 'Results'), the day–night spatial shift of the home range was estimated. For daytime and nighttime home ranges, the values for latitude and longitude (shown as decimal degrees with six significant digits) were averaged and defined as the 'center' of the home range. Then, the distance between the centers in the daytime and nighttime was estimated using the 'survey calculation site' provided by the Geospatial Information Authority of Japan (https://vldb.gsi.go.jp/sokuchi/surveycalc/surveycalc/bl2stf.html). This distance is defined as the 'inter-center distance'. A GLM was run to clarify the relationship between the inter-center distance and total length using the above-mentioned procedure.

Estimation of the precision of the returning ability

Spawning of *E. ongus* occurs during the last quarter of the moon (Nanami et al. 2013a) and a spawning aggregation was actually found on 21 May 2014 (last quarter of the moon, Nanami et al. 2017). Thus, the spawning date was assumed to be 21 May 2014 during the present study. Therefore, the study period between 22 April and 20 May 2014 was defined as the 'period before spawning', while the study period between 22 May and 20 June 2014 was defined as the 'period after spawning'.

In order to confirm the spawning migration to the spawning ground, 18 automated monitoring acoustic receivers (VR2, VEMCO) were deployed in the spawning ground (Yonara Channel). This spawning ground is designated as an MPA during the spawning period (Nanami et al. 2014, 2017). Ten and 8 receivers were deployed on the eastern and the western sides of the spawning ground, respectively (Fig. 1c). The distance between the 2 sides was approximately 450 m. The receivers were placed approximately 80 m apart from each other, resulting in 100 × 900 m and 100 × 500 m detection areas for the eastern and western sides of the spawning ground, respectively. This placement design was based on the results of the field survey that was conducted in May 2011, i.e. the receivers were placed in the area where the highest density of the spawning aggregation was found (Nanami et al. 2017). It has previously been confirmed that almost all *E. ongus* individuals in the study site migrate into the Yonara Channel during the spawning migration (Nanami et al. 2015).

Among the 17 individuals, 10 were detected over 20 times by the VPS at the home ground in the period after spawning (Table 1). All 10 individuals were also detected in the spawning ground. Thus, the degree of precision of the returning ability was estimated for these 10 individuals as follows: (1) the position data obtained by VPS were plotted on the aerial photograph so as to plot the location of each detection; (2) the inter-center distance between the home ranges during the periods before and after spawning was estimated using the above-mentioned procedure (see 'Day–night spatial shift of home range'). Smaller values for the inter-center distance represent a more precise returning ability.

Some individuals showed a relatively low number of VPS detections (ID 8, 11, 12, 17) or no VPS detections after the spawning migration (ID 1, 15) (Table 1). However, this does not mean low site fidelity for the individuals. VPS detections are only possible when signals from a tagged fish can be simultaneously detected by more than 3 receivers (VEMCO 2013). If the signals from a tagged fish are only detected by 1 or 2 receivers, a VPS detection is not possible even though the tagged fish remains in the home ground. Indeed, detections by VR2W receivers (detections that showed the presence of tagged individuals within the 19 receiver array) were abundant at the home ground after the spawning migration (Fig. S2 in Supplement 1, Table S1 in Supplement 2 at www.int-res.com/articles/suppl/m606p119_supp2.xlsx).

RESULTS

No remarkable time period variations in accuracy and precision were found for any of the 3 reference tags (Table S2 in Supplement 2). On average, accuracy was 6.861 ± 3.642 m (mean ± SD) and precision was 0.131 ± 0.124 m.

Home range size difference among time periods

Home range size was greatest in the nighttime and smallest in the daytime (Fig. 2, Table 2, and Fig. S3 in Supplement 1), whereas home range size at dawn and dusk was intermediate between daytime and

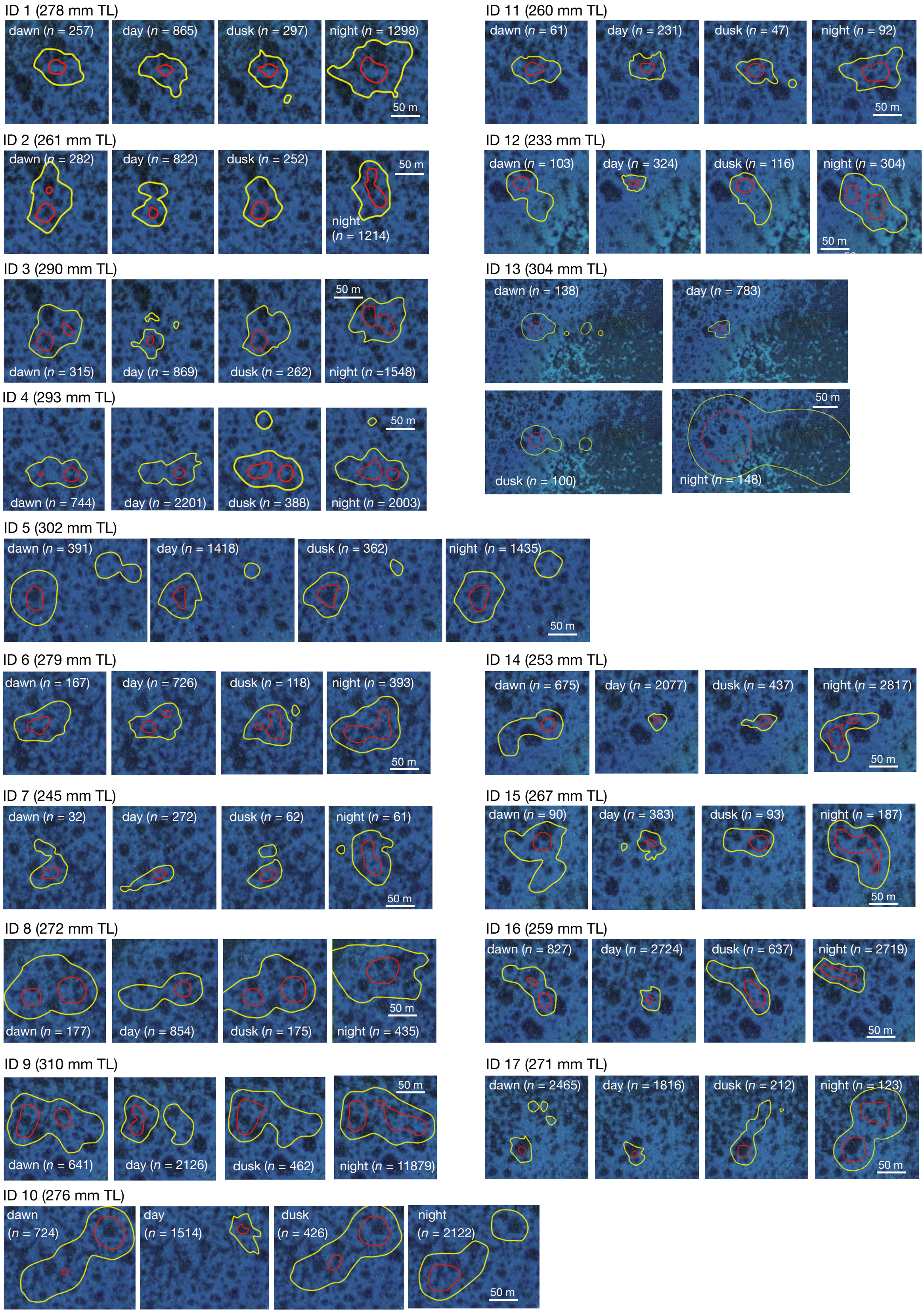

Fig. 2. Home range arrangement of 17 *Epinephelus ongus* individuals in their home ground as estimated by kernel utilization distributions (KUDs). Numbers in parentheses represent the number of VEMCO Positioning System (VPS) detections for home range size estimation. The boundaries of the core home range (50% KUDs, red line) and overall home range (95% KUDs, yellow line) are shown. The dark and light areas in the aerial photographs show hard substrates (coral colonies and dead corals) and sandy sea bottom, respectively. TL: total length. See also Fig. S1 in Supplement 1 for detailed locations of each home range. Aerial photographs were provided by the International Coral Reef Research and Monitoring Center

Table 2. Summary of *Epinephelus ongus* home range sizes at the home ground estimated by the kernel utilization distribution method (KUDs). For definition of daytime and nighttime, see 'Materials and methods'. TL: total length

ID	TL (mm)	Home range size by 50% KUDs (m^2) Dawn	Daytime	Dusk	Nighttime	Home range size by 95% KUDs (m^2) Dawn	Daytime	Dusk	Nighttime
1	278	204.2	138.8	140.8	416.9	1193.1	1082.9	952.6	2769.1
2	261	310.4	84.3	192.8	388.9	1790.5	856.9	1232.4	1531.2
3	290	335.9	49.9	218.6	431.7	1747.0	485.6	1565.8	1781.6
4	293	202.1	129.2	440.3	413.9	1219.1	1092.5	2064.4	1896.7
5	302	356.7	227.9	318.6	337.9	2605.6	1303.4	1544.7	2145.6
6	279	291.5	201.4	378.0	711.5	1428.9	1194.9	1544.5	2551.8
7	245	150.5	76.3	128.5	394.6	867.6	490.3	760.9	1576.8
8	272	858.1	191.7	667.4	637.9	3874.7	1655.6	3722.4	4178.8
9	310	803.0	298.9	654.6	1083.7	3314.6	1788.3	3311.9	3713.2
10	276	821.9	696.8	809.1	588.9	4443.1	480.6	4230.1	3372.8
11	260	178.3	117.3	137.7	314.0	868.3	683.9	729.7	1532.3
12	233	182.4	48.9	168.4	542.7	1153.2	229.0	1152.8	2170.9
13	304	329.4	117.9	463.4	6090.5	2350.3	703.2	2937.3	32792.3
14	253	18.3	30.4	58.7	275.2	131.4	166.7	385.3	1336.2
15	267	306.1	73.7	211.2	741.1	2183.2	416.3	1093.9	2499.9
16	259	236.7	28.8	289.9	293.8	1137.8	219.0	1410.0	1061.3
17	271	56.2	29.3	154.4	1360.7	681.7	221.3	1580.7	5122.6
Average	273.7	331.9	149.5	319.6	883.8	1823.0	768.8	1777.6	4237.2

nighttime (Fig. 2). Average daytime and nighttime home ranges estimated using 50% KUDs were 149.5 ± 160.8 m^2 (mean ± SD) and 883.8 ± 1373.0 m^2, respectively. The nighttime home range was 5.9-times larger (883.8/149.5) than the daytime home range (Table 2). Average dawn and dusk home ranges were 331.9 ± 254.7 m^2 and 319.6 ± 219.4 m^2, respectively. The dawn and dusk home ranges were 2.2-times (331.9/149.5) and 2.1-times (319.6/149.5) larger than the daytime home range (Table 2).

The average daytime and nighttime home ranges estimated using 95% KUDs were 768.8 ± 508.5 m^2 and 4237.2 ± 7439.7 m^2, respectively. The nighttime home range was 5.5-times larger (4237.2/768.8) than the daytime home range (Table 2). The average dawn and dusk home ranges were 1823.0 ± 1176.6 m^2 and 1777.6 ± 1112.8 m^2, respectively. The dawn and dusk home ranges were 2.4-times (1823.0/768.8) and 2.3-times (1777.6/768.8) larger than the daytime home range (Table 2).

RM-ANOVA revealed that the night home range size was significantly greater than the daytime, dawn, and dusk home range sizes for estimation with both 50% KUDs (F = 16.453, df = 3, $p < 0.05$) and 95% KUDs (F = 14.331, df = 3, $p < 0.05$). The dawn and dusk home ranges were also significantly larger than the daytime home range for estimation with both 50% KUDs and 95% KUDs ($p < 0.05$). In contrast, no significant difference in home range size was shown between the dawn and dusk home ranges for estimation with both 50% KUDs and 95% KUDs ($p > 0.05$).

The GLM revealed that there was a significant positive relationship between total length and daytime home range size for estimation with 95% KUDs (Fig. 3: for coefficient −26.419, t = −2.587, and p = 0.02; for coefficient 5.879, t = 3.229 and $p < 0.01$; df = 16 for null deviance). In contrast, although there was a positive trend, there was no significant relationship between total length and home range size at dawn, dusk, and night.

Day–night shift of home range

The inter-center distance ranged from 3.0 to 67.9 m. Two individuals (ID 1, 6) showed a less than 5 m difference. In contrast, 1 individual (ID 10) showed a difference of over 60 m, indicating that the location of the core home range (estimated using 50% KUDs) was remarkably different between daytime and nighttime (Fig. 2). The average inter-center distance was 22.5 ± 4.2 m (mean ± SE) (Table 3). The GLM revealed that there was no significant relationship between the inter-center distance and total length (Fig. 4).

Degree of precision of returning ability after spawning migration

The departure date for the migration to the spawning ground was between 9 and 19 May 2014

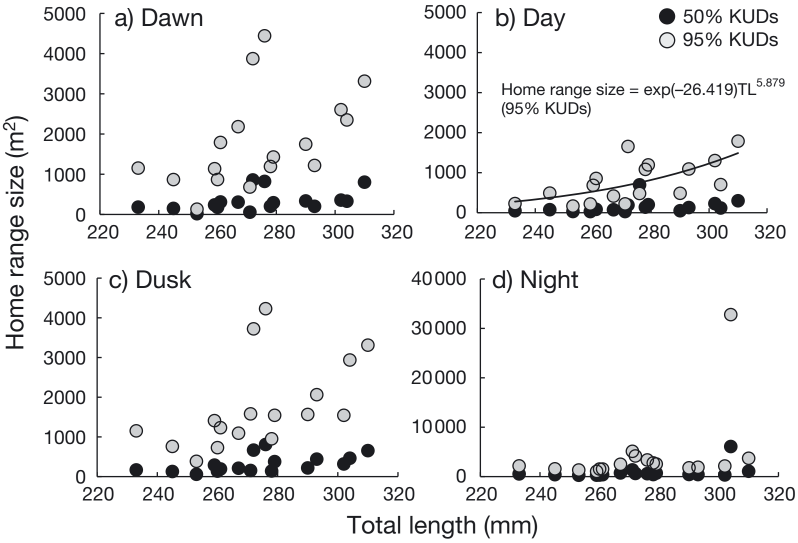

Fig. 3. Relationship between *Epinephelus ongus* total length and home range size, for both core home range (50 % KUDs, ●) and overall home range (95 % KUDs, ●), for (a) dawn, (b) day, (c) dusk, and (d) night. The black line in (b) indicates the significant relationship for overall home range determined by GLM. Note that the scaling of the vertical axis in (d) differs from that in (a,b,c)

and the return date to the home ground was between 24 and 30 May 2014 (Table 1). The inter-center distance between the home ranges in the 2 periods ranged from 1.8 to 23.4 m and the average was 8.1 ± 2.2 m (mean ± SE) (Table 4). Most individuals (8 individuals: ID 2, 4, 5, 11, 12, 14, 16, 17) showed an inter-center distance of less than 10 m. For these 8 individuals, daytime VPS detections during the period after spawning were on the same patchy substrates that were used during the period before spawning (Fig. 5). For 6 out of the 8 individuals (ID 2, 4, 5, 12, 14, 16), nighttime VPS detections during the period after spawning were also in the same areas that were used during the period before spawning.

DISCUSSION

Diel difference in home range size at home ground

The present study is the first to clarify home range size and its diel difference for *Epinephelus ongus*. The results show that all of the *E. ongus* individuals had a greater home range size in the nighttime than in the daytime, and at dawn and dusk. Since the main prey items of *E. ongus* are crustaceans including crabs and shrimps (Kawabata et al. 2014) and crustaceans are more active in the nighttime (Masuda et al. 2012, Ory et al. 2014), this suggests that the larger home range in the nighttime is an adaptation for nocturnal foraging.

Some previous studies have shown clear diel activity for groupers. Red-spotted grouper *E. akaara* is more active at night (Masuda et al. 2012). In contrast, Carter et al. (1994) have shown that Nassau grouper *E. striatus* is most active at dawn and dusk (just after sunrise and just prior to sunset). Gibran (2007) has also observed feeding activity of dusky grouper *E. marginatus* at twilight. Zeller (1997) has shown that coral trout *Plectropomus leopardus* is more active in the daytime than in the nighttime. Thus, the results of the present study differ from these previous studies, suggesting that diel activity is species-specific for groupers.

Table 3. Center of *Epinephelus ongus* home ranges at daytime and nighttime, and inter-center distance between daytime and nighttime home ranges. For definition of 'center', 'inter-center distance', 'daytime' and 'nighttime', see 'Materials and methods'

ID	Daytime Latitude (°N)	Daytime Longitude (°E)	Nighttime Latitude (°N)	Nighttime Longitude (°E)	Inter-center distance (m)
1	24.305673	123.992300	24.305700	123.992294	3.0
2	24.305104	123.992070	24.305266	123.992146	19.5
3	24.305088	123.992069	24.305143	123.992103	7.0
4	24.304634	123.992195	24.304652	123.992090	10.8
5	24.303982	123.991756	24.304001	123.991802	5.1
6	24.304393	123.991425	24.304350	123.991429	4.8
7	24.304522	123.991415	24.304673	123.991386	17.0
8	24.304702	123.991433	24.304899	123.991294	26.0
9	24.304978	123.992906	24.304995	123.993091	18.9
10	24.304687	123.992659	24.304343	123.992106	67.9
11	24.304770	123.992951	24.304753	123.993073	12.5
12	24.304648	123.993386	24.304466	123.993529	24.9
13	24.304653	123.993412	24.304637	123.993910	50.6
14	24.304696	123.993325	24.304563	123.993007	35.5
15	24.305162	123.993803	24.305083	123.993710	12.9
16	24.304845	123.993269	24.305046	123.992997	35.5
17	24.305241	123.993867	24.305492	123.994008	31.2
Mean ± SE					22.5 ± 4.2

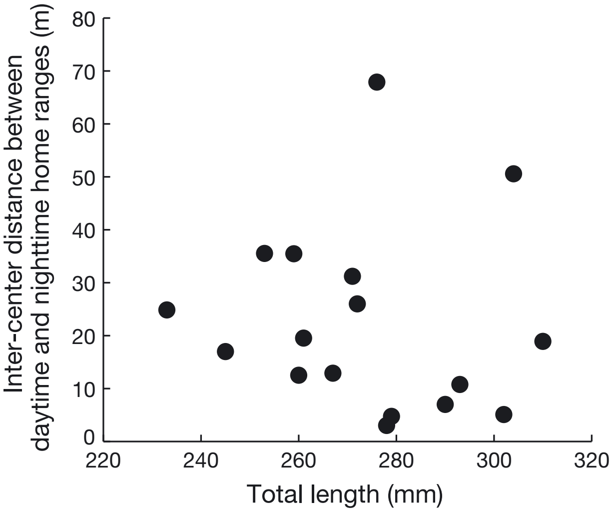

Fig. 4. Relationship between *Epinephelus ongus* total length and inter-center distances between daytime and nighttime home ranges (for definition of 'inter-center distance', see 'Materials and methods'). The GLM revealed no significant relationship

Table 4. Center of *Epinephelus ongus* home ranges before and after spawning, and inter-center distance between home ranges during the 2 periods. For definition of 'center' and 'inter-center distance', see 'Materials and methods'

ID	Before spawning		After spawning		Inter-center distance (m)
	Latitude (°N)	Longitude (°E)	Latitude (°N)	Longitude (°E)	
2	24.305220	123.992109	24.305280	123.992106	6.6
4	24.304642	123.992087	24.304628	123.992169	8.4
5	24.304014	123.991828	24.303976	123.991836	4.3
8	24.304773	123.991305	24.304776	123.991550	16.6
9	24.305011	123.993014	24.304916	123.993220	23.4
11	24.304765	123.992938	24.304774	123.992953	1.8
12	24.304602	123.993439	24.304559	123.993466	5.5
14	24.304636	123.993164	24.304619	123.993171	2
16	24.304942	123.993129	24.304886	123.993189	8.7
17	24.305262	123.993871	24.305240	123.993849	3.4
Mean ± SE					8.1 ± 2.2

Day–night home range shift

Inter-center distance between the daytime and nighttime home ranges varied individually. This suggests that the resting site in the daytime and foraging site in the nighttime were different for those individuals that had a greater inter-center distance. Total length was not the main factor responsible for the size of the day–night home range shift. Although the precise causes remain unknown, spatial variations in food resources (i.e. prey items) might play a role. If individuals inhabit corals that support only a low density of potential prey items, these individuals would hunt around their resting site for prey. As a result, the core home range would change spatially between the daytime and nighttime. This might be the reason why no significant relationship between total length and home range size was found in the nighttime. Since the study area was covered by a sandy sea bottom with patchily distributed coral colonies, food resources would not be uniformly distributed but would be aggregated patchily. Thus, expanding home range size would not necessarily guarantee increased food resources. Therefore, despite expanding its home range, an individual would not acquire sufficient food resources if few coral colonies with rich prey items were included in the expanded home range. In contrast, if an individual could inhabit a coral colony with rich prey items, it would acquire sufficient food resources on the coral colony without substantially expanding its home range.

Although it is difficult to estimate the spatial variation in prey item abundance in the wild, experimental studies might be useful for testing the relationship between prey item abundance and the day–night home range shift. The results of the present study suggest that the appropriate size and location of an MPA for *E. ongus* should be determined based on the day–night home range shift at their home ground.

Returning ability after spawning migration

The inter-center distances between the home ranges for the periods before and after spawning were all under 25 m. In fact, it was less than 10 m for most individuals. This suggests that *E. ongus* are able to return with high precision after the spawning migration.

Some species use olfaction and vision for homing (Mitamura et al. 2005) and others use topographical characteristics (Mazeroll & Montgomery 1995, 1998, Kaunda-Arara & Rose 2004). Kaunda-Arara & Rose (2004) conducted an artificial displacement experiment for 1 grouper species (*E. tauvina*). In this experiment, tagged *E. tauvina* individuals were released 0.5 to 2.6 km away from the capture site. As a result, 8 out of 12 individuals returned to their initial capture sites. In contrast, the present study

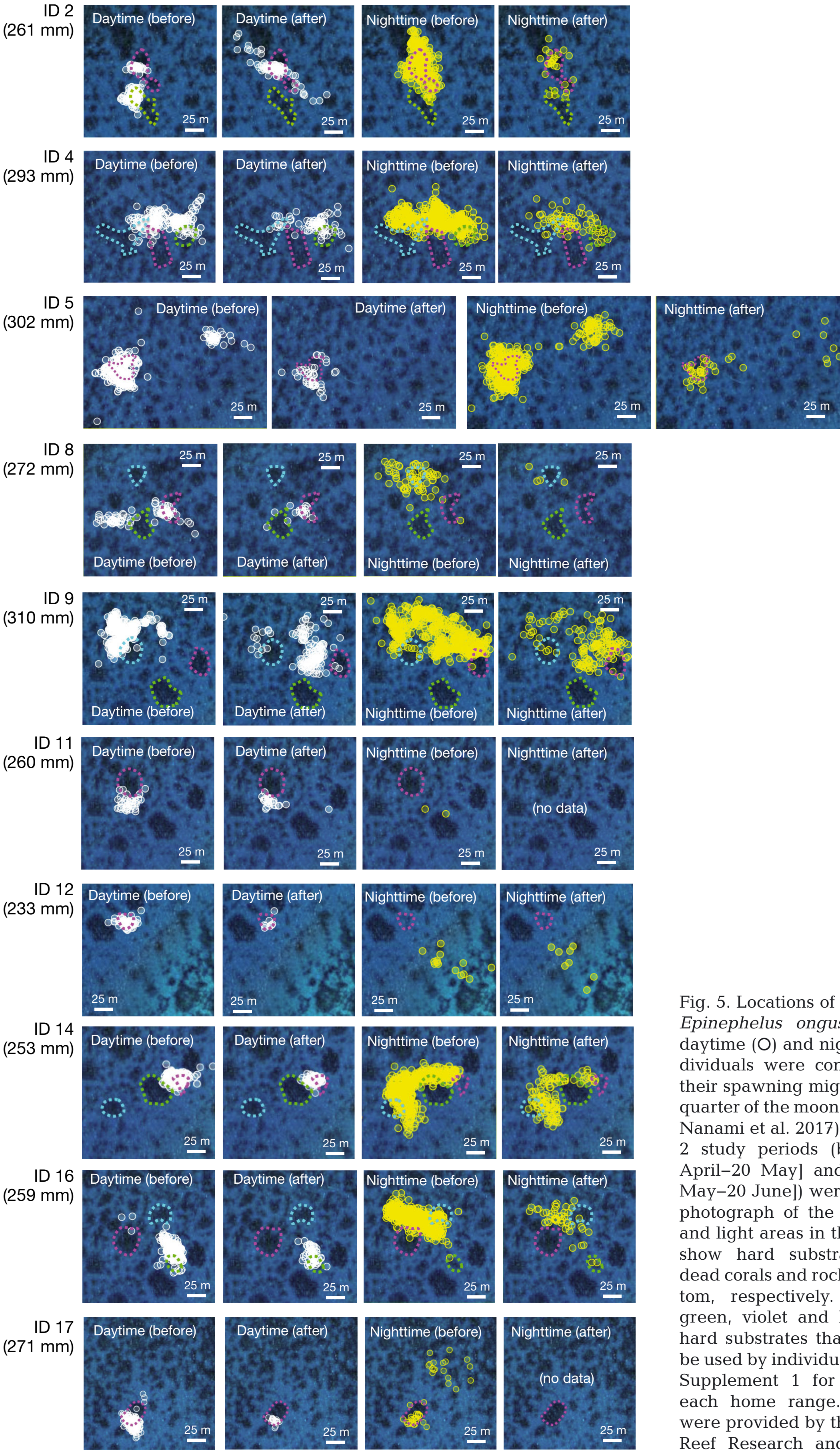

Fig. 5. Locations of VPS detections for 10 *Epinephelus ongus* individuals in the daytime (O) and nighttime (●). These individuals were confirmed to undertake their spawning migration around the last quarter of the moon in May (21 May 2014, Nanami et al. 2017). The locations for the 2 study periods (before spawning [21 April–20 May] and after spawning [22 May–20 June]) were plotted on an aerial photograph of the study site. The dark and light areas in the aerial photographs show hard substrates (coral colonies, dead corals and rocks) and sandy sea bottom, respectively. Dotted lines (light green, violet and light blue) show the hard substrates that were considered to be used by individuals. See also Fig. S1 in Supplement 1 for detailed location of each home range. Aerial photographs were provided by the International Coral Reef Research and Monitoring Center

revealed precise returning ability after the spawning migration even though the distance between the home ground and the spawning ground was approximately 6 km. Although the exact mechanisms of the returning ability of *E. ongus* remain unknown, the present study is the first to clearly show the ability of grouper to return to their home ground precisely after the spawning migration under natural conditions (i.e. *E. ongus* was not artificially released into an area outside of their home ground in the present study).

Implications of establishing MPAs using behavioral characteristics

Since the site fidelity of *E. ongus* was high in the daytime, the habitat that is used in the daytime should be included in the MPA. Some individuals showed day–night habitat shifts of several tens of meters. Furthermore, the returning precision after the spawning migration was high. Since *E. ongus* are captured during both the daytime and nighttime, both daytime and nighttime home ranges should be included in the MPA. Thus, the establishment of an appropriate MPA for *E. ongus* in their home ground would involve the following: (1) the daytime core home range (i.e. substrates in which *E. ongus* individuals are found in the daytime) could be designated as the center of the MPA; (2) an area with a radius of several tens of meters from the daytime core home range would be an appropriate size for the MPA during the non-spawning period.

Since some coral reef fish species change their home ground during the non-spawning period (Chateau & Wantiez 2008), long-term monitoring of the site fidelity of *E. ongus* should be conducted. The maximum age and age at maturity of *E. ongus* are 20 and 4 yr, respectively (Ohta & Ebisawa 2015, 2016). Thus, *E. ongus* undergo spawning migrations multiple times during their lifetime (maximum can be 16 times). If long-term site fidelity of *E. ongus* is observed, i.e. if the location of their home ground remains almost the same throughout their adult lifetime due to their precise returning ability after the spawning migration, then the selection of an appropriate location for an MPA will ensure the long-term protection of individuals at their home ground. Since clear microhabitat association has been found for *E. ongus* (Nanami et al. 2013b), further research will be useful. Namely, in order to determine the appropriate MPA location, the density and spatial distribution of the *E. ongus* population, as well as the extent of suitable habitat should be investigated before MPA establishment.

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LITERATURE CITED

Afonso P, Fontes J, Holland KN, Santos RS (2008) Social status determines behaviour and habitat usage in a temperate parrotfish: implications for marine reserve design. Mar Ecol Prog Ser 359:215–227

Calenge C (2015) Home range estimation in R: the adehabitatHR package. https://cran.r-project.org/web/packages/adehabitatHR/vignettes/adehabitatHR.pdf

Carter J, Marrow GJ, Pryor V (1994) Aspects of the ecology and reproduction of Nassau grouper, *Epinephelus striatus*, off the coast of Belize, Central America. Proc Gulf Caribb Fish Inst 43:65–111

Chateau O, Wantiez L (2008) Movement patterns of four coral reef fish species in a fragmented habitat in New Caledonia: implications for the design of marine protected area networks. ICES J Mar Sci 66:50–55

Currey LM, Heupel MR, Simpfendorfer CA, Williams AJ (2015) Assessing fine-scale diel movement patterns of an exploited coral reef fish. Anim Biotelem 3:41

Davis K, Carlson PM, Lowe CG, Warner RR, Caselle JE (2017) Parrotfish movement patterns vary with spatiotemporal scale. Mar Ecol Prog Ser 577:149–164

Di Franco A, Plass-Johnson JG, Di Lorenzo M, Meola M and others (2018) Linking home ranges to protected area size: the case study of the Mediterranean Sea. Biol Conserv 221:175–181

Di Lorenzo M, D'Anna G, Badalamenti F, Giacalone VM, Starr RM, Guidetti P (2014) Fitting the size of no-take zones to species movement patterns: a case study on a Mediterranean seabream. Mar Ecol Prog Ser 502: 245–255

Di Lorenzo M, Fernández TV, Badalamenti F, Guidetti P and others (2016) Diel activity and variability in habitat use of white sea bream in a temperate marine protected area. Mar Environ Res 116:1–9

Domeier ML (2012) Revisiting spawning aggregations: definitions and challenges. In: Sadovy de Mitcheson Y, Colin PL (eds) Reef fish spawning aggregations: biology, research and management. Fish Fish Ser, Vol 35. Springer Verlag, Berlin, p 1–20

Espinoza M, Farrugia TJ, Webber DM, Smith F, Low CG (2011) Testing a new acoustic telemetry technique to quantify long-term, fine-scale movements of aquatic animals. Fish Res 108:364–371

Gibran FZ (2007) Activity, habitat use, feeding behavior, and diet of four sympatric species of Serranidae

(Actinopterygii: Perciformes) in southeastern Brazil. Neotrop Ichthyol 5:387–398
Green AL, Maypa AP, Almany GR, Rohdes KL and others (2015) Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. Biol Rev Camb Philos Soc 90:1215–1247
Holland KM, Peterson JD, Christopher G, Wetherbee BM (1993) Movements, distribution and growth rates of the white goatfish *Mulloides flavolineatus* in a fisheries conservation zone. Bull Mar Sci 52:982–992
Holland KN, Lowe CG, Weltherbee BM (1996) Movement and dispersal patterns of blue trevally (*Caranx melampygus*) in a fisheries conservation zone. Fish Res 25:279–292
Honda K, Uy WH, Baslot DI, Pantallano ADS, Nakamura Y, Nakaoka M (2016) Diel habitat-use patterns of commercially important fishes in a marine protected area in the Philippines. Aquat Biol 24:163–174
Kaunda-Arara B, Rose GA (2004) Homing and site fidelity in the greasy grouper *Epinephelus tauvina* (Serranidae) within a marine protected area in coastal Kenya. Mar Ecol Prog Ser 277:245–251
Kawabata Y, Okuyama J, Asami K, Yoseda K, Arai N (2008) The post-release process of establishing stable home ranges and diel movement patterns of hatchery-reared black-spot tuskfish *Choerodon schoenleinii.* J Fish Biol 73:1770–1782
Kawabata Y, Noda T, Nakashima Y, Nanami A and others (2014) Use of a gyroscope/accelerometer data logger to identify alternative feeding behaviours in fish. J Exp Biol 217:3204–3208
Kawabata Y, Nanami A, Yamamoto K, Sato T and others (2015) Duration of migration and reproduction in males is dependent on energy reserve in a fish forming spawning aggregations. Mar Ecol Prog Ser 534:149–161
Krumme U (2009) Diel and tidal movements by fish and decapods linking tropical coastal ecosystems. In: Nagelkerken I (ed) Ecological connectivity among tropical coastal ecosystems. Springer Verlag, Berlin, p 271–324
Lembo G, Fleming IA, Okland F, Carbonara P, Spedicato MT (1999) Site fidelity of the dusky grouper *Epinephelus marginatus* (Lowe, 1834) studied by acoustic telemetry. Mar Life 9:37–43
Lembo G, Spedicato MT, Økland F, Carbonara P and others (2002) A wireless communication system for determining site fidelity of juvenile dusky groupers *Epinephelus marginatus* (Lowe, 1834) using coded acoustic transmitters. Hydrobiologia 483:249–257
Levin PS, Grimes CB (2002) Reef fish ecology and grouper conservation and management. In: Sale PF (ed) Coral reef fishes. Academic Press, San Diego, p 377–389
Masuda R, Matsuda K, Tanaka M (2012) Laboratory video recordings and underwater visual observations combined to reveal activity rhythm of red-spotted grouper and banded wrasse, and their natural assemblages. Environ Biol Fishes 95:335–346
Matley JK, Tobin AJ, Lédée EJI, Heupel MR, Simpfendorfer CA (2016) Contrasting patterns of vertical and horizontal space use of two exploited and sympatric coral reef fish. Mar Biol 163:253
Mazeroll AI, Montgomery WL (1995) Structure and organization of local migrations in brown surgeonfish (*Acanthurus nigrofuscus*). Ethology 99:89–106
Mazeroll AI, Montgomery WL (1998) Daily migrations of a coral reef fish in the Red Sea (Gulf of Aqaba, Israel): initiation and orientation. Copeia 1998:893–905
Mitamura H, Arai N, Sakamoto W, Mitsunaga Y and others (2002) Evidence of homing of black rockfish *Sebastes inermis* using biotelemetry. Fish Sci 68:1189–1196
Mitamura H, Arai N, Sakamoto W, Mitsunaga Y and others (2005) Role of olfaction and vision in homing behaviour of black rockfish *Sebastes inermis.* J Exp Mar Biol Ecol 322:123–134
Mitamura H, Uchida K, Miyamoto Y, Arai N and others (2009) Preliminary study on homing, site fidelity, and diel movement of black rockfish *Sebastes inermis* measured by acoustic telemetry. Fish Sci 75:1133–1140
Nanami A (2015) Pair formation, home range, and spatial variation in density, size and social status in blotched foxface *Siganus unimaculatus* on an Okinawan coral reef. PeerJ 3:e1280
Nanami A, Yamada H (2008) Size and spatial arrangement of home range of checkered snapper *Lutjanus decussatus* (Lutjanidae) in an Okinawan coral reef determined using a portable GPS receiver. Mar Biol 153:1103–1111
Nanami A, Sato T, Ohta I, Akita Y, Suzuki N (2013a) Preliminary observations of spawning behavior of white-streaked grouper (*Epinephelus ongus*) in an Okinawan coral reef. Ichthyol Res 60:380–385
Nanami A, Sato T, Takebe T, Teruya T, Soyano K (2013b) Microhabitat association in white-streaked grouper *Epinephelus ongus*: importance of *Acropora* spp. Mar Biol 160:1511–1517
Nanami A, Kawabata Y, Sato T, Yamaguchi T, Kawabe R, Soyano K (2014) Spawning migration and returning behavior of white-streaked grouper *Epinephelus ongus* determined by acoustic telemetry. Mar Biol 161:669–680
Nanami A, Ohta I, Sato T (2015) Estimation of spawning migration distance of the white-streaked grouper (*Epinephelus ongus*) in an Okinawan coral reef system using conventional tag-and-release. Environ Biol Fishes 98: 1387–1397
Nanami A, Sato T, Kawabata Y, Okuyama J (2017) Spawning aggregation of white-streaked grouper *Epinephelus ongus*: spatial distribution and annual variation in the fish density within a spawning ground. PeerJ 5:e3000
Nash KL, Welsh JQ, Graham NAJ, Bellwood DR (2015) Home-range allometry in coral reef fishes: comparison to other vertebrates, methodological issues and management implications. Oecologia 177:73–83
Nemeth RS, Blondeau J, Herzlieb S, Kadison E (2007) Spatial and temporal patterns of movement and migration at spawning aggregations of red hind, *Epinephelus guttatus*, in the U.S. Virgin Islands. Environ Biol Fishes 78: 365–381
Ohta I, Ebisawa A (2015) Reproductive biology and spawning aggregation fishing of the white-streaked grouper, *Epinephelus ongus*, associated with seasonal and lunar cycles. Environ Biol Fishes 98:1555–1570
Ohta I, Ebisawa A (2016) Age-based demography and sexual pattern of the white-streaked grouper, *Epinephelus ongus* in Okinawa. Environ Biol Fishes 99:741–751
Ohta I, Ebisawa A (2017) Inter-annual variation of the spawning aggregations of the white-streaked grouper *Epinephelus ongus*, in relation to the lunar cycle and water temperature fluctuation. Fish Oceanogr 26: 350–363
Ory NC, Dudgeon D, Duprey N, Thiel M (2014) Effects of predation on diel activity and habitat use of the coral-reef shrimp *Cinetorhynchus hendersoni* (Rhynchocinetidae). Coral Reefs 33:639–650

R Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.R-project.org/

Rhodes KL, McIlwain J, Joseph E, Nemeth RS (2012) Reproductive movement, residency and fisheries vulnerability of brown-marbled grouper, *Epinephelus fuscoguttatus* (Forsskål, 1775). Coral Reefs 31:443–453

Sadovy de Mitcheson Y, Cornish A, Domeier M, Colin PL, Russell M, Lindeman KC (2008) A global baseline for spawning aggregations of reef fishes. Conserv Biol 22: 1233–1244

Sadovy de Mitcheson Y, Craig MT, Bertoncini AA, Carpenter KE and others (2013) Fishing groupers towards extinction: a global assessment of threats and extinction risks in a billion dollar fishery. Fish Fish 14:119–136

Smith CL, Tyler JC (1972) Space resource sharing in a coral reef fish community. Bull Nat Hist Mus Los Angel Cty 14: 125–170

Taylor BM, Mills JS (2013) Movement and spawning migration patterns suggest small marine reserves can offer adequate protection for exploited emperorfishes. Coral Reefs 32:1077–1087

Teesdale GN, Wolfe BW, Lowe CG (2015) Patterns of home ranging, site fidelity, and seasonal spawning migration of barred sand bass caught within the Palos Verdes Shelf Superfund Site. Mar Ecol Prog Ser 539:255–269

VEMCO (2013) VEMCO Positioning System (VPS). VPS Datasheet (4722-04), AMIRIX Systems. https://vemco.com/wp-content/uploads/2014/01/vps.pdf

Welsh JQ, Bellwood DR (2012) Spatial ecology of the steephead parrotfish (*Chlorurus microrhinos*): an evaluation using acoustic telemetry. Coral Reefs 31:55–65

Zeller DC (1997) Home range and activity patterns of the coral trout *Plectropomus leopardus* (Serranidae). Mar Ecol Prog Ser 154:65–77

Zeller DC, Russ G (1998) Marine reserves: patterns of adult movement of the coral trout (*Plectropomus leopardus* (Serranidae)). Can J Fish Aquat Sci 55:917–924

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