Fish Sci (2009) 75:1109–1116
DOI 10.1007/s12562-009-0136-7

ORIGINAL ARTICLE Biology

Site fidelity, size, and spatial arrangement of daytime home range of thumbprint emperor *Lethrinus harak* (Lethrinidae)

Atsushi Nanami · Hideaki Yamada

Received: 16 March 2009 / Accepted: 8 June 2009 / Published online: 11 July 2009

Abstract Although emperors (Lethrinidae) are commercially important fisheries resources in tropical and subtropical waters, their home range size and its spatial arrangement have not been sufficiently clarified. In the present study, the size and spatial arrangement of the daytime home range of the thumbprint emperor *Lethrinus harak* were investigated by using a portable GPS receiver. In a 150 m × 200 m quadrat, 21 individuals of the species were identified by their color pattern, and individuals were divided into four arbitrary size classes (class 1 $<$ 20 cm TL $\leq$ class 2 $<$ 25 cm TL $\leq$ class 3 $<$ 30 cm TL $\leq$ class 4). Fish tracking by snorkeling was conducted with the portable GPS receiver. Daytime site fidelity of this species was high and there was a significant positive correlation between the home range size and fish total length. Home ranges of same-sized individuals abutted each other (20.3% area overlap), whereas those of different-sized individuals overlapped (48.3% area overlap). Agonistic behavior (attacking) occurred significantly more frequently between same-sized individuals than between different-sized individuals. These results suggest that daytime home ranges of *Lethrinus harak* can be regarded as territories against same-sized individuals, but not different-sized individuals.

Keywords Home range · Intraspecific interaction · *Lethrinus harak* · Site fidelity · Spatial arrangement

A. Nanami (✉) · H. Yamada
Ishigaki Tropical Station, Seikai National Fisheries Research Institute, Fisheries Research Agency, Fukai-Ota 148-446, Ishigaki, Okinawa 907-0451, Japan
e-mail: nanami@fra.affrc.go.jp

Introduction

Emperors (Lethrinidae) are one of the important fisheries resources in tropical and subtropical waters [1]. Several previous studies have clarified their reproduction [2–9], settlement [10, 11], and feeding ecology [12, 13]. However, despite their economical significance, the site fidelity, home range size, and spatial arrangement of the home ranges for lethrinid species have received limited attention, although this information is important for their management [14–20].

Little is also known regarding the relationship between home range arrangement and intraspecific interaction for lethrinid species, although several previous studies have demonstrated that intraspecific interaction is responsible for the spatial arrangement of home ranges in some species [21–23].

The thumbprint emperor, *Lethrinus harak* (Forsskål), is one of the lethrinid species that is widely distributed in the Indian Ocean and western Pacific including the Red Sea and East Africa [1]. This species inhabits shallow waters and is a benthic carnivore [1]. Although it remains an important fisheries resource in the Indo-Pacific region [1], little is known regarding details of its home range (site fidelity, size, and spatial arrangement). Furthermore, behavioral aspects of the species including intraspecific interactions have not been sufficiently studied. Thus, the specific aim of this study was to answer the following questions for *L. harak*: (1) does the species exhibit high site fidelity? (2) how large are its home ranges? (3) is there any particular spatial arrangement of its home ranges? and (4) are any intraspecific interactions among the conspecifics found? based on observations in an Okinawan seagrass bed by using a portable GPS receiver. As far as we are aware, this is the first attempt to detect home range size, spatial arrangement of home range, and intraspecific interactions of lethrinid species.

Materials and methods

Study site and fish

Fieldwork for this study was conducted in a seagrass bed at Urasoko Bay on the fringing reef off Ishigaki Island, Okinawa, Japan (24°27′N, 124°13′E). Seagrass species consisted of *Cymodocea serrulata* and *Thalassia hemprichii*. Water depth was about 2 m at high tide and 0.8 m at low tide. A 150 m × 200 m quadrat was set on the study site, since preliminary surveys for the species showed that this quadrat size was sufficient to include various size class individuals. During July 2007 to June 2008, all individuals of *L. harak* in the quadrat were identified individually according to the patterns of black spots on the middle of the body side (Fig. 1). Such identification method has been used by several previous studies [21, 22]. Since one black spot is located on each side of the body, two black spots were found for each individual. The morphological traits of the two black spots were sketched on waterproof paper while observing the fish using snorkeling [23]. The waterproof paper was always carried and the morphological traits for each individual were checked at each visual observation. Individuals were readily differentiated based on this pigmentation pattern and showed minimal change in this morphological trait over the study period in all individuals. Since the spawning season is considered to be during April to November in Okinawan region [5], it is reasonable to consider that both the spawning and nonspawning seasons were included in the present study.

The total length (TL) of each fish was estimated underwater to the nearest 0.5 cm using a scale carried by the researcher. The estimated TL ranged from 18.0 to 31.0 cm. Individuals were divided into four arbitrary size classes (class 1 $<$ 20 cm TL $\leq$ class 2 $<$ 25 cm TL $\leq$ class 3 $<$ 30 cm TL $\leq$ class 4) for subsequent data analyses. Since the maximum total length of most individuals is ca. 30 cm for the species [1] and the maximum total length recorded in the Okinawan region is ca. 33 cm [5], it is reasonable to consider that most of the size range of the species in Okinawan region was covered in the present study. Consequently, a total of 21 individuals (5, 5, 8, and 3 individuals for the four respective size classes) were found in the quadrat. All of the individuals were present for the whole study period. Neither courtship behavior nor spawning was observed at the study site during the study periods.

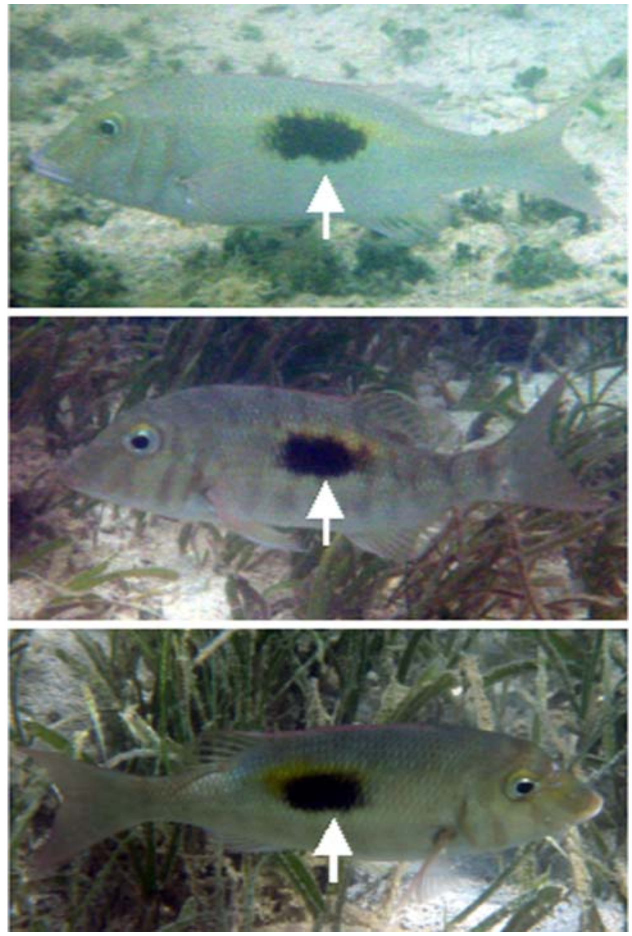

Fig. 1 Lateral view of *Lethrinus harak* showing the black spot on the middle of the body side (*white arrows*). Three individuals are shown as concrete examples in order to illustrate the difference in patterns of the *black spots*

Fish tracking by snorkeling

Fish tracking was conducted using a portable GPS receiver (GARMIN GPSmap 60CS). The measurement error of location detection was 0–3.08 m and the average measurement error was 0.62 m [23]. During the visual observations, the GPS receiver was sealed in a waterproof case and placed in a box made of styrene foam on the water surface. Then, a researcher with the box slowly approached a focal fish using snorkeling and followed the fish. Escape behaviors of fish from the researcher were rarely observed for most individuals during fish tracking. Each individual's position was recorded at 1-s intervals, and each individual was followed for ca. 20 min in a focal observation. These visual observations were made between 09:00 and 18:30 hours. This procedure was repeated four to seven times for each individual (total observation time ca. 80–140 min for each individual).

Home range size estimation

To estimate the home range size, the data logged by the GPS receiver were plotted for each individual using MapSource^{TM} software (GARMIN). The data from four to seven swimming track surveys that were obtained for each individual were pooled. Then, the edge of the pooled tracking data was enclosed and regarded as the home range, in accordance with previous studies [21, 22].

In order to estimate whether four to seven trackings were sufficient to estimate the home range sizes, the relationship between the number of trackings and the rate of increase of the home range size was determined by using five individuals (20.0–31.0 cm TL), in accordance with previous study [23]:

$$\text{Rate of additional home range size } (\%) = [(A_i - A_{i-1})/(A_{i-1})] \times 100;$$

where A_i is the home range estimated by using all fish trackings from the first to the ith tracking ($i = 2$–7). The rate of additional home range size will tend to zero as the number of trackings increases if the site fidelity of the fish is high and a sufficient number of trackings are used.

Intraspecific interactions

In order to clarify whether any intraspecific interactions among the *L. harak* individuals occurred in the study site, intraspecific interactions of *L. harak* were recorded as follows: (1) agonistic behavior (rushing to other conspecific individuals) and (2) no interaction (recorded if no noticeable interactions occurred when the fish were within 50 cm of each other). Intraspecific interactions were recorded during fish tracking by snorkeling and GPS receiver.

Feeding behavior

In order to clarify what types of substrata were used by *L. harak*, foraging behavior was recorded for all individuals in the study area. Foraging behavior was recorded during fish tracking. Six substrata used by the individuals were recorded: (1) sand, (2) surface of seagrass, (3) coral rubble, (4) rocks, (5) living massive coral, and (6) surface of seaweed (brown algae). In order to analyze the size class difference in the foraging sites, one-way analysis of variance (ANOVA) was conducted, with the proportion of use of each substrate arcsin-transformed for analysis.

Data analyses

Relationship between home range size and TL of home range owners was obtained as follows: $\log_{10}$ (home range size) = $a\log_{10}$(TL) + b, where a and b are coefficients.

The degree of home range overlap was calculated for each home range owner in accordance with Matsumoto [22] as follows: (total area overlapping with the home ranges of other individuals)/(home range area of the resident) $\times$ 100. One-way analysis of variance (ANOVA) was carried out to clarify if the degree of home range overlap of same-sized individuals was significantly different from that of different-sized individuals. In this procedure, the values of home range overlap were arcsin-transformed for analysis.

In order to test for any significant difference in the frequency distribution of intraspecific interaction between same-sized and different-sized individuals, 2 $\times$ 2 contingency table analysis was carried out. Frequency data obtained from four size classes was pooled for analysis.

Results

Site fidelity and reliability of home range size estimation

The trackings obtained from the same *L. harak* individual were close and/or overlapped although the tracks were obtained on different days and/or times (Fig. 2), and therefore it is reasonable to consider that all identified individuals had high site fidelity and stable home ranges during the study period. The rate of additional home range size was calculated for two to seven trackings, and four to seven trackings was concluded to be sufficient to estimate the home range size for this species (Fig. 3).

Daytime home range size and spatial arrangement

During the study period, all *L. harak* individuals were found to be swimming individually and no conspecific schools or aggregations were observed in the study area. Figure 4 shows the spatial arrangement of home ranges of *L. harak*. For individuals of size classes 1 and 4, the home ranges of individuals abutted each other (Fig. 4a, d). For size classes 2 and 3, home ranges of same-sized individuals did not strictly abut each other (Fig. 4b, c). These results were quantitatively confirmed by the degree of home range overlap (Table 1). Among same-sized individuals, the average degree of home range overlap for the four size classes was 20.3% ± 10.1 SE (size class 1 = 2.7% ± 1.0 SE; size class 2 = 26.3% ± 11.2 SE; size class 3 = 46.2% ± 7.0 SE; size class 4 = 6.0% ± 3.3 SE). In contrast, among different-sized individuals, the average degree of home range overlap for the four size classes was 48.3% ± 3.2 SE (size class 1 = 41.9% ± 14.0 SE to 67.0% ± 10.6 SE; size class 2 = 40.8% ± 8.8 SE to 71.5% ± 11.9 SE; size class 3 = 40.7% ± 10.6 SE to

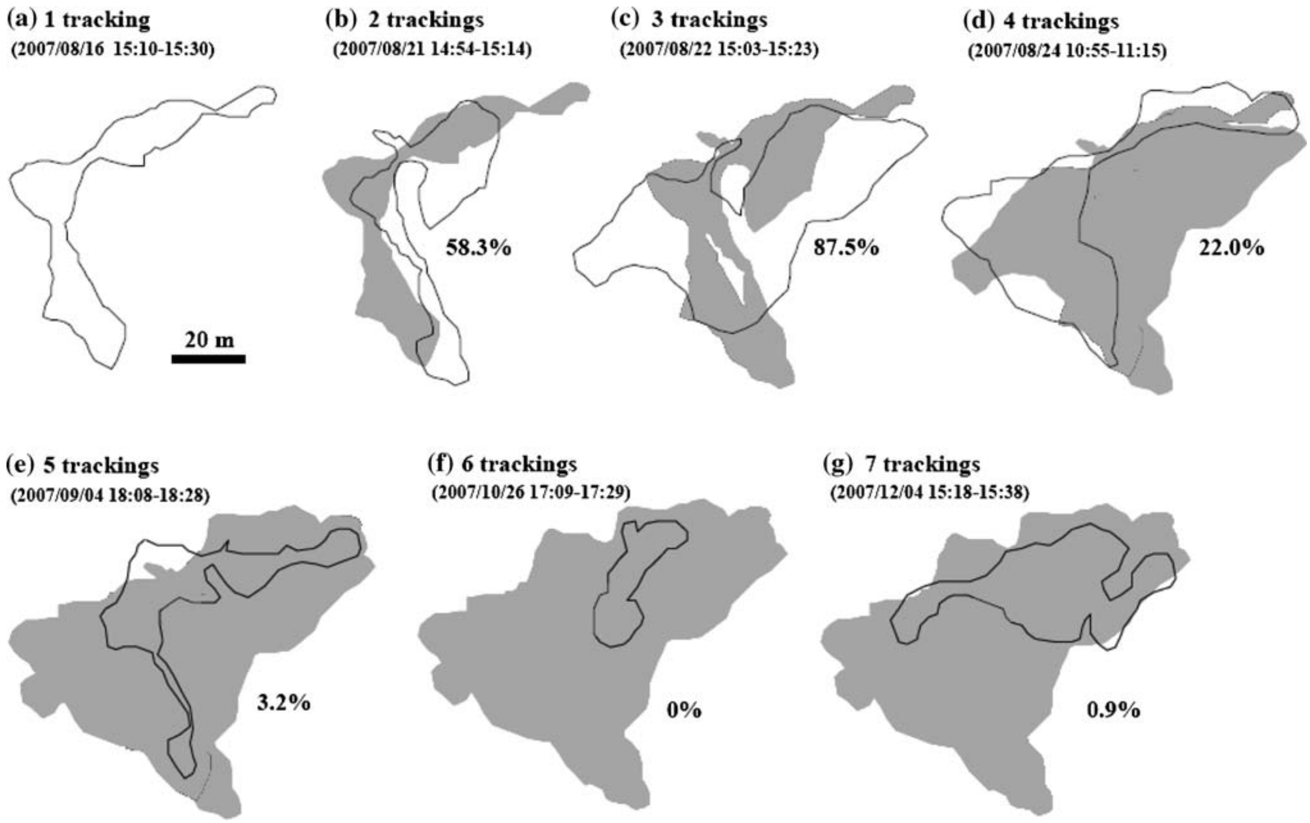

Fig. 2 Procedure of home range size estimation of *Lethrinus harak*. In this figure, seven trackings were obtained for the focal individual (31.0 cm TL). The *enclosed white* and *shaded areas* represent the estimated home range for the focal tracking and the estimated home range by using all trackings obtained just before the focal tracking, respectively. For the second to seventh trackings, the rates of additional home range size (see text for definition) are also shown as percentages (**b–g**)

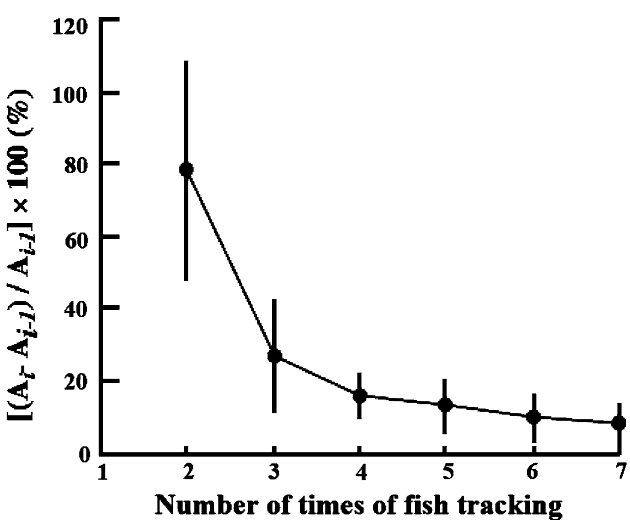

Fig. 3 Relationship between the number of trackings and the increase rate of the estimated home range size (see text for definition). *Bars* represent standard deviation ($n = 5$: 20.0–31.0 cm TL)

51.2% ± 8.5 SE; size class 4 = 32.5% ± 12.5 SE to 52.8% ± 11.7 SE). The home range overlap among same-sized individuals was significantly lower than that among different-sized individuals (one-way ANOVA, $P < 0.05$).

The home range size ranged from 690.8 to 4864.7 m^2. There was a significantly positive relationship between the home range size and the total length of the home range owner: $\log_{10}$(home range size) = 1.301 $\log_{10}$(TL) + 1.451 ($R^2 = 0.270$, $P < 0.05$) (Fig. 5).

Intraspecific interactions

Agonistic behavior tended to occur more frequently between same-sized individuals (Fig. 6) (same-sized individuals:different-sized individuals = 25.0%:0–8.3% for size class 1; 22.2%:0–20.0% for size class 2; 7.0%:0% for size class 3; 33.3%:0% for size class 4). Overall, significant agonistic behavior occurred more frequently between same-sized individuals than between different-sized individuals (2 × 2 contingency table analysis: $\chi^2 = 9.60$, $df = 1$, $P < 0.01$).

Feeding behavior

Sand was mainly used as the feeding site for all individuals in the study area (Table 2). One-way ANOVA revealed that there was no significant difference in substrate use as

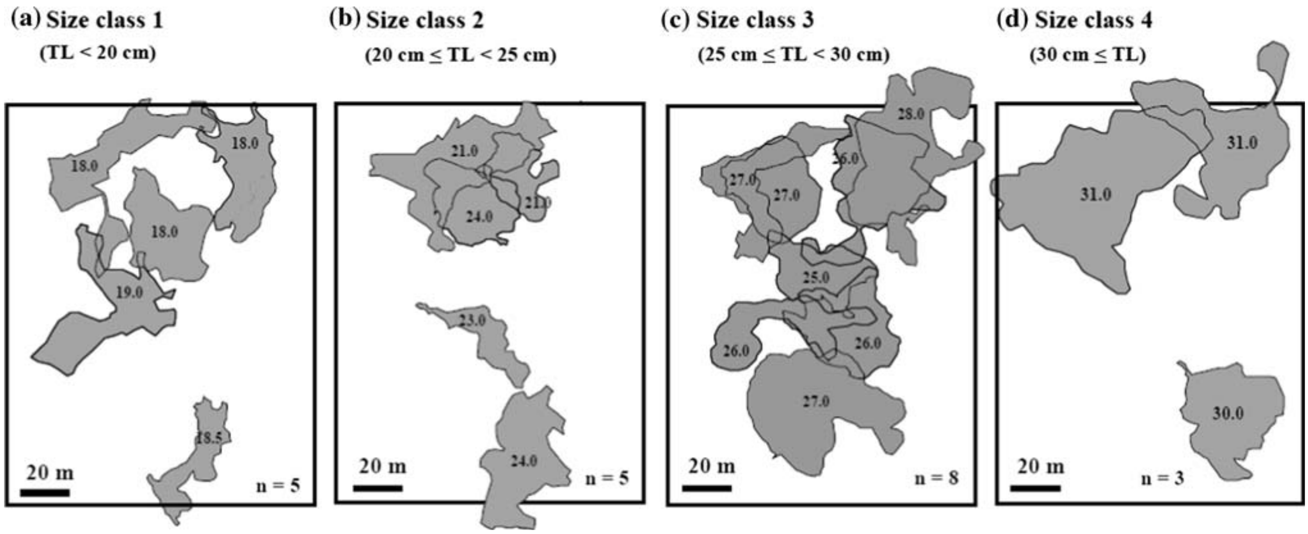

Fig. 4 Spatial arrangement of home ranges of *Lethrinus harak* in the quadrat (150 m × 200 m) ($n = 21$). *Areas* enclosed by lines are the home ranges for each size class (**a–d**). *Square* represents the quadrat (150 m × 200 m). *Numbers in areas* represent the total length of the individual (cm)

Table 1 Degree of home range overlap among the four size classes of *Lethrinus harak* (% ± SE)

Fish size class	*n*	Overlapping with same-sized individuals	Overlapping with different-sized individuals				
			Size class 1	Size class 2	Size class 3	Size class 4	Average
Size class 1 (TL < 20 cm)	5	2.7 ± 1.0	–	46.0 ± 15.6	67.0 ± 10.6	41.9 ± 14.0	51.6 ± 7.8
Size class 2 (20 cm ≤ TL < 25 cm)	5	26.3 ± 11.2	40.8 ± 8.8	–	71.5 ± 11.9	51.8 ± 17.3	54.7 ± 12.5
Size class 3 (25 cm ≤ TL < 30 cm)	8	46.2 ± 7.0	51.2 ± 8.5	40.7 ± 10.6	–	49.1 ± 15.0	47.0 ± 4.3
Size class 4 (30 cm ≤ TL)	3	6.0 ± 3.3	34.7 ± 11.4	32.5 ± 12.5	52.8 ± 11.7	–	40.0 ± 6.4
Average		20.3 ± 10.1					48.3 ± 3.2

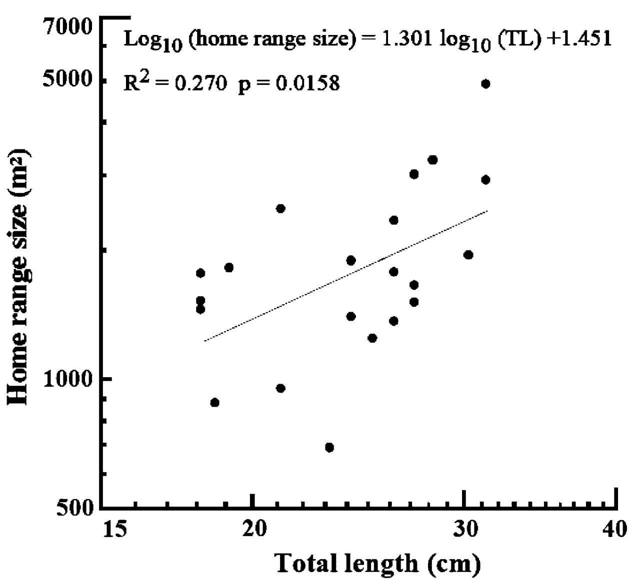

Fig. 5 Relationship between home range size and total length of home range resident of *Lethrinus harak* ($n = 21$)

feeding site among the four size classes ($P > 0.05$ for all substrates).

Discussion

Daytime site fidelity

The present study showed high daytime site fidelity for *Lethrinus harak*. Although lethrinid fishes are generally considered as nocturnal feeders, some lethrinid species are daytime feeders [24]. In this study, *L. harak* frequently dwelled on sandy bottom and caught benthic animals including crustaceans and mollusks at daytime during the study period (Nanami, unpublished data). Some marine fishes inhabit shallow area at daytime but move to other habitats at nighttime [25, 26]. There is a possibility that *L. harak* inhabit seagrass bed only at daytime. Nevertheless, as high and long-term daytime site fidelity of *L. harak* appears to be certain, it is reasonable to conclude that

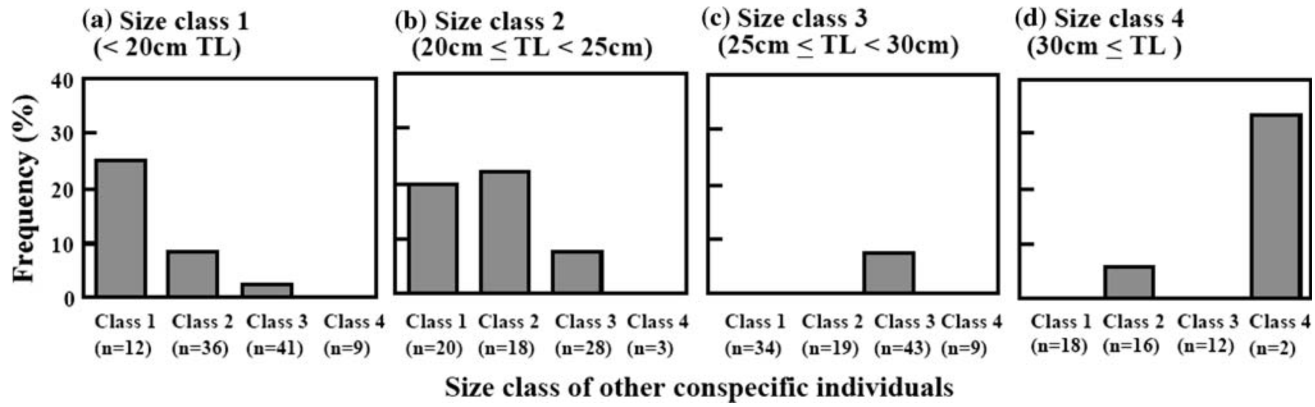

Fig. 6 Frequency distribution of intraspecific interactions between individuals of *Lethrinus harak*. *Bars* represent agonistic behavior. Individuals belonging to the same size classes were pooled for analyses. *Numbers in parenthesis* represent the observed number of intraspecific interactions

Table 2 Feeding sites of *Lethrinus harak* as percentage substrate use (±SD)

Size class	*n*	Foraging sites					
		Sand	Seagrass	Coral rubble	Rocks	Coral patches	Seaweed
Size class 1 (TL < 20 cm)	5	91.2 ± 10.6	8.8 ± 10.6	0	0	0	0
Size class 2 (20 cm < TL < 25 cm)	5	88.9 ± 5.1	9.3 ± 7.4	1.0 ± 2.3	0	0	0.7 ± 1.6
Size class 3 (25 cm < TL < 30 cm)	6[a]	83.7 ± 27.1	10.8 ± 15.7	0	0	5.6 ± 13.6	0
Size class 4 (30 cm < TL)	3	89.6 ± 12.0	2.0 ± 3.4	2.0 ± 3.4	3.9 ± 6.8	2.6 ± 4.4	0

[a] Although eight individuals were found in the study area, feeding behavior was found for six individuals in the size class

L. harak has high site fidelity. Such high site fidelity of lethrinid species has not been reported in the previous studies. In contrast, some previous studies demonstrated by using mark-recapture method that some individuals of two lethrinid species (*Lethrinus mahsena* and *L. miniatus*) showed long-distance movements at coastal Kenya, although the site fidelity of most individuals of the two lethrinid species was high [27, 28]. Thus, degree of site fidelity of lethrinid species might be different among species and/or localities. The present study was not able to detect nocturnal activity of *L. harak*, and site fidelity and home range size of the species at nighttime remains unclear. Another method such as ultrasonic telemetry, which does not rely on visual census, would be useful to detect nocturnal activity of the species in the future.

Spatial arrangement of home ranges in relation to intraspecific interactions

The present study demonstrates the size and spatial arrangement of home ranges of lethrinid species for the first time. In fishes that have a harem as a social behavioral system, territories of larger males enclose territories of smaller females, i.e., females cohabit within the male's territory [29]. Although some lethrinid species are considered to be protogynous hermaphrodites [4, 5, 30], the sex ratio (% female) increased for large size individuals (>ca. 30 cm) of *L. harak* [5, 6]. Thus, the possibility that large males enclose territories of smaller females seems minimal. Indeed, it is observed that larger-sized individuals of *L. harak* did not keep smaller-sized individuals in their territories, suggesting that territories of *L. harak* do not seem to exhibit a harem structure. Since the species forms spawning aggregations [1], the spatial arrangement of the home ranges of this species does not seem to be related to the spawning behavior.

Agonistic behavior occurred significantly more frequently between same-sized individuals whereas it was rarely found among different-sized individuals, and home ranges of same-sized individuals abutted whereas that of different-sized individuals overlapped. Thus, the home range of *L. harak* is considered as territory against same-sized individuals, not different-sized individuals.

Similar spatial arrangements of home ranges have been reported for a freshwater cichlid *Lobochilotes labiatus* [21] as well as the marine teleosts *Goniistius zonatus* [22] and *Lutjanus decussatus* [23], in which the spatial arrangement of territories was defined as "overlapping territory." Although the factors which are responsible for determining the overlapping territory of *L. harak* are beyond of the scope of the present study, several previous studies have suggested the ecological factors that are responsible for overlapping territories in fish [21, 22]. These studies have suggested that overlapping territory of fishes is concerned with feeding behavior, not with spawning behavior. *L. harak* was observed to feed frequently during the daytime and most individuals fed on prey on sandy sea bottom areas in the seagrass bed (Nanami, unpublished data). Since there was no significant difference in the foraging sites among the four size classes, the overlapping territory of the species might be maintained by the size-specific prey size difference. Stomach contents analysis would be useful to clarify the mechanisms that are responsible for the overlapping territory of *L. harak* in the future.

Based on the results of the present study, it is suggested that: (1) the maximum population density of the species can be estimated in a study area and (2) the density for each size class can be estimated independently. Further studies in terms of the generality of the behavioral traits (i.e., overlapping territory) and spawning behavior should be investigated in the future for effective management of this species. Since daytime site fidelity clearly occurs, appropriate setting of marine protected area (MPA) would be useful to protect the *L. harak* population. However, to be able to determine the appropriate size of the MPA, details of nighttime home range size are necessary.

Acknowledgments We are grateful to the staff of Ishigaki Tropical Station, Seikai National Fisheries Research Institute. Constructive comments on the manuscript from C. P. Norman and K. Yoseda were much appreciated. The present study complies with current laws in Japan.

References

1. Carpenter KE, Allen GR (1989) Emperor fishes and large-eye breams of the world (Family Lethrinidae). An annotated and illustrated catalogue of lethrinid species known to date. FAO species catalogue, vol 9. FAO, Rome
2. Ebisawa A (1990) Reproductive biology of *Lethrinus nebulosus* (Pisces: Lethrinidae) around Okinawan waters. Nippon Suisan Gakkaishi 56:1941–1954
3. Ebisawa A (1997) Some aspects of reproduction and sexuality in the spotcheek emperor, *Lethrinus rubrioperculatus*, in waters off the Ryukyu Islands. Ichthyol Res 44:201–212
4. Ebisawa A (1999) Reproductive and sexual characteristics in the Pacific yellowtail emperor, *Lethrinus atkinsoni*, in waters off the Ryukyu Islands. Ichthyol Res 46:341–358
5. Ebisawa A (2006) Reproductive and sexual characteristics in five *Lethrinus* species in waters off the Ryukyu Islands. Ichthyol Res 53:269–280
6. Kulmiye AJ, Ntiba MJ, Kisia SM (2002) Some aspects of the reproductive biology of the thumbprint emperor, *Lethrinus harak* (Forsskål, 1775), in Kenyan coastal waters. West Indian Ocean J Mar Sci 1:135–144
7. Bean K, Mapstone BD, Davies CR, Murchie CD, Williams AJ (2003) Gonad development and evidence of protogyny in the red-throat emperor on the Great Barrier Reef. J Fish Biol 62:299–310
8. Sumpton W, Brown I (2004) Reproductive biology of the red throat emperor *Lethrinus miniatus* (Pisces: Lethrinidae) from the southern Great Barrier Reef, Australia. Bull Mar Sci 74:423–432
9. Williams AJ, Davis CR, Mapstone BD (2006) Regional patterns in reproductive biology of *Lethrinus miniatus* on the Great Barrier reef. Mar Freshw Res 57:403–414
10. Kanashiro K (1998) Settlement and migration of early stage spangled emperor, *Lethrinus nebulosus* (Pisces: Lethrinidae) in the coastal waters off Okinawa Island, Japan. Nippon Suisan Gakkaishi 64:618–625
11. Arvedlund M, Takemura A (2006) The importance of chemical environmental cues for juvenile *Lethrinus nebulosus* Forsskål (Lethrinidae, Teleostei) when settling into their first benthic habitat. J Exp Mar Biol Ecol 338:112–122
12. Hiatt RW, Strasburg DW (1960) Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol Monogr 30:65–127
13. Carpenter KE (1996) Morphometric pattern and feeding mode in emperor fishes (Lethrinidae, Perciformes). In: Marcus LF, Corti M, Lay A, Naylor GJP (eds) Advances in morphometrics. NATO Advanced Science Series. Series A, Life Sciences, vol 284. Plenum Publishing, New York, pp 479–487
14. Holland KN, Lowe LG, Wetherbee BM (1996) Movements and dispersal patterns of blue trevally (*Caranx melampygus*) in a fisheries conservation zone. Fish Res 25:279–292
15. Zeller DC (1997) Home range and activity patterns of the coral trout *Plectropomus leopardus* (Serranidae). Mar Ecol Prog Ser 154:65–77
16. Zeller DC (1999) Ultrasonic telemetry: its application to coral reef fisheries research. Fish Bull 97:1058–1065
17. Kramer DL, Chapman MR (1999) Implications of fish home range size and relocation for marine reserve function. Environ Biol Fish 55:65–79
18. Parsons DM, Babcock RC, Hankin RKS, Wills TJ, Aitken JP, O'Dor RK, Jackson GD (2003) Snapper *Pagrus auratus* (Sparidae) home range dynamics: acoustic tagging studies in a marine reserve. Mar Ecol Prog Ser 262:253–265
19. Meyer CG, Holland KN (2005) Movement patterns, home range size and habitat utilization of the bluespine unicornfish, *Naso unicornis* (Acanthuridae) in a Hawaiian marine reserve. Environ Biol Fish 73:201–210
20. Meyer CG, Holland KN, Papastamatiou YP (2007) Seasonal and diel movements of giant trevally *Caranx ignobilis* at remote Hawaiian atolls: implications for the design of Marine protected areas. Mar Ecol Prog Ser 333:13–25
21. Kohda M, Tanida K (1996) Overlapping territory of the benthophagous cichlid fish, *Lobochilotes labiatus*, in Lake Tanganyika. Environ Biol Fish 45:13–20
22. Matsumoto K (2001) Overlapping territories of a benthophagous fish, *Goniistius zonatus* (Teleostei: Cheilodactylidae). Ecol Res 16:715–726
23. 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
24. Healey J (1997) Encyclopedia of Australian wildlife. Reader's Digest, Sydney
25. Holland KN, Peterson JD, Lowe CG, 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
26. Meyer CG, Holland KN, Wetherbee BM, Lowe CG (2000) Movement patterns, habitat utilization, home range size and site fidelity of whitesaddle goatfish, *Parupeneus porphyreus*, in a marine reserve. Environ Biol Fish 59:235–242

27. Kaunda-Arara B, Rose GA (2004) Out-migration of tagged fishes from marine reef National Parks to fisheries in coastal Kenya. Environ Biol Fish 70:363–372
28. Kaunda-Arara B, Rose GA (2004) Long-distance movements of coral reef fishes. Coral Reefs 23:410–412
29. Thresher RE (1984) Reproduction in reef fishes. TFH Publications, Neptune City
30. Young PC, Martin RB (1982) Evidence for protogynous hermaphroditism in some lethrinid fishes. J Fish Biol 21:475–484