Laboratory video recordings and underwater visual observations combined to reveal activity rhythm of red-spotted grouper and banded wrasse, and their natural assemblages

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Abstract The diel activity rhythm of red-spotted grouper *Epinephelus akaara* was studied both in captivity and in the wild. Behavior of solitary grouper (58 to 397 mm in total length) in a tank was video recorded using infrared illuminators under 11L/10D and two 1.5-h twilight transition periods, and was compared to that of banded wrasse *Halichoeres poecilopterus*, a typical diurnal fish. Underwater observations using SCUBA were also conducted in their natural habitat to reveal the behavioral activity together with a visual census of adjacent fish and crustacean assemblages. Red-spotted grouper showed a strong nocturnal activity in a tank regardless of body size as opposed to the strongly diurnal banded wrasse. Activity of groupers in natural waters was high at dawn and dusk, low at noon, and only a few individuals were observed at night. Visual census in the habitat revealed that fish abundance and species richness was highest at noon, lowest at night, and intermediate at dawn and dusk. The opposite trend was found in crustacean assemblages. Absence of groupers at night may reflect their nocturnal feeding migration away from the study area. Alternatively, the crepuscular activity of groupers in the wild is suggested to be an adaptation to feed on small fishes that shift between daytime activity and nighttime rest and/or on nocturnal crustaceans that show the opposite activity pattern.

Keywords Crepuscular activity, Diel variation, *Epinephelus akaara*, Fish assemblages, Twilight, Underwater visual census

Introduction

Groupers, the subfamily Epinephelinae of the family Serranidae, are generally at or near the top trophic level of the food chain and thus play an important role in reef ecosystems through top-down control (Shpigel and Fishelson 1989). They are also important food sources especially in tropical and subtropical regions, where fishing often results in over-exploitation of this group of fish. The depressed fisheries have stimulated studies of their feeding (Harmelin-Vivien and Bouchon 1976), migration and mating (Bolden 2000; Whaylen et al. 2004). Such basic biological information has been applied to the management of grouper populations, as is reported in the successful population management of the red hind (*Epinephelus guttatus*) (Beets and Friedlander 1999).

Red-spotted grouper (*Epinephelus akaara*), reported from 20°–39°N and 109°–143°E, is one of 85 species of *Epinephelus* groupers and is found in the northern margin of the distribution of this genus (Bailly N et al. 2011, http://www.fishbase.org. Cited 26 Feb 2011). Because of its high commercial value and restricted distribution range, populations of this species are highly depleted and the species is ranked as endangered in the International Union for Conservation of Nature and Natural Resources (ICUN) Red List of Threatened Species (Morris et al. 2000). Although it is intensively targeted for aquaculture in China (Ou-yang et al. 2010) and stock enhancement in Japan (Kayano 2001), only limited information is available on its behavior and ecology. Underwater visual census, however, revealed that this species is relatively abundant in its northern distribution margins, *i.e.*, Wakasa Bay, Sea of Japan (Fig. 1; Masuda 2008; Masuda et al. 2010), providing opportunities to conduct *in situ* observations and laboratory studies.

In general fish behavioral and ecological studies are biased to diurnal aspects despite that some species are more active at other times of the day (Griffiths 2001), and this focus may misdirect understanding of the ecology and conservational management of the target species. Red-spotted grouper has a local name "yonezu" in the Sea of Japan area, meaning that "not sleeping at night". Indeed fishermen often catch large individuals of this species while fishing in late evenings. Present research is aimed to reveal the diel activities of red-spotted grouper both in captivity and in the wild. Knowledge on such behavioral traits together with the diel change of fish assemblages in their habitat may well be applicable to the management of its population. Behavioral rhythm in captivity was also analyzed in banded wrasse (*Halichoeres poecilopterus*) collected in the same area as an example of a typical diurnal fish for comparison.

Materials and Methods

Video recording in laboratory

Eleven individuals of red-spotted grouper were collected from August to October 2004 and August to September 2005; eight of them were captured using cage traps, one was caught by hook and line fishing and two were purchased from a local fish market providing live individuals caught in local set nets. All of them were from Maizuru Bay (35°29'N lat. and 135°22'E long.) and adjacent areas (Fig. 1). Total length (TL) and body weight of the groupers ranged from 58 to 397 mm and 5.3 to 823 g, respectively. Five individuals of banded wrasse were also collected using cage traps in Maizuru Bay from August to September 2005. Their TL and body weight ranged from 173 to 261 mm and 61 to 205 g, respectively. Following capture each individual was initially stocked in a 500l black polycarbonate tank and then within a 24 hour period moved to the observation tank.

A transparent acrylic tank (45 × 90 × 45 cm height) was used as an observation tank. Within the observation tank a structure with two compartments was made by arranging ten pieces of red bricks (10.5 × 22 × 5.5 cm each). The inner dimension of the compartments was 11 × 36 × 24 cm height and 8 × 24 ×

11 cm height for the large and the small compartment, respectively. The tank was filled with filtered seawater with a depth of 37 cm. Water was exchanged with a rate of 1000 ml/min and aeration was provided at a rate of 200 ml/min. The observation tank with its adjacent area (3.5 × 2.5 m) was surrounded by a black curtain to minimize visual disturbances from the outside. The recording system was similar to that reported by Yokota et al. (2007a). In brief, a video camera (AI18CIR-AFM, HOGA, Kyoto, Japan) and an infrared illuminator (C4-170, HOGA) were set inside the curtain. The camera was connected to a time-lapse video recorder (WDV-960H/100, HOGA) and a TV monitor (LC-13E1-S, Sharp, Tokyo, Japan). Behavior of fish was recorded for 48 hours starting from daytime (09:00 to 15:00 h). A 24-hour event was recorded in a two-hour videotape using the recorder. The infrared illuminator was on throughout the observation period, providing illumination during hours of darkness. During daylight hours three 100 W light bulbs were turned on at 05:30 h and their intensity gradually increased until 07:00 h, and decreased from 18:00 to 19:30 h using a light manager (NQ28641, Matsushita Electric Industrial, Kadoma, Japan) (Fig. 2a). The photoperiod approximately corresponded with the one observed in the season at which fish were collected. The light intensity in the daytime (435 lux) was much lower than the one in the field, yet preliminary observation revealed that red-spotted grouper showed normal daytime acitivity at this level of light intensity. The total length and body weight of fish were measured after the video recording.

Videotape recordings of the second day after moving the fish into the observation tank were analyzed, as a preliminary observation revealed that the behavior on the first day tended to be variable depending on the individual. As the criteria of activity, the time at large from the structure was measured hourly for each individual. Because the recording was conducted at a speed of 1/12 of the standard speed, a video replay for 5 minutes provided a 1-hour event. The time at large from the structure was measured by using a stopwatch, and was multiplied by 12 to estimate the actual time at large. Fish were considered to be at large when more than half of the body was outside the structure. The hourly number of turning was also counted as a criterion of activity. Fish was considered to have turned when the direction of the body axis changed *c.* 180°. Criteria of the activity (time at large from the structure and the number of turns) were compared between daytime (08:00 – 16:00 h) and night (20:00 – 04:00 h), excluding dawn and dusk, for each fish species using the Mann-Whitney U-test.

As the criteria of nocturnal activity, a nocturnal at large index and a nocturnal turning index were defined as follows:

Nocturnal at large index

= (time at large during night) / {(time at large during night) + (time at large during day)}

Nocturnal turning index

= (the number of turning during night) / {(the number of turning during night) + (the number of turning during day)}

Both indexes were expected to be above 0.5 when fish were nocturnal. Correlation between fish total length and the above indexes were analyzed by Spearman's signed rank test.

Underwater observations

Underwater observations were conducted during 20 scuba dives from 5 to 30 October 2003 near Otomi, Fukui, Japan (35°32'N lat. and 135°30'E long.; Fig. 1). The location has been maintained as a leisure diving area and receives relatively low fishing pressure, as spear fishing with SCUBA is forbidden by local regulations. At the study site the shore is covered by a breakwater of concrete blocks. Shallow areas are dominated by rocky reef and offshore areas have a sandy substrate. The research area included both natural vertical structure with large rocks and artificial structure such as small shipwrecks. The maximum depth of the observation area was 5 m. Observations were conducted along a pre-determined course of *c.* 300 m in length (Fig. 1c). All the red-spotted grouper found within 3 m distance on both sides of the course (thus 1800 m^2 in area) were recorded. When a grouper was found an observation was conducted for a minimum of 5 minutes. After visually estimating and recording the TL of the fish, the height of the fish from the sea bottom was estimated and recorded. The total distance traveled by the fish and the total number of body turns during the 5 minutes was also recorded.

Observations were conducted during four different time periods; morning starting from 05:30 to 06:15 h, noon starting from 12:00 h, evening starting from 17:00 to 17:45 h, and night starting either at 20:30 h or 00:00 h. Observations were conducted five times in each time period, and each observation took 75 to 90 min. Underwater flashlights, used for the nighttime observations, were occasionally turned on and off to confirm that they did not attract or repel fish to any great extent, however, we avoided directly shining the light on a fish for long periods to minimize disturbance. Light intensity measured at water surface ranged from < 0.1 – 30000 lux in mornings, 8000 – 80000 lux during noon periods, 900 – 0 in evenings, and < 0.1 at nights. Note, however, that attenuation coefficient of sea water in this area is ca. 0.27, and thus light will be attenuated to about 10% at 5 m depth from the surface (Nishigaki et al. 2005). Sea water temperature ranged 21.1 – 23.4 °C. The number of groupers, their TL, height from the bottom, distance traveled and number of turns were compared among different time periods using Kruskal-Wallis test.

Visual census was also conducted along the course for 12 times, 3 times in each time period. The number of individuals of all fish and crustacean species found within a distance of 3 m on either side of the census course were recorded. The abundance and species richness of the fish and crustacean species were compared among time periods using ANOVA followed by Tukey's HSD test. Abundance data was $\log_{10}(x+1)$ transformed prior to the analysis to improve the homogeneity of variance.

Results

Video recording in the laboratory

Overall, the grouper showed a clear nocturnal activity whereas the wrasse showed a typical diurnal activity. In groupers the time at large from the structure gradually decreased from 80% at midnight to 60% at 05:00 h, then rapidly decreased during the dawn period and remained at a constant value of *c*. 25 %, increased again during dusk twilight reaching a plateau at 80% (Fig. 2b). Their time at large at night (*i.e.* from 20:00 to 04:00 h) was significantly higher than in the daytime (08:00 to 16:00 h) ($p<0.05$, Mann-Whitney U-test). Wrasse always stayed inside the structure from midnight to 05:00 h, time at large from the structure was above 80% at dawn, relatively high (*c.* 40%) during the daytime, very high activity again at dusk, and no activity at all after 20:00 h. The time at large in darkness was significantly lower than that in the daytime in wrasse ($p<0.05$, Mann-Whitney U-test). The number of turns showed similar trends as that of the time at large both in the grouper and wrasse (Fig. 2c). The number of turns was significantly fewer in the daytime in the grouper, whereas the opposite was true for the wrasse ($p<0.05$, Mann-Whitney U-test).

All the red-spotted grouper showed a nocturnal at large index of more than 0.5, and ten out of eleven individuals showed nocturnal turning index of more than 0.5 (Fig. 3). Neither index had a significant correlation with fish total length ($p = 0.23$ and 0.39 for at large and turning, respectively).

Underwater observations

Most groupers were found near structures such as a large rock. In most cases they were either adjacent to a rock (Fig. 4a) or under a ledge. More individuals stayed off the bottom in the morning and in the evening ($p<0.05$, Kruskal-Wallis test followed by Dunnet test) (Fig. 4b). There was no major shift of distribution between the different time periods except that more individuals tended to be found over the sand area in the morning.

Most groupers were found during the morning observation period, followed by noon, evening, and fewest at night (Fig. 5a). Significantly more individuals were found in the morning than at night ($p<0.05$, Kruskal-Wallis test followed by Dunnet test). The TL of grouper ranged from 140 to 240 mm (Fig. 5b). TLs of grouper found in the morning and evening were significantly smaller than those found at night ($p<0.05$, Kruskal-Wallis test followed by Dunnet test). The average distance traveled was significantly longer in the evening than in the noon and at night (Fig. 5c; $p<0.05$, Kruskal-Wallis test followed by Dunnet test), and exactly the same trend was observed in the number of turns (Fig. 5d). The height of hovering (gently swimming while remaining largely stationary) was significantly higher in the morning and evening than compared to those at night (Fig. 5e). At the beginning of the morning observation when the light intensity was still low, groupers often stayed under the ledge or settled on the bottom, and then more individuals were found in the water column as the light intensity increased.

Feeding behavior was observed as follows. One grouper was observed to bite an octopus and another to try to consume a rabbitfish *Siganus fuscescens* juvenile in the morning. One grouper in the daytime ingested a leg of a shore swimming crab *Charybdis japonica* but regurgitated it. One individual was observed to attack a school of anchovy *Engraulis japonicus* in the evening.

A total of 37 fish species were identified during the surveys of fish community, among which 32 species overlapped with the fishes observed in Nagahama, Maizuru reported by Masuda (2008). The five numerically dominant fish species were Japanese anchovy, rabbitfish, pygmy filefish *Rudarius ercodes*, rainbow wrasse *Halichoeres tenuispinnis* and barface cardinalfish *Apogon semilineatus* with this order (Table 1). Most species tended to be abundant in noon and morning but rare during evening and night, and this tendency was clear in labrid species. Scorpionfish *Scorpaenopsis cirrosa*, rockfish *Sebastiscus marmoratus* and barface cardinal fish tended to be few during the noon period with no significant difference. The number of fish species and of individuals was highest at noon, followed by morning, evening and fewest at night (Fig. 6a, b). The opposite trend was found in the number of crustacean species and individuals.

Anchovy and rabbitfish formed large schools during midday (Fig. 4c). Such schools were absent at night and rabbitfish were only found using seaweed or behind other structures as cover at night (Fig. 4d). In the early morning rabbitfish started to form schools as the light intensity increased (Fig. 4e). Few fish species were observed to be active at night except for black rockfish and barface cardinal fish remaining motionless in the water column, and a conger eel that moved at night (Fig. 4f).

Discussion

Video analysis revealed the typical nocturnal activity of red-spotted grouper with activity decreasing at dawn and increasing during dusk. Our underwater observation of distance moved, number of turns and the distance of grouper from the bottom suggest that this species is most active during dusk and dawn; however, we found only four individuals at night. The relatively few number of groupers found at night suggest that most individuals had left their daytime habitat, presumably for a feeding ground. This speculation is supported by the findings by Itani et al. (2005) who tracked red-spotted grouper using acoustic telemetry; they successfully tracked two individuals released at an offshore artificial reef and found that the number of received signals decrease after sunset and increase after sunrise, suggesting nocturnal feeding trip outside the range of the fixed receiver. Further acoustic telemetry tracking studies using several signal receivers located in a wider range of area, as have been conducted in other species of *Epinephelus* groupers (Lembo et al. 2002; Eklund and Schull 2001), should provide better documentation of their nocturnal migration.

Video analysis also revealed that banded wrasse in a tank was most active at dawn and dusk, relatively active in the daytime, and showed essentially no activity at night. Most wrasses are considered typical diurnal fish (Helfman 1993). Gerkema et al. (2000) reported that yellow wrasses (*Halichoeres chrysus*) showed clear daytime activity and disappeared in the sand substrate before lights went off, suggesting the internal rhythm adjusted to the conditioned 12:12 light-dark cycle. Domm and Domm (1973) found labrid fishes to disappear first in dusk and appear latest in dawn in a coral reef fish community in the Great Barrier Reef. Arendt et al. (2001) revealed diurnal activity and nocturnal quiescence in *Tautoga onitis*, another labrid fish, in Chesapeake Bay. High activity at dawn and dusk in the banded wrasse may represent such a shift of activity rhythm. Alternatively, it may be related to their feeding activity, as many piscivorous and planktivorous fishes are crepuscular feeders. Hobson and Chess (1976) revealed that relatively large crustaceans (mysids, gammarideans) swim up from the bottom at 20 to 40 minutes after the sunset. Therefore planktivores are likely to be actively feeding at that time of the day. High activity of banded wrasse in our laboratory observations may also reflect such a feeding tendency at dawn and dusk. Furthermore, diel feeding rhythm is reported to change seasonally in European sea bass (*Dicentrachus labrax*) and gilthead sea bream (*Sparus aurata*) (Reviewed by López-Olmeda and Sánchez-Vázquez 2010), implying that seasonal observation would be required to confirm a species-specific diel activity.

Thedinga et al. (2011) emphasized the importance of conducting diel sampling in order to properly evaluate nearshore fish assemblages. Research studying diel variations of fish abundance has reported either replacement of species between day and night typically observed in coral reef and seagrass habitats (Hobson 1972; Robblee and Zieman 1984), increased number was observed in temperate shallow waters at night (Horn 1980; Griffiths 2001) or reduced abundance in a mangrove habitat (Rooker and Dennis 1991) and a temperate kelp forest (Ebeling and Bray 1976) at night. Visual census in the present research revealed that most fishes were more abundant in the daytime and few at night, with typical examples in pomacentrid, girellid, labrid, gobiid and siganid species, whereas the opposite but non-significant trend was observed in scorpaenid and apogonid species. Robblee and Zieman (1984) suggested that active nocturnal fish were all carnivores equipped with large eyes and mouths; rockfish and barface cardinal fish in the present research fit in this category. Conger eel found at night in the present study is also a nocturnal predator but relies on olfaction rather than vision for their feeding, as is typically observed in Anguilliformes (Hobson 1974; Dou and Tsukamoto 2003).

Major prey items of red-spotted grouper are reported to be crustaceans and small fishes (Tamaki 1981; Kayano 2001) and our observations of their feeding confirmed that. Crepuscular activity of the grouper may optimize feeding on crustacean preys that become active in darkness or to feed on small fishes that shift between diurnal activity and nighttime rest in dawn and dusk. La Mesa et al. (2002) assessed microhabitat preferences in dusky grouper *Epinephelus marginatus* and found that this species prefers cavities and recesses and stays close to the bottom, in contrast to two other serranids *Serranus cabrilla* and *S. scriba*. This is coincident with our observations on red-spotted grouper during daytime and is likely to be a common feature of *Epinephelus* groupers.

We expected to see some ontogenetic shift from daytime to nocturnal activity in the red-spotted grouper but failed to find any such shift in the size range from 58 to 397 mm TL. Tamaki (2000) reported that red-spotted grouper recruit from offshore to coastal shallow (< 5 m in depth) water at 80-100 mm TL, then gradually shift their habitat to deeper waters. Hobson and Chess (1976) reported that olive rockfish *Sebastes serranoides* shifts from diurnal to nocturnal feeding at about 55 mm TL. Such a shift in the grouper might have occurred at a smaller stage than the size range at which we conducted our observations. Because it is difficult to attain wild individuals smaller than 58 mm TL, further research should be conducted using hatchery-reared grouper juveniles, yet they might show a distinct behavioral rhythm from the wild counterpart (Yokota et al. 2007b).

Red-spotted grouper typically shows protogynous hermaphroditism changing from female to male at about 30 cm TL, although small size (= 18 cm TL) males and large size (= 40 cm TL) females have also been reported (Tanaka et al. 1990). Most of the red-spotted grouper found in our research are likely to be either immature or females judging from the size range (14-24 cm TL). Larger individuals are more common in offshore reefs (Masuda R, unpublished data).

Despite that the red-spotted grouper is listed as an Endangered species in IUCN Red List, this species seems to be relatively abundant in Wakasa Bay, Sea of Japan. The present visual census in Otomi recorded 8.6, 6.6, 5.2 and 0.8 individuals in the 1800 m^2 area in morning, noon, evening and night, respectively, and the average density would be estimated as 2.97×10^{-3} m^{-2}. In our previous studies the density of this species estimated in the daytime was 3.19×10^{-4} m^{-2} in a rocky reef habitat off Nagahama, Maizuru (asterisk in Fig. 1b, Masuda 2008) and 2.19×10^{-3} m^{-2} in the habitat of artificial reefs deployed in Nagahama (Masuda et al. 2010). The relatively high density suggests that there is a major spawning biomass in the Sea of Japan. It is therefore important to protect such spawning stocks probably located along offshore reefs for the management of red-spotted grouper.

Groupers are generally capable predators for piscine prey especially when they attain large enough sizes (St John 1999). Recent loss of algae and kelp vegetations in rocky reef is partly attributable to the increased feeding pressure by herbivorous fishes such as rabbitfish (Yamauchi et al. 2006). Conservation of groupers and other top predators may thus partially mitigate the loss of algal vegetation and maintain healthy and productive rocky reef ecosystems. Furthermore, the coloration of red-spotted grouper, *i.e.* red-orange spots on violet brown background with vague and irregular vertical bands on its trunk, is likely to work as an effective camouflage in surroundings with *Sargassum* spp. and other brown algae vegetation. Therefore conservation of this species should be combined with that of brown algae. Collectively we suggest that the implementation of no-take marine reserves focusing on ecosystem protection is the most appropriate approach as a protection measure of red-spotted grouper and its habitat. For the implementation of adequate marine protected areas further study is required to reveal the range of habitat utilization covering any seasonal/reproductive migration of red-spotted grouper.

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Figure captions

Fig. 1 (a), (b) Location of the study area for sample collections in Maizuru and underwater observations in Otomi, Wakasa Bay, Sea of Japan. (c) Schematic drawing of the area for underwater observations in Otomi. Major underwater structure such as ship wrecks and large rocks are shown in dark grey, and the thick line is the course taken by the divers.

Fig. 2 (a) Light intensity during the laboratory video recording. (b) Average (±SE) proportion of time at large from the structure in the red-spotted grouper (n=11) and the banded wrasse (n=5). (c) Average (±SE) number of turns per hour in the red-spotted grouper (n=11) and the banded wrasse (n=5).

Fig. 3 Nocturnal activity represented by at large from the structure and the number of turns in relation to the total length of the red-spotted grouper.

Fig. 4 (a) Red-spotted grouper at noon, (b) red spotted grouper in the morning, (c) rabbitfish in noon, (d) rabbitfish sleeping at midnight, (e) rabbitfish started to form a school in morning in a school of cardinal fish, (f) conger eel actively moving in midnight. All the photographs were taken by the senior author in and around the observation area at Otomi.

Fig. 5 The average, range and quartiles in (a) the number of individuals, (b) total length, (c) distance traveled, (d) the number of turns and (e) the height off the bottom in the red-spotted grouper found in relation to time of the day.

Fig. 6 The average (±SE) number of (a) species and (b) individuals in fishes and crustaceans found along the transect at Otomi.

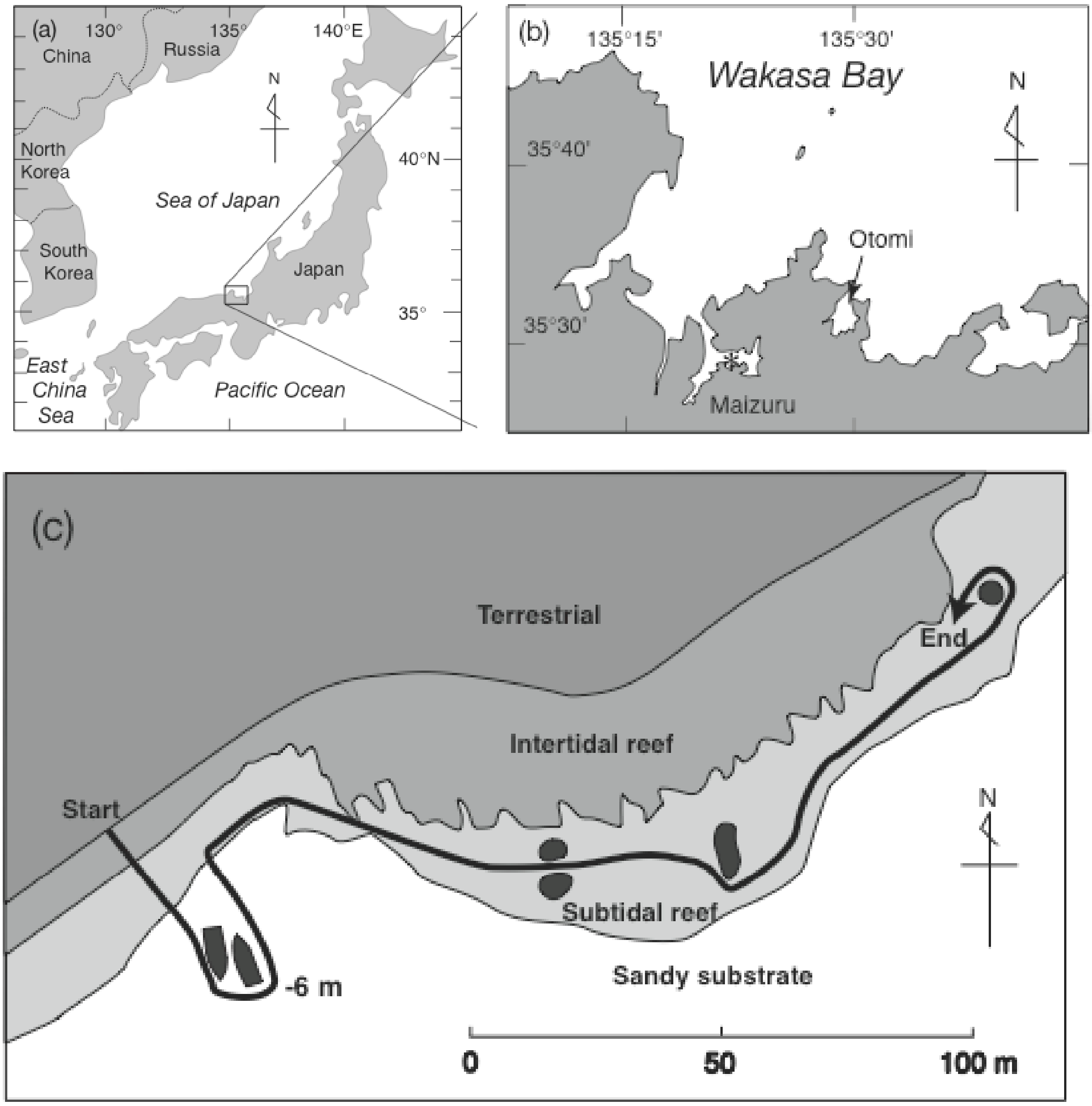
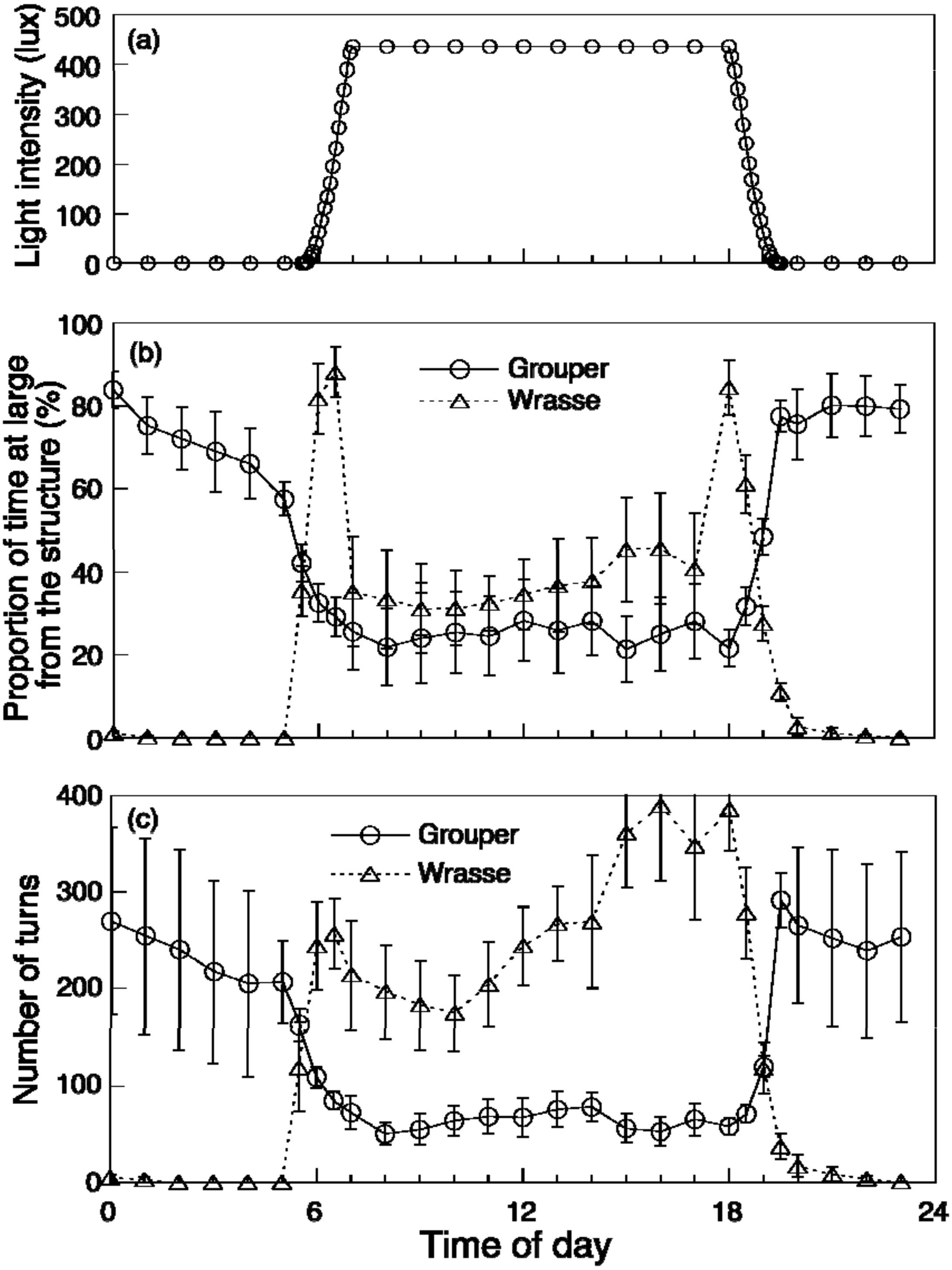
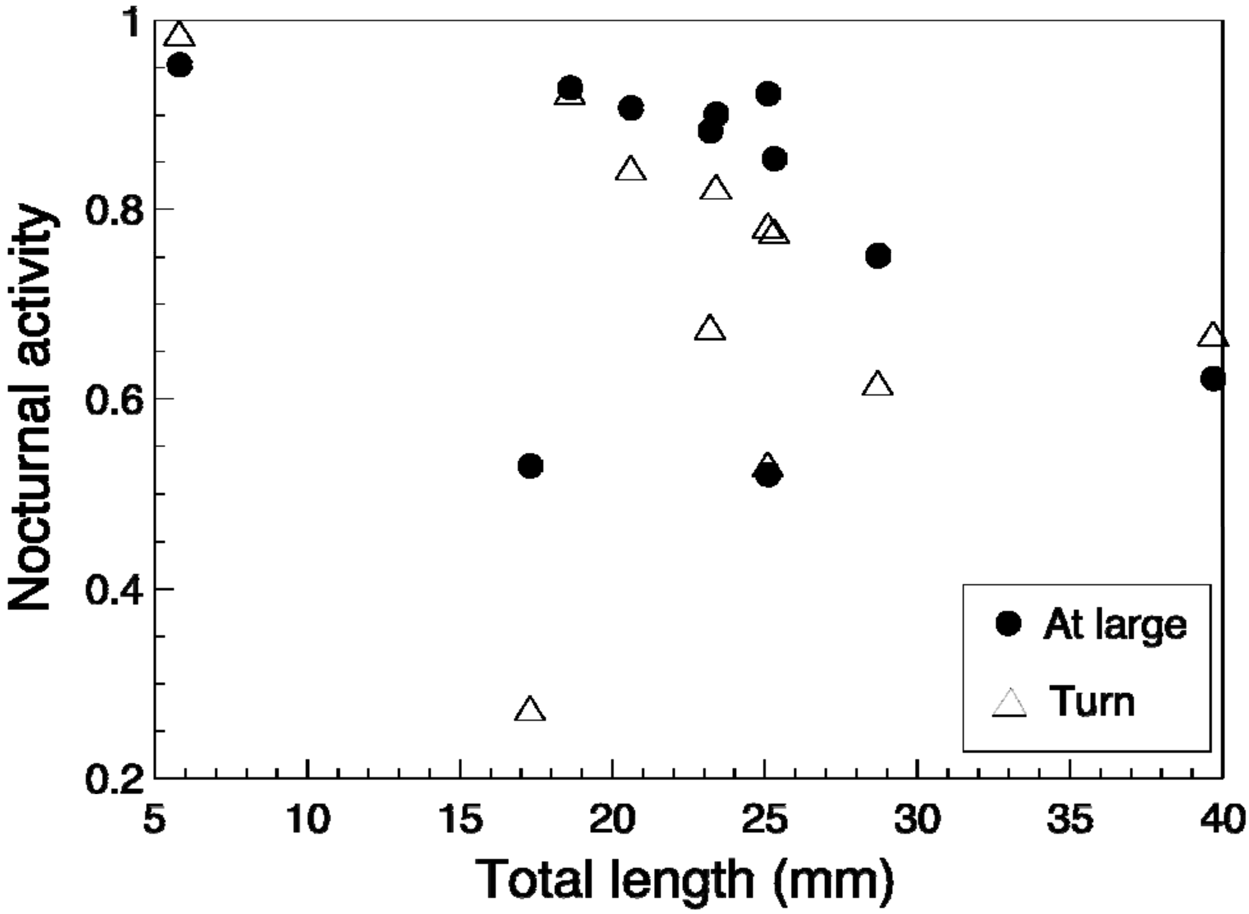

(a)
130°
135°
140°E
China
Russia
N
North Korea
40°N
Sea of Japan
South Korea
Japan
35°
East China Sea
Pacific Ocean
(b)
135°15'
135°30'
Wakasa Bay
N
35°40'
Otomi
35°30'
Maizuru
(c)
Terrestrial
End
Intertidal reef
Start
N
Subtidal reef
-6 m
Sandy substrate
0
50
100 m

Fig. 1



(a)
Light intensity (lux)
500
400
300
200
100
0
(b)
Grouper
Wrasse
Proportion of time at large from the structure (%)
100
80
60
40
20
0
(c)
Grouper
Wrasse
Number of turns
400
300
200
100
0
0
6
12
18
24
Time of day

Fig. 2



Nocturnal activity
1
0.8
0.6
0.4
0.2
5
10
15
20
25
30
35
40
Total length (mm)
At large
Turn

Fig. 3

(a)

QuickTimeý Ç²
êLí£ÉvÉçÉOÉâÉÄ
Ç™Ç±ÇÃÉsÉNÉ`ÉÉÇ¾å©ÇÈÇžÇ½Ç…ÇÕïKóvÇ-ÇÅB

(b)

QuickTimeý Ç²
êLí£ÉvÉçÉOÉâÉÄ
Ç™Ç±ÇÃÉsÉNÉ`ÉÉÇ¾å©ÇÈÇžÇ½Ç…ÇÕïKóvÇ-ÇÅB

(c)

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(d)

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(e)

QuickTimeý Ç²
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Ç™Ç±ÇÃÉsÉNÉ`ÉÉÇ¾å©ÇÈÇžÇ½Ç…ÇÕïKóvÇ-ÇÅB

(f)

QuickTimeý Ç²
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Ç™Ç±ÇÃÉsÉNÉ`ÉÉÇ¾å©ÇÈÇžÇ½Ç…ÇÕïKóvÇ-ÇÅB

Fig. 4

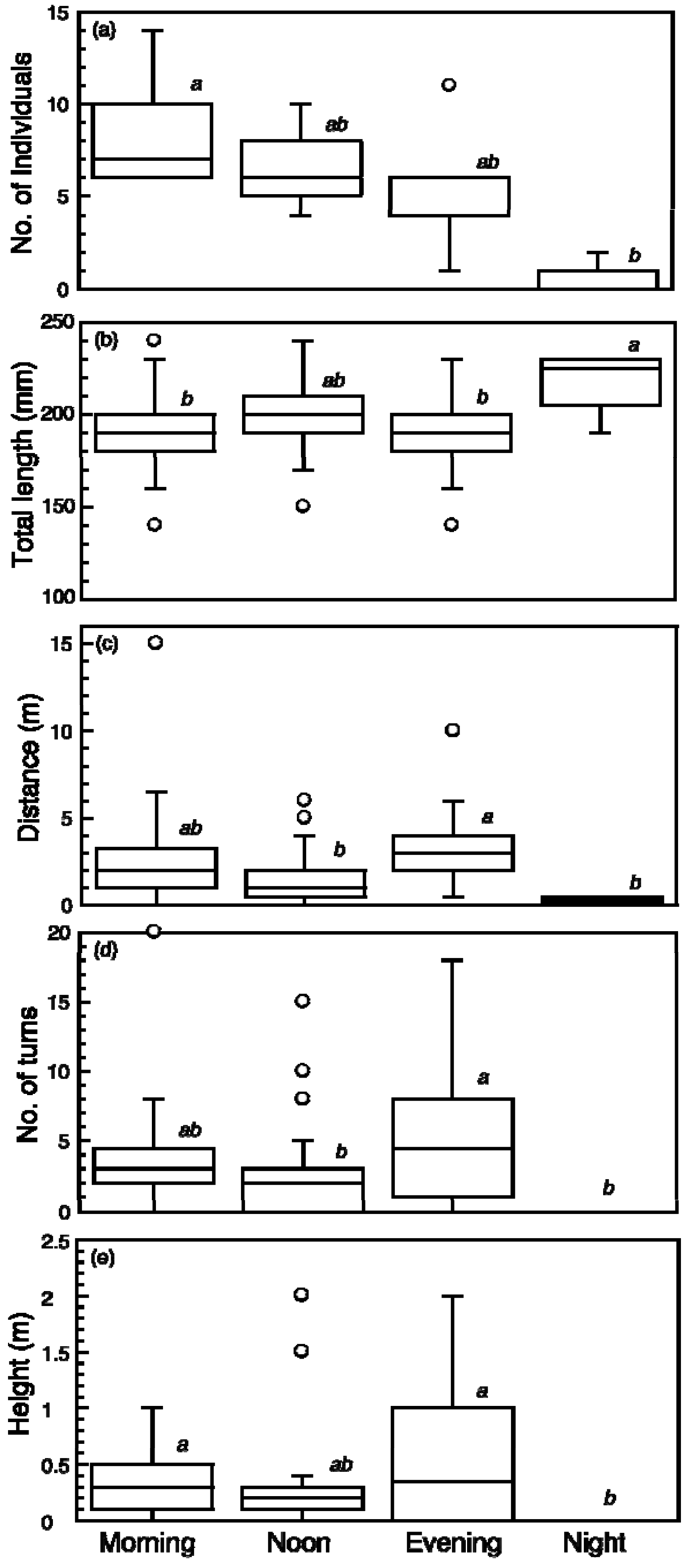
(a)
No. of Individuals
15
10
5
0
a
ab
ab
b
(b)
Total length (mm)
250
200
150
100
b
ab
b
a
(c)
Distance (m)
15
10
5
0
ab
b
a
b
(d)
No. of turns
20
15
10
5
0
ab
b
a
b
(e)
Height (m)
2.5
2
1.5
1
0.5
0
a
ab
a
b
Morning
Noon
Evening
Night

Fig. 5

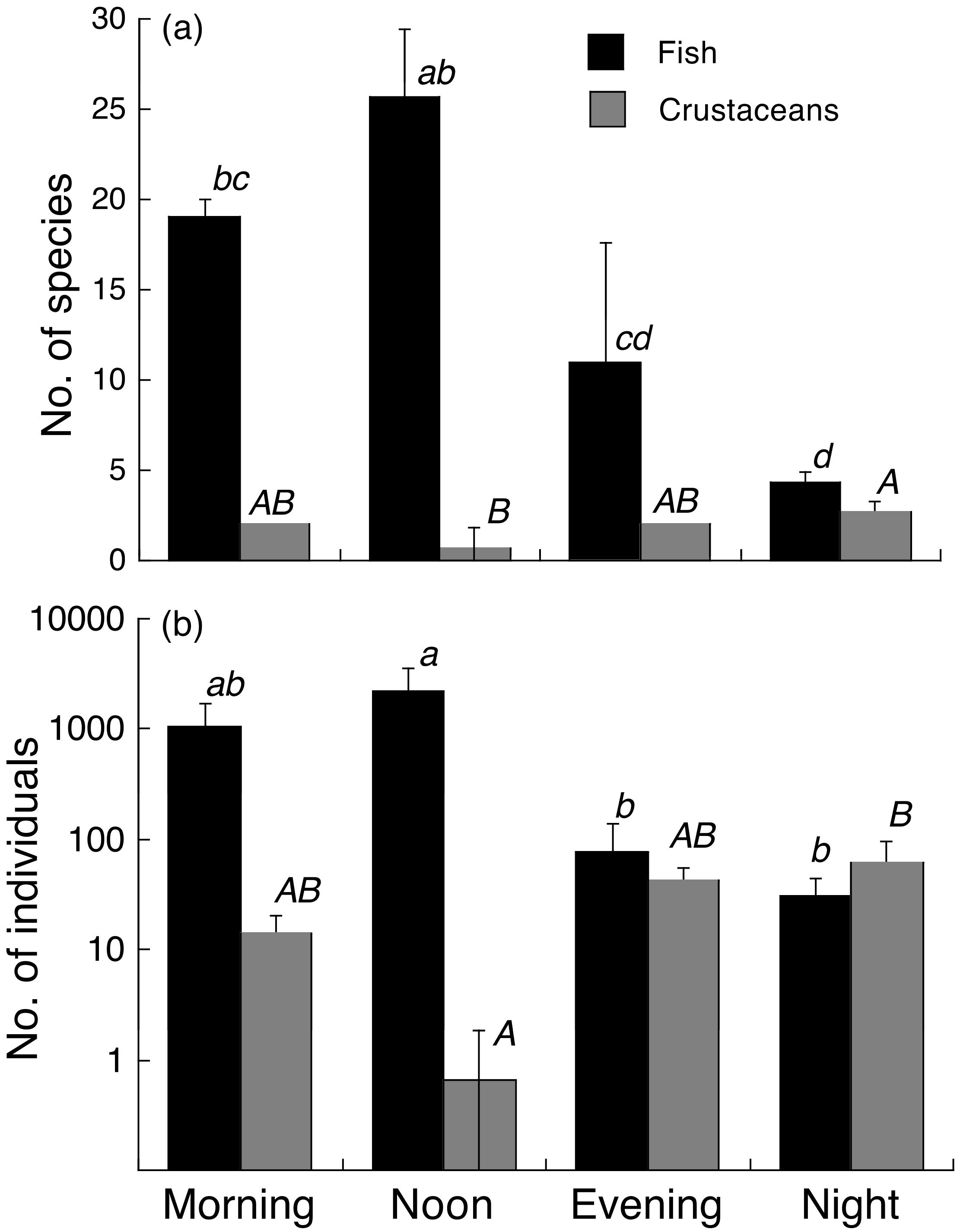
(a)
Fish
Crustaceans
No. of species
30
25
20
15
10
5
0
bc
AB
ab
B
cd
AB
d
A
(b)
No. of individuals
10000
1000
100
10
1
ab
AB
a
A
b
AB
b
B
Morning
Noon
Evening
Night

Fig. 6

TABLE 1. Families and species of fish found in the visual census, as well as the mean body length, size range, and mean ± SE number of specimens observed. Only species which were observed three times or more are included in the table.

Family	Species	Body length (cm)		No. of individuals, mean ± SE			
		Mean	Range	Morning	Noon	Evening	Night
Engraulidae	*Engraulis japonicus*	3.5	2–5	450±290	1400±720	0	0
Scorpaenidae	*Scorpaenopsis cirrosa*	20.0	18–25	1.0±1.0	0.33±0.33	0	0.67±0.33
	Sebastiscus marmoratus	17.6	14-25	2.3±0.67	0.67±0.33	1.0±0.58	1.3±0.88
	Sebastes inermis	13.1	6–18	2.3±0.88 ^{ab}	2.7±0.33 ^{a}	0.67±0.33 ^{bc}	0 ^{c}
Serranidae	*Epinephelus akaara*	19.1	14–24	8.0±1.7 ^{a}	6.7±2.3 ^{a}	3.3±1.3 ^{ab}	0.33±0.33 ^{b}
Apogonidae	*Apogon semilineatus*	5.0	2-8	67±38	18±3.5	48±24	26±7.3
Carangidae	*Trachurus japonicus*	6.8	5-9	13±7.9	13±10	5.0±5.0	0
Gerreidae	*Gerres equulus*	2.7	2-13	7.0±7.0	49±28	2.7±2.1	1.3±0.88
Mullidae	*Upeneus japonicus*	4.6	4–6	0.67±0.67	1.7±0.67	0	0
Pomacentridae	*Chromis notata*	2.6	1–4	40±8.4 ^{a}	41±11 ^{a}	0.67±0.67 ^{b}	0 ^{b}
	Pomacentrus coelestis	2.7	2–4	1.7±1.7 ^{ab}	11±4.4 ^{a}	0 ^{b}	0 ^{b}
Girellidae	*Girella punctata*	5.0	3–5	34±34 ^{ab}	68±16 ^{a}	0 ^{b}	0 ^{b}
Labridae	*Pteragogus aurigarius*	7.4	5–12	2.3±0.67 ^{b}	13±1.5 ^{a}	0.67±0.33 ^{bc}	0 ^{c}
	Pseudolabrus sieboldi	8.8	5–9	2.3±1.2 ^{ab}	6.7±1.5 ^{a}	0.33±0.33 ^{b}	0 ^{b}
	Stethojulis interrupta	8.1	5–11	12±5.6 ^{a}	12±4.4 ^{a}	0.33±0.33 ^{b}	0 ^{b}
	Halichoeres poecilopterus	11.0	6–15	2.7±1.7 ^{ab}	5.0±1.5 ^{a}	0.33±0.33 ^{b}	0 ^{b}
	H. tenuispinnis	5.1	1.5–12	37±10 ^{b}	140±17 ^{a}	0.33±0.33 ^{c}	0 ^{c}
Blennidae	*Petroscirtes breviceps*	5.5	2–9	3.3±1.9 ^{ab}	13±5.2 ^{a}	0 ^{c}	0 ^{c}
Callionymidae	*Repomucenus curvicornis*	8.8	6–12	0 ^{b}	1.3±0.33 ^{a}	0 ^{b}	0 ^{b}
Gobiidae	*Pterogobius zonoleucus*	4.4	3–5	3.0±5.2 ^{ab}	14±12 ^{a}	0 ^{b}	0 ^{b}
	Istigobius campbelli	6.0	2–9	5.7±3.2 ^{ab}	32±15 ^{a}	3.7±2.2 ^{b}	0 ^{b}
Siganidae	*Siganus fuscescens*	3.6	2–8	200±170 ^{ab}	210±59 ^{a}	6.3±3.2 ^{bc}	0.33±0.33 ^{c}
Monacanthidae	*Rudarius ercodes*	2.0	1–3	170±16 ^{a}	130±76 ^{a}	0.33±0.33 ^{b}	0 ^{b}
	Stephanolepis cirrhifer	8.3	6–11	1.3±0.88	2.3±0.33	1.3±0.33	0.33±0.33
	Paramonacanthus japonicus	6.5	3–9	0.33±0.33	0.33±0.33	0.67±0.33	0