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Minimum daytime brightness recognized by Japanese spiny lobster

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Abstract : The Japanese spiny lobster shows nocturnal habit, and a clear diurnal variation is observed in its activity. We reproduced diurnal brightness variation in our experimental tank by setting a 12-hour bright period (daytime) and a 12-hour dark period (nighttime), alternatively. The lobster was habituated in the condition of the 3.3×10^2 *lx* daytime brightness and of the 0 *lx* nighttime brightness for several days prior to each experimental run. Then, the daytime brightness was changed to 0 *lx*, and the lobster was put into a long-lasting dark condition (control run). The lobster sustains its diurnal variation pattern even after the chage of condition, but the variation period tends to be shortened. Several similar experiments were conducted by decreasing the changing rate of the daytime brightness, and compared with the results of the control run. When the daytime brightness is changed to lower than a threshold value, the lobster behaves just as in the control run. When the brightness is larger than this threshold value, the activity variation of the lobster occurs just in phase with the brightness variation, and no change in variation period occurs. The threshold brightness was shown to be about 2.3×10^{-5} *lx*, and this value would be understood as the minimum daytime brightness recognized by the lobster.

1. Introduction

Spiny lobsters show nocturnal habit (*e.g.*: SUTCLLIFFE, 1956; IWAI and HAYASHI, 1990; LIPCIUS and COBB, 1994). They move actively at night, and are almost at rest at daytime. KOIKE *et al.* (1993, 1995) investigated the diurnal variation of activity of Japanese spiny lobsters *Panulirus japonicus* in a small water tank, and showed that the nighttime activity is strongly controlled by underwater brightness. Spiny lobsters move actively under nighttime brightness less than 2.3×10^{-5} *lx* just as in a pitch-dark condition (0 *lx*). The nighttime activity is considerably suppressed if the nighttime brightness is set to be higher than 5.2×10^{-3} *lx*. KOIKE *et al.* (1993, 1995) adapted 3.3×10^2 *lx* as the standard daytime brightness in their experiments, but they showed that the diurnal activity variation is almost unchanged if the daytime brightness is kept higher than 3.5×10^{-2} *lx*. However, the lower limit of the daytime brightness that spiny lobsters are able to identify as the daytime was not obtained.

A lobster was kept in the standard conditions of 3.3×10^2 *lx* daytime brightness and of 0 *lx* nighttime brightness for several days as a habituation period. Then, the daytime brightness was lowered to a prescribed value. Even if the daytime brightness is changed to 0 *lx*, and if the lobster is kept in pitch-dark condition thereafter, the lobster preserves the similar diurnal variation pattern as in the habituation period. After several days, however, the transition time from low activity to high activity period tends to shift gradually, and occurs earlier and earlier day after day.

It was shown that the shift of the transition time occurs when the daytime brightness is lowered to a finite values smaller than a threshold value. Above this threshold value, the diurnal variation of the lobster activity occurs just in phase with given brightness variation. The threshold brightness was shown to be about 2.3×10^{-5} *lx*, and this value would be understood as the minimum daytime brightness recognized by the lobster.

2. Experimental procedure

Our experiment ws conducted in small water

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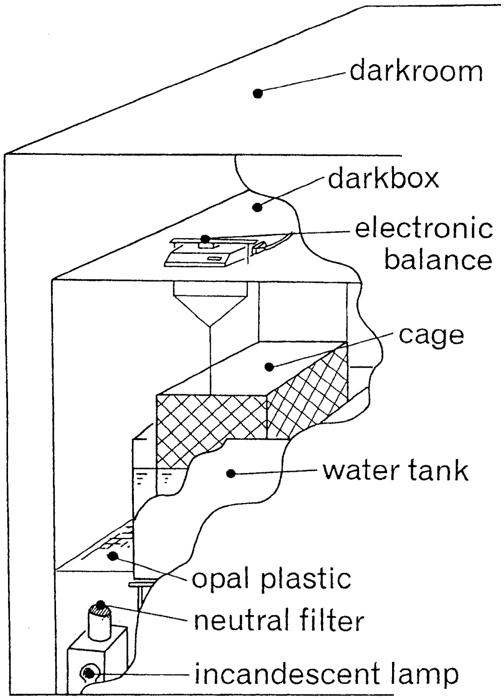

Fig. 1. Schematic view of the experimental apparatus.

tanks in the Fisheries Research Laboratory of the Mie University which is located in Zaga Island in Ago Bay, Mie Prefecture. The tanks are kept in the dark box as shown schematically in Fig. 1. Each lobster was kept in a cage of 40 cm length, of 30 cm width and, of 30 cm depth. The cage is hanged by three wires, one of which is connected to an electric balance. The variation of its tension caused by lobster movements is measured and recorded automatically. The water in the tank is replaced by sea water pumped up from the depth of about 5 m at the rate of 3 l per min. The water is drained from two outlets placed near the water surface and near the bottom of the tank, respectively, in order to keep the water inside clean. We use incandescent lamps as light source. Only the reflected light from the ceiling is allowed to reach the tank surface, and the downward light flux at the surface at the center of the tank is used as a measure of the brightness. The light intensity is adjusted by putting various semitransparent neutral filters on front of lamps. The lamps are switched on at 6:00 and off at 18:00 by using a timer. The daytime is modeled by 12 hours bright period with a constant brightness, and the nighttime by 12 hours period of 0 *lx*.

The tension of the wire averaged over 9 sec recorded for every 15 sec. By assuming that the tension change larger than 2 gw indicates a significant lobster movement, the occurrence frequency of such changes is used as a measure of the lobster activity. The 2 gw change in tension corresponds to the movement of the lobster of 250 gw (about 25 gw in the sea water) over the distance of 3.2 cm in the longitudinal direction. The apparatus and the experimental procedure are the same as used in the previous papers (KOIKE *et al.* 1993, 1995).

The combination of the daytime and nighttime brightnesses for each experimental run is shown in Table 1, together with other experimental parameters. The nighttime brightness is fixed to be 0 *lx* throughout our experiments. The daytime brightness is set to be 0 *lx* in run 1 (control run), 6.8×10^{-8} *lx* in run 2, 2.3×10^{-5} *lx* in run 3, 5.2×10^{-3} *lx* in run 4, and 3.5×10^{-2} *lx* in run 5, respectively. The lobster was kept in the standard condition of the 3.3×10^{2} *lx* daytime brightness for more than 1 week (habituation period) prior to the experiments of run 1 through run 3. The behaviors of the lobster in run 2 through run 5 will be discussed in comparison with that in the control run (run 1).

Table 1. Experimental conditions of the five experimental runs conducted in the present study.

Run No.	Brightness(lx) daytime	nighttime	Water temp. (℃)	Dates	
1	0	0	19.0–22.4	May.28–Jul.15	1993
2	6.8×10^{-8}	0	21.7–22.5	Jul. 3–Jul.25	1993
3	2.3×10^{-5}	0	19.6–23.7	Sep.21–Oct.31	1993
4	5.2×10^{-3}	0	22.5–27.8	Jul. 1–Jul.15	1990
5	3.5×10^{-2}	0	23.1–26.0	Jun.17–Jun.30	1990

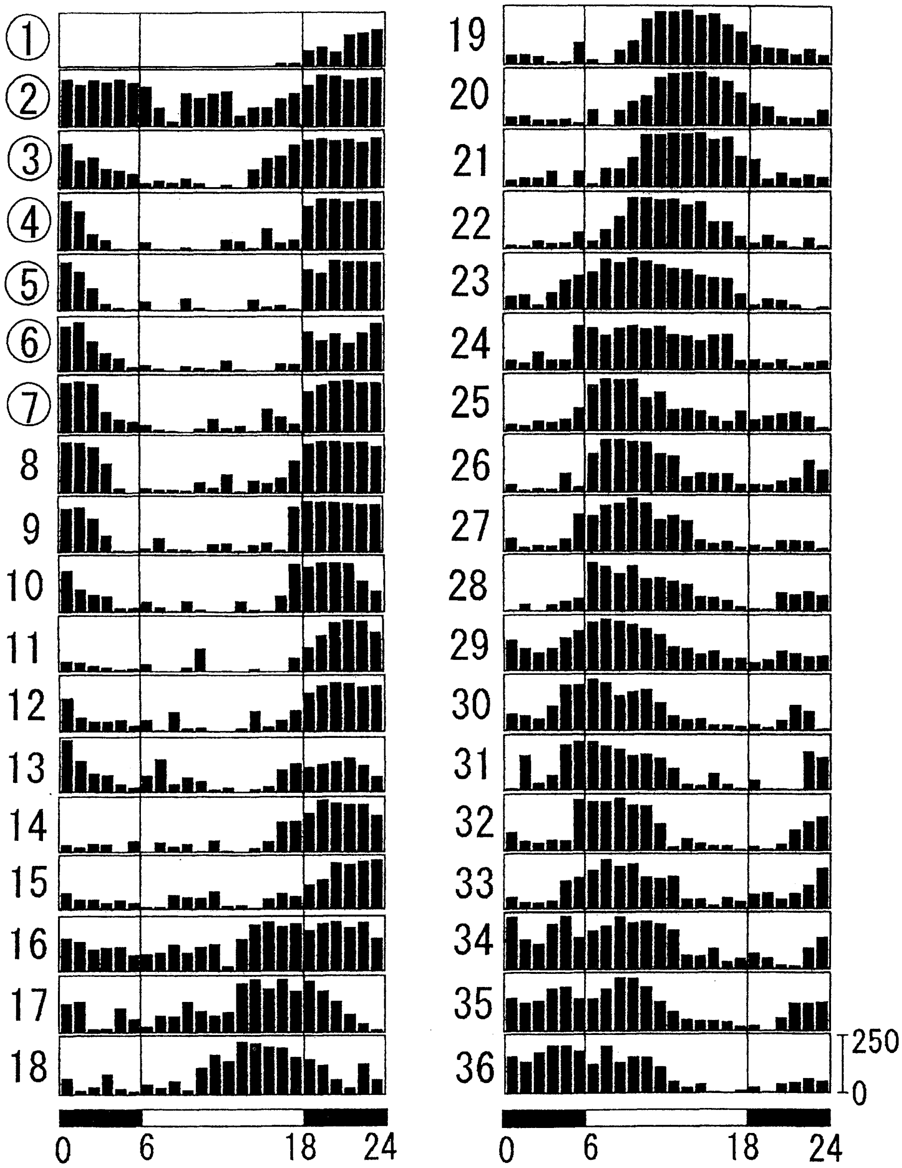

Fig. 2. Daily variation of the diurnal activity change of the lobster in run 1. The activity frequency per hour is taken in the ordinate, and its scale is shown at the under right corner. The time of day is taken in the abscissa. The nighttime is shown with black horizontal bars and the daytime with white bars. The numerals attached on left side of each figure show the day number, and those with circle indicate that they are in the habituation period.

We used the lobsters which had been caught in the sea off Wagu of the Shima Peninsula, Mie Prefecture. Only the male lobsters having carapace length from 7.0 to 8.5 cm and having weight from 250 to 350 gw. The lobsters can be usually used more than one year. No significant change is observed in their moving characteristics, though the magnitude of activity frequency strongly depends on water temperature as discussed later. The same lobster was used in the experiments of run 1 through run 3, but the lobsters used in run 4 and run 5 were different to one another. The lobster in the tank is fed with 150–250 gw living mussels

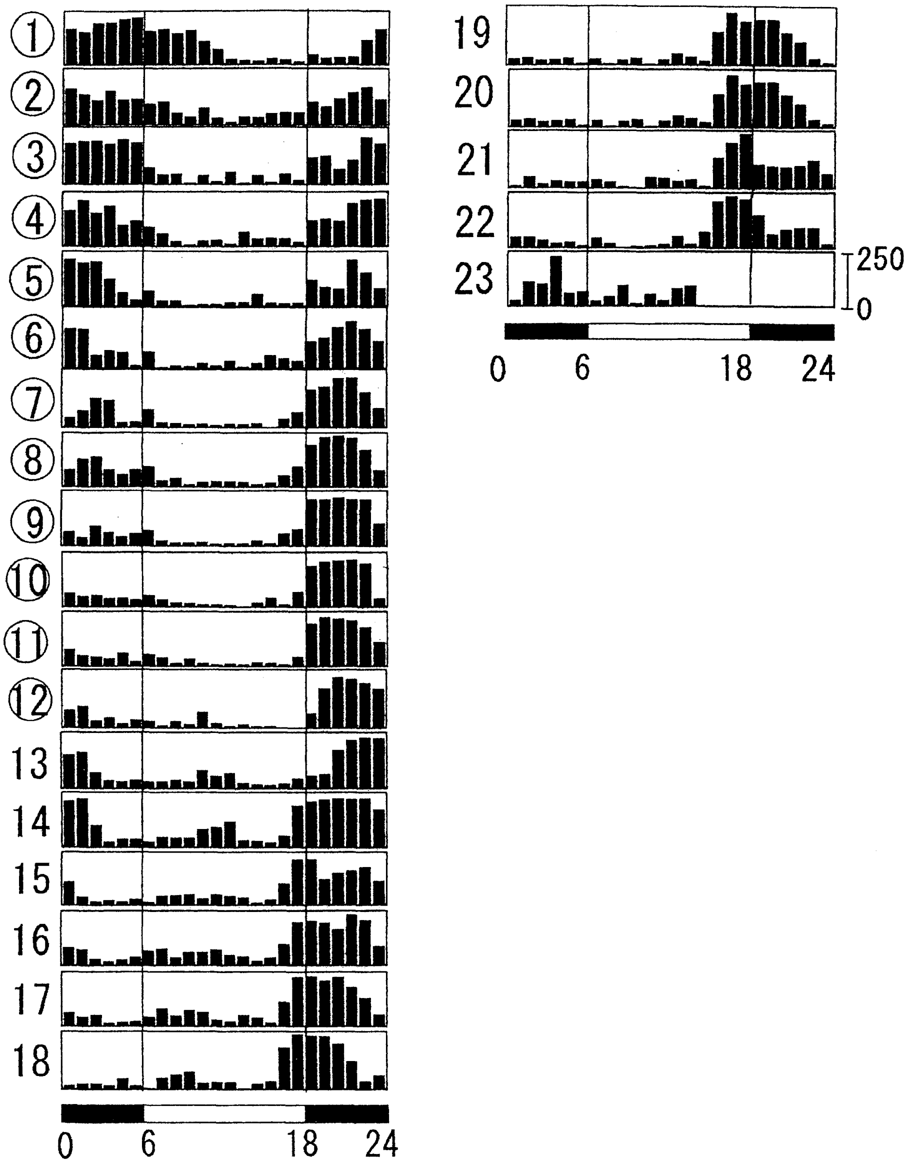

Fig. 3. The same as in Fig. 2, except for run 2.

Mytitlus edulis once a week. The weight of the mussels ranges from 3 to 10 gw, and their shells are partly broken so as that the lobster can easily eat them. The mussels are sometimes found living three days after, but all of the mussels have been eaten up before the next feeding time. The feeding was made in the middle of the day, and the water temperature in the tank was measured with a thermistor at the time of feeding.

3. Diurnal variation of the lobster in the standard condition

The diurnal variations of the lobster activity are shown in Fig. 2 for the period from May 28 to July 2, 1993 (run 1) and in Fig. 3 for the period from July 3 to July 25, 1993 (run 2), respectively. The first 7 days in run 1 and the first 12 day in run 2 are the habituation period in the standard condition. The pattern of the diurnal variation appears to be disturbed for a few

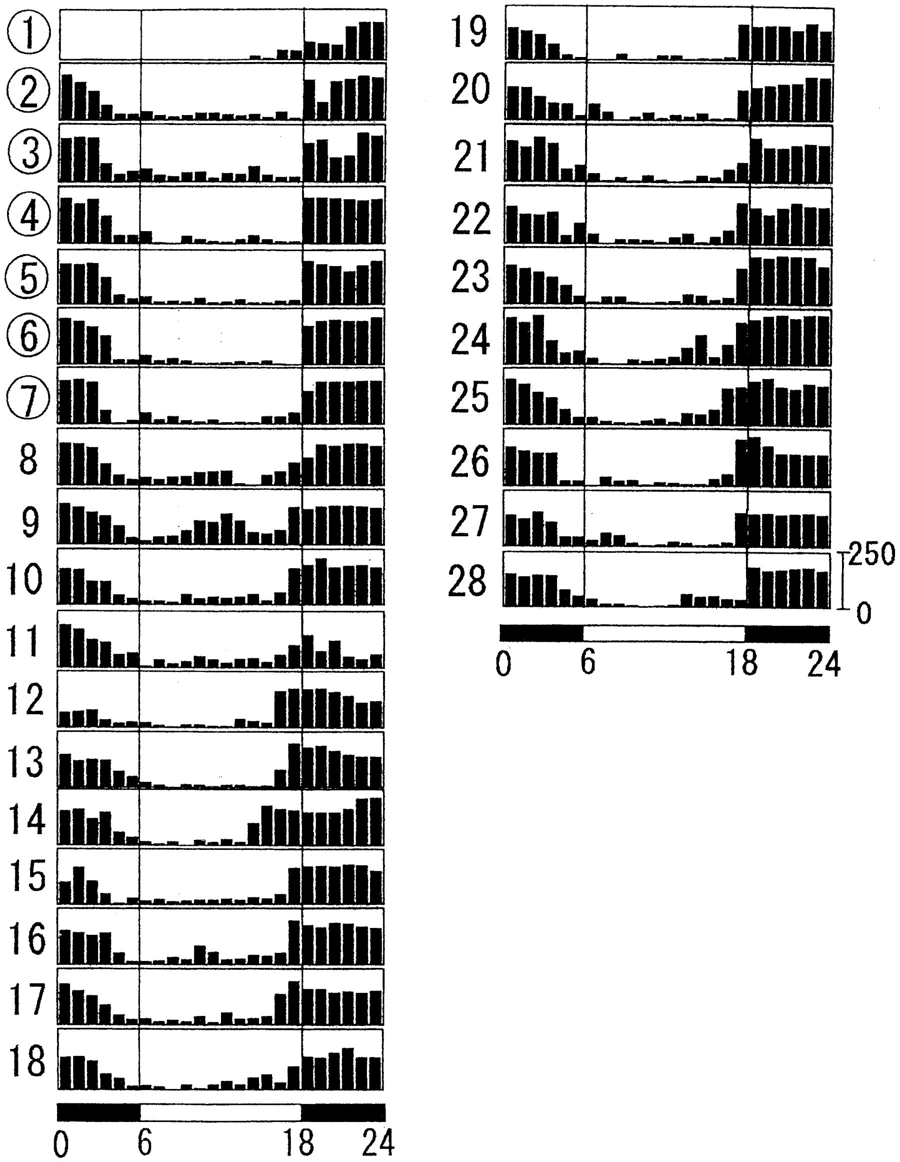

Fig. 4. The same as in Fig. 2, except for run 3.

days untill the lobster becomes familiar with its new circumstance. Then, the lobster activity usually shows a clear diurnal variation in phase with the diurnal brightness variation. The length of the habituation periods adopted in our present experiments is arbitrary and depends mainly on the time needed for set up our experimental apparatus. The data taken in the first few disturbed days are included in our analysis as it does not affect on our experimental results significantly.

The diurnal activity variations measured in the period from September 21, 1993 to Octover 31, 1993 (run 3) are shown in Fig. 4. The lobster had been kept in the standard condition for about 1 month, but the data is available only the last 7 days due to a trouble in our recording system. The diurnal activity variations for these 7 days are shown as in habituation period in the figure.

Table 2. Activity frequencies per hour for nighttime (N) and for daytime (D) for each ,habituation period and for each sub-period of one week length. The sub-period in each run may be shorter than one week, and 4 days (*) or 6 days (**). The standard deviations are also ahown. The variation periods (in hour) obtained by the periodgram analysis are shown in parentheses. The brightness conditions are reproduced in the left side columns.

Run No.	Brightness (lx)		habituation	first week	second week	third week	fourth week
	N	0	155.0±25.2	128.5±27.8	81.8±38.9	45.1±6.9	91.1±11.9
1	D	0	38.2±32.3	37.4±7.8	129.5±37.2	144.7±14.3	111.2±14.6
			(24.0)	(24.0)	(22.8)	(23.6)	(23.8)
	N	0	119.5±9.8	104.7±25.9	49.3±7.3 *		
2	D	6.8×10^{-8}	25.7±5.4	58.3±9.9	53.2±20.4 *		
			(24.0)	(23.4)	(23.8) *		
	N	0	136.4±30.9	127.3±21.0	128.0±10.1	145.7±16.0	
3	D	2.3×10^{-5}	19.8±7.2	46.6±16.1	34.1±9.2	37.6±8.8	
			(24.0)	(23.8)	(24.2)	(24.0)	
	N	0		86.8±9.7	66.8±11.0		
4	D	5.2×10^{-3}		19.5±10.8	12.6±2.4		
				(24.0)	(24.0)		
	N	0		62.4±13.4	81.2±13.5 **		
5	D	3.5×10^{-2}		14.7±4.8	9.4±1.3 **		
				(24.0)	(24.0) **		

The diurnal activity variations for these habituation periods give a pattern with very low activity in daytime and with high activity in nighttime. The activity frequency averaged separately for daytime and for nighttime for each habituation period is shown in the left-hand side column of Table 2, together with its standard deviation. It can be seen that the activity frequency in nighttime is remarkably higher than that in daytime. The magnitude of the activity frequency, however, appears to be changeable run by run even for the same lobster. Activity frequencies accumulated for 24 hours are calculated for the days when the water temperature was measured. In Fig. 5, the accumulated frequencies in the habituation (standard) condition are plotted against the water temperature. The data of the previous experiments and of run 4 and run 5 are also included, as the lobster shows a clear diurnal variation patterns as just as in the standard condition. The data are well aligned near a str aight line, and the activity decreases linearly with temperature increase. The straight line drawn in Fig. 5 is obtained by the least square method, and is given by

$$F=9569-301T$$

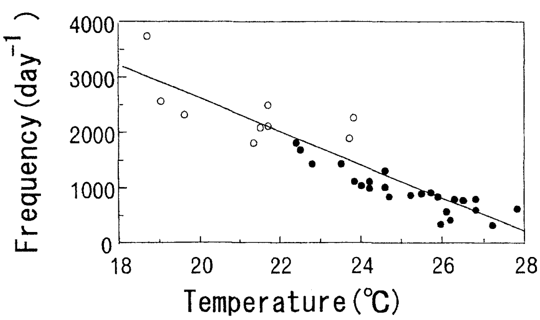

Fig. 5. Relation between the water temperature (℃) and the accumulated activity frequency per day. The straight line in the figure is obtained by the least square method. Data points shown with white circles are obtained in the present experiments, and those with black circles in the previous experiments.

where F is the activity frequency per day, and T the water temperature in ℃. This relation could not be applicable for lower temperatures as the lobster activity is very low in winter time. The relation suggests that the lobster activity is determined mainly by water temperature. This might be resulted partly from the facts that we used male lobsters of medium sizes only and that significantly inactive lobsters are intentionally removed prior to the experiments. The individuality of the lobster appears not to affect our present experimental results significantly.

The transition from the low activity to the high activity occurs just when the light is turned off (at 18:00). However, the transition from the high activity to the low activity does not always coincide with the time when the light is put on (at 6:00). The lobster used in run 1 through run 3 tends to stop its activity a few hours before the start of the daytime. The lobsters used in runs 4 and 5 tend to continue to move for a little while after the light is on. The transition time from high activity to low activity may depend on individuality of lobsters.

In order to describe the periodicity of the diurnal variation of the lobster activity objectively, a periodgram analysis (see, for sample, TABATA, 1991; WADA, 1983) is applied for the data in each habituation period, and the obtained period is given in parenthesis in each column of Table 2. The period in each habituation period is exactly 24.0 hours.

4. The behavior of the lobster after the daytime brightness is changed to 0 *lx*

We shall see how the behavior of the lobster is changed after the daytime brightness is lowered to 0 *lx* (from the 8-th day to the 36-th day in Fig. 2: run 1). For the first several days, the lobster keeps its diurnal variation pattern as just as in the habituation period even in pitch dark condition. Then, the transition time from low activity to high activity shifts earlier and earlier day by day. On the 18-th day, the high activity period occurs from 6:00 to 18:00: the phase of the diurnal activity variation becomes just opposite to that of the original brightness variation.

After the 21-th day, the diurnal pattern of the activity variation appears to be disturbed: the length of the high activity period tends to increase and that of the low activity to decrease, and the peak of the high activity appears sometimes twice a day (on the 32-th and 33-th days in Fig. 2). For this period, the phase shift of the variation pattern is hardly recognized.

We divided the period, after the day when the 24 hours pitch-dark condition starts, into several sub-periods having the length of a week (the length of the last sub-period of each run may be shorter than one week). The activity frequency and its standard deviation for the daytime (defined as from 6:00 to 18:00 also in the pitch-dark condition for convenience' sake) and the nighttime (defined as from 18:00 to 6:00) are calculated for each sub-period, and shown in Table 2. The shift of the diurnal activity variation mentioned above is recognized as increases of daytime activity and decreases of nighttime activity.

The periodgram analysis was applied also for each sub-period, and the obtained period of the diurnal variation is shown for each colums in Table 2. No phase shift occur in the first week of run 1, and the period is just 24.0 hours. The period in the second week decreases to 22.8 hours indicating that the transition time moves earlier and earlier. The periods in the third and fourth weeks are also shorter than 24.0 hours, but the period tends to increase toward the 24.0 hours as the time elapses.

The phase shift and the shorter variation period seen in the second and third weeks might suggest that the diurnal activity variation of Japanese spiny lobster is strongly controlled by the brightness conditions, and the 24.0 variation period is not their inherent nature. However, the variation period increases gradually again near to 24.0 hours, if it is kept long enough in a pitch-dark condition, though the variation pattern tends to become ambiguous. The further elaborated experiments would be needed to get definite conclusions.

5. Minimum daytime brightness recognized by Japanese spiny lobster

If we change the daytime brightness to a level lower than the minimum brightness recognized by a Japanese spiny lobster after keeping a lobster in the standard condition, the lobster in the tank would exhibit just as the same behavior as described in the previous section. The daytime brightness is lowered to 6.8×10^{-8} *lx* from the 13–th day in run 2 (Fig. 3). Though some disturbance is seen for the first few days, the transition timee from low activity to high activity shifts clearly earlier and

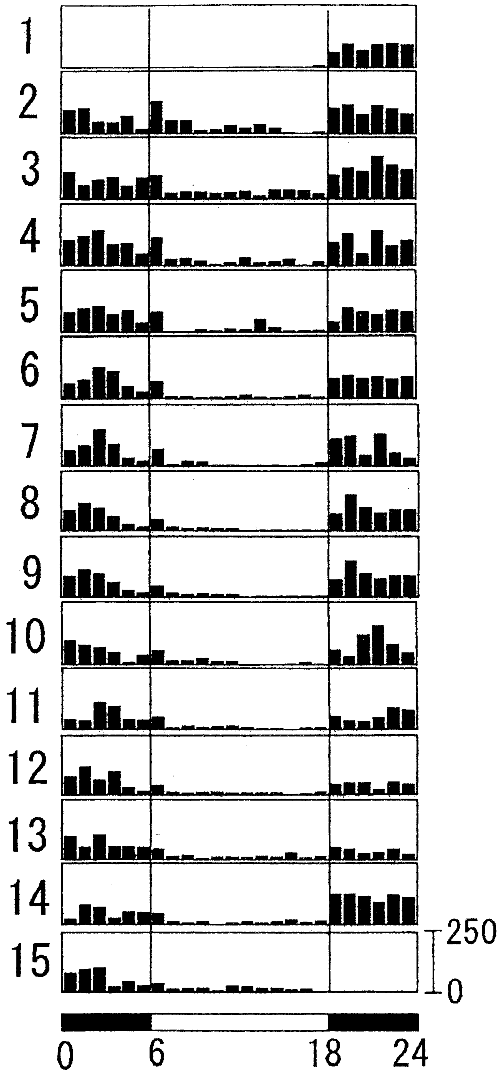

Fig. 6. The same as in Fig. 2 except for run 4. No habituation period is set in this run.

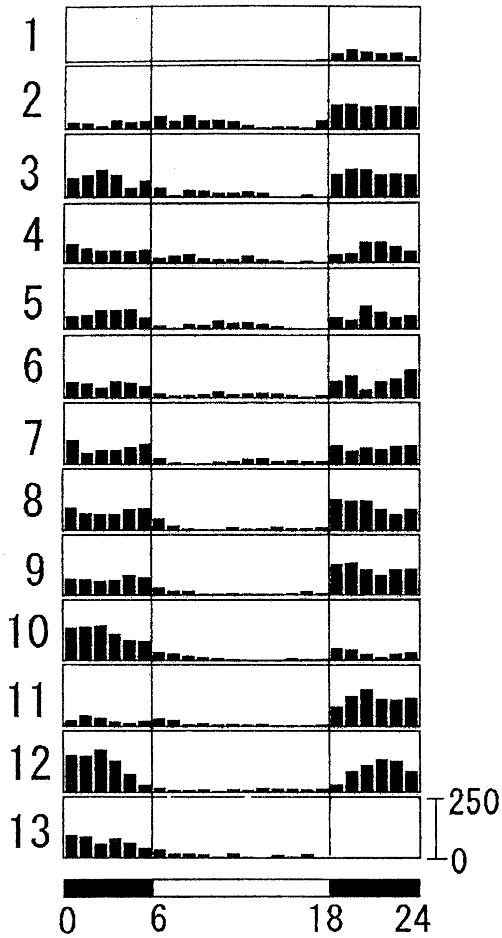

Fig. 7. The same as in Fig. 2 except for run 5. No habituation period is set in this run.

earlier after the 14-th day. The activities for daytime (6:00 – 18:00) and for nighttime (18:00–6:00) and their standard deviations for each one-week sub-period are shown in Table 2, together with the period obtained from the periodgram analysis. The behavior of the lobster in run 2 is very similar to that in run 1. We conclude that the lobster cannot identify the brightness of 6.8×10^{-8} *lx* as daytime.

The daytime brightness is lowered to 2.3×10^{-5} *lx* from the 8-th day in run 3 (Fig. 4). The variation pattern for the first few days are disturbed, and the lobster activity is rather high even in daytime, especially in the 8-th and 9-th days. The shift of the transition time from high activity to low activity shifts forwards from the 12-th day to the 14-th day. However, the transition time goes back and occurs at 17:00 in the 15-th day (one hour before the brightness change). The similar forward shift is observed in the period from the 15-th day to the 18-th day, but the transition backs again and occurs at 17:00 in the 19-th and 20-th days. In general, the transition time is not exactly in

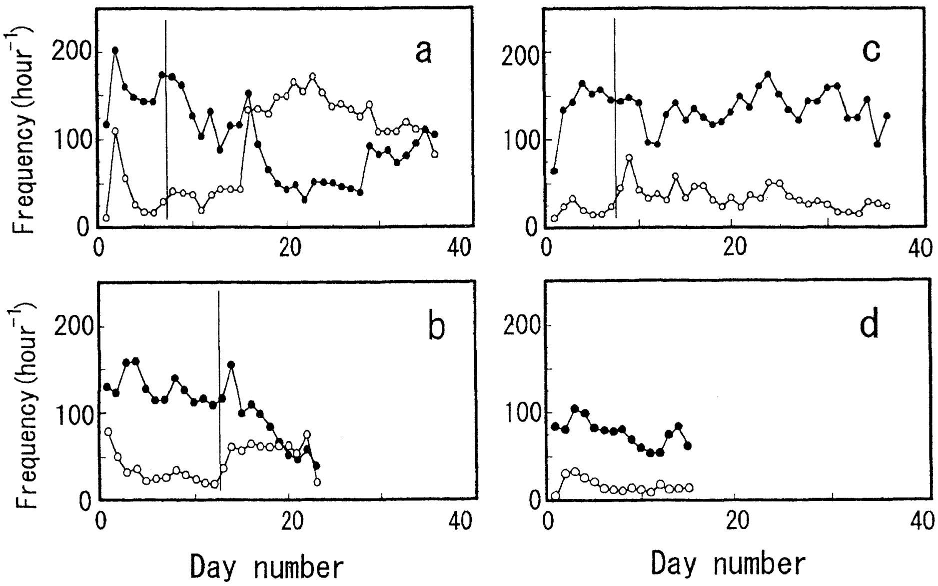

Fig. 8. Temporal changes of the lobster activity frequencies per hour averaged over nighttime (black circles) and over daytime (white circles) for each day: **a** is for run 1, **b** for run 2, **c** for run 3, and **d** for run 4, respectively. The day number is taken in the abscissa. The left-hand side of the vertical line indicates the habituation period.

phase to the brightness variation. These results suggest that the lobster appears to be confused, but identifies more or less the brightness of 2.3×10^{-5} lx as daytime.

The diurnal lobster activity variations for the daytime brightness of 5.2×10^{-3} lx (run 5) and of 3.5×10^{-2} lx (run 6) are shown in Figs. 6 and 7, respectively. Though no habituation period is set for these experiments, and though some disturbed patterns appear for the first few days, the transition from low to high activity occurs always at 18 : 00, namely at the time that the light is put off. The difference between daytime and nighttime activity and the variation period are as just as in the standard condition (Table 2). We conclude that the lobster recognizes these brightness as daytime.

6. Summary and conclusion

The change of the diurnal variation pattern of the Japanese spiny lobster for the various daytime brightness is investigated in the experimental tank. The results are summarized in Fig. 8 where day to day variations of the lobster activity frequencies in daytime and in nighttime are shown for each experimental runs. The variation patterns for the daytime brightness of 2.3×10^{-5} lx and of 5.2×10^{-3} lx are almost identical to that in the habituation period. When the daytime brightness is lowered to 6.8×10^{-8} lx, the transition time from low to high activity is shifted earlier and earlier, and the nighttime activity (18 : 00–6 : 00) decreases on reflecting such phase change. For the case of 2.3×10^{-5} lx daylight brightness, the clear shift of the transition time is not observed, but the transition time is somewhat variable day by day. This brightness value appears to be detected by the lobster but with some perplexity. Our results suggest that the minimum daytime brightness recognized by Japanese spiny lobster is about 2.3×10^{-5} lx. This is consistent with the result given by Koike *et al.* (1993, 1995) where they reported that the lobster activity in nighttime is very high if the nighttime brightness is lower than this value. It is also consistent to the results given by Archiga and Atkinson (1975): they reported the brightness value of 10^{-5} lx as the minimum brightness recognized by Burrowing prawn *Nepherops norvegicus*.

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References

ARECHIGA H. and R. J. A. ATKINSON (1975): The eye and some effects of light on locomotor activity in *Nephrops norvegicus*. *Mar. Biol.*, **32**, 63–76.

IWAI, T. and I. HAYASHI (1990): Kiso Suisan Dobutsugaku (Basic Fisheries Zoology), Kosei-sha-Koseikaku, pp. 266. (in Japanese)

KOIKE, T., Y. MORIKAWA, M. MAEGAWA and T. MORINAGA (1993): Effects of underwater brightness on Japanese spiny lobster behavior during nighttime scotophase. *Nippon Suisan Gakkaishi*, **59**, 1689–1694, (in Japanese).

KOIKE, T., Y. MORIKAWA and M. MAEGAWA (1995): Underwater brightness in nighttime and behaviors of Japanese spiny lobsters. *La mer*, **33**, 37–46.

LIPCIUS, R. N. and J. S. COBB (1994): Ecology and fishery biology of spiny lobsters. in Spiny Lobster Management (B. F. PHILLIPS, J. S. COBB and J. KITTAKA eds.), Blackwell Scientific Publications, Oxford., 1–30.

SUTCLLIFFER, W. H. (1956): Effect of light intensity on the activity of the Bermuda spiny lobster *Panulirus argus*. *Ecology*, **37**, 200–201.

TABATA, M. (1991): Photoreceptor organs and circadian locomotor activity in fishes, in Rhythms in Fishes (ALI, M. A. ed.), Plenum Press, 223–224.

WADA, M, (1983): Periodgram. in Jitsuyo-Program-Shu, Life-Science-personal-computer-Series No. 4, Baifuukan, Tokyo, 208–214. (in Japanese)

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