Burrow Usurpation and Duration of Surface Activity in *Scopimera globosa* (Crustacea : Brachyura : Ocypodidae)

By

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With Text-figures 1–2 and Tables 1–4

Abstract Burrow usurpation and duration of surface activity were studied for the ocypodid crab *Scopimera globosa* in the Fukuro River Estuary, southern Honshu, Japan. Burrow owners were displaced frequently during an exposure period, where burrow usurpation accounted for almost half of the causes of burrow abandoning. In most instances of burrow usurpation, the usurper was larger than its opponent, irrespective of the sex. The duration of surface activity during an exposure period was not correlated with crab size. Based on these facts, the reason for size variations in spatial distribution of *S. globosa* is discussed.

For some ocypodid crabs inhabiting intertidal sand or mud flat, it has been reported that larger crabs tend to occur at higher level than smaller conspecific ones: for *Scopimera inflata* by Fielder (1971), *Dotilla fenestrata* by Hartnoll (1973), *Ocypode cursor* by Shuchman & Warburg (1978), *Ocypode quadrata* by Fisher & Tevesz (1979), *Uca lactea* by Frith & Brunenmeister (1980), and *Scopimera globosa* & *Ilyoplax pusillus* by Wada (1983). But mechanisms involved in such intraspecific distributional difference have not so far been fully analyzed. With the purpose of discussing this problem for *Scopimera globosa* De Haan, 1835, I have made experimental observations in the field, and present, in this paper, data on displacement of burrow owners and the relation between the duration of surface activity and crab size. In this connection, few works have been done on burrow abandoning or burrow obtaining in ocypodids in the field; Hyatt & Salmon (1978) reported the size relationships between wandering crabs and residents evicted by the former for *Uca pugilator* and *U. pugnax*, and Bertness & Miller (1984) examined crab recruitment to artificial burrows for *U. pugnax*. Furthermore, the duration of surface activity has not so far been studied in relation to individual size in ocypodids.

Field study was conducted on an intertidal sand flat of the Fukuro River Estuary, Japan (33°38′N 135°24′E). Four fixed areas were established along the middle level (ca. 42 cm above M.T.L.) of *S. globosa* distributional range which measured about 30 m across the shore. On each day of spring and neap tides of summer (June 5 & 14, 1984) and of autumn (October 2 & 12, 1984), surface activities of crabs in the fixed areas were continuously recorded with four video cameras for 4.5 to 7 hours within daytime exposure periods. It was only on 12 October that recording almost fully extended over an entire exposure period. Data on observation time & area, number of burrows observed, and

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Table 1. Relevant data of four observations by video cameras.

Date	Tidal condition	Observation time	Observation area (m^2)[1]	No. burrows observed[2]	Max. number of active crabs/0.25 m^2 [3]
5 June	Neap	1005–1700	0.40	15	13.1
14 June	Spring	0938–1636	0.71	16	5.6
2 Oct.	Neap	0949–1632	0.43	42	16.3
12 Oct.	Spring	1043–1509	0.54	41	23.1

1) Total area observed by four cameras.
2) Total no. of burrows observed by four cameras.
3) Maximum of the values recorded by each of four cameras.

maximum density of active crabs on each day are shown in Table 1. During each observation period, the study area was under sunny or overcast condition. From this record, the following aspects were examined, coupled with crab size: 1) duration of surface activity for each crab, inclusive of intermittent short hiding inside the burrow, 2) frequency of displacement of burrow owners, and 3) in case of burrow abandoning, frequencies of voluntary abandoning and of abandoning by usurpation. Crab size was estimated by measuring the carapace width (CW) of each crab on the screen of the video monitor, but the sex of each crab could not be determined.

In addition to the above observation by tape recording, the following field experiment was made on 10 days between 17 April and 12 October 1984. Crabs of both sexes were collected near the fixed areas, and their CW were measured. Immediately after the measurements, they were released on nearby areas to see how they obtained their new burrows. When they usurped burrows owned by other crabs, the latter (evicted crabs) were captured to determine their sex and CW. The procedure was followed for each released crab separately.

Results

1. Displacement of burrow owners.

During each tape-recording period, displacement of burrow owners occurred at least once in more than half the burrows observed (Table 2). The maximum

Table 2. Displacement of burrow owners recorded during each observation. No. burrows: number of burrows, owners of which were displaced at least once during observation, and its proportion (%) to the number of observed burrows. Burrow abandoning: observed frequencies of burrow abandoning for two causes, and χ^2-test. CW: Carapace width.

Date	No. burrows (%)	Burrow abandoning				
		Size range in C.W. (mm)	Voluntary	By usurpation	χ^2	P
5 June	14 (93.3)	4–8	10	14	0.67	<0.5> 0.3
		9–13	20	16	0.44	<0.7> 0.5
14 June	10 (62.5)	3–8	13*	5*	—	—
		9–13	8	8	—	—
2 Oct.	22 (52.4)	2.5–4	14	20	1.06	<0.5> 0.3
		5–8	10	11	0.05	<0.9> 0.8
12 Oct.	21 (51.2)	2.5–4	13	10	0.39	<0.7> 0.5
		5–9	6	11	1.47	<0.3> 0.2

*: P=0.048, Test of a binomial proportion.

frequency of owner's displacement for a burrow was 10 on 5 June, 6 on 14 June, 7 on 2 October and 5 on 12 October. On each day, the frequencies of burrow abandoning were compared between the voluntary case and the case by usurpation, separately for two size groups divided arbitrarily (Table 2). No significant differences were seen between the two cases in either size group.

Table 3. Number and its proportion (%) to the total (in parenthesis) of released crabs which obtained new burrows by each of different means.

	Burrowing	Obtaining a vacant burrow	Usurping	Total
Male	8 (6.7)	27 (22.5)	85 (70.8)	120
Female	2 (2.8)	19 (26.4)	51 (70.8)	72

In crab-release experiment, irrespective of the sex, about 70% of the released crabs usurped other crab's burrows, and the rest obtained empty burrows or excavated new ones (Table 3). In most cases that the released crabs succeeded in burrow usurpation, the usurpees were smaller than the usurpers, though not smaller than three-fifths of usurpers in CW, irrespective of the sex (Figs 1 & 2).

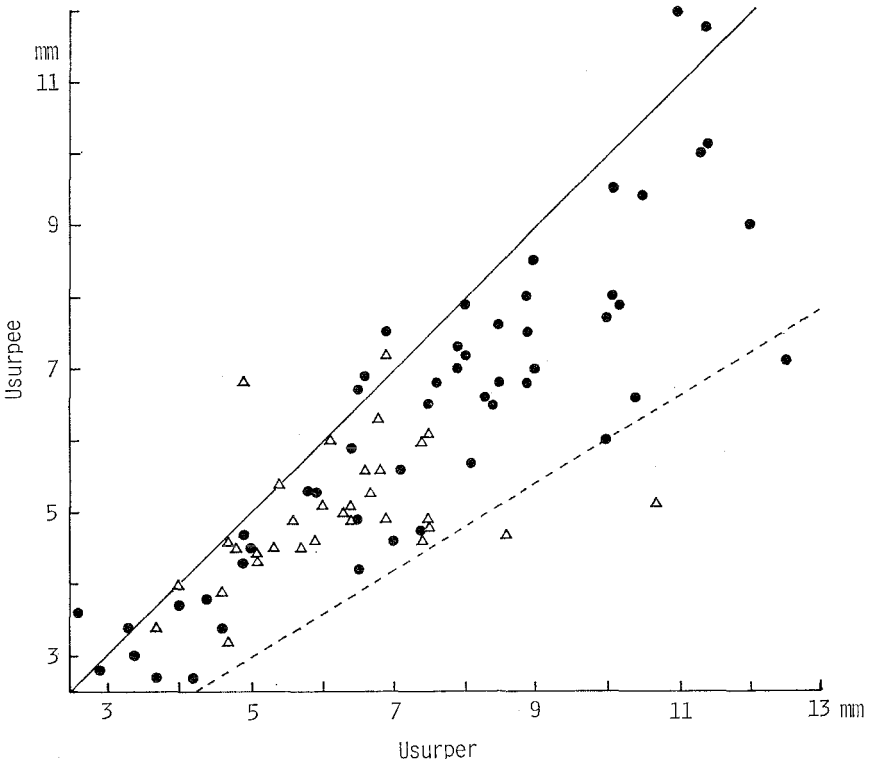

Fig. 1. Burrow usurpation; sizes (carapace width in mm) of the male usurper and its male (●) or female (△) opponent (usurpee) in the crab release experiments. Solid line: usurper and usurpee sizes equal. Broken line: usurpee size 3/5 of usurper size.

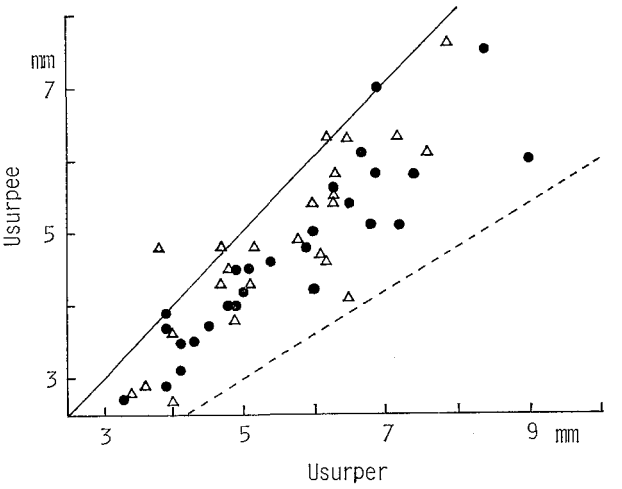

Fig. 2. Burrow usurpation; sizes (carapace width in mm) of the female usurper and its male (●) or female (△) opponent (usurpee) in the crab release experiments. Solid line: usurper and usurpee sizes equal. Broken line: usurpee size 3/5 of usurper size.

2. Duration of surface activity.

From the tapes recorded on 2 and 12 October, activities of crabs could be traced over the whole observation period for 15 and 19 individuals, respectively. These crabs were divided into three size groups: large ($\geqq$8 mm in CW), middle ($<$7 mm $>$5 mm in CW) and small ($\leqq$4 mm in CW), and durations of surface activity were compared among the groups (Table 4). No significant differences were seen among

Table 4. Duration (hr.) of surface activity of each crab of large ($\geqq$8 mm in carapace width [CW]), middle ($<$7 mm$>$5 mm in CW) and small ($\leqq$4 mm in CW) groups within the observation period of Oct. 2 and 12, and comparison of the values among the three groups by Kruskal-Wallis analysis of variance of ranks.

		Large	Middle	Small	H′	P
2 Oct.		0.32	0.68	0.12		
		0.37	0.87	0.13		
		0.52	1.02	0.68		
		1.57	1.90	0.80		
		1.77	2.37	1.80		
	$\overline{X}$	0.91	1.37	0.71	3.2608	$>$0.1
12 Oct.		0.62	0.17	0.22		
		0.65	0.17	0.47		
		0.78	0.45	0.80		
		1.27	0.77	1.43		
		4.43	0.82	1.95		
			0.82	2.67		
			0.88			
			1.55			
	$\overline{X}$	1.55	0.70	1.26	1.1639	$>$0.5

the three groups. The duration was variable within each size group, with almost all the values being less than half the whole observation period.

From the tapes recorded on 5 and 14 June, activities of crabs could be traced over the whole observation period for only 1 and 3 individuals, respectively. Respective values of durations of their surface activities were 0.03 hr. on 5 June, and 0.4, 0.7 and 4.8 hr. on 14 June.

Discussion

In *S. globosa,* displacement of burrow owners occurred frequently within an exposure period, as seen in the present study. Almost half of the observed cases of burrow abandoning was caused by the burrow usurpation by other crabs. In the crab-release experiment, about 70% of new burrow obtaining was achieved by usurpation of other's burrows. These facts suggest that burrow usurpation is a common phenomenon for *S. globosa.* Present study also demonstrated that burrow usurpation succeeded when the usurper was larger than its opponent, as already shown in other ocypodids such as *Uca pugilator* and *U. pugnax* by Hyatt & Salmon (1978). It is, therefore, expected that larger crabs occupy their favorable burrowing sites, expelling smaller crabs. If so, and if larger crabs burrow at the higher level, some smaller crabs would be forced to burrow at the lower level, as predicted by Wada (1983).

It is highly probable that crabs of different sizes have different preferences for environmental conditions and such a size-dependent difference in preference together with the effect of their size-dependent dominancy causes the size variation in spatial distribution. As one of the possible cases, it can be assumed that larger crabs require longer surface activity. In this case, larger crabs should prefer to burrow at higher levels, because longer surface activity is allowed there. But, as far as can be seen from the present data, there was no clear relation between the duration of surface activity and size. Moreover, the duration of surface activity was greatly variable even in a size group. This fact does not support the assumed case; rather, it implies that the duration of surface activity depends on some size-independent conditions, e.g. intermolt stages, as molt cycle alterations in some behaviors such as feeding and locomotion have been reported for other crustaceans (see Lipcius & Herrnkind, 1982). However, the present presumption on the surface activity is based on a very limited record that was obtained only in October and at the middle level of their distributional range. Further data in other seasons and at other levels should be accumulated before denying the relationship between crab size and required time for surface activity. In addition to these data, possible size-dependent preferences for other environmental factors such as deeper water table at higher levels should be examined for discussing their spatial distribution.

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