Swimming behavior of the marine copepod *Oithona davisae*: internal control and search for environment

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Abstract

The swimming behavior of the marine cyclopoid copepod *Oithona davisae* Ferrari and Orsi, collected in Tokyo Bay, Japan, between 1980 and 1983, was studied after acclimation to various food concentrations. Males and females exhibited forward and circular swimming movements. Males search mainly for mates, not for food. Their circular swimming behavior may serve for the mate search. The spiraling movement during mate-pursuit is peculiar to males. Circular swimming in females may function as a spontaneous search behavior for rich food areas and less crowded conditions. Females acclimated to a low food concentration, with net production about zero, responded sensitively to the increased food concentration by decreasing their swimming distance per unit time. Females acclimated to higher levels also responded similarly, but less sensitively. On the other hand, females kept without food exhibited no changes in swimming behavior and exhibited a stereotyped behavior at every food level. Females, when exposed to a low food level, may prefer to search for richer areas rather than capture food. The combined effect of the degree of internal activity (DIA) and the intensity of external stimulus (IES) determines the behavior pattern of *O. davisae*. The behavioral response to IES depends on DIA.

Introduction

Copepods perceive various information from the ambient environment and respond individually to the information, especially to information about food (Bainbridge 1949, Conover 1966, Lillelund and Lasker 1971, Strickler and Bal 1973, Ambler and Frost 1974, Poulet and Marsot 1978, 1980, Kerfoot et al. 1980, Landry 1980, Poulet and Quellet 1982). The quest for food constitutes the most important aspect of their life, and they exhibit a looping movement when searching for food (Fryer 1957, Kerfoot and Peterson 1980). Male copepods also exhibit a similar looping move-

ment when searching for mates (Katona 1973). These looping movements may be a search behavior for information sources (food and mates), triggered by physical or chemical information. Before behaving in a particular manner, copepods must primarily encounter the information itself. If the encounter occurs through spontaneous behavior, not by chance, then the behavior may be an environment-search behavior and can be categorized as appetitive (Craig 1918) or as exploratory (Barnett 1958). Information about their environment-search behavior may contribute to the understanding of the way copepods live under environmental conditions varying temporally and spatially, but little is known of the behavior of copepods in different environmental situations.

Copepods vary their feeding behavior under different food conditions (Alcaraz et al. 1980, Williamson and Gilbert 1980, Williamson 1981, Cowles and Strickler 1983). The feeding behavior is also subject to different starvation levels (Williamson 1980, 1983). Feeding activity (ingestion ability and digestive enzyme activity) depends on a previous feeding history and tends to be higher for copepods prestarved in laboratory experiments (Mayzaud and Poulet 1978, Donaghay and Small 1979, Donaghay 1980, Hassett and Landry 1983, Landry et al. 1984). On the other hand, much shorter starvation periods (1 to 2 d) lowered the ability of female *Oithona davisae* Ferrari and Orsi, a marine cyclopoid copepod, to capture conspecific nauplii (Uchima and Hirano 1986 b). The present findings indicate that the ability to resist starvation varies amongst copepod species, and suggest that the feeding behavior of copepods is controlled by internal factors which differ from environmental stimuli. Ivlev (1955) noted in fish the influence of emaciation through starvation on the ability to resist physical and chemical factors. Starvation or undernutrition in organisms generally lowers their physiological activities (Imai 1978, Braunwald et al. 1987). The reduction of physiological activity may affect various behavioral abilities (Ivlev 1955). Little is known of the influence of internal factors on the swimming behavior of copepods.

This problem was examined for *Oithona davisae* adults whose physiological activity could be changed by short-term starvation, as mentioned above. We report on their swimming behavior in various food situations and on the mechanisms by which their swimming behavior is determined.

Materials and methods

Individuals of *Oithona davisae* were sorted from plankton samples taken from the innermost brackish-water region of Tokyo Bay between 1980 and 1983, and transferred to a 30-ml Petri dish (55 mm diam.) containing either unfiltered natural seawater or filtered seawater. Their behavior was studied under a stereomicroscope. Filtered seawater was prepared by boiling and filtering (0.45 μm Millipore filter) oceanic water and diluted to 20‰ S. A mixture of *Chlamydomonas* sp., *Dunaliella* sp. and *Platymonas* sp. (each of the same concentration; hereafter called the food mixture) was supplied as food at various concentrations. The behavior of adults, which had previously been kept at a given food concentration for conditioning (CFC) or at a given rearing density (RD), was examined in isolation at various food concentrations as an environmental stimulus (EFC).

(I) Conditioning: Young adult males or females were initially maintained in 30-ml dishes containing filtered seawater and the food mixture at given CFC. There were seven levels for CFC's ranging from 0 to 45×10^4 cells ml^{-1}. A distinction between younger and older adults has been drawn by Uchima (1985). Dishes were kept at 20 °C in darkness for several days and the water was changed every 12 h except of CFC of 900 cells ml^{-1} in which water was changed every 6 h. A total of 11 sets, each containing 10 females, were kept at each CFC of 0, 900, 7 500, 15 000 and 12×10^4 cells ml^{-1}. A total of 17 sets, each containing 10 females, were kept at 3 000 cells ml^{-1} and 1 set at 45×10^4 cells ml^{-1}. Three sets of 10 males each were kept without food and 3 sets at CFC of 12×10^4 cells ml^{-1}. Eight sets of females were also maintained for 4 d at RD of 4 (5 sets), 10 (2 sets) and 100 (1 set) females in 30-ml dishes, respectively, with a food mixture of 3 000 cells ml^{-1}. Their behavior constituted the findings of the experiment on crowding.

(II) Observation: After being conditioned, the females from the sets were transferred individually to 15-ml Petri dishes (41 mm diam) containing food mixtures of 0, 900, 3 000, 7 500, 15 000 and 12×10^4 cells ml^{-1}, respectively, as the EFC. Each of the conditioned males was exposed to EFC of 0, 15 000 and 12×10^4 cells ml^{-1}. One minute after transfer, the number of each individual's swimming movements was counted for 5 min. The behavior of females maintained at CFC of 3 000 cells ml^{-1} for 8 d was observed for 3 min every 2 d. Three types of forward swimming movements of females (ca. 550 μm in body length) were observed. These movements were based on distance covered per movement (d), D1 (d > 1.5 mm), D2 (1.5 mm $\geqq$ d > 0.5 mm) and D3 (0.5 mm $\geq$ d). These movements were counted for 3 min at EFC of 0, 3 000, 45 000, 12×10^4 and 45×10^4 cells ml^{-1} for individuals from the 5 sets of 10 females each, condi-

tioned at CFC of 6 levels. The behavior pattern of each of the 10 females maintained at 45×10^4 cells ml^{-1} for 99 h was examined for 3 min during each of the 18 observations. The swimming movements of the 20 females conditioned at a given RD were counted for 3 min.

Additional experiments were conducted to examine the change in behavior of females exposed alternately to different food levels (0, 3 000 and 12×10^4 cells ml^{-1}) every 12 or 24 h after sampling. Three sets of five females each were prepared. Their swimming movements were counted for 3 min during each observation. In order to examine the effect of food concentrations on adult survival, newly-molted adult males and females were kept at various food concentrations (0 to 12×10^4 cells ml^{-1}) of EFC.

The average rates of individual swimming categories at various EFC or CFC or RD were compared using the Newman-Keuls method (Snedecor and Cochran 1980) at 0.05 level of significance.
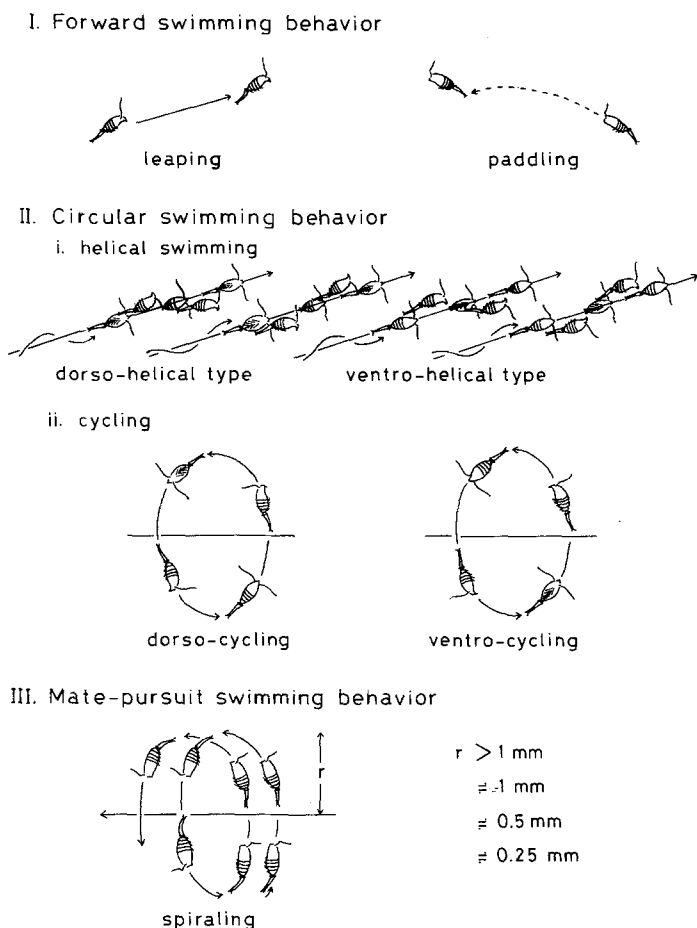
Results

I. Swimming movements

Oithona davisae makes forward, circular and spiraling swimming movements (Fig. 1). Nauplii, copepodites and adult females swim forward by leaping without hopping and sinking (Strickler 1977). Leaping is along a straight line (Fig. 1-I). Adult males advance by paddling, which is an erratic, curved movement consisting of continuous small hops. At times the leaping or paddling was followed by several seconds of rest. Nauplii, copepodites and adults made one rapid leaping movement before a raptorial feeding movement. *Oithona davisae*, which feeds on motile organisms (Uchima and Hirano 1986a), usually reacted to prey organisms at distances less than its body length and ingested a single prey individual in one raptorial feeding movement.

Circular behavior consists of helical swimming and cycling. During dorso-helical swimming, the dorsal body surface of the individual faces the axis of displacement (Fig. 1-II i) and during ventro-helical swimming, the ventral body surface faces the axis of displacement. Cycling is in a vertical plane, only occasionally in an oblique or horizontal plane. Unlike helical swimming, cycling does not result in displacement; individuals displayed tight somersaults (Fig. 1-II ii).

Mate-persuit behavior is peculiar to adult males. Once a male has approached or traversed the trail of a female ready for copulation, he begins a tight-radius spiraling to pursue her (Fig. 1-III, see Uchima and Murano 1988). The radius of the spiral decreases gradually from more than 1 mm to ca. 0.25 mm as the male approaches the female. This shorter radius leads to a faster spiraling.
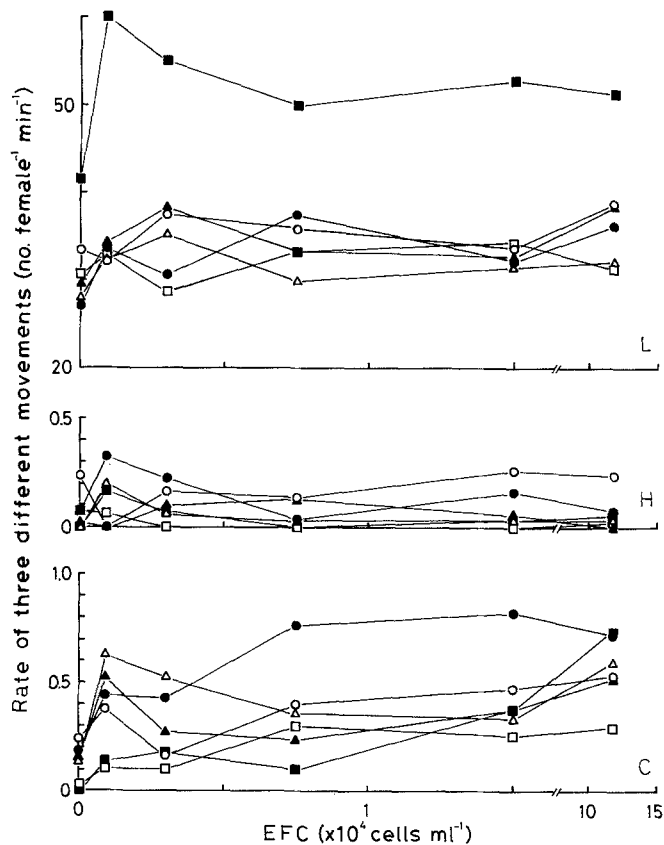
II. Change in behavior pattern

(i) Females maintained for 3 d at CFC of 0, 900, 3 000, 7 500, 15 000 and 12×10^4 cells ml^{-1}, respectively: At six

I. Forward swimming behavior

leaping   paddling

II. Circular swimming behavior
   i. helical swimming

dorso-helical type   ventro-helical type

   ii. cycling

dorso-cycling   ventro-cycling

III. Mate-pursuit swimming behavior

r > 1 mm
≑ -1 mm
≑ 0.5 mm
≑ 0.25 mm

spiraling

Fig. 1. *Oithona davisae*. Swimming movements of copepodites and adults. (I) Except for adult paddling males, copepods swim forward by leaping; (II) all copepods make circular swimming behavior; (III) mate-pursuit behavior is peculiar to adult males whose spiraling occurs when they traverse or approach the trail of females ready for copulation

Fig. 2. *Oithona davisae*. Behavior of females at food concentrations (EFC) of 0, 900, 3 000, 7 500, 15 000 and 12×10^4 cells ml^{-1} observed for 5 min after the 3 d conditioning to each food level. Conditioning food concentrations (CFC; $\times 10^3$ cells ml^{-1}): 0 (o), 0.9 (•), 3 (△), 7.5 (▲), 15 (□), 120 (■). Each plotted value is mean of 10 replicates; significant differences are noted in text. L: leaping; H: helical swimming; C: cycling

EFC of the same concentrations as those of CFC, there was no significant difference as to the rates of leaping swimming movements (Fig. 2). At EFC of 900 cells ml^{-1} or more, the leaping rates for females conditioned to CFC of 12×10^4 cells ml^{-1} were above 50 female^{-1} min^{-1} and significantly higher (10 to 30) than those of females conditioned to lower CFC (Table 1). Of the three swimming movements, leaping constituted over 98% at all EFC regardless of CFC. Helical-swimming rates at each CFC did not differ significantly among all EFC. In a no-food situation, the rate was significantly higher for females conditioned without food than for those conditioned to 900 cells ml^{-1} or more (Table 1). The mean helical swimming rate in all EFC tended to decrease from 0.17 to 0.05 female^{-1} min^{-1} with an increase in CFC from 0 to 12×10^4 cells ml^{-1} (Fig. 2). For females conditioned to 12×10^4 cells ml^{-1}, cycling rates were significantly higher at EFC of 12×10^4 cells ml^{-1} than at lower EFC (Fig. 2). Cycling rates at 7 500 cells ml^{-1} or less EFC were lower for females conditioned to higher CFC though significant differences were seldom detected (Fig. 2 and Table 1).

(ii) Females maintained at 3 000 cells ml^{-1} for 8 d: Both the rates of helical swimming and of cycling were below 0.3 female^{-1} min^{-1} and no significant difference existed among EFC in individual rates; these rates tended to decrease with the prolongation of conditioning periods (Table 2). Leaping rates tended to decrease with time until Day 6, especially at EFC of 7 500 cells ml^{-1} or less (Fig. 3). On Day 6 the rate at 7 500 cells ml^{-1} or less EFC was significantly lower than that at higher EFC. The former rate increased again on Day 8 when 20 to 40% of the females died, though the mean rate in all EFC was significantly lower than those on Days 2 and 4 (Fig. 3 and Table 2). With the progress of time, females became more sensitive to different food concentrations while reducing their swimming activity.

(iii) Females maintained for 4 d at 3 000 cells ml^{-1} at RD of 4, 10 and 100 females 30 ml^{-1}, respectively: Leaping rates were not much influenced by the change in RD, but the rate at each RD was somewhat, though not significantly ($p < 0.05$; Student's t-test) lower on Day 4 than on Day 2 (Table 3). Leaping constituted more than 99% of all movements at all RD regardless of conditioning periods. Helical-swimming rates in all RD were not significantly different from each other. Cycling rates were significantly higher at

Table 1. *Oithona davisae.* Statistics of rates of swimming movements of females conditioned at six levels of food concentrations (CFC) for 3 d. At every food concentration as an environmental stimulus (EFC), comparisons of mean rates among CFC were made by Newman-Keuls method at 0.05 level of significance. No significant differences exist among CFC bracketed, and > shows a significantly higher rate at CFC on left-hand side

EFC ($\times 10^3$ cells ml^{-1})	Significant difference among CFC ($\times 10^3$ cells ml^{-1})
Leaping movement	
0	Not detected
0.9 ⎫	
3 ⎪	
7.5 ⎬	Present: 120 > (0, 0.9, 3, 7.5, 15)
15 ⎭	
120	Present: 120 > (0, 3, 15)
Helical swimming movement	
0	Present: 0 > (0.9, 3, 7.5, 15, 120)
0.9 ⎫	
3 ⎪	
7.5 ⎬	Not detected
15 ⎪	
120 ⎭	
Cycling movement	
0 ⎫	
0.9 ⎬	Not detected
3 ⎭	
7.5	Present: 0.9 > (0, 7.5, 15, 120)
15 ⎫	
120 ⎬	Not detected

Table 2. *Oithona davisae.* Statistics of rates of swimming movements of females kept at CFC of 3 000 cells ml^{-1} for 8 d. On Day 8, 20 to 40% of females died in all experiments. At every EFC, comparisons of mean rates among conditioning periods (2, 4, 6 and 8 d) were made by Newman-Keuls method at 0.05 level of significance. No significant differences exist between days bracketed, and > shows a significantly higher rate on day on left-hand side

EFC ($\times 10^3$ cells ml^{-1})	Significant difference between days
Leaping movement	
0	Present: 2 > 4 > 8 > 6
0.9	Present: 2 > (4, 8) > 6
3	Present: (2, 4) > 8 > 6
7.5	Present: 2 > 8 > 6, 4 > 6
15	Present: (2, 4) > 8
120	Present: (2, 4) > (6, 8)
Helical swimming movement	
0	Present: 8 > 6
0.9	Present: 4 > 8
3	Present: 2 > (4, 6, 8)
7.5	Not detected
15	Present: 2 > 4
120	Present: 2 > (4, 6, 8)
Cycling movement	
0	Present: 6 > 2, (4, 6) > 8
0.9	Not detected
3	Present: 2 > (4, 6, 8)
7.5	Present: 6 > 8
15	Present: 2 > 6, (2, 4) > 8
120	Not detected

Table 3. *Oithona davisae.* Swimming behavior of females kept at 3 000 cells ml^{-1} under various crowding conditions for 4 d. Figures show rates (number female^{-1} min^{-1}) of leaping (L), helical swimming (H) and cycling (C) examined for 3 min 2 and 4 d after conditioning

| Crowding conditions (females 30 ml^{-1})	Rates of movements (mean ± 1 SE; $N=20$)		
	L	H	C
(Day 2) 4	40.3 ± 1.96	0	0
10	48.0 ± 2.91	0.03 ± 0.02	0.03 ± 0.02
100	44.7 ± 2.73	0.05 ± 0.03	0.12 ± 0.04
(Day 4) 4	35.2 ± 3.22	0	0
10	35.0 ± 2.77	0	0
100	35.9 ± 2.86	0.03 ± 0.03	0.18 ± 0.06
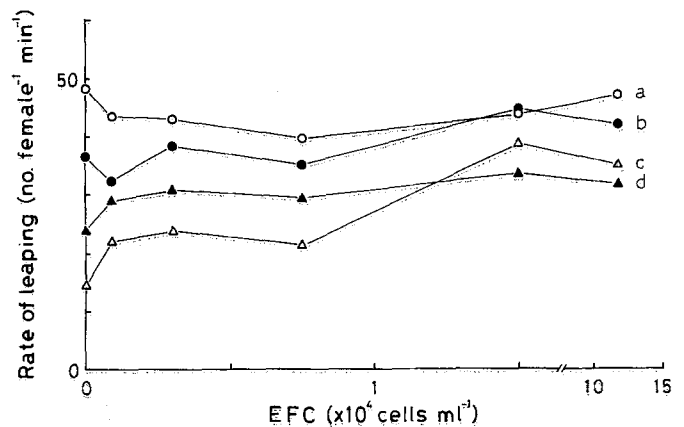
Fig. 3. *Oithona davisae.* Changes in rate of leaping movements of females at the food concentrations (EFC) of 0, 900, 3 000, 7 500, 15 000 and 12×10^4 cells ml^{-1}. Each female was observed for 3 min 2 (a), 4 (b), 6 (c) and 8 (d) d after being maintained at 3 000 cells ml^{-1}. Each plotted value is mean of 10 replicates, except for 6 on Day 8 when 20 to 40% of females died

RD of 100 females 30 ml^{-1} than at 10 or less; the high value was maintained for 4 d (Table 3).

(iv) Males maintained for 3 d at CFC of 0 and 12×10^4 cells ml^{-1}: For both starved and nourished males the rates of paddling, helical swimming and cycling did not differ significantly in the individual rates among all EFC (Fig. 4). Paddling rates were significantly lower for starved males than for nourished males at every EFC. On the contrary, cycling rates for starved males were significantly higher at every EFC, and the rates of their helical swimming also were higher though significant differences existed only in a no-food situation (Fig. 4). The mean rate of helical swimming in all EFC for starved males was almost equal to that for starved females, whereas the starved males had 9-fold the mean rate of cycling of the starved females (Fig. 4).
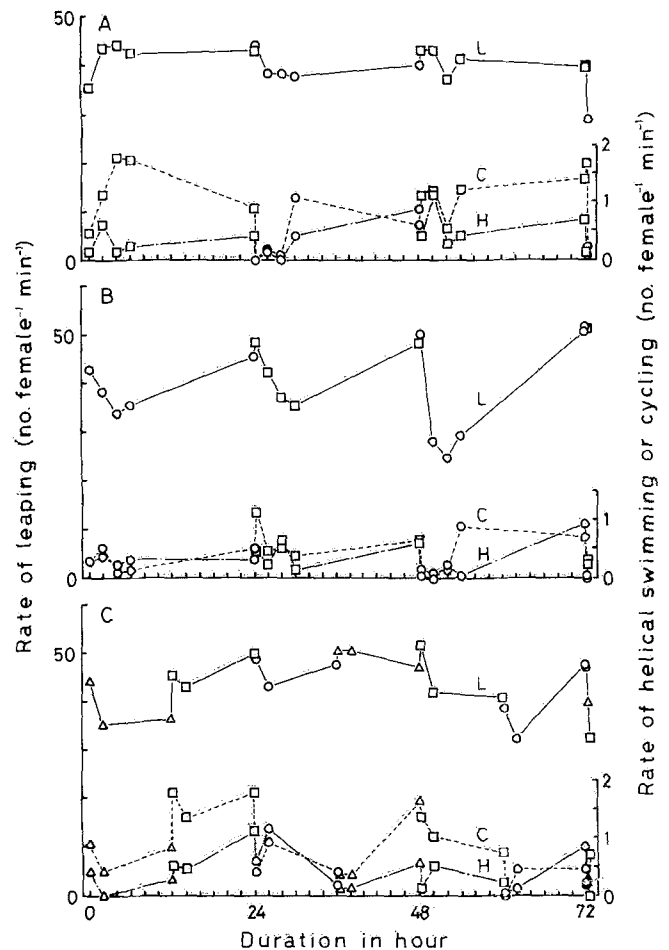
(v) Variation of behavior pattern in changing environment: The behavior pattern of females depended on changing patterns of the ambient environment (Fig. 5). The fluctuation in the leaping rates during 3 d was larger in females
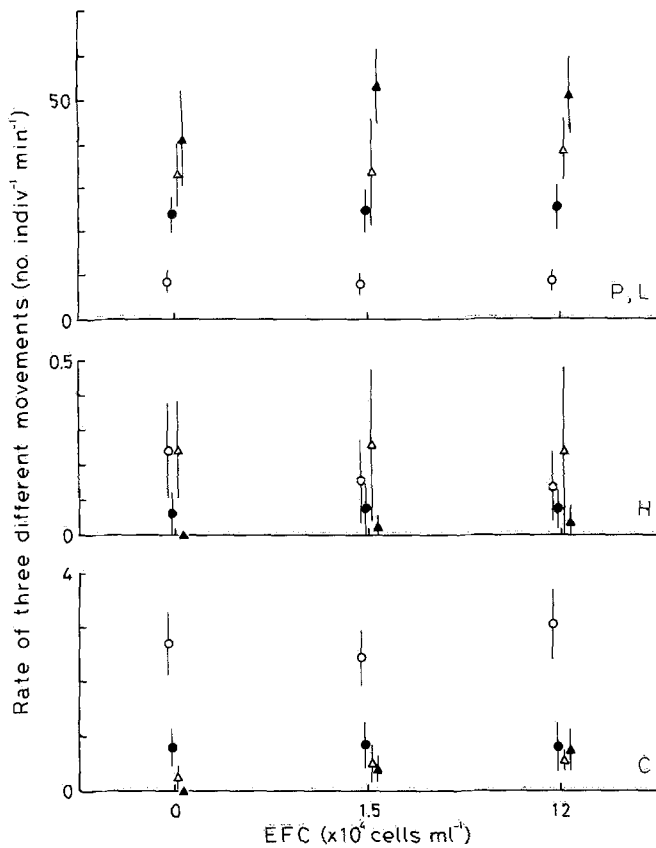
Fig. 4. *Oithona davisae.* Behavior of males and females at food concentrations (EFC) of 0, 15 000 and 12 × 10⁴ cells ml⁻¹ observed for 5 min after 3 d conditioning with or without food. Conditioning food concentrations (CFC; cells ml⁻¹): 0 (o), 12 × 10⁴ (●) for males; 0 (△), 12 × 10⁴ (▲) for females. Each plotted value is mean ±95% C.I. of 10 replicates; values for females are the same as those shown in Fig. 2. L: female's leaping; P: male's paddling; H: helical swimming; C: cycling

Fig. 5. *Oithona davisae.* Changes in behavior pattern of females exposed to different food concentrations at 24-h (A, B) or 12-h (C) intervals. Each female was observed for 3 min repeatedly over 17 to 21 times. Food concentrations (× 10³ cells ml⁻¹): 0 (o), 3 (△), 120 (□). Each plotted value is mean of 5 replicates. L: leaping; H: helical swimming; C: cycling

exposed to longer-term starvation. Females kept without food for the first 24 h after sampling exhibited greater variations in the rate of swimming movements in a changing environment than those supplied with the food mixture of 12 × 10⁴ cells ml⁻¹, although much of this variation represented a return to rates reached before transfer to a new food concentration (Fig. 5 A, B). Under the same food conditions, the females were not excited when transferred to new dishes every 2 h, but were stimulated when transferred after a longer stationary period. Females exposed to the change in EFC every 12 h displayed a variable pattern of behavior, adjusting to environmental changes (Fig. 5 C). The females acclimated to a new environment within 2 h regardless of their previous history; hence, the term "conditioning" in the present study can be exchanged for "acclimation".

(vi) Pattern of forward swimming behavior of females conditioned for 2 d to CFC of 0, 900, 3 000, 7 500, 15 000 and 12 × 10⁴ cells ml⁻¹, respectively: The percentage of the shortest leaping movement (D3) increased and that of the longer leaping movements (D1) and (D2) decreased with increasing EFC, regardless of conditioning (Fig. 6). These patterns also were demonstrated by the leaping rate itself.

Let Ym be the minimum or the maximum percentage of any leaping movement. Then the actual percentage Y of the leaping movement at the EFC X (cells ml⁻¹) can be expressed by the following equation:

$$Y = (Ym - i)(1 - \exp(-sX)) + i$$

where i = percentage in a no-food situation and s = sensitivity coefficient (see Appendix). If the minimum and the maximum percentage are 0 and 100, respectively, then the relation between the percentage of each type of leap and the EFC is expressed by the equations noted in Fig. 6.

A difference between the actual and the expectant values in the percentage of each type of leaping movement in a no-food situation was smaller for females kept at 900 cells ml⁻¹ or less CFC and largest for females kept at 3 000 cells ml⁻¹. In the latter, female sensitivity coefficients were largest and hence, the response curves of D1, of D2 and of D3 to EFC were sharpest (Figs. 6 and 7). In other words, starved females responded less sensitively to food conditions and displayed an almost stereotyped behavior; thus the relative ratio of leaping movements was almost
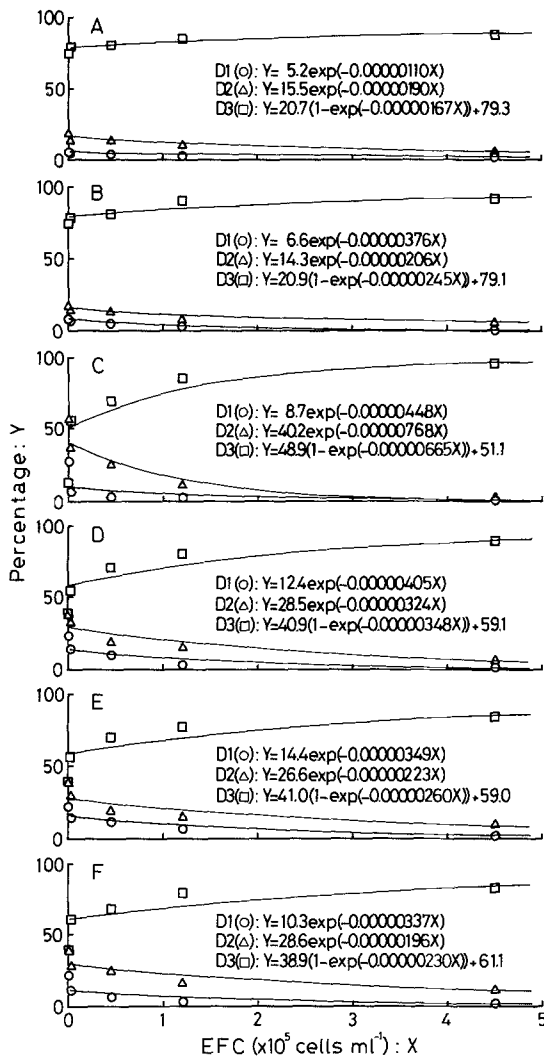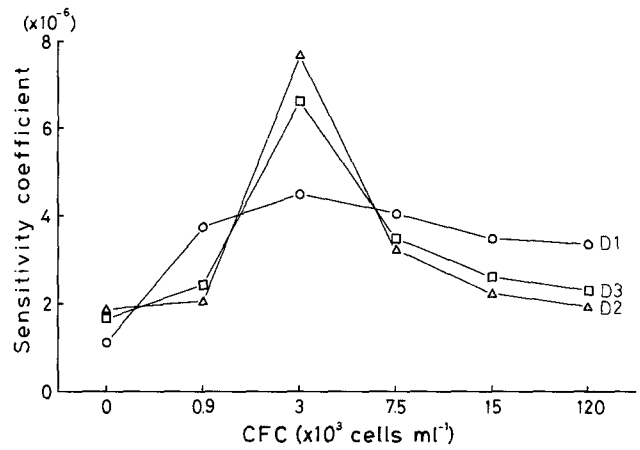
Fig. 6. *Oithona davisae*. Changes in forward swimming behavior of females at food concentrations (EFC) of 0, 3 000, 45 000, 12 × 10⁴ and 45 × 10⁴ cells ml⁻¹ observed for 3 min after 2-d conditioning to different food levels. Conditioning food concentrations (CFC; × 10³ cells ml⁻¹): 0 (A), 0.9 (B), 3 (C), 7.5 (D), 15 (E), 120 (F). Leaping movements were divided into three types, D1, D2 and D3, according to distance covered per movement (d). (D1) d > 1.5 mm, (D2) 1.5 mm ≧ d > 0.5 mm, (D3) 0.5 mm ≧ d. Each plotted value is mean of 10 replicates

Fig. 7. *Oithona davisae*. Response of sensitivity coefficients of females to conditioning food concentrations (CFC). D1, D2 and D3 mean three types of leaping movements

Fig. 8. *Oithona davisae*. Swimming distance (mm) per minute of females shown in Fig. 6, assuming distance covered per movement in D1, D2 and D3 being 2.5, 1 and 0.3 mm, respectively. Conditioning food concentrations (CFC; × 10³ cells ml⁻¹): 0 (○), 0.9 (●), 3 (△), 7.5 (▲), 15 (□), 120 (■). Each plotted value is mean of 10 replicates
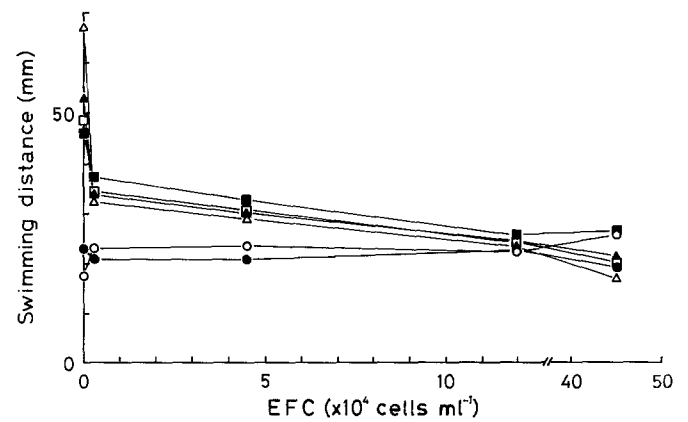
constant regardless of EFC. On the other hand, females kept at CFC of 3 000 cells ml⁻¹, with net production about zero (Uchima unpublished data) were most sensitive to environmental changes. Females responded to higher CFC by the lowered sensitivity and stereotyped behavior (Figs. 6 and 7).

The swimming distance covered per minute was estimated at every EFC, assuming that the distance per leap in D1, D2 and D3 was 2.5, 1 and 0.3 mm, respectively (Fig. 8). Females conditioned to 900 cells ml⁻¹ or less swam almost the same distance at every EFC. Females conditioned to 3 000 cells ml⁻¹ swam the longest distance in a no-food situation; the distance decreased sharply when they encountered food. In females conditioned to higher concentrations, the distance decreased more gently with an increase in EFC.

(vii) Behavior pattern of females maintained for 99 h at 45 × 10⁴ cells ml⁻¹: Females seldom swam in D1 (Fig. 9).

Fig. 9. *Oithona davisae*. Behavior pattern and swimming distance (mm) per minute of females maintained at food concentration of 45 × 10⁴ cells ml⁻¹. Each female was observed for 3 min. Behavior pattern was shown as relative percentage of three types of leaping movements, D1 (○), D2 (△) and D3 (□) (see Figs. 6 and 8). Each plotted value is mean ±95% C.I. of 10 replicates

The relative percentage of three types of leaping movements remained almost unchanged for 99 h. Swimming distance per minute was also almost constant, though it fluctuated slightly between 47 and 50 h.

Discussion

Living animals perceive, discriminate and react to various information scattered in their environment. The ability to perceive suitable information swiftly can allow copepods to avoid encounters with predators (Strickler and Bal 1973), and the information mediates contact with food and mates. Copepods must primarily search for the information itself. Their information-search behavior can be categorized into an appetitive behavior if it is followed by a consummatory reaction (Craig 1918). Particularly the search behavior taken spontaneously, but not connected with any particular stimulus, is categorized into an exploratory behavior (Barnett 1958), although the distinction between appetitive and exploratory behavior is not clear.

Circular swimming in copepods is the behavior displayed in response to an escaping prey animal (Fryer 1957, Kerfoot 1977, 1978, Gilbert and Williamson 1978, Li and Li 1979, Williamson 1980, 1981, 1983), to a cladoceran egg (Kerfoot and Peterson 1980) or to a mate (Parker 1902, Katona 1973, Kittredge et al. 1974, Griffiths and Frost 1976, Gerritsen 1980, Jacoby and Youngbluth 1983, Watras 1983). This swimming behavior as a search and pursuit behavior is functionally similar to the mate-pursuit behavior not circular movements, of male *Oithona davisae*. The swimming patterns also are similar (cf. Fryer 1957 and present Fig. 1-II, III). *O. davisae* displayed a circular swimming behavior in situations without food or mates (Figs. 2, 4, 5). Females acclimated to more crowded conditions displayed this behavior more frequently even when they were isolated from each other (Table 3). Hence, the circular swimming behavior of *O. davisae* may be the spontaneous environment-search behavior, i.e., exploratory behavior.

Oithona davisae females swam by cycling less frequently and by leaping more actively when they were transferred from acclimated richer food conditions ($\geq 15\,000$ cells ml^{-1}) to poorer conditions (Figs. 2 and 8). On the contrary, females acclimated to 3 000 to 7 500 cells ml^{-1}, at which the net production was about zero (Uchima unpublished data), had higher cycling rates at lower concentrations except for 0. Cycling rates were lower in the absence of food than at higher food levels, regardless of the conditioning food concentration (CFC), but in the former situation they tended to increase with lowering CFC (Fig. 2). These results suggest that the behavioral response of females to new food conditions depends on their internal, nutritional conditions. It may be of urgent necessity for females starved in poor food areas to discover richer areas and it may be more important for them to avoid much poorer areas than is the case for unstarved females. Females cycling in a rich food area can return to the same area even if they encounter poorer food conditions while cycling. On the contrary, leap-

ing females once moved out of a rich food area must search for environments and locomote again to return to the rich area. The cycling movements of females may lead to more careful detection of high concentrations of food patchily distributed on an ultra micro-scale, i.e., at a μm or mm level, and the leaping movements may allow them to explore more extensively. Helical swimming may be an intermediate movement between cycling and leaping. Starved females tend to adopt this swimming movement more frequently than unstarved females (Fig. 4), but the function is not clear.

Starved males displayed cycling movements at a much higher rate than both starved females and unstarved males, regardless of food conditions (Fig. 4). The survival days in starved males were much shorter than those in starved females (Fig. 10). This result suggests that males swim more actively in the absence of food than females. The ingestion rate for males was more or less stable and is much lower than that for females at every food condition, regardless of the previous food history, though the rate was almost equal for the two sexes of Copepodite V (Uchima unpublished data). These results suggest that the sexually-motivated males prefer to search for a mate rather than obtain food, and their cycling movements serve for the mate search. Once males perceive the signal from females ready for copulation, they change their paddling movements and occasional circular swimming for spiraling movements (Uchima and Murano 1988 and present Fig. 1-III). The former two movements may be a spontaneous mate-search behavior and can be regarded as an appetitive behavior; the spiraling mate-pursuit behavior is the consummatory behavior.

The present results reveal that the behavior of *Oithona davisae* is influenced by an environmental stimulus (external stimulus) but is more strongly controlled by the internal factor concerned with nutritional conditions (Figs. 2, 3, 4, 5, 6, 8). The acclimation to a given food concentration also depends on the internal condition. Hassett and Landry (1983) and Landry et al. (1984) found higher feeding activities in *Calanus pacificus* acclimated to lower food concentrations. On the other hand, Ivlev (1955) reported that both
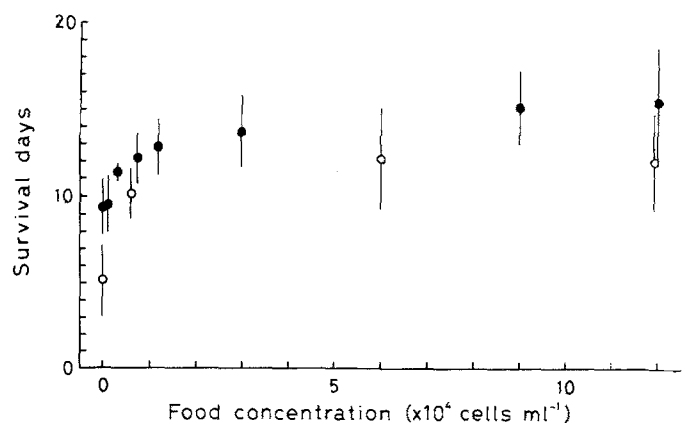

Fig. 10. *Oithona davisae*. Survival of adults at 20 °C and various food levels. Food concentrations ($\times 10^3$ cells ml^{-1}): 0, 6, 60, 120 for males (o); 0, 0.9, 3, 7.5, 12, 30, 90, 120 for females (•). Each plotted value is mean $\pm 95\%$ C.I. of 5 replicates

swimming and feeding abilities of fish decrease with an in-
crease in the degree of emaciation through starvation. Lille-
lund and Lasker (1971) noted that the vigor of the starved
carnivorous copepods declined with time. The decline
caused a decrease in their swimming activity, which was
reflected in a lower respiration rate, and resulted in the
lowering of the ability to capture fish larvae. *O. davisae*
females also exhibited less swimming and feeding ability
with decreasing CFC or with lengthening starvation periods
(Uchima and Hirano 1986 b and present Figs. 2 and 8). The
dependency of behavioral ability or of survival (Fig. 10) on
nutritional conditions may closely be related to the physio-
logical activity (internal activity), i.e., digestion, absorption,
metabolism, ability to resist sickness, etc. (Imai 1978, Braun-
wald et al. 1987). Although direct measurements were not
made in the present study, the decrease in CFC may lower
the degree of internal activity (DIA). Starved and inactive
O. davisae females displayed an almost stereotyped behav-
ior, regardless of the food concentration as an environ-
mental stimulus, EFC (Fig. 6). It is likely that such a be-
havior depresses the energy loss (Fig. 8), and that the
internal activity above a certain, critical level (critical level of
internal activity, CLIA) is necessary to respond sensitively
to changing environments.

Williamson (1980, 1983) showed in the encounter of
Mesocyclops edax and prey zooplankters that the rates of
looping movements and of attack on prey animals are higher
in starved *M. edax* than in unstarved individuals. Frost
(1972) and Runge (1980) found that *Calanus pacificus* ex-
posed to short-term starvation has a higher ingestion rate
than unstarved individuals. Starved copepods were active
feeders, particularly in low prey densities (Yen 1983) though
they exhibited less selectivity (Stemberger 1985). Their DIA
may have been higher than CLIA because of the high starva-
tion tolerance (Threlkeld 1976, Dagg 1977). Feeding activity
is lower in starved, inactive *C. pacificus* than in starved,
active individuals (Cox and Willason 1981, cf. Hassett and
Landry 1983). This fact also indicates that DIA higher than
CLIA is necessary to adapt to the food-level change. DIA
may be dependent on a previous history.

Oithona davisae females starved for 2 d did not capture
animal prey (Uchima and Hirano 1986 b). They were more
easily collected with a pipet (1 mm diam.) at any EFC with
lengthening starvation periods. Although the pipet, an arti-
ficial predator, raised hydrodynamic information, it also
easily captured females transferred from an acclimation
level of 12×10^4 flagellate cells ml^{-1} into higher concentra-
tions. The less sensitive response was not entirely attribut-
able to the confused hydrodynamic information in a crowd
of flagellates because of the lower acclimation levels
($\leq 15\,000$ cells ml^{-1}) allowing the ease of evasion. The same
trends were also found in nauplii and copepodites, though
adult males were comparatively easily captured regardless of
acclimation food levels. These results suggest that the low
sensitivity caused by very high DIA or by DIA lower than
CLIA produces an almost stereotyped behavior (Figs. 6
and 7) and consequently, increases the difficulty in escaping
from predators. The ability to remain motionless may be

generally more effective than the escape response to avoid
the attack of fish (Zaret 1980 b). However, even if *O. davisae*
keeps still, it may be discovered easily by fish because of the
red-colored part on each postero-lateral side of the first
thoracic somite (see Kerfoot et al. 1980). Females must
adopt the largest leaping movement, D 1, under every food
condition as a momentary movement for escaping from the
visionary field of the fish (Confer and Blades 1975, Zaret
1980 a, b) or from its suction field (Drenner et al. 1978) even
if the escape response involves high energy expenditure
(Strickler 1977), or to avoid chaetognath attacks even if the
response is more disadvantageous than a motionless drift
(Newbury 1972, Feigenbaum and Reeve 1977).

The stereotyped behavior may be inhibited by the ad-
dition of an environment-dependent behavior, which is
elicited by an environmental stimulus through sensitivity to
the environment-independent behavior occurring in a no-
food situation (see Appendix). The behavior pattern ap-
proaching the complete stereotype with increase in EFC
should be broken, especially in females acclimated to high
food concentrations suitable for feeding. However, the
swimming behavior pattern does not break at 45×10^4 cells
ml^{-1} (Fig. 8) though the feeding rate fluctuates hourly
(Uchima unpublished data). The latter fact probably indi-
cates that DIA has the upper limit and the maximum DIA
does not adjust with the very high intensity of an external
stimulus (IES). In other words, very high IES presumably
represses the force of internal activity controlling sensitivity
and behavior. Therefore, prey *Oithona davisae* will avoid
entering or remaining in very rich food environments if the
high food levels do not interfere with the foraging behavior
of predators, though actually they do. In nature, the patchy
food environment present on a small scale (Dagg 1977) may
inhibit the stereotyped behavior.

In conclusion, the present results indicate that the com-
bined effects of the degree of internal activity (DIA) and the
intensity of external stimulus (IES) determine the behavior
pattern of *Oithona davisae*; the behavioral response to the
given IES depends on DIA. By this mechanism they are able
to adapt their swimming behavior to ambient food condi-
tions changing temporally and spatially. However, their be-
havior is not completely adapted to obtain food, because of
the necessity of searching for more preferable food condi-
tions and of escaping from predators. Particularly, males
must search for a mate. In order to maintain adaptable, but
not stereotyped, *O. davisae* has to maintain a degree of inter-
nal activity (DIA) that is higher than the critical level of
internal activity (CLIA).

Appendix

The behavior pattern of *Oithona davisae* was modified by
the food concentration as an environmental stimulus. The
relative ratios of three types of leaping movements (D 1, D 2
and D 3) asymptotically decreased or increased with increase
in food concentrations (Fig. 6). These data suggest a behav-
ioral dependency upon environmental stimuli. The behavior

is not an entire dependency because of the food independent behavior taken in a situation without food, i.e., individuals still respond with various kinds of leaping movements in the absence of food. Higher sensitivity to the change in food concentrations presumably causes larger modification of behavioral patterns.

(I) Behavior promoted by the increase in food concentration: The ratios of three types of leaping movements sum up to 100% at every food concentration. Using the rate (number of leaps per unit time) instead of the ratio (%), then $Ym =$ the total number of leaps per unit time and constant, 100, regardless of food concentrations. Let $Y =$ the rate of D3, and the summed rate, R, of D1 and D2 is expressed by

$$R = Ym - Y \qquad (1),$$

and when $Y = i$ in a situation without food stimuli,

$$R = Ym - i.$$

The rate of D3 is promoted by a fraction of food concentration, dX. The increase beyond the food independent rate i is $Rs\,dX$, where $s =$ the coefficient of sensitivity or of food dependency (per unit food concentration). Then,

$$Y = i + Rs\,dX.$$

The increase of $Y =$ the decrease $- dR$ of the summed rate of D1 and D2; i.e.,

$$Rs\,dX = - dR \qquad (2).$$

Since $R = Ym - Y$, and since $R = Ym - i$ when $X = 0$, integrating Eq. (2) for the range $(0, X)$, and hence $(Ym - i, R)$, we obtain

$$Y = (Ym - i)(1 - \exp(- sX)) + i \qquad (3).$$

(II) Behavior depressed by the increase in food concentration: Let $Y =$ the rate of D1 or D2, and let $i =$ the food independent rate. The decrease in Y, depressed by a fraction of food concentration, dX, is $Ys\,dX$, where $s =$ the sensitivity coefficient, and then,

$$Ys\,dX = - dY \qquad (4).$$

Since $Y = i$ when $X = 0$, integrating Eq. (4) for the range $(0, X)$, and hence (i, Y), we obtain

$$Y = i\exp(- sX) \qquad (5).$$

Substituting 0 for Ym in Eq. (3), we obtain Eq. (5), as a natural consequence of the agreement between the increase in one behavior and the decrease in the other behavior; i.e., $R = - Y$ when $Ym = 0$ in Eq. (1).

The complementary relation between the relative ratios of behavior is almost satisfied, but not perfectly completed in the present study since the behavior comprises three, not two, types whose ratios all vary asymptotically with food concentrations (Fig. 6).

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