# カイアシ類Oithona davisaeの餌料とその幼生の成長に及ぼす摂食開始時の餌料密度の影響


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# Food of *Oithona davisae* (Copepoda : Cyclopoida) and the Effect of Food Concentration at First Feeding on the Larval Growth[1), 2)]

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**Abstract**

Neither diatom nor detritus was suitable as food for *Oithona davisae* throughout all developmental stages. Except for zooplankters which are too large to capture, Nauplius I (NI) fed on motile organisms (flagellates, dinoflagellates and oligotrichines) of the same species and approximate size as adult females. *Oithona davisae* commenced feeding soon after hatching and did not grow beyond NI below the threshold concentration of food, which fell within a range from 900 cells $ml^{-1}$ (54 ngC $ml^{-1}$) to 1,500 cells $ml^{-1}$ (90 ngC $ml^{-1}$) and consisted of a mixture of *Chlamydomonas* sp., *Dunaliella* sp. and *Platymonas* sp. NI needed a food concentration above 4,500 cells $ml^{-1}$ (270 ngC $ml^{-1}$) to reach Copepodite I (CI). A shortage of food for only 1 h after hatching prevented most nauplii from reaching CI. NI did not feed within 1 h after hatching at a concentration of 1,000 *Dunaliella* cells $ml^{-1}$ (60 ngC $ml^{-1}$), whereas 30-70 % of NI ingested *Chlamydomonas*, *Dunaliella* or *Platymonas* at 5,000 cells $ml^{-1}$ (300 ngC $ml^{-1}$). Their feeding ability was poor during the initial 30 (especially 20) minutes period after hatching. Adult females carry eggs in a pair of egg-sacs until hatching. This type of egg-laying strategy may compensate for the insufficient ability of newly-hatched nauplii to forage under conditions with little available food and/or to migrate into more favorable environments.

Copepod egg-laying strategy may be divided into two types (MARSHALL & ORR 1954, SEKIGUCHI 1985); here referred to as egg-releasing and egg-carrying types. Many calanoid copepods belong to the egg-releasing type in which females lay eggs freely in the water, whereas cyclopoid oithonid copepods carry eggs in a pair of egg-sacs attached to the female's genital openings until nauplii emerge (egg-carrying type). In the egg-releasing type, even if the nauplii hatch in an area of insufficient food concentration, they are vigorous enough to pass through their early developmental stages without feeding, as reported by MARSHALL & ORR (1956) for Nauplius I (NI) and II (NII) of *Calanus finmarchicus*. The swimming and foraging abilities of later stage nauplii are greater than those of the earlier stage nauplii because of their larger size.

The first feeding stage varies in both herbivorous and predatory copepods (RAYMONT 1983). *Oithona similis* commences feeding at the 1st naupliar stage (EATON 1971). If an egg-carrying female locates and stays in an area which is rich in food of NI until eggs hatch, the newly-hatched nauplii will survive successfully.

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[2)] カイアシ類 *Oithona davisae* の餌料とその幼生の成長に及ぼす摂食開始時の餌料密度の影響

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Many observations and experiments have been made mainly for adult females of calanoid copepods in relation to feeding habit, food selection, feeding (or filtering) rate, etc. (cf. MARSHALL 1973, RAYMONT 1983). Feeding behavior in the nauplii is little known. Their feeding impact on the population of prey organisms and on co-existing animals having a similar food requirements is of importance in an aquatic ecosystem. The population growth may depend upon the success of the first feeding at a naupliar stage.

*Oithona davisae* Ferrari & Orsi, a marine cyclopoid copepod, is one of the dominant copepod species in the innermost part of Tokyo Bay (UCHIMA unpubl.). We examined the food of both adult females and NI, the effect of first feeding on the growth of nauplii, and the threshold concentration of food for growth.

## Materials and Methods

Adult females of *Oithona davisae* carrying fertilized eggs were isolated from plankton samples taken from the innermost brackish-water region of Tokyo Bay in 1982, 1983 and 1985. Those carrying the 1st egg batch near hatching (FE) were used for examining foods suitable for the successive egg production. Other females were individually reared in 10 ml Petri dishes (41 mm in diameter) without food until their eggs hatched. FE and newly-hatched nauplii were reared in 15 or 30 ml Petri dishes (41 or 55 mm in diameter, respectively) under various food conditions at given temperatures depending on natural water temperatures. The culture water was prepared by boiling and filtering (0.45 $\mu$m Millipore filter) oceanic water which was then adjusted to 20‰ salinity.

### *Food*

Various phytoplankters were examined for suitability as food for adult females and NI. The flagellates *Chlamydomonas* sp., *Dunaliella* sp. and *Platymonas* sp. were cultured at 20‰ salinity in a slightly modified Føyn's Erd-Schreiber medium (PROVASOLI et al. 1957), to which vitamin $B_{12}$ was added instead of soil-extract. These flagellate diets had been found suitable for the growth and egg production of *O. davisae* (UCHIMA 1979, 1985). Other phytoplankters, *Chattonella antiqua*, *Chlorella* sp., *Ditylum brightwellii*, *Heterosigma* sp., *Phaeodactylum tricornutum* and *Skeletonema costatum*, were cultured at 20‰ salinity in SW II medium (IWASAKI 1961). They were separately supplied as food at different concentrations to FE having mature oocytes in ovaries and newly-hatched nauplii; the 2nd egg batch nutritionally originating from natural food was laid by the FE within 1 day at 20°C. These females are expected to lay or to carry the 3rd egg batch between days 4 and 7 at 20°C under suitable conditions (UCHIMA 1985).

*Oithona* did not ingest *Skeletonema* in the dark, however they fed on flagellates regardless of light conditions (UCHIMA 1979, 1985). Because of possible light stimulant for feeding on diatoms, 10 FE or 10 newly-hatched nauplii were kept in a 30 ml dish at 20°C under a 12-h L (0600–1800): 12-h D photoperiod. The light was about 1,500 lx. Water was changed daily.

Observations on feeding behavior were made under a binocular microscope for all develop-

mental stages of *O. davisae* maintained in 2, 15 or 30 ml dishes with unfiltered natural seawater, from which large zooplankters were removed. Sometimes detritus, plants and animals (oligotrichines, tintinnids and rotifers) taken by a towing net (mesh aperture: 59 $\mu$m) were added to bottle-sampled water.

*First Feeding*

For examining the first feeding, sets of 15 newly-hatched nauplii each were kept in 15 ml dishes with phytoplankton at different concentrations ranging from 1,000 to $4\times10^4$ cells $ml^{-1}$ at 20°C in darkness. For phytoplankton species *Chlamydomonas* and *Platymonas* 4 sets (60 indiv.) and for *Dunaliella* 10 sets (150 indiv.) of larvae were used for the experiment. Feeding on flagellates was determined by counting the nauplii having green particles in the gut under a microscope. Counting within 10 min was done 10, 20 and 60 min after hatching.

*Effect of Food Concentration on Larval Growth*

The effect of food concentration on development was examined for 10 newly-hatched nauplii, which were reared in a 30 ml dish at concentrations of 900, 1,500, 3,000, 4,500, 6,000 and $12\times10^4$ cells $ml^{-1}$ of a mixture of the above three species of flagellates (each of the same concentration) at 20, 23 or 27°C in the dark. The other 10 newly-hatched nauplii were reared in a 30 ml dish at $12\times10^4$ cells $ml^{-1}$ after exposure to a concentration of 0 or 900 cells $ml^{-1}$ for the first 1–2 h at 23 or 27°C in darkness. Counting of nauplii retaining food in the gut was made daily when they were transferred to a new culture medium.

## Results

*Food*

*Chlorella* sp., *Ditylum brightwellii*, *Phaeodactylum tricornutum* and *Skeletonema costatum* allowed neither adult females of *Oithona davisae* to produce eggs nor NI to reach NII (Table 1), as the copepods did not ingest these diatoms. Rapid movements of feeding appendages were occasionally seen in females when *Chlorella* was supplied, but these movements differed from normal raptorial feeding motions. The flagellates *Chlamydomonas* sp., *Dunaliella* sp. and *Platymonas* sp., almost equal in size (13–15 $\mu$m long and 5–7 $\mu$m wide), were all ingested by both females and NI, as reported by UCHIMA (1979, 1985). *Chattonella antiqua* (>100 $\mu$m long) was rarely ingested by females but never taken by NI, whereas *Heterosigma* sp. (40–50 $\mu$m long) was fed on by both females and NI and resulted in their egg production and growth. Both females and NI fed on *Heterosigma* survived more successfully than those on other food types (Table 1). Microscopic observations of feeding behavior indicated that *O. davisae* at all developmental stages fed on flagellates, dinoflagellates and oligotrichines (*Strobilidum* spp. and *Strombidium* spp.: 10–30 $\mu$m long) in natural seawater. They did not ingest diatoms (*Chaetoceros*, *Coscinodiscus*, *Ditylum*, *Nitzschia*, *Rhizosolenia*, *Skeletonema*, *Thalassiosira*) and detrital particles of different sizes. Adult females occasionally caught rotifers (*Brachionus* sp.) and tintinnids (*Tintinnopsis beroidea* and *Favella ehrenbergii*). These foods were probably too large for nauplii to capture.

TABLE 1. RESPONSE OF EGG-LAYING AND LARVAL DEVELOPMENT OF *Oithona davisae* TO VARIOUS FOOD CONDITIONS. TEN FEMALES AND 10 NI WERE REARED IN 30 ML OF WATER AT 20°C IN DUPLICATE.

| Food cells $ml^{-1}$ | Stage | Survival (%) Day 4 | Survival (%) Day 7 | Most advanced developmental stage Day 4 | Most advanced developmental stage Day 7 | % of females laying 3rd egg batch between days 4 and 7 |
|---|---|---|---|---|---|---|
| *Chattonella antiqua* | Female | 100 | 40 | | | 10 |
| $5\times10^3$ | NI | 40 | 0 | NI | NI | |
| *Chlorella* sp. | Female | 100 | 10 | | | 0 |
| $4\times10^6$ | NI | 80 | 20 | NI | NI | |
| *Ditylum brightwellii* | Female | 100 | 10 | | | 0 |
| $5\times10^3$ | NI | 45 | 0 | NI | NI | |
| *Heterosigma* sp. | Female | 100 | 100 | | | 100 |
| $4\times10^4$ | NI | 100 | 55 | NIV | CI | |
| *Phaeodactylum tricornutum* | Female | 100 | 40 | | | 0 |
| $2\times10^5$ | NI | 85 | 5 | NI | NI | |
| *Skeletonema costatum* | Female | 100 | 10 | | | 0 |
| $2\times10^4$ | NI | 40 | 0 | NI | NI | |

TABLE 2. OCCURRENCE OF FIRST FEEDING IN NI OF *Oithona davisae* UNDER DIFFERENT FOOD CONDITIONS AT 20°C. FIGURES SHOW THE PERCENTAGE OF FEEDING INDIVIDUALS AMONG 7 TO 11 NAUPLII. EXPERIMENT WAS DUPLICATED FOR *Dunaliella* SP.

| Food $\times10^4$ cells $ml^{-1}$ | Time after hatching (min) 10 | 20 | 30 | 60 | 70 |
|---|---|---|---|---|---|
| *Chlamydomonas* sp. | | | | | |
| 0.5 | 0 | 14 | | 30 | |
| 1 | 0 | 75 | | 100 | |
| 2 | 40 | 86 | | 100 | |
| 4 | 80 | 100 | | 100 | |
| *Platymonas* sp. | | | | | |
| 0.5 | 25 | 50 | | 44 | |
| 1 | 29 | 100 | | 100 | |
| 2 | 64 | 91 | | 100 | |
| 4 | 64 | 100 | | 100 | |
| *Dunaliella* sp. | | | | | |
| 0.1 | 0 | 0 | | 0 | |
| 0.5 | 14 | 60 | | 67 | |
| 1 | 57 | 100 | | 100 | |
| 2 | 50 | 100 | | 100 | |
| 4 | 100 | 100 | | 100 | |
| 0.1 | 0 | 0 | | 0 | |
| 0.5 | 43 | 57 | | 71 | |
| 1 | 43 | 71 | | 100 | |
| 2 | 43 | 100 | | 100 | |
| 4 | 71 | 100 | | 100 | |

*Occurrence of First Feeding under Various Food Conditions*

Feeding in NI commenced soon after hatching (Table 2). The percentage of fed NI became higher with increase in food concentration and with time after hatching. This percentage was different among three species of flagellates at given concentrations for the first 30, especially 20, min. The difference was also shown by the experiments repeated for *Dunaliella*. NI, when supplied with 1,000 *Dunaliella* cells $ml^{-1}$, did not feed within 1 h after hatching. All NI indicated the first feeding within 1 h after hatching when *Chlamydomonas*, *Dunaliella* or *Platymonas* was given at concentrations of $1\times10^4$ cells $ml^{-1}$ or more.

*Effect of Food Concentration on Larval Growth*

NI did not molt into NII at a concentration of 900 cells $ml^{-1}$ of a mixture of food at 20 and 27°C (Table 3). At 20°C all NI obtained food during 2 days after hatching (Fig. 1), but the assimilated energy seemed insufficient for normal growth and molting. A decrease in the percentage of fed NI preceded an increase in mortality (Fig. 1); dead NI did not retain any food particles in the gut. At 27°C fed NI were not observed. More than 50 % of NI died on day 3 after hatching at 27°C and on day 5 at 20°C (Fig. 1). At concentrations of 1,500 cells $ml^{-1}$ or more, NI grew to at least NV at 20°C; the development time was shorter and the survival rate was higher with increase in food concentration (Table 3). NI required a concentration above 4,500 cells $ml^{-1}$ to reach Copepodite I (CI). Dead nauplii were found to have empty guts. A short-term shortage of food after hatching affected the development of NI (Table 4). A constant food supply of $12\times10^4$ cells $ml^{-1}$ allowed 60 % of NI to reach CI at 23°C. When food was not supplied to NI for the first 1 h, only 15 % of NI reached CI at 23°C and 10 % at 27°C. Though results were not shown in Table 4, an initial 2 h period

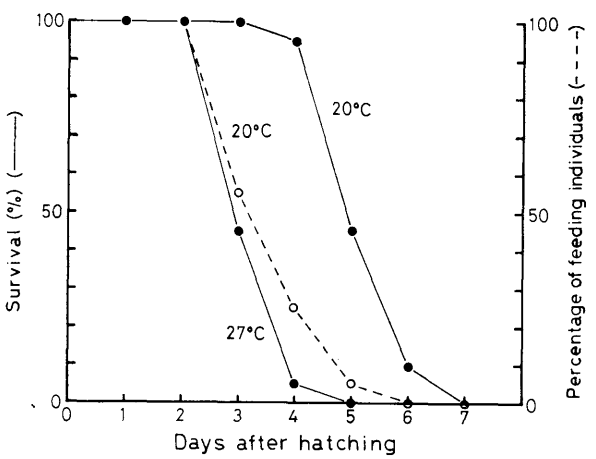


Fig. 1. Survival rate and percentage of feeding individuals of NI of *Oithona davisae* at 20 and 27°C. Ten NI were reared in 30 ml of water with a mixture of equal number of cells of *Chlamydomonas* sp., *Dunaliella* sp. and *Platymonas* sp. at a total concentration of 900 cells $ml^{-1}$. Each value is the mean of two replicates. Feeding was not observed at 27°C.

TABLE 3. EFFECTS OF FOOD CONCENTRATION ON LARVAL DEVELOPMENT OF *Oithona davisae*. TEN NI WERE REARED IN 30 ML OF WATER WITH A MIXTURE OF EQUAL NUMBER OF CELLS OF *Chlamydomonas* SP., *Dunaliella* SP. AND *Platymonas* SP.

| Food concentration $\times 10^3$ cells $ml^{-1}$ | Temperature °C | Survival (%) of NI to NII | Survival (%) of NI to CI | Survival (%) and development time (days) to NV % | Days Mean (range) |
|---|---|---|---|---|---|
| 0.9* | 20 | 0 | 0 | 0 | not determined |
| 0.9* | 27 | 0 | 0 | 0 | not determined |
| 1.5 | 20 | 70 | 0 | 10 | 7.0 |
| 3 | 20 | 90 | 0 | 50 | 6.8 (6-9) |
| 4.5 | 20 | 100 | 0 | 70 | 6.0 |
| 6 | 20 | 100 | 30 | 70 | 5.7 (5-6) |

* Experiment was done in duplicate.

TABLE 4. EFFECTS OF FOOD SHORTAGE FOR 1-2 H AFTER HATCHING ON LARVAL DEVELOPMENT OF *Oithona davisae*. AFTER VARIOUS INITIAL FOOD CONDITIONS, A MIXTURE OF EQUAL NUMBER OF CELLS OF *Chlamydomonas* SP., *Dunaliella* SP. AND *Platymonas* SP. WAS SUPPLIED AT A CONCENTRATION OF $12 \times 10^4$ CELLS $ML^{-1}$ TO 10 NI KEPT IN 30 ML OF WATER.

| Initial food conditions $\times 10^3$ cells $ml^{-1}$ | Duration of food shortage (h) | Temperature °C | Survival (%) to CI | Development time in days from NI to CI Mean (range) |
|---|---|---|---|---|
| 120* | 0 | 23 | 60 | 7.8 (6-10) |
| 0* | 1 | 23 | 15 | 7.0 |
| 0 | 1 | 27 | 10 | 7.0 |
| 0 | 2 | 27 | 0 | not determined |
| 0.9* | 1 | 27 | 0 | not determined |

* Experiment was done in duplicate.

without food allowed NI to develop up to NV at 27°C. Exposure to a concentration of 900 cells $ml^{-1}$ for the first 1 h resulted in only 10 % of NI reaching NVI at 27°C.

## Discussion

*Oithona davisae*, unlike *O. nana* (MURPHY 1923, HAQ 1965, LAMPITT 1979, LAMPITT & GAMBLE 1982) and *O. similis* (LEBOUR 1922, MARSHALL & ORR 1962, 1966, EATON 1971), did not feed on diatoms. Algal diets eaten by adult females of *O. davisae* were the same as those taken by NI (Table 1). Both females and NI exclusively ingested motile, unicellular organisms such as flagellates and dinoflagellates. *Chattonella antiqua* was not ingested by NI and by most females which could capture larger zooplankters. ITOH & IMAI (1986) reported that *Oithona* sp. did not feed on *Chattonella marina*, but larger copepod species did. *Chattonella* may be too large for NI of *O. davisae* to catch. The type and the size of diets of the females may be determined by their suitability as food for NI. Microscopic observations indicated that females fed more frequently on phytoplankters than on zooplankters in natural seawater. *Oithona davisae*, unlike *O. minutus* and *O. similis* reported on by PETIPA et al. (1970), may

not shift their omnivorous habit to a carnivorous one with growth.

*Oithona davisae* commenced feeding soon after hatching (Table 2), unlike calanoid copepods (MARSHALL & ORR 1956, LEWIS 1967, MULLIN & BROOKS 1967, SEKIGUCHI 1974, UYE 1980, UYE & ONBÉ 1975). Assuming that the flagellates *Chlamydomonas* sp., *Dunaliella* sp. and *Platymonas* sp. are spherical with a diameter of 9 $\mu$m, each single cell will contain 59.65 pgC according to the equation presented by STRATHMANN (1967). NI did not molt into the next stage at a concentration of 900 cells $ml^{-1}$ (54 ngC $ml^{-1}$) of a mixture of food, but reached NV at 1,500 cells $ml^{-1}$ (90 ngC $ml^{-1}$) (Table 3). These results show that the threshold concentration of food for the growth of *O. davisae* is somewhere between 54 and 90 ngC $ml^{-1}$. The first feeding may be difficult to accomplish for newly-hatched nauplii in waters where suitable foods are scarce. The difficulty may be especially large soon after hatching (Table 2). A shortage of food within the first 1 h did not permit most NI to reach CI (Table 4). OMORI (1979) stated that poor feeding ability and poor nutrient condition were probably the primary causes of high mortality in the first feeding larvae (the 1st protozoeal stage) of the oceanic shrimp *Sergestes similis*. Higher mortality in the nauplii of *O. davisae* at lower food levels (Table 3) may be attributable to their poor feeding ability in the first feeding and to their vulnerability to starvation.

NI, when exposed for the first 1 h to a low food concentration, did not reach CI; whereas when kept without food 10–15 % of NI did reach CI (Table 4). The former NI probably spent more energy in swimming during the period. At a low food level NI died earlier at 27°C with more difficulty in feeding than at 20°C (Fig. 1). NI must emerge in food rich waters, particularly when the ambient temperature is high.

Microscopic observations indicated that females continued feeding throughout the period of embryonic development. Egg-carrying females must stay in areas with a food concentration above the threshold value for the development of NI. The higher the concentration of food acceptable to females the easier will be the first feeding of NI. Egg-carrying in oithonid copepods is viewed as a way of protecting eggs against lethal factors such as predation (FISH 1936, KOGA 1973, 1984). Another interpretation of this strategy is as compensation for the insufficient ability of newly-hatched nauplii to forage under conditions with little available food and/or to migrate into more favorable environments.

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