

Production and Loss of Eggs in the Calanoid Copepod *Centropages abdominalis* Sato in Fukuyama Harbor, the Inland Sea of Japan^{1), 2)}

DONG LIANG³⁾, SHIN-ICHI UYE³⁾ AND TAKASHI ONBÉ^{3), 4)}

*Faculty of Applied Biological Science, Hiroshima University,
4-4 Kagamiyama 1 Chome, Higashi-Hiroshima 724*

Abstract

The calanoid copepod *Centropages abdominalis* occurred in the plankton from November 1986 to May 1987 (temperature range: 8.9 – 19.7 °C) in Fukuyama Harbor, in the central part of the Inland Sea of Japan. Its fecundity was estimated by two methods: the incubation method and the egg-ratio method. The incubation fecundity ranged from 39 to 142 eggs female⁻¹ d⁻¹, with a corresponding carbon weight specific rate ranging from 0.19 to 0.70 d⁻¹. The specific egg production rate (*SEPR*, d⁻¹) can be estimated from temperature (*T*, °C) and chlorophyll (*P*, µg l⁻¹) with the multiple regression equation: $SEPR = 0.330 \ln T + 0.125 \ln P - 0.678$. The egg-ratio fecundity, however, was extremely low (0.6 – 45 eggs female⁻¹ d⁻¹) compared to the incubation fecundity. The difference between these two fecundities was regarded as loss of eggs caused by various factors. This loss was higher in March–May (mean: 94.2%) than that in November – February (mean: 81.0%). We attribute it mainly to sinking from the water column and predation, including cannibalism, by omnivorous copepods (i.e. late copepodites of *C. abdominalis* and *Acartia omorii*). Higher loss of eggs in April and May may also be related to the production of diapause eggs.

Keywords: *Centropages abdominalis*, egg production, egg loss, the Inland Sea of Japan

Although a variety of physical and biological factors affect the population dynamics of copepods, the variation in egg production rate is a major factor affecting the population abundance, because it often determines the birth rate of the population. Previous studies demonstrated that food supply (MARSHALL & ORR 1952, DURBIN et al. 1983, BECKMAN & PETERSON 1986) and temperature (DAGG 1978, VAN RIJSWIJK et al. 1989) influence the fecundity of copepods. UYE (1981) and AMBLER (1986) have respectively developed a simple model equation to predict the egg production rate of the genus *Acartia* and shown that its fecundity can be adequately estimated from the model equation by only knowing ambient temperature and chlorophyll concentrations. However, all the eggs produced do not hatch into nauplii, but they are subjected to various losses in the water column. From the viewpoint of population dynamics of the planktonic copepods, the recruitment rate into the planktonic phase provides important informa-

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3) 梁 棟・上 真一・遠部 卓, 広島大学生物生産学部

4) Present address: 2-60-406 Saijyo Nishihonmachi, Higashi-Hiroshima 724

tion as compared from the egg production rate. LANDRY (1978) and UYE (1982a) found that only 10–20% of the eggs produced can survive to a certain early naupliar stage (NII or NIII) for the genus *Acartia*.

Centropages abdominalis Sato is an omnivorous copepod, which is distributed in the boreal and temperate coastal waters of the North Pacific (CHEN & ZHANG 1965), although this species was discovered recently to populate in Patagonian waters, southern Chile (HIRAKAWA 1986). In the Inland Sea of Japan, this species occurs only in cold seasons, and becomes an important component of the zooplankton (HIROTA 1979). KASAHARA et al. (1975) found that this species spends its life in a form of resting eggs in the bottom sediment during warm seasons.

At the first step to elucidate the population dynamics and production of *C. abdominalis* in Fukuyama Harbor, this paper reports the egg production rate and loss of eggs throughout the season of its occurrence.

Materials and Methods

Field Sampling

A series of samplings were carried out at a station (Figure 1) in Fukuyama Harbor, in the central part of the Inland Sea of Japan, at intervals of 3–5 days from 7 November, 1986 to 8 November, 1987. Zooplankton was taken by oblique hauls of a plankton net (mouth diameter: 0.45 m, length: 2 m, mesh aperture: 62 μm) from the bottom (depth: 7–8 m) to the surface, within the period 1 h before and after the nighttime high tide (between 17:00–07:00 hrs). The volume of water filtered through the net was estimated from the reading of a flowmeter. Samples were preserved in 5–10% formalin-seawater. Temperature and salinity at 1 m depth were recorded with a thermo- and salinometer (YSI, Model 33). The surface water of 50–200 ml was filtered with a glassfiber filter (Whatman GF/C) for fluorometric determination of chlorophyll *a* concentration.

Identification and Enumeration of Developmental Stages

Centropages abdominalis from split subsamples (1/8 to 1/16 of original samples) were staged, sexed and counted under a binocular stereomicroscope. Its eggs, the morphological characteristics of which were described by KASAHARA et al. (1974), were also counted. Egg diameter and female prosome length were measured to the nearest 1 μm and 5 μm , respectively, with an eyepiece micrometer.

Egg Production Experiments

The fecundity of *C. abdominalis* was estimated using the following two methods. In one approach, the egg-ratio technique (EDMONDSON et al. 1962, PETERSON 1985) was employed: $F = E/(A \times D)$, where F is fecundity (eggs female⁻¹ day⁻¹), E is egg abundance (eggs m⁻³), A is female abundance (females m⁻³), and D is egg development time (days). For determining the D , 20–30 eggs, which had been laid for recent 2 hrs, were incubated at different temperatures ranging from 4.5 to 19.5 °C. Their hatching was monitored at intervals of 1–5 hrs.

Another approach was to incubate recently captured females in seawater containing natural assemblage of phytoplankton (DAGG 1978, UYE 1981). For this experiment, live zooplankton was transported to our laboratory by being

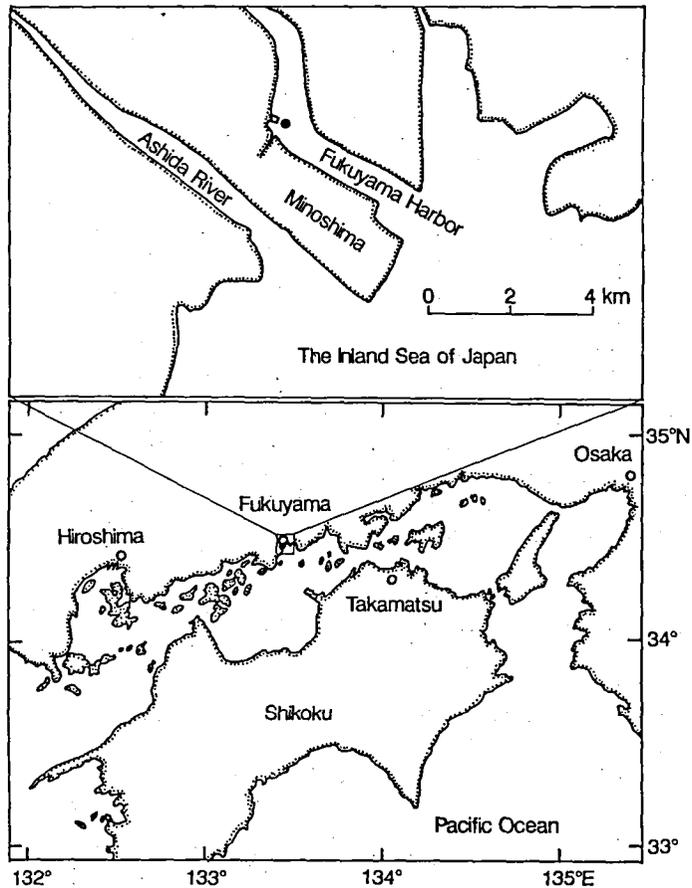


Fig. 1. Map showing the location of a sampling station (solid circle) in Fukuyama Harbor, in the central part of the Inland Sea of Japan.

kept into 2-liter plastic bottles in an insulated box, within 0.5 h of collection. Two to three healthy-appearing females of *C. abdominalis* with dark oocytes in the ovary and oviducts were pipetted into glass bottles containing 450 ml of filtered (148 μm mesh) seawater taken from 1 m depth of the sampling site. The bottles were secured on a rotating wheel (1 rpm) in a temperature- and light-controlled incubator. Temperature was adjusted to ambient surface temperature and light was adjusted to a 10 h light: 14 h dark photoperiod. After 24 h, the contents of the bottles were retained on a 40 μm sieve and preserved with formalin. Later, eggs and hatched nauplii were enumerated.

To offset the effect of female body size and egg size, specific egg production rate (*SEPR*, day^{-1}) was determined on a carbon base. The carbon weight of an egg was calculated from a composite relationship between egg carbon (C_E , μg) and egg diameter (ED , μm), which was obtained for 12 calanoid species (UYE unpublished): $C_E = 10^{-7.27} \times ED^{3.04}$. Female body carbon weight (C_F , μg) was determined from its prosome length (μm) with the regression equation given by UYE (1982 b): $C_F = 10^{-8.19} \times PL^{2.97}$.

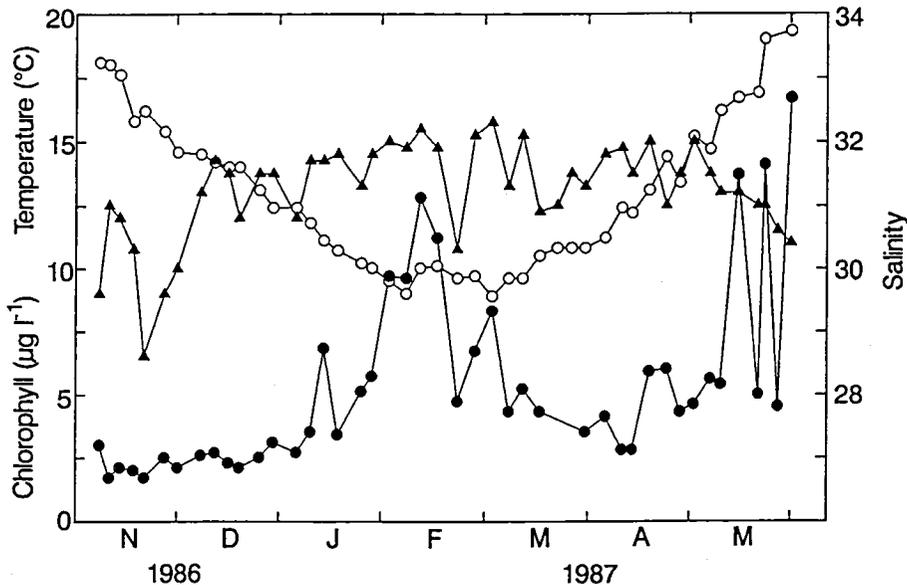


Fig. 2. Seasonal variations in temperature (open circles), salinity (solid triangles) and chlorophyll *a* concentration (solid circles) in Fukuyama Harbor from November 1986 to May 1987, when *Centropages abdominalis* occurred in the plankton.

Results

Environmental Variables

Since *Centropages abdominalis* occurred in the plankton mainly from November to May, descriptions of environmental parameters are confined to that period (Figure 2). In this period, temperature ranged from 8.9 to 19.7 °C, and salinity ranged from 28.6 to 32.3. Chlorophyll *a* concentrations varied from 1.7 to 16.7 $\mu\text{g l}^{-1}$ with significant peaks in February and May.

Seasonal Fluctuations in Abundance and Size of Females and Eggs

Significant numbers of adult female *C. abdominalis* first occurred in the plankton on 26 November when temperature was 15.4 °C. Their density increased markedly from January through February to reach a peak density (3,200 females m^{-3}) on 11 March (Figure 3). Then, it decreased gradually to disappear completely from the plankton on 2 June, when temperature was 20.7 °C. Numerical abundance of eggs in the plankton followed an almost similar pattern to that observed in female abundance (Figure 3). A peak density (11,900 eggs m^{-3}) was observed on 20 February.

The prosome length of adult females was small in November and December, increased to a maximum size in February, and then decreased gradually thereafter (Figure 4). The mean prosome length varied from 945 to 1300 μm , which corresponds to a carbon weight ranging from 4.7 to 11.4 μg . However, egg diameter did not change significantly over the study period (Figure 4), ranging from 74.3 to 77.3 μm (corresponding carbon weight: 0.026 to 0.029 μg), with an overall mean of 75.3 μm (carbon weight: 0.027 μg).

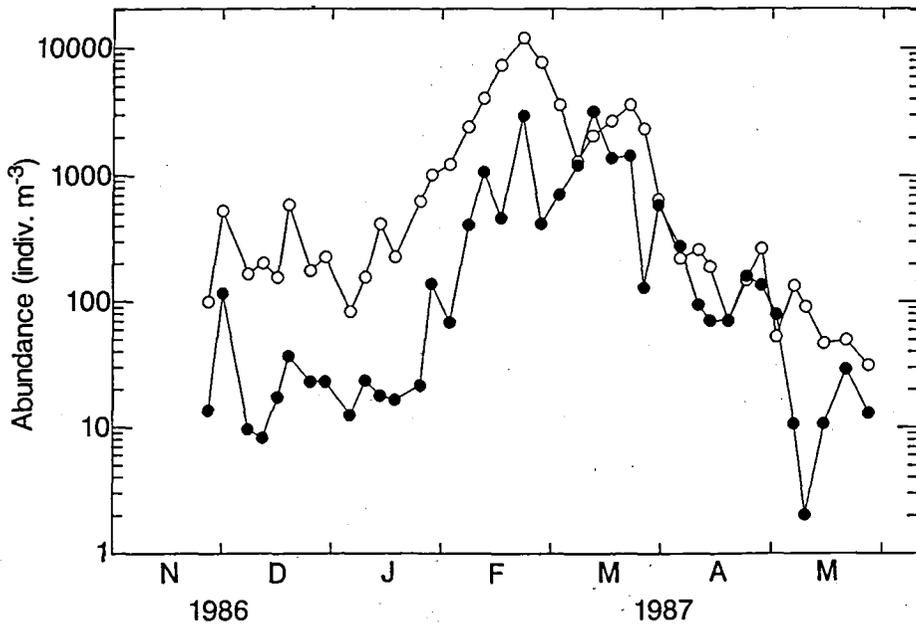


Fig. 3. Seasonal variations in abundance of adult females (solid circles) and eggs (open circles) of *Centropages abdominalis*.

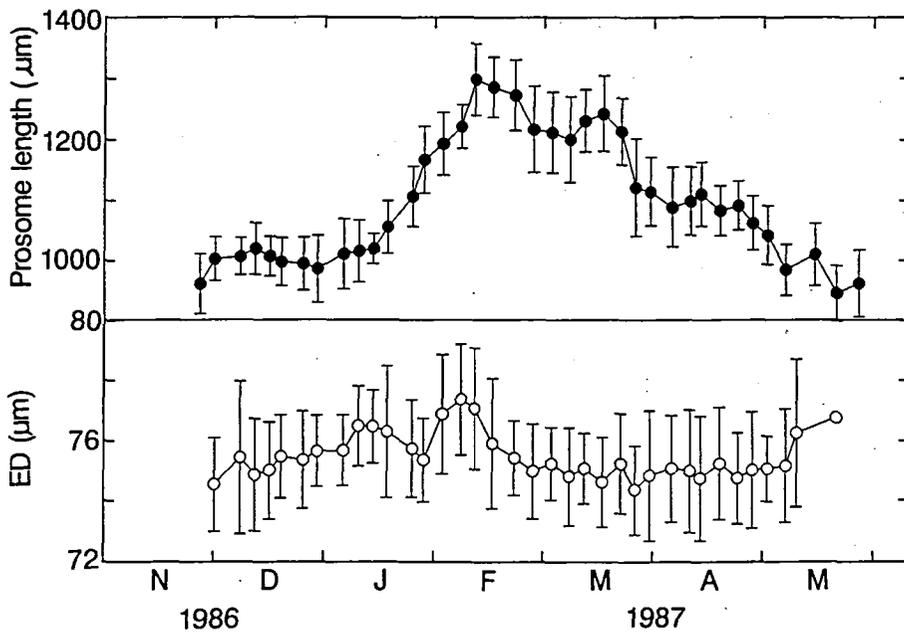


Fig. 4. Seasonal variations in prosome length of adult females (solid circles) and diameter of eggs (ED, open circles) of *Centropages abdominalis*. Vertical lines denote SD.

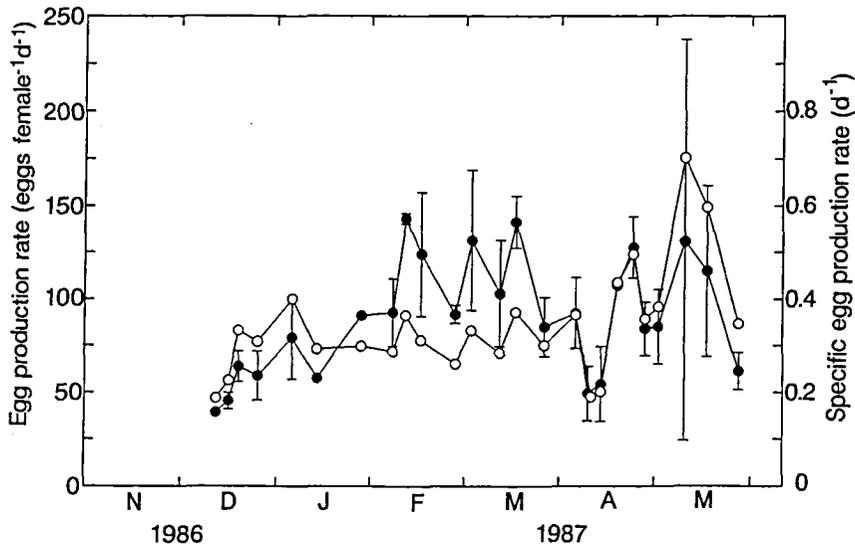


Fig. 5. Seasonal variations in egg production rates (solid circles, left ordinate) and corresponding specific egg production rates (open circles, right ordinate) of *Centropages abdominalis* estimated from incubation method. Vertical lines denote SD.

Egg Production Rates Estimated by Incubation Method

The fecundity of *C. abdominalis* by means of a bottle incubation technique ranged from 39 to 142 eggs female⁻¹ day⁻¹ (Figure 5). It was constantly high in February and March, dropped in early April, and increased again in late April and early May. The corresponding carbon specific rate of egg production (*SEPR*) was relatively constant from late December to early April (mean: 0.32 d⁻¹). After the drop in early April, it increased to the highest value (0.70 d⁻¹) on 9 May (Figure 5).

A multiple regression analysis was performed taking *SEPR* as a dependent variable and temperature (T , °C) and chlorophyll (P , µg l⁻¹) as independent variables. The resulting equation: $SEPR = 0.330 \ln T + 0.125 \ln P - 0.678$ was significant ($r^2 = 0.42$; $F_{2,23} = 7.98$, $p < 0.05$). Partial correlation coefficients of temperature ($r = 0.57$) and chlorophyll ($r = 0.58$) with *SEPR* were also significant ($p < 0.05$).

Since the mean carbon content of an egg is 0.027 µg, the in situ egg production rate (F , eggs female⁻¹ d⁻¹) can be calculated from the following equation:

$$F = C_f (0.330 \ln T + 0.125 \ln P - 0.678) / 0.027.$$

Egg Production Rate Estimated by Egg-Ratio Method

The development time of eggs (D , days) was strongly dependent on temperature (T , °C) (Figure 6), which was expressed by the Bělehraděk function:

$$D = 159 (T + 3.18)^{-1.58}.$$

Fecundity estimated by the egg-ratio method ranged from 0.6 to 45 eggs female⁻¹ day⁻¹ (Figure 7). It was extremely low in March and April.

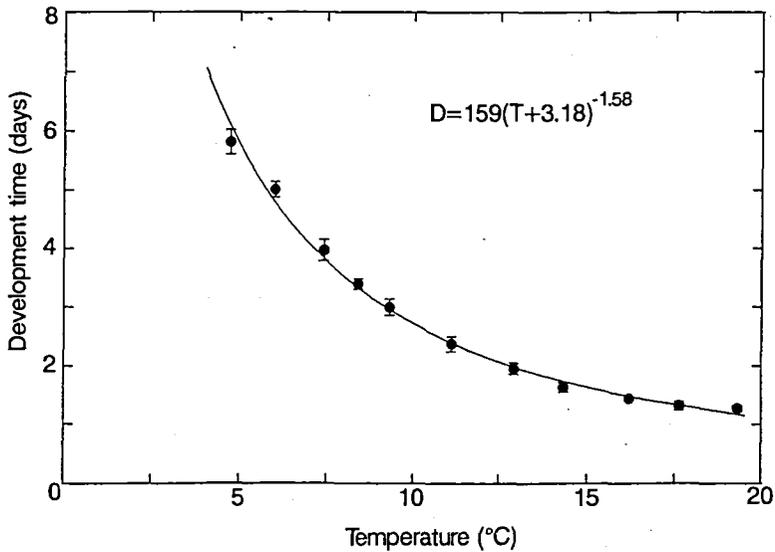


Fig. 6. Relationship between temperature and egg development time of *Centropages abdominalis*. Vertical lines denote SD.

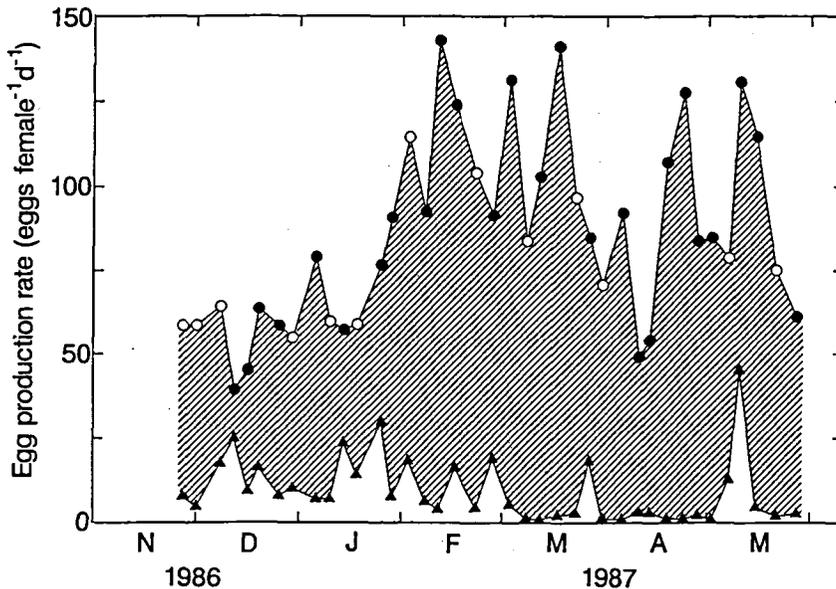


Fig. 7. Seasonal variations in fecundity by means of incubation method (solid circles) and of egg-ratio method (solid triangles) of *Centropages abdominalis*. Open circles denote predicted fecundity (see text). Hatched area denotes loss of eggs.

Loss During Egg Stage

When the incubation experiment was not conducted, the egg production rate was estimated by substituting temperature, chlorophyll and female body carbon weight on that date into the multiple regression equation given above. Incubation

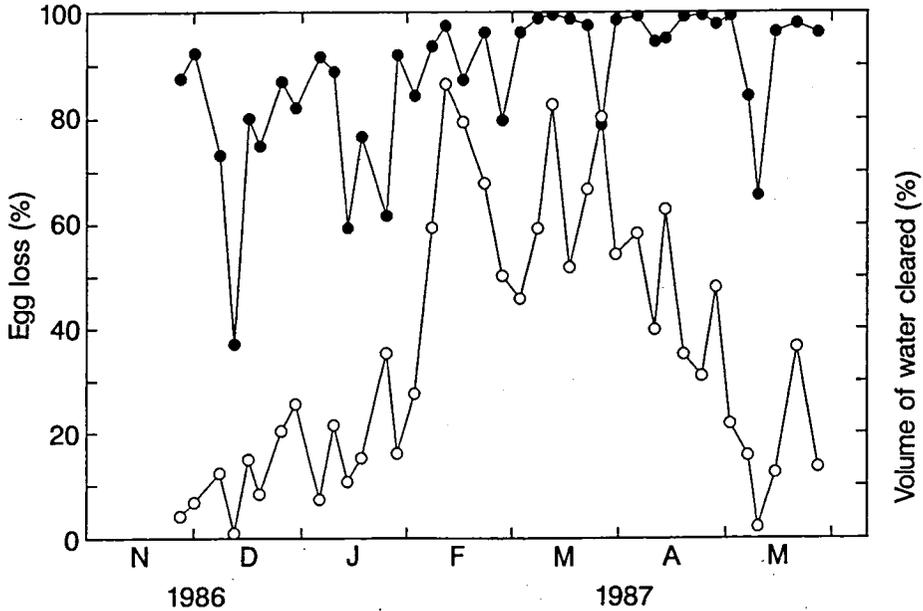


Fig. 8. Seasonal variations in percentage loss of eggs (solid circles, left ordinate) of *Centropages abdominalis* and percentage volume of water cleared by late copepodites of *C. abdominalis* and *Acartia omorii* (open circles, right ordinate, see text).

fecundity and egg-ratio fecundity were then compared (Figure 7). The former is higher than the latter throughout the study period. The differences between these two fecundity were as losses attributed to various sources. These losses ranged from 36.9 to 99.3%, with a mean of 87.5% (Figure 8). They were relatively small between November and February (mean: 81.0%), and large between March and May (mean: 94.2%).

Discussion

Since there is a time lag of 8–24 h between ingestion of food and production of eggs in copepods (MARSHALL & ORR 1961, TESTER & TURNER 1990), the fecundity of *Centropages abdominalis* measured during the 24 h incubation should adequately represent the egg production in the natural environment. However, egg cannibalism might occur during the incubation period, since we occasionally found egg membranes in its fecal pellets. Nevertheless, no correction was made for the cannibalism because we did not know at what extent it actually occurred, and hence our incubation fecundity is somewhat underestimated. *C. abdominalis* females oscillate between a dark, ripe stage of oogenesis and a light, unripe stage of primary oocytes. IANORA (1990) found that there is a 2-fold difference in egg deposition rate between dark, gravid females and light, non-gravid ones for *Centropages typicus*. In the present study, we used dark females only, and hence our incubation results may be close to actual potential rates of egg production for field populations of *C. abdominalis*.

Our estimate of egg production rate for *C. abdominalis* by the incubation

Table 1. Comparison of egg production rate (EPR) and specific egg production rate (SEPR) by incubation method in the genus *Centropages*. -: no data.

Species	Location	Temp. (°C)	EPR (eggs f ⁻¹ d ⁻¹)	SEPR (d ⁻¹)	Reference
<i>C. typicus</i>	New York Bight	15	5-230	0.01-0.16*	DAGG (1978)
	New York Bight	8-20	28-55	0.03-0.04	SMITH & LANE (1985)
	New York Bight	8.8-18.5	23-76	0.01-0.06	SMITH & LANE (1987)
	Gulf of Naples	16-24	15-102	-	IANORA et al. (1992)
<i>C. hamatus</i>	Kattegat	3-19	1-80	-	NIELSEN (1990)
	Skagerrak	9-19	1-77	-	TISELIUS et al. (1991)
<i>C. abdominalis</i>	Inland Sea of Japan	8.9-19.7	39-142	0.19-0.70	Present study

*: calculated assuming that carbon weight is 0.45 dry weight.

Table 2. Comparison of egg production rate (EPR) and specific egg production rate (SEPR) among calanoid copepods occurring in the Inland Sea of Japan.

Species	Temp. (°C)	EPR (eggs f ⁻¹ d ⁻¹)	SEPR (d ⁻¹)	At 10 °C		Reference
				EPR	SEPR	
<i>Acartia omorii</i> *	5.9-23.2	5-55	0.005-0.71	30	0.19	UYE (1981)
<i>Pseudodiaptomus marinus</i>	7.0-25.3	1-17	0.001-0.30	3	0.04	UYE et al. (1982)
<i>Sinocalanus tenellus</i>	6.5-35	9-60	0.006-0.41	19	0.12	KIMOTO et al. (1986)
<i>Paracalanus</i> sp.	7.8-28	4-64	0.03-0.53	6	0.08	UYE & SHIBUNO (1992)
<i>Centropages abdominalis</i>	8.9-19.7	39-142	0.19-0.70	109	0.30	Present study

* Referred as *Acartia clausi* by UYE (1981) for specimens from Onagawa Bay. Its fecundity is assumed to be similar to that of *A. omorii* from the Inland Sea of Japan.

method is higher than or similar to the results reported for other species of the genus *Centropages* (Table 1). *C. typicus* in the New York Bight (DAGG 1978, SMITH & LANE 1985, 1987) seems to produce eggs almost similar to those produced by *C. abdominalis*. Since *C. typicus* has larger body carbon weight (10.4-19.7 μ g, DAGG & GRILL 1980) and smaller egg diameter (70 μ m, DAGG 1978) than those of *C. abdominalis* (4.7-11.4 μ g, 75 μ m, respectively), the specific egg production rate of the latter is higher than the former. By contrast, *Centropages hamatus* in Kattegat (NIELSEN 1990) and Skagerrak (TISELIUS et al. 1991) is less fecund than *C. abdominalis*.

A comparison of egg production rate is also made among calanoid species occurring in the Inland Sea of Japan (Table 2). In terms of egg number, *C. abdominalis* is most fecund. In particular, its egg production rate is remarkably high at low temperatures. For instance, at 10 °C, it produces as many as 109 eggs per day, while the other species produce less than 30 eggs per day (Table 2). Its specific egg production rate is also higher than that of other species by factors of 1.5-7 (Table 2). These facts suggest that *C. abdominalis* is highly adapted to low temperatures and probably the most successful copepod species in cold seasons in the Inland Sea of Japan.

BECKMAN & PETERSON (1986) determined both incubation fecundity and egg-ratio fecundity for *Acartia tonsa* in Long Island Sound, and suggested that a comparison of fecundities between these two techniques is a useful way of gaining some insight into the extent of egg predation in the field. In Long Island Sound, approximately 50% of *A. tonsa* eggs produced were lost within the water column (depth: 30 m). In our study, however, the loss of *C. abdominalis* eggs was much

higher (overall mean: 87.5%) than *A. tonsa*. As suggested by BECKMAN & PETERSON (1986), this loss might be attributed to at least two sources. The first one is sinking of eggs from the water column, because our sampling station is shallow (mean depth: 7.5 m), and the second one is predation, because the size and nutritive value of copepod eggs make them favorable prey for planktivorous predators including suspension feeding copepods (LANDRY 1978, RUNGE 1984).

The most important predators on *C. abdominalis* eggs were late copepodites (CIV-CVI) of its own species and *Acartia omorii*, since they are capable of eating the eggs (LIANG et al. unpublished.) and they occurred as many as 39,000 indiv. m^{-3} . True carnivores such as fish larvae, chaetognaths, jellyfish and ctenophores were absent or extremely rare during our study period.

The percentage of the volume of water swept clear by suspension-feeding copepods (TF, d^{-1}) can be calculated by:

$$TF = \{1 - (1 - F)^N\} \times 100$$

where F is the clearance rate of a predator ($l \text{ predator}^{-1} d^{-1}$), and N is the predator density ($\text{predators } l^{-1}$) (HADA & UYE 1991). Clearance rate of the genus *Centropages* and *Acartia* were reported by several authors (PAFFENHÖFER & KNOWLES 1980, AYUKAI 1987, BERGGREEN et al. 1988), which ranged from 15 to 91 $ml \text{ predator}^{-1} d^{-1}$ when relatively large-sized prey was used. Here, we assume that the average clearance rate of the late copepodites of *C. abdominalis* and *A. omorii* is 50 $ml \text{ predator}^{-1} d^{-1}$. Their abundance varied from 0.2 to 39 $\text{predators } l^{-1}$. It is calculated that 1-86 % of the water column can be cleared by them per day (Figure 8). However, this value does not directly account for the loss of eggs, but may be a better indicator showing relative strength of predation.

The predation pressure on eggs was highest between February and April (Figure 8), and before and after this time it was relatively unimportant, indicating that sinking was the main source of the loss. Although the physiological property of eggs of *C. abdominalis* has not been investigated yet, this species is likely to lay subitaneous eggs before February, which will hatch immediately to nauplii. On the other hand, after April it is likely that this species produce diapause eggs, whose hatching is arrested for several months (UYE 1985). If diapause eggs were produced between April and June, our calculated egg-ratio fecundity was overestimated, since embryonic development time for these eggs is nearly infinite. Production of diapause eggs in this period is also evidenced by much fewer density of young *C. abdominalis* nauplii in the plankton samples.

In conclusion, *C. abdominalis* is the most successful calanoid copepod in cold seasons by displaying the highest reproductive rate under low temperatures among calanoid species in the Inland Sea of Japan. However, the loss of its eggs is significantly high. In addition to the loss by sinking, predation, including cannibalism, by omnivorous copepods may account for a significant part of the loss when the predators are abundant. *C. abdominalis* presumably produces diapause eggs during the latter part of its planktonic occurrence. The loss by sinking thereby increase, but the eggs accumulated on the sea-bottom undergo a resting state until the next season.

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