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Population dynamics and production of the planktonic copepods in a eutrophic inlet of the Inland Sea of Japan. I. *Centropages abdominalis*

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Abstract Population dynamics and production of the calanoid copepod *Centropages abdominalis* were studied from November 1986 to November 1987 in Fukuyama Harbor, in the central part of the Inland Sea of Japan. This species was present in the plankton during a cold-water period from November to June (temperature range: 8.9 to 21.1 °C), with a peak abundance (23 600 ind m^{-3}) in February. During this period, six generations could be detected, and each generation time agreed well with that predicted from food-satiated laboratory experiments, indicating that the natural population was not food-limited. The population suffered extremely high mortality during the period from egg to naupliar stage (N) II: only 0.02 to 4% of the eggs survived to NII. However, the mortality in stages older than NII was almost negligible. The growth rate of *C. abdominalis* increased exponentially with increasing temperature. Its biomass and production rate showed marked seasonal variations largely in parallel with numerical abundance. The estimated production between 7 November 1986 and 29 May 1987 was 355 mg C m^{-3} or 2.66 g C m^{-2}, 95% of which occurred during February and March. The daily production rate to biomass ratio increased exponentially with temperature from 0.18 at 8.9 °C to 0.37 at 19 °C.

Introduction

Copepods are the major constituents of zooplankton in the ocean, and many species show marked seasonal changes in abundance, particularly in temperate regions. Therefore, understanding the processes controlling abundance and production of copepods in the ocean is a major objective in biological oceanography. Earlier studies indicate that a variety of physical and biological factors influence the abundance and population structure of planktonic copepods. Among them, water temperature (McLaren 1978; Colebrook 1982a, b), food availability (Durbin et al. 1983; Frost 1985; Runge 1985; Osgood and Frost 1994) and predation (Ohman 1986; Hada and Uye 1991) are important factors. An effective way to investigate limiting factors for population growth is to sample natural populations at frequent intervals, and then analyze various population parameters (e.g. egg production rate, recruitment rate into the population, survival rate through developmental stages) in relation to various biotic and abiotic environmental conditions. Such an approach was used in studies by Landry (1978), Uye (1982a) and Durbin et al. (1983) for various *Acartia* species, and by Peterson (1980) for *Calanus marshallae.*

Centropages abdominalis Sato is an omnivorous copepod distributed in the boreal and temperate waters of the North Pacific (Chen and Zhang 1965), and was also discovered recently in Patagonian waters, southern Chile (Hirakawa 1986). In the central Inland Sea of Japan, this species is a dominant copepod in winter and spring seasons (Hirota 1964, 1979; Kasahara et al. 1975). However, no detailed investigations have been conducted on its population dynamics and production.

In the present paper, we describe population dynamics and production rate of *Centropages abdominalis* by integrating field and laboratory data. We frequently sampled the zooplankton in Fukuyama Harbor, a temperate eutrophic inlet, during the course of a year. The seasonal change in fecundity of this species has been reported elsewhere (Liang et al. 1994).

Materials and methods

Study area, sampling methods and sample processing

Fukuyama Harbor is located in the central part of the Inland Sea of Japan (Fig. 1). There is no significant inflow of freshwater into the

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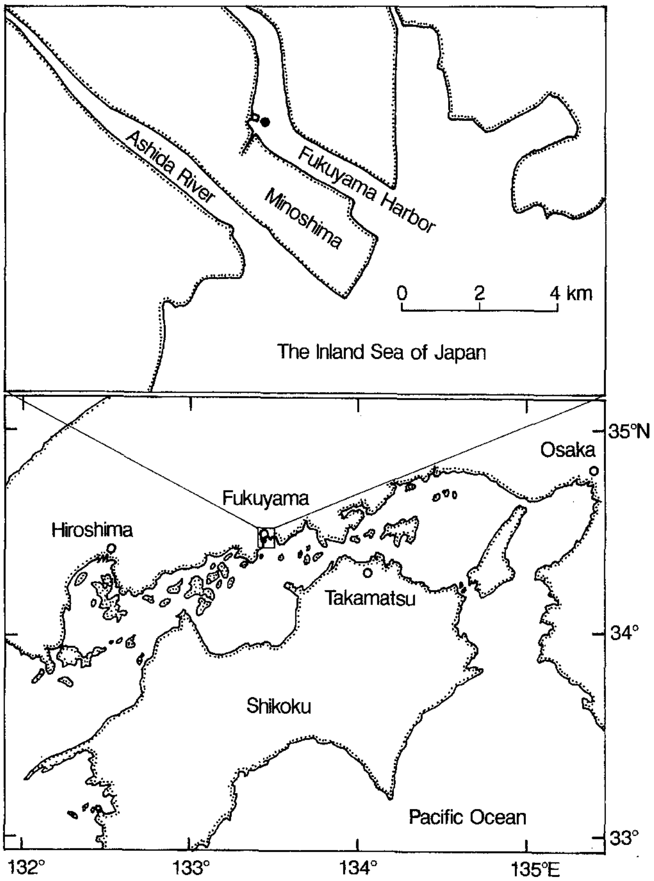

Fig. 1 Map showing the location of the sampling station (*filled circle*) in Fukuyama Harbor, in the central part of the Inland Sea of Japan

Harbor. However, this area receives nutrient-rich water from a nearby sewage plant, which provides secondary treatment to waste water. Hence, red-tides and anoxic conditions at the bottom often occur in summer.

The samplings were carried out from the floating pier of a ferry terminal, at intervals of 3 to 5 d 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, equipped with a flow meter) from the bottom (depth: 7 to 8 m) to the surface, within the period 1 h before and after the nighttime high tide (between 17.00 and 07.00 hrs). This procedure minimized the sampling variability caused by patchy distribution (the distributions of inlet copepods are more homogeneous during nighttime, e.g. Ueda 1987) and tidal cycle (Sameoto 1975; Lee and McAlice 1979). Samples were preserved in 5 to 10% formalin-seawater. Temperature and salinity at 1 m depth were recorded with a thermo- and salinometer (YSI, Model 33). Surface water (50 to 200 ml) was filtered with a fiber glass filter (Whatman GF/C) for fluorometric determination of chlorophyll *a* concentration.

Centropages abdominalis Sato from whole samples or split subsamples (1/8 to 1/16 of the original sample) were staged, sexed and counted under a binocular stereomicroscope. A congeneric species, *Centropages tenuiremis*, was also identified and counted. The separation between these species was made following the morphological descriptions of their developmental stages by Koga (1960) and Li and Fan (1990). Body length of nauplii and prosome length of copepodites and adults of *C. abdominalis* were measured to the nearest 1 and 5 µm, respectively, by an eyepiece micrometer.

Laboratory experiments to determine development rate

Live zooplankton samples were collected in Fukuyama Harbor and kept in 2 liter insulated bottles during transportation to our laboratory (< 2 h). A total of 20 adult females of *Centropages abdominalis* with dark oocytes were isolated and kept in 1 liter glass beakers containing fiber glass (Whatman GF/C) filtered seawater taken from the sampling site to let them spawn. Approximately 1000 eggs produced during the preceding 12 h were introduced into two 3-liter glass beakers containing 2.5 liter of filtered seawater. The beakers were placed in temperature-controlled rooms (12 h light:dark photoperiod), one at 16 ± 1 °C and the other at 10.5 ± 1 °C. After hatching, nauplii were provided with a mixture of the cultured diatom *Thalassiosira weissflogii* (1 to 5×10^4 cells ml^{-1}) and the chrysophyte *Isochrysis galbana* (1 to 2×10^5 cells ml^{-1}) as food. At 12 to 24 h intervals, fecal pellets and residual food on the bottom of the beakers were carefully pipetted or siphoned out, and freshly prepared medium was added. For the culture at 16 °C, 10 to 20 ind were removed daily with a large-mouthed pipette or by decanting a part of the cultures and were preserved with formalin. Later, their developmental stages were examined, and their body size was measured. Due to high mortality in the culture at 10.5 °C, fewer individuals were taken, which enabled only determination of the time of the beginning of each developmental stage.

Estimation of growth and production rate

The instantaneous growth rate in stage i (g_i, d^{-1}) is given by:

$$g_i = (\ln W_{i+1} - \ln W_i)/D_i, \tag{1}$$

where W_i and W_{i+1} are body carbon weight (µg C) of Stage i and Stage i+1, and D_i is instar duration of Stage i (d). The carbon content of an individual was estimated from the following length–weight relationships:

$$W = BL^{2.10} \times 10^{-6.02}, \tag{2}$$

for nauplii (Liang et al. unpublished), and

$$W = PL^{2.97} \times 10^{-8.19}, \tag{3}$$

for copepodites and adults (Uye 1982b), where BL is body length (µm) and PL is prosome length (µm).

Population production rate (P, $\mathrm{mg\,C\,m^{-3}\,d^{-1}}$) can be calculated as:

$$P = \sum_{\mathrm{NII}}^{\mathrm{CV}} (B_i \times g_i) + B_f \times G_f, \tag{4}$$

where B_i and B_f are biomass ($\mathrm{mg\,C\,m^{-3}}$) of Stage i and adult females, and G_f is specific egg production rate (d^{-1}). The G_f was estimated from the empirically derived multiple regression equation (Liang et al. 1994):

$$G_f = 0.330 \ln T + 0.125 \ln S - 0.678, \tag{5}$$

where T is temperature (°C) and S is chlorophyll *a* concentration ($\mu\mathrm{g\,l}^{-1}$). However, production by naupliar stage (N) I and adult males was assumed to be negligible.

Results

Field investigations

Environmental variables

Temperature followed a general seasonal variation in a temperate zone in the northern hemisphere, with

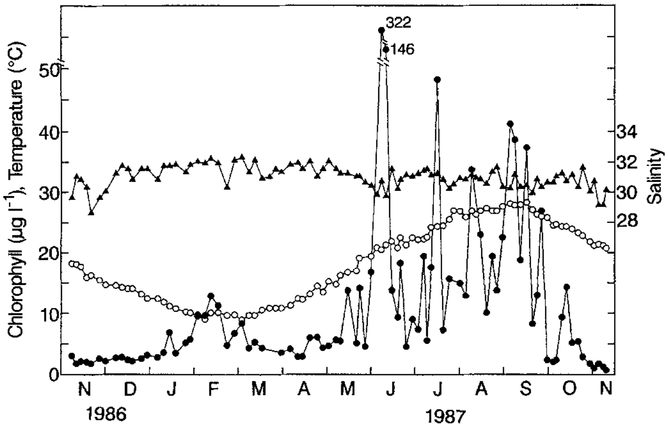

Fig. 2 Seasonal variations in temperature (*open circles*), salinity (*filled triangles*) and chlorophyll *a* concentration (*filled circles*) in Fukuyama Harbor from November 1986 to November 1987

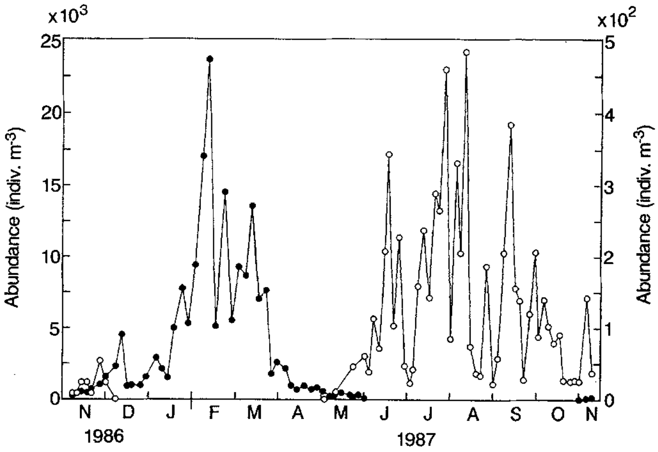

Fig. 3 *Centropages abdominalis* and *C. tenuiremis*. Seasonal variations in total (nauplii + copepodites + adults) abundance. *C. a.*: *filled circles*, left ordinate. *C. t.*: *open circles*, right ordinate

minimum and maximum temperatures of 8.9 °C on 2 March and 28.2 °C on 11 September 1987, respectively (Fig. 2). Salinity ranged from 28.6 to 32.3‰, and generally was lower and more variable in summer and fall than in winter and spring (Fig. 2). There was a remarkable variation in chlorophyll *a* concentration (Fig. 2). It was extremely high from May to September, due to occurrence of red-tides of *Chattonella marina* and *Heterosigma akashiwo* (both Raphidophyceae).

Seasonal variation in abundance of two Centropages species

Centropages abdominalis is a winter–spring species and *Centropages tenuiremis* is a summer–fall form (Fig. 3). The former species already occurred in the plankton on the first sampling date (7 November 1986), gradually increased to the maximum (23 600 ind m^{-3}) in early February, and disappeared from the plankton by 12 June 1987. A reestablishment of the population was observed on 2 November 1987. On the other hand, *C. tenuiremis* occurred from 2 May to 6 December. Its density was much lower than the former, and the maximum density was only ca. 500 ind m^{-3}.

The seasonal changes in abundance of various developmental stages, including eggs, of *Centropages abdominalis* are shown in Fig. 4. On 7 November 1986, its nauplii and early copepodites already appeared in the plankton, whereas its eggs, late copepodites and adults did not appear until 26 November. The abundance of each developmental stage fluctuated greatly during the study period.

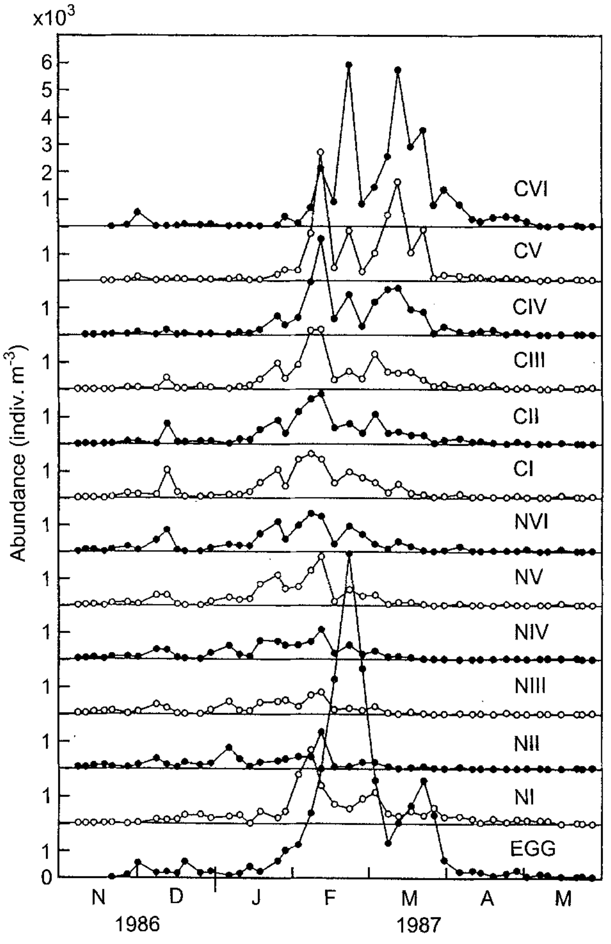

Fig. 4 *Centropages abdominalis*. Seasonal variation in stage-specific abundance

Seasonal variation in body size

Body size of *Centropages abdominalis* fluctuated seasonally in all developmental stages but NI and NII; it was larger in winter and early spring and smaller in fall and early summer (Fig. 5). Mean body length of each developmental stage older than NIII was inversely related to temperature at the time of sampling. To

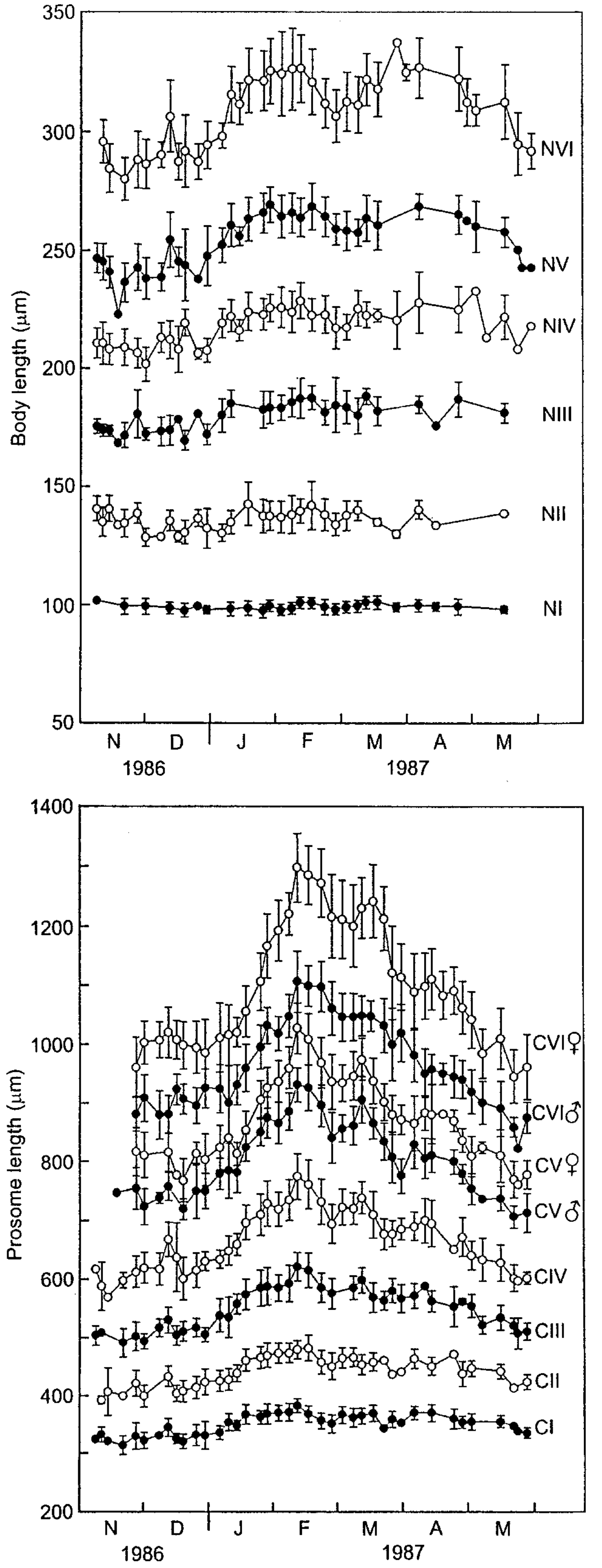

Fig. 5 *Centropages abdominalis.* Seasonal variation in body size (body length for nauplii and prosome length for copepodites and adults) of each developmental stage. *Error bars* denote SD

Table 1 *Centropages abdominalis.* Regression equations describing the relationship between body size and water temperature (T, °C). Body length (BL, µm) for nauplii and prosome length (PL, µm) for copepodites and adults. (r correlation coefficient)

Stage/sex	Regresion equation	r
NIII	$BL = 205\ (T - 4.26)^{-0.06}$	− 0.70***
NIV	$BL = 237\ (T - 6.00)^{-0.05}$	− 0.65***
NV	$BL = 308\ (T - 4.01)^{-0.09}$	− 0.70***
NVI	$BL = 392\ (T - 3.37)^{-0.11}$	− 0.72***
CI	$PL = 393\ (T - 6.81)^{-0.07}$	− 0.73***
CII	$PL = 514\ (T - 6.62)^{-0.09}$	− 0.76***
CIII	$PL = 654\ (T - 7.06)^{-0.11}$	− 0.84***
CIV	$PL = 910\ (T - 5.71)^{-0.17}$	− 0.90***
CV male	$PL = 1049\ (T - 6.38)^{-0.16}$	− 0.89***
CV female	$PL = 1060\ (T - 7.16)^{-0.13}$	− 0.86***
CVI male	$PL = 1270\ (T - 6.26)^{-0.16}$	− 0.90***
CVI female	$PL = 1374\ (T - 7.25)^{-0.15}$	− 0.86***

*** $p < 0.005$

express their relations by Bělehrádek's functions, non-linear least-squares were applied (Table 1).

Seasonal variation in sex composition

Although the sexes can be distinguished starting at copepodite Stage (C) IV in *Centropages abdominalis*, the sex composition was investigated only for CV and adult stages. The composition varied irregularly with season, but overall sex ratio was nearly 1 : 1 for both CV and adult.

Generation analysis

Numerical abundance of NIII, relative abundance of copepodites and adults within total abundance, and frequency distribution of prosome length of adult females were used to supplement the generation analysis. From November 1986 to May 1987, six generations could be detected, as the peaks in NIII abundance were followed by peaks in relative abundance of copepodites and adults and then the change in adult female body size (Fig. 6). The generation time varied depending on water temperature, being longer in cold months and shorter in warm months.

Postembryonic development in the laboratory

The stage succession based on median development time was determined only at 16 °C (Fig. 7). The stage duration was shortest in NI, but compensatingly longer in NII, the first-feeding stage. The stage duration was nearly constant between NIII and NVI, beyond which it tended to increase. There was no significant sexual difference in stage durations in CIV and CV. The

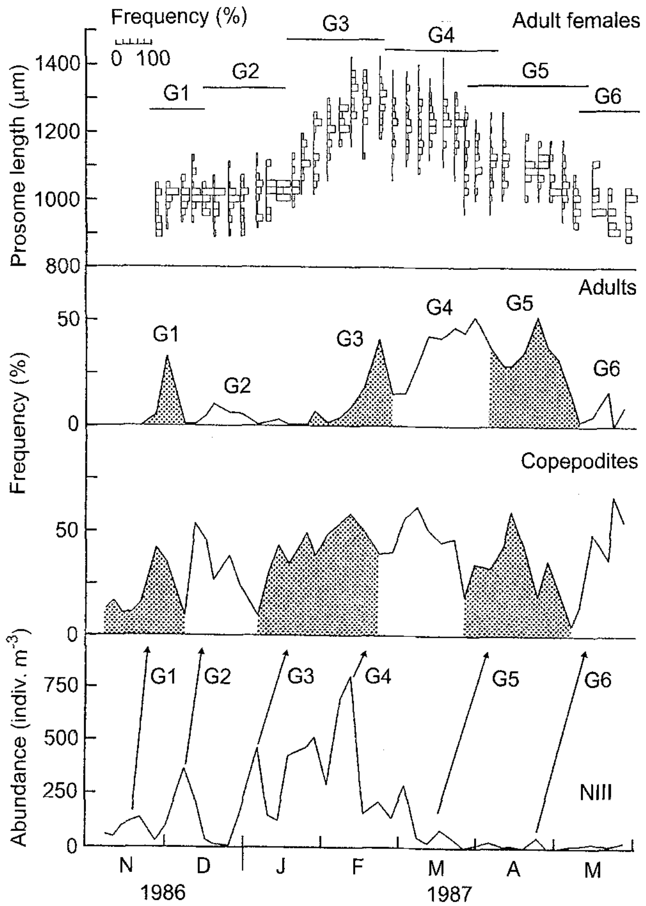

Fig. 6 *Centropages abdominalis.* Generation analysis based on numerical abundance of NIII, relative abundance of copepodites and adults in total abundance, and prosome length of adult females

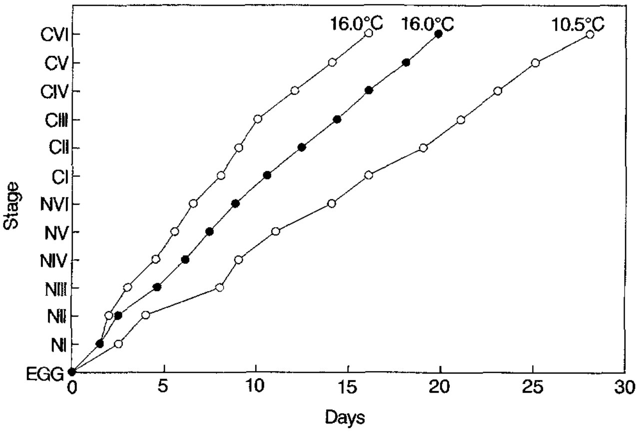

Fig. 7 *Centropages abdominalis.* Post-embryonic development at 10.5 and 16 °C. *Open* and *filled circles* denote minimum development time and median development time, respectively

development time from egg-laying to the first occurrence of an adult was 28 and 16 d at 10.5 and 16 °C, respectively, and the time at which 50% of individuals had molted into adult was 19.8 d at 16 °C (Fig. 7).

Liang et al. (1994) have previously reported the relationship between embryonic development time (DS_{NI}, d) of *Centropages abdominalis* and temperature (T, °C), which is expressed by the Bělehrádek's function:

$$DS_{\mathrm{NI}} = 159\ (T + 3.18)^{-1.58}. \tag{6}$$

Assuming that *Centropages abdominalis* follows the "equiproportional" rule of development (Corkett 1984), as observed for *C. typicus* (Fryd et al. 1991), the time required from egg-laying to reach developmental Stage i (DS_{i}, d) can be calculated from the embryonic duration by multiplication of a proportional constant (M) (Corkett and McLaren 1970), i.e.

$$DS_{\mathrm{i}} = \mathrm{M} \times DS_{\mathrm{NI}}. \tag{7}$$

The multipliers for successive stages were as follows: 1.68 (NII), 3.10 (NIII), 4.10 (NIV), 5.00 (NV), 5.95 (NVI), 7.10 (CI), 8.40 (CII), 9.68 (CIII), 10.9 (CIV), 12.2 (CV) and 13.4 (adult). Thus, the times from egg-laying to CI and adult were expressed by:

$$DS_{\mathrm{CI}} = 1131(T + 3.18)^{-1.58} \tag{8}$$

and

$$DS_{\mathrm{CVI}} = 2123(T + 3.18)^{-1.58} \tag{9}$$

respectively (Fig. 8).

Comparisons were made between the generation times observed in nature, which were simply defined as periods between pulses in abundance of NIII, and the

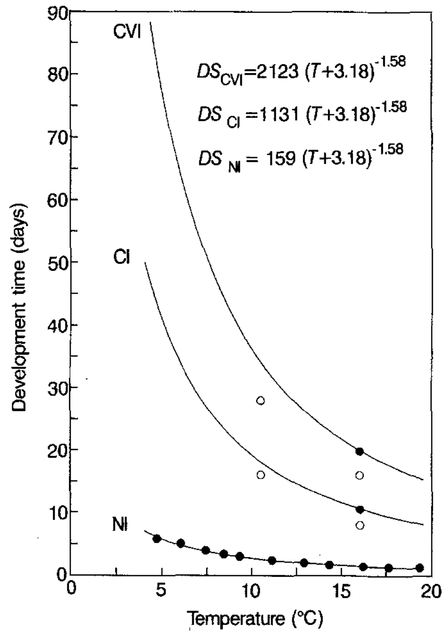

Fig. 8 *Centropages abdominalis.* Relationship between water temperature and development time from egg-laying to hatching, to CI and to adult. *Continuous lines* calculated from egg development times using Equations (6) and (7). *Open* and *filled circles* denote minimum development time and median development time, respectively

Table 2 *Centropages abdominalis.* Comparison between generation times in the field and development times from egg-laying to adult predicted from laboratory experiments

Generation	Average temperature (°C)	Generation time (d)	
		Observed	Predicted
G1	15.5	20	20.9
G2	13.7	28	24.5
G3	10.6	36	33.8
G4	9.8	40	37.1
G5	12.0	32	29.0

development times from egg-laying to adult calculated from the above equations by substituting average temperature during the period (Table 2). Although the laboratory-determined development times did not include the time from molting into an adult to the onset of egg production (ca. 2 to 3 d at 15 °C, our unpublished data), the times derived from the two different methods were in fairly good agreement.

Population dynamics

Population egg production rate

Seasonal change in egg production rate of *Centropages abdominalis* was investigated by incubating freshly collected females in glass bottles containing a natural assemblage of phytoplankton for 24 h at field temperatures (see Liang et al. 1994). This incubation fecundity was assumed to represent in situ egg production rates. Population egg production rate was given as a multiple of individual egg production rate and adult female density (Fig. 9). It was highest in February and March due to high density of females.

Daily midstage abundance

Assuming steady state of the population near each sampling date, the number of individuals per day passing through the midpoint of each stage can be calculated by:

$$DMA_i = N_i/D_i, \qquad (10)$$

where DMA_i is the daily midstage abundance of Stage i (ind $m^{-3}d^{-1}$), N_i is the abundance of Stage i (ind m^{-3}) and D_i is the duration of Stage i (d) (Fager 1973). This calculation was performed on each sampling date and results are shown in Fig. 9.

The daily midstage abundance of NI, which also represents the recruitment rate to the planktonic population, was roughly in parallel with the population egg production rate from December to early February. From late February to early April, there was a large gap between them.

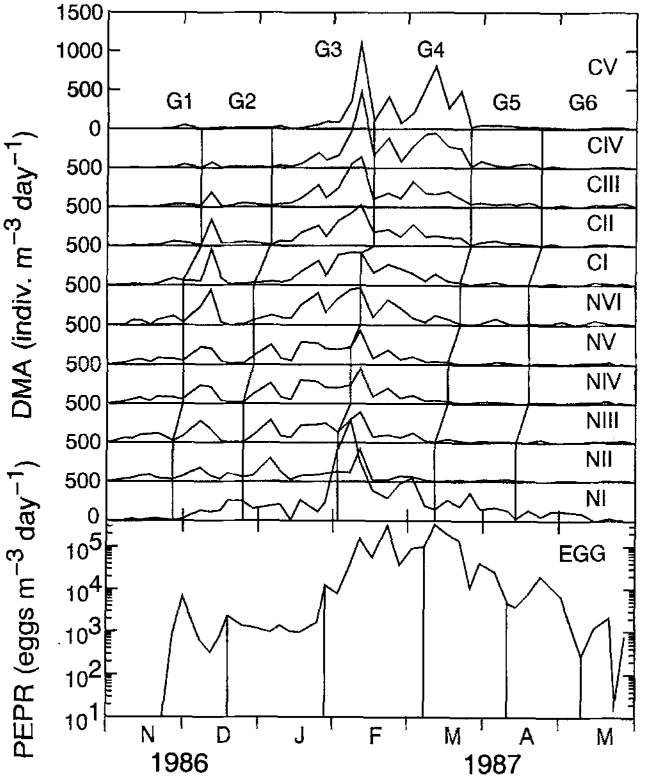

Fig. 9 *Centropages abdominalis.* Seasonal variation in population egg production rate (*PEPR*, in logarithmic scale) and daily midstage abundance (*DMA*) of each stage. Each generation is delimited by *vertical lines*

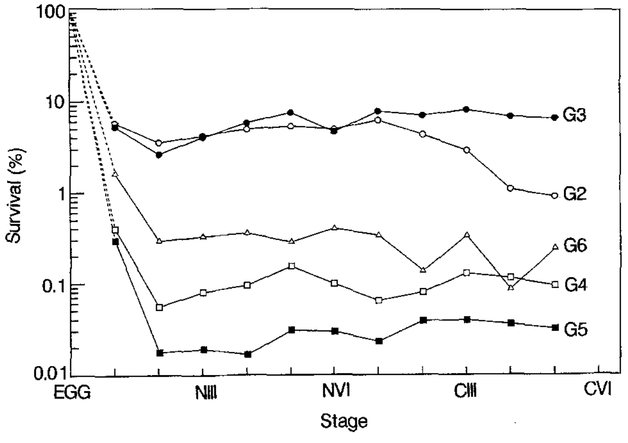

Fig. 10 *Centropages abdominalis.* Survival curves for generations G2 to G6

Generation survival curve

As described in the section "Generation analysis", there might be six generations during our study period. From the illustration of the seasonal variation in daily midstage abundance of each stage versus time, a sequence of pulses was traced to define a generation which was subjectively delimited by boundaries in time for each developmental stage (Fig. 9). Hence, a survival curve for each generation could be generated by using the mean egg production rate and the mean daily abundance of each developmental stage of a given generation.

A survival curve for the first generation (G1) could not be determined, since this generation was derived from resting eggs in the bottom sediment. Survival curves for the other generations (G2 to G6) are given in Fig. 10. The most striking feature was extremely high mortality between egg and NI. In G2 and G3, this mortality was lower (94.3 and 94.8%, respectively) than that in G4 (99.6%), G5 (99.7%) and G6 (98.4%). The mortality was also higher between NI and NII in G4 to G6. On the contrary, the mortality in stages older than NII was almost negligible.

Growth rate

An assumption that *Centropages abdominalis* in Fukuyama Harbor develops at the same rate as in a well-fed laboratory population was substantiated as described in the section "Postembryonic development in the laboratory". The instantaneous growth rate of the field population was calculated for each stage, and the means for nauplii and copepodites are plotted against temperature (Fig. 11). The following equations were derived:

$$g_N = 0.068\,e^{0.080T}, \qquad (11)$$

for nauplii, and

$$g_C = 0.087\,e^{0.082T} \qquad (12)$$

for copepodites.

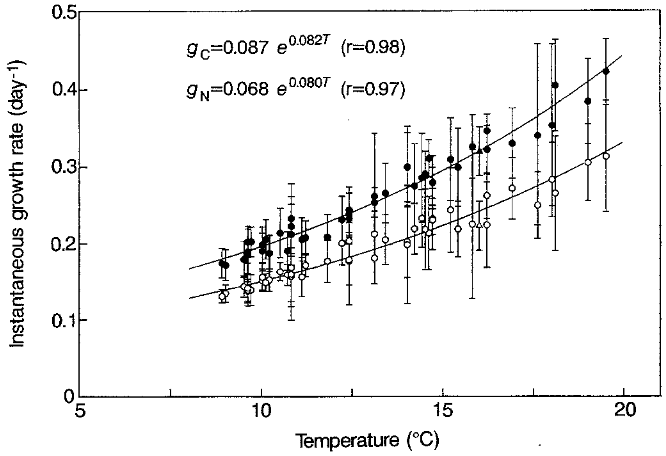

Fig. 11 *Centropages abdominalis.* Relationship between mean instantaneous growth rate of nauplii (*open circles*) and copepodites (*filled circles*) and water temperature. *Error bars* denote SD. *Open* and *filled triangles* denote the mean instantaneous growth rate of nauplii and copepodites respectively, determined for the laboratory-reared population at 16 °C

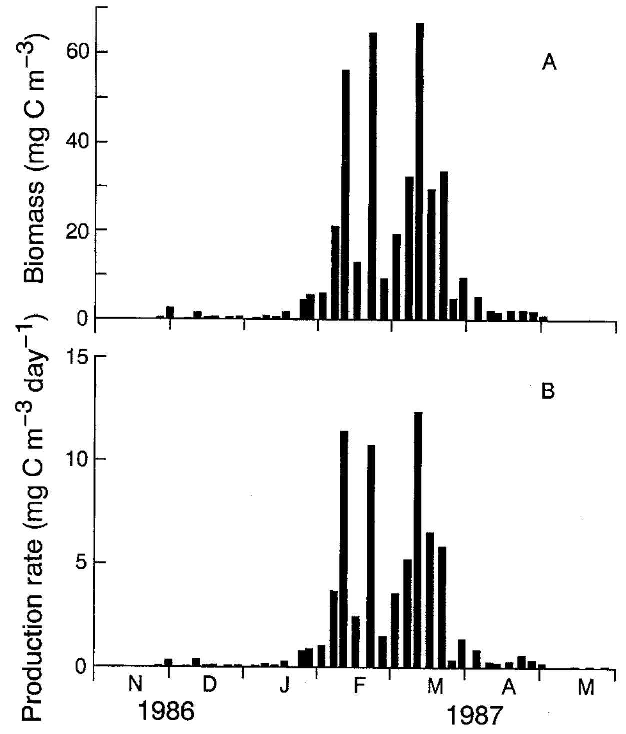

Fig. 12 *Centropages abdominalis.* Seasonal variation in **A** biomass and **B** production rate

Seasonal variation in biomass and production rate

The biomass of *Centropages abdominalis* was less than 5 mg C m^{-3} until late January and became high in February and March (Fig. 12). The maximum biomass of 67.1 mg C m^{-3} was recorded on 11 March 1987.

The pattern of the seasonal variation in production rate was similar to that of biomass (Fig. 12). The maximum production rate (12.4 mg C m^{-3} d^{-1}) was also recorded on 11 March 1987. Cumulative production between 7 November 1986 and 29 May 1987 was 355 mg C m^{-3} or 2.66 g C m^{-2}. The contribution of nauplii to the population production was minor (overall mean: 8.6%), and primarily owed to copepodites (57.8%) and adult females (33.6%).

The empirical relationship between the ratio of daily production rate to biomass (P/B) and temperature was examined (Fig. 13). The ratio increased exponentially with increasing temperature (T, °C), and the following equation was derived:

$$P/B = 0.086\,e^{0.064T}. \qquad (13)$$

Discussion

Seasonal occurrence and population dynamics

As seen in Fig. 3, a clear pattern of alternation in the plankton was evident for *Centropages abdominalis* and

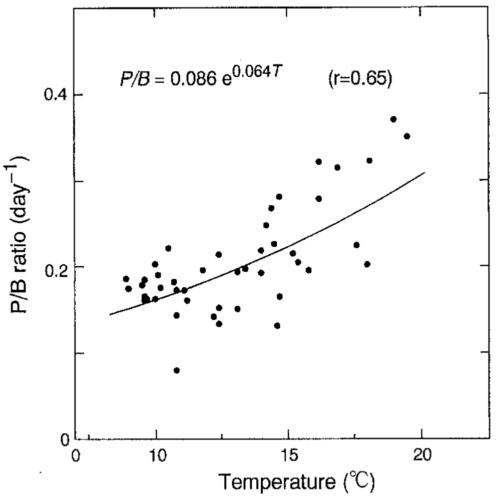

Fig. 13 *Centropages abdominalis.* Relationship between daily production/biomass ratio (*P*/*B*) and water temperature

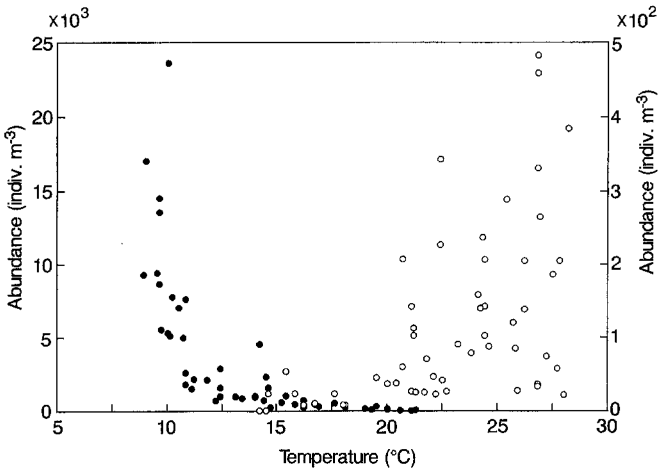

Fig. 14 *Centropages abdominalis* and *C. tenuiremis.* Relationship between abundance and temperature. *C. a.*: *filled circles*, left ordinate. *C. t.*: *open circles*, right ordinate

Centropages tenuiremis. Fig. 14 shows the relationship between the abundance of both species and temperature. *C. abdominalis* appeared in the plankton when temperature was below 21.1 °C, and its density was higher at temperatures below 10 °C. On the contrary, *C. tenuiremis* appeared when temperature was higher than 14.5 °C, and became abundant at temperatures above 21 °C. Replacement seems to occur within a temperature range between 14.5 and 21.1 °C. During an unfavorable temperature period, either species can exist as resting eggs on the sea-bottom (Kasahara et al. 1974, 1975). Thus, temperature is the prime determinant of their occurrence in the plankton.

Within the thermal range of *Centropages abdominalis*, the density and age structure of the population are explained by temporal variations in the balance between fecundity and mortality. The fecundity of this species varied from 39 to 142 eggs female^{-1} d^{-1}, and the weight-specific egg production rate was positively correlated to both temperature and chlorophyll *a* concentration (Liang et al. 1994). The population egg production rate depended largely on the density of adult females, and hence it was highest in February and March (Fig. 9). The fraction surviving from egg to NII was extremely low and variable in this species (Fig. 10). In G2, although the population egg production rate was lowest, the fraction surviving to NII was highest (i.e. 4.0%). In G5, it was vice versa, and only 0.02% of the eggs spawned survived to NII. Landry (1978) previously reported that approximately 80% of the eggs never survived to NII for *Acartia clausi* in a temperate lagoon in Washington, USA, and Uye (1982a) found that mortality of 80 to 90% occurred from egg to NIII for *Acartia omorii* (formerly referred to as *A. clausi*) in Onagawa Bay, Japan. Liang et al. (1994) recently assessed the loss of eggs by comparing incubation fecundity and egg-ratio fecundity of *C. abdominalis*: 37 to 99% (mean: 87.5%) of the spawned eggs were lost during egg stage within the water column. Hence, mortality in early life is probably concentrated in the egg stage.

A significant part of the loss might be attributed to predation, including cannibalism, in addition to loss by sinking (Liang et al. 1994). Furthermore, the mortality was also higher between NI and NII in G4 to G6 (February–May) (see Figs. 9, 10). True carnivores such as fish larvae, chaetognaths, medusae and ctenophores were absent or extremely rare, while adults and late copepodites (CIV to CV) of *Centropages abdominalis* and *A. omorii* (both omnivorous copepods) occurred with as many as 39 000 ind m^{-3} during this period. Assuming the clearance rate of each individual is 50 ml ind^{-1} d^{-1}, 1 to 86% of the water column was estimated to be cleared by *C. abdominalis* and *A. omorii* per day (Liang et al. 1994). This suggested that predation, including cannibalism, by these copepods might also be the main source of mortality during these stages. A similar predation (i.e. cannibalism) impact was also found by Hada and Uye (1991) for the omnivorous copepod *Sinocalanus tenellus* in a brackish-water pond of Fukuyama, Japan.

Although the hatching success of eggs of *Centropages abdominalis* was not investigated in the present study, another possible source for the higher mortality in the early life stages was low egg viability, Ianora et al. (1992) found that hatching success of *Centropages typicus* eggs in the Gulf of Naples varied from 41 to 94%, and the variation was related to neither breeding intensity nor environmental variables such as chlorophyll and temperature. Furthermore, Ianora and Poulet (1993) and Poulet et al. (1994) found that several species of diatoms inhibited copepod embryonic development causing higher egg mortality. In Fukuyama Harbor, the phytoplankton community (cell diameter $>$ ca. 10 μm) consisted almost entirely of diatoms (e.g.

Table 3 Comparison of development time from egg-laying to adult (*D*) and instantaneous growth rate (*g*) at various temperatures within the genus *Centropages*. (– no data)

Species	Temp. (°C)	D (d)	g (d^{-1})	Source
C. typicus	18–19	22	–	Lawson and Grice (1970)
	10	48	–	Smith and Lane (1985)
	15	33	–	Smith and Lane (1987)
	17	16	0.37	Fryd et al. (1991)
C. hamatus	15	20	0.31	Klein Breteler et al. (1982)
	17	18	0.27	Fryd et al. (1991)
C. abdominalis	16	20	0.28	Present study

Skeletonema costatum, *Chaetoceros* spp.) from mid-January to the end of March, when higher mortality of *C. abdominalis* in the early life stages occurred. The effect of inhibitory compounds from diatoms upon egg mortality of *C. abdominalis* remains to be investigated in future.

Development, growth and production

As observed for *Centropages typicus* (Fryd et al. 1991), *Centropages abdominalis* had a relatively brief prefeeding stage (NI) which was followed by compensatingly longer first-feeding stage (NII). Between NIII and NVI, the development was nearly isochronal, and beyond NVI the stage durations tended to be longer. Agreement of the generation times both predicted from the well-fed laboratory population and analyzed from the field population (Table 2) suggested that *C. abdominalis* in Fukuyama Harbor was not food-limited. However, this might not be so for the egg production rate by adult females, since the rate was dependent on both temperature and chlorophyll *a* concentration (Liang et al. 1994).

A comparison is made of the development time among three *Centropages* species, i.e. *C. typicus*, *C. hamatus* and *C. abdominalis* (Table 3). They develop at almost the same rate; at temperatures around 17 °C it takes approximately 20 d for them to develop from egg to adult, although the development time of *C. typicus* according to Smith and Lane (1987) is longer than that of the other species.

The instantaneous growth rate of *Centropages abdominalis* is similar to that of the other *Centropages* species (Table 3). Fryd et al. (1991) found that the growth rate is constant over the all developmental stages for *C. hamatus* and *C. typicus*. For *C. abdominalis*, however, the growth rate is higher in copepodites than in nauplii. Moreover, the growth rate of *C. abdominalis* is high compared to those of the other calanoid species occurring in the low temperature period in the Inland Sea of Japan (Table 4).

Davis (1987) has forcefully argued that estimation of species-specific growth rate of zooplankton may be the only route to the accurate determination of zooplankton production rate. In the present study, the estimate of production was based on the instantaneous growth rate of each developmental stage and its biomass on each date, hence our estimation may be close to the actual production rate of a field *C. abdominalis* population. The main characteristic feature of this species is an elevated production rate during the coldest season because of its relatively high growth rate and the culmination of its biomass. The annual production of *C. abdominalis* was 355 mg C m^{-3} or 2.66 g C m^{-2}, 95% of which was attained in February and March. During the same coldest months, the production of *Acartia omorii* was estimated to be 280 mg C m^{-3} or 2.10 g C m^{-2} (Liang and Uye unpublished). Thus these two species are the most important secondary producers during the coldest season in Fukuyama Harbor.

Table 4 Comparison of the instantaneous growth rate (*g*) at 10°C among calanoid copepods occurring in the Inland Sea of Japan

Species	g at 10 °C	Source
Calanus sinicus	0.19[a]	Uye (1988)
Paracalanus sp.	0.18[a]	Uye (1991)
Centropages abdominalis	0.20	Present study
Pseudodiaptomus marinus	0.10[a]	Uye et al. (1983)
Acartia omorii	0.14[a]	Uye (1982a)

[a] g is recalculated from the original data

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