Vol. 224: 133–148, 2001 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published December 19

Development and egg production in *Centropages typicus* (Copepoda: Calanoida) fed different food types: a laboratory study

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ABSTRACT: The effects of different types of food on the growth, development, reproduction, egestion and grazing of the copepod *Centropages typicus* Krøyer was studied in the laboratory at 15°C. The copepods were reared from eggs to NVI using *Isochrysis galbana* as food, and from NVI onwards with a range of diets: a single food source consisting of 1 of 2 algae (the haptophyceaen *Hymenomonas elongata* and the diatom *Thalassiosira weissflogii*), a single food source consisting of the ciliate *Strombidium sulcatum*, and a mixture consisting of each type of algae and the ciliate. The results, based on daily sampling, show that growth, development rate and egg production were dependent on food type. The food types that induced the shortest development times (*H. elongata*, *S. sulcatum*) did not necessarily result in the highest production rates. The daily specific growth rate for copepodid stages was significantly lower with *T. weissflogii* (0.045 d^{-1}) than with the other diets (0.09 to 0.15 d^{-1}). The combination of variable development and variable growth rates with the different diets induced a high variability in mean weight within developmental stages. The weights recorded are amongst the highest observed for this species. Length did not differ significantly within the same development stage between different diets. Mixed food sources were more efficient than a single food source in terms of egg production and viability. No relationship was established between hatching success, female age or copepodid mortality rate and food type. A pure diet of *T. weissflogii* resulted in a sex ratio skewed towards males, whereas the other diets produced a balanced sex ratio. The present results indicate the mixture phytoplankton/ciliate to be the most favourable for development, growth and egg production, suggesting that omnivory is the best feeding strategy for *C. typicus*.

KEY WORDS: *Centropages typicus* · Development · Growth · Egg production · Hatching rate · Phytoplankton prey · Microzooplankton preyos

INTRODUCTION

The importance of food quality has been demonstrated by many authors studying a range of processes in copepods: e.g. ingestion and assimilation (Paffenhöfer 1971, Checkley 1980, Cowles et al. 1988, Klein Breteler et al. 1990, Reinfelder & Fisher 1991), egg production and hatching success (Checkley 1980, Ianora & Poulet 1993, Miralto et al. 1995, 1999, Jónasdóttir & Kiørboe 1996) and faecal pellet production (Ianora & Poulet 1993, Butler & Dam 1994). A few major studies have demonstrated an influence of food quality on their life cycle (Klein Breteler et al. 1990, Støttrup & Jensen 1990, Twombly & Burns 1996, Koski et al. 1998, Twombly et al. 1998). Kleppel (1993) stated that dietary diversity is a nutritional requirement, which changes ontogenetically from copepodid to adult stage. Juvenile copepods must feed on different food size spectra during the course of their development (Berggreen et al. 1988, Klein Breteler et al. 1995), as the adult is about 10

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to 20 times larger than the Nauplius I. Moreover juveniles have different bioenergetic needs linked to their various developmental stages (growth, appearance of sexual characters, reproduction).

Thus, the growth and reproduction of these organisms depends on their present and recent-past feeding history in terms of both food quantity and food quality. However, apart from their recent feeding history, nothing is known about the previous nutrition of individuals in the majority of developmental studies in the laboratory (Mayzaud et al. 1998).

The role of protozoans in the zooplankton diet has been little studied in the laboratory, since they are not easily detectable in the gut contents of zooplankton collected in the field (Stoecker & Govoni 1984). Nevertheless, *in situ* studies have shown the importance of microzooplankton (Azam et al. 1983), which consume primary production in a size spectrum inaccessible to copepods, and then serve as prey for the mesozooplankton. For most copepods, omnivory seems to be a frequent strategy (Corner et al. 1974, Paffenhöfer & Knowles 1980, Dam et al. 1994), as demonstrated by fatty acid and amino acid tracers (Ederington et al. 1995), and predation on protozoans is thought to be important, since they consitute a source of nutrients essential for survival and production (Ohman & Runge 1994).

Laboratory studies on the development of *Centropages typicus* (Smith & Lane 1985, Davis & Alatalo 1992) have not considered microzooplankton prey as a food source. In the laboratory, Wiadnyana & Rassoulzadegan (1989) and Caparroy et al. (1998) have shown that *C. typicus* feeds actively on the protozoan *Strombidium sulcatum*, but there is no data in the literature describing the effects of its ingestion on the development rate and egg production of this copepod.

The present study therefore investigated the effect of food quality on the development of the copepod *Centropages typicus* over 1 complete generation, including egg production of the subsequent generation. Different cohorts were reared on specific diets of pure algae or pure ciliate, or mixtures of both food types, in order to examine the effect of dietary diversity on growth, development, egg production and hatching success.

MATERIALS AND METHODS

Cultures and experimental set up. Algal cultures were grown in Guillard *F*/2 medium and exposed to the same light:dark cycle (12:12 h) as *Centropages typicus. B*acterial suspensions used to feed the protozoan *Strombidium sulcatum* were cultured by adding 20 g of protease peptone and 2.5 g of yeast extract to 1 l of filtered seawater (0.22 µm). The algae and protozoan used were in the exponential growth phase (7 to 10 d for the algae, 3 to 4 d for protozoa). Cell sizes of the food items were measured under a microscope. Ten ml of cultures were filtered through combusted GF/F filters and measured with a Model 10 fluorometer (Turner Designs, Sunnyvale, CA) for chl *a* or a CHN analyzer (LEICO 900) for C and N content.

Zooplankton were collected at the entrance of Villefranche Bay (Mediterranean Sea) with a WP2 net at 100 m depth. Three hundred to 400 adult female *Centropages typicus* Krøyer were placed in a 5 l plexiglas cylinder (200 µm bottom mesh) filled with filtered seawater containing *Hymenomonas elongata* (Haptophyceae) at a concentration of 5000 cells ml^{-1} at 15°C. After 1 d, the females were separated from the eggs. A concentration of 100 000 cells ml^{-1} of *Isochrysis galbana* (Prymnesiophyceae) was offered as food during naupliar development. When the cohort reached the NVI/CI stages, it was divided into 5 sub-cohorts which were fed different food sources: (1) the haptophyceaen *H. elongata*, (2) the diatom *Thalassiosira weissflogii*, (3) the ciliate *Strombidium sulcatum*, (4) *H. elongata* + *S. sulcatum*, or (5) *T. weissflogii* + *S. sulcatum*. Table 1 presents the food concentrations and the initial copepod concentrations for the different cohorts studied. The cultures were sampled and mixed daily.

Food concentrations were chosen based on previous studies on *Centropages typicus* such that *Hymenomonas elongata* and *Strombidium sulcatum* were offered at near optimal concentrations to achieve maximal ingestion rates (Bonnet 1998, Caparroy 1998, Caparroy et al. 1998), and *Thalassiosira weissflogii* was offered at concentrations that would ensure maximal egg production rates (Smith & Lane 1985). The subcohorts were sampled daily, and food concentrations were adjusted as necessary. Optimum algal concentrations

Table 1. Initial densties of *Centropages typicus* and concentrations of its food sources in the mesocosms

Cohort	Initial Copepodite I density (ind. l^{-1})	Diet	Cells ml^{-1}
Nauplii		*Isochrysis galbana*	100 000
Subcohorts			
A	580	*Hymenomonas elongata*	5000
B	440	*Thalassiosira weissflogii*	5000
C	590	*Strombidium sulcatum*	45
D	820	*H. elongata* + *S. sulcatum*	5000 + 45
E	400	*T. weissflogii* + *S. sulcatum*	5000 + 45

were used in the single diet to achieve a maximum ingestion response. In mixed cultures, the addition of phytoplankton cells to *S. sulcatum* yields a ciliate carbon/phytoplankton chl *a* ratio of 3.6, a value similar to those found by Dolan & Marrasé (1995) in the Mediterranean Sea. All sub-cohorts *Centropages typicus* were reared at 15°C under a 12:12 h light:dark cycle.

Development and growth. Sample volume varied daily as a function of the population density of a cohort, so that the first sample represented 1% of the total volume (at the beginning) and the last sample represented 4% of the final volume (4.5 l) and consisted of 20 to 40 individuals. The samples were fixed and preserved in 4% formalin, and stage distribution determined under a binocular microscope. Stage durations were calculated using the median development time of stage frequencies defined as the time for 50% of the cohort to moult to the next stage (Klekowski & Duncan 1975, Landry 1975). Only the CV and CVI stages were considered for determining the male to female ratio, and the final ratio is an average of daily values. Mortality rates were calculated for the whole copepodid development (CI to CVI) for each food source as well as for the nauplii lifespan (egg to NVI) by fitting decreasing exponential curves to the data.

To measure body length of each stage, formalin samples from successive dates were pooled to obtain 30 individuals for each stage. Cephalothorax length of copepodids and total length of nauplii were measured. All individuals were subsequently washed with ammonium formiate (68 g l^{-1}), dried at 70°C for 72 h, and finally weighed with a microbalance. Length-weight relationships were determined for each diet (±1 µg). Copepod dry weights were converted to carbon assuming that carbon represents 37.6% of the dry weight (Gorsky et al. 1988). When 50% of the population had reached the CVI stage, the cultures were discontinued.

Ingestion rates from grazing experiments rate. Ingestion experiments were made on NVI and CIII stages: NVI from the initial cohort reared on *Isochrysis galbana* (8 groups of 30 individuals) and CIII from the sub-cohorts reared on different food sources (3 groups of 50 individuals taken from each cohort) were incubated in bottles of 125 and 1000 ml, respectively, under the same food conditions as the cohorts from which they were taken. The bottles with copepods as well as those without (controls) were fixed on a Ferris wheel and gently rotated (1.5 rpm) for 24 h in the same conditions. After 24 h, samples were taken to determine cells concentrations in the bottles, and mortality of the copepods was estimated. Algal cells and the protozoan were preserved in 2% acid Lugol solution and counted with a Lemaur or Malassez cell under a microscope for the algae and with an inverted microscope after sedimentation in an Utermöhl chamber for the ciliate. Ingestion rates were calculated according to Frost (1972).

Egg production, egestion and egg viability. When 50% of a sub-cohort population had reached the adult stage, adult females (<3 d old) were taken from the sub-cohort, divided into 4 groups of 10 individuals each and placed in 300 ml beakers with a 200 µm-mesh filter on the bottom so that adults could not feed on their eggs. Three males were introduced to each beaker to ensure fertilisation. Copepods were fed with the same food source used during their development. The incubation medium was changed every day, and egg and faecal pellet number and female mortality were measured. At least 30 of the eggs produced each day were divided between a series of 10 ml chambers, and their hatching success was observed until the non-hatched eggs were decomposing. The experiments were run until all the females had died.

Differences among experiments on ingestion, egg and faecal pellet production, hatching success, sex ratio and mortality were statistically tested using an ANOVA followed by a Tukey's HSD test. For non-homogeneous variance, the non-parametric Kolmogorov-Smirnov test was used.

RESULTS

Characteristics of diets offered

The C, N and chl *a* content of the food types are presented in Table 2. For *Centropages typicus* nauplii, a small (6 µm) alga *Isochrysis galbana* was used, whereas for the copepodid stages, 2 further algae *Hymenomonas elongata* and *Thalassiosira weissflogii*

Table 2. Equivalent spherical diameter (ESD), carbon, nitrogen and chl *a* content of cells offered as food source to *Centropages typicus*. *Strombidium sulcatum* length includes hair length. Data are means ± SD

Diet	ESD (µm)	C (pg $cell^{-1}$)	N (pg $cell^{-1}$)	C/N	chl (pg $cell^{-1}$)	C/chl *a*
Isochrysis galbana	6.00 ± 1.06	15.39 ± 1.12	1.66 ± 0.09	9.27	0.243 ± 0.002	64.13
Hymenomonas elongata	13.00 ± 2.55	286.55 ± 13.24	17.62 ± 0.72	16.26	2.440 ± 0.034	117.44
Thalassiosira weissflogii	11.77 ± 1.81	159.68 ± 4.36	29.53 ± 1.06	5.41	2.002 ± 0.130	79.84
Strombidium sulcatum	86.41 ± 12.23	4267.22 ± 257.51	977.5 ± 50.39	4.36	–	–

Table 3. Initial cell concentrations and C, N and chl *a* contents of diets fed to *Centropages typicus*

Cohort	Diet	cells ml^{-1}	µg C l^{-1}	µg N l^{-1}	µg chl *a* l^{-1}
Nauplii	*Isochrysis galbana*	100 000	1539	166	24.3
Subcohorts					
A	*Hymenomonas elongata*	5000	1433	88.1	12.2
B	*Thalassiosira weissflogii*	5000	799	147.6	10
C	*Strombidium sulcatum*	45	192	44	–
D	*H. elongata* + *S. sulcatum*	5000 + 45	1433 + 192	166 + 44	12.2
E	*T. weissflogii* + *S. sulcatum*	5000 + 45	799 + 192	147.6 + 44	10

of the same size (12 µm) and with the same chl *a* content (~2 pg cell^{-1}) were offered. *H. elongata* has a very high C/N ratio compared to *T. weissflogii*. The ciliate *Strombidium sulcatum*, the largest prey (85 µm), has a low C/N ratio compared to the algae. These characteristics of the food sources enabled us to estimate the concentrations offered in terms of C, N and chl *a* (Table 3). In general, the concentrations were very high: >192 µg C l^{-1}, >44 µg N l^{-1} and >10 µg chl *a* l^{-1}.

Egg and naupliar development

Fifty percent of the eggs had hatched after 33.6 h, and 95% after 72 h. A few stragglers remained for up to 5 d (Fig. 1, Table 4). Development of nauplii fed *Isochrysis galbana* lasted for ca 12 d. During naupliar development, there was good synchronism in the moult of the whole population *I. galbana*. Only 5 to 10% stragglers were observed, and this ratio was stable and did not increase with time. The NI stage was short compared to the other naupliar stages, which are feeding stages, NIV was the longest naupliar stage (Fig. 1, Table 4).

Copepodite development and adult sex ratio

Single food sources induced different copepodite development rates. CIV and CV took up around 62% of the cumulative copepodid duration with *Thalassiosira weissflogii* as food source, 53% with *Hymenomonas elongata*, *Strombidium sulcatum* and *H. elongata* + *S. sulcatum*, *T. weissflogii*, and 44% with *T. weissflogii* + *S. sulcatum*. CV stage was the longest of the copepodid stages regardless of food type.

The combinations of *Hymenomonas elongata* + *Strombidium sulcatum*, or *Thalassiosira weissflogii* + *S. sulcatum* resulted in an intermediate stage duration compared to the development times with either food source alone. Stragglers were oserved for the CI and CII stages in the *H. elongata* cohort and for the CI instar in the populations fed *H. elongata* + *S. sulcatum* or *T. weissflogii* (Fig.1).

Sex ratios are also shown in Table 4. Diet had a significant effect on sex ratio (ANOVA: calculated F_c = 2.57; theoretical $F_{\text{theo }(4;63;5\%)}$ = 2.52; $p < 0.05$). The culture reared on *Thalassiosira weissflogii* had a particularly low sex ratio (females/males = 0.535) (Tukey's HSD: $p < 0.05$), whereas the other diets produced a more equal balance of females and males.

Mortality rates

The mean mortality rate from eggs to NVI was estimated at 0.01 d^{-1}. Mean copepodid mortality rates were equal to 0.09 and 0.15 d^{-1}, in cultures with *Thalassiosira weissflogii* + *Strombidium sulcatum* and

Table 4. *Centropages typicus.* Duration of development stages at 15°C as a function of food source. Also shown are mortality rates and sex ratios (Female CV + CVI)/(Male CV + CVI) of cohorts fed different food sources (mean ± SD)

Diet	Development stage duration (d)							Cumulative duration (d)	Mortality rate (d^{-1})	Sex ratio
	Egg	**N1**	**N2**	**N3**	**N4**	**N5**	**N6**	**Egg–N6**		
Isochrysis galbana	1.40	0.95	1.90	1.05	2.75	1.65	1.85	11.55	0.0106	
	CI	**CII**	**CIII**	**CIV**	**CV**			**CI–CV**		
Hymenomonas elongata	0.83	1.93	4.07	2.71	4.79			14.33	0.1086	0.943 ± 0.562
Thalassiosira weissflogii	0.90	3.00	5.50	7.13	8.25			24.78	0.1173	0.535 ± 0.282
Strombidium sulcatum	0.85	2.09	4.55	3.91	5.00			16.40	0.1676	0.843 ± 0.567
H. elongata + *S. sulcatum*	0.88	2.15	4.56	4.09	5.00			16.68	0.1458	1.107 ± 0.758
T. weissflogii + *S. sulcatum*	1.20	3.90	4.90	2.30	5.80			18.10	0.0861	1.054 ± 0.506

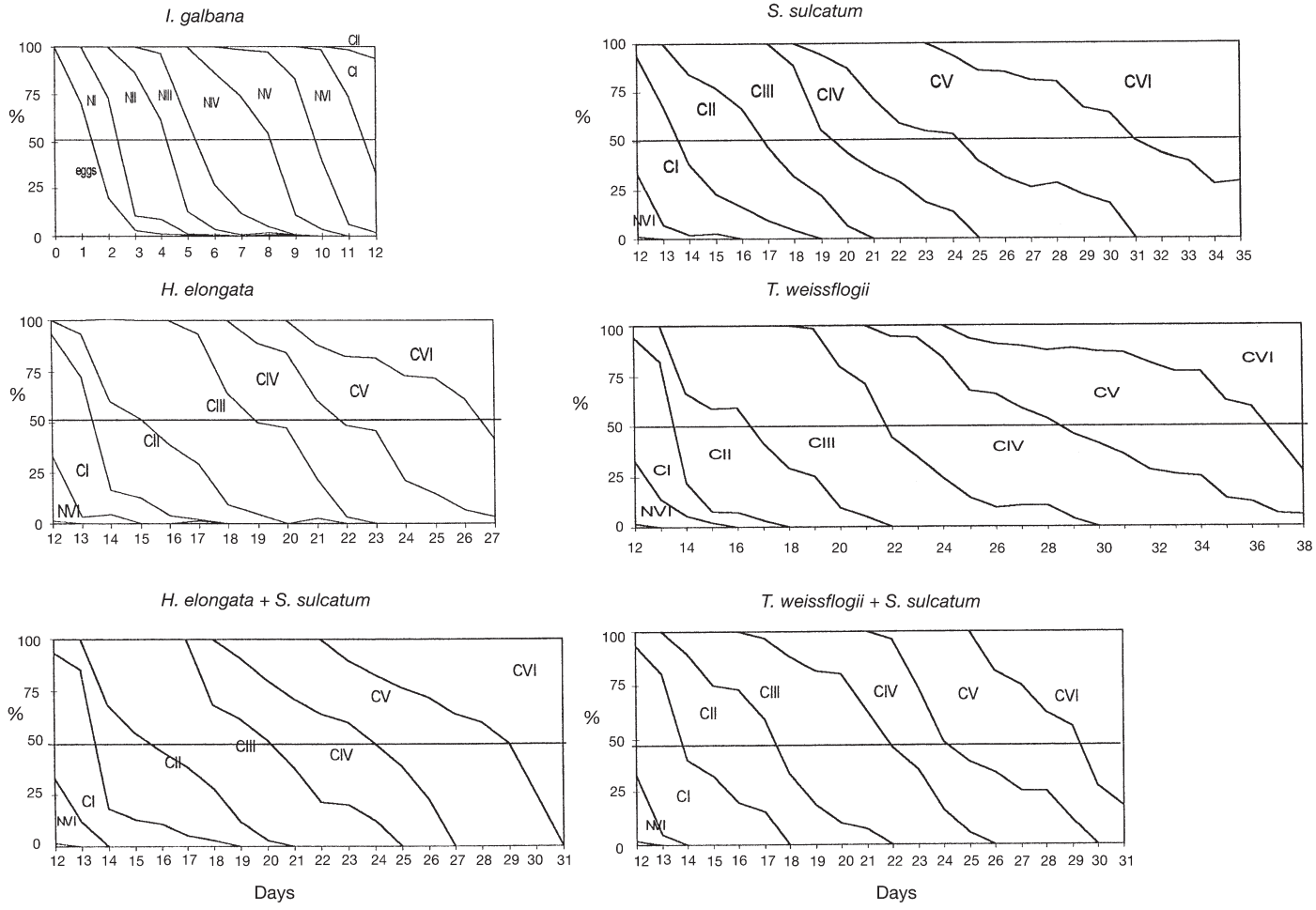

Fig. 1. *Centropages typicus.* Distribution of development stages (%) as a function of food type. Full specific names are given in Table 1

Hymenomonas elongata + *S. sulcatum* diets, respectively. *H. elongata*, *T. weissflogii* and *S. sulcatum* induced mean copepodid mortality rates of 0.11, 0.12 and 0.17 d^{-1}, respectively (Table 4). There was no significant influence of the diets offered on copepodid mortality rates (ANOVA: $F_c = 5.36$; $F_{theo(4;17;5\%)} = 8.91$). The mortality rates included mortality due to daily sampling (1 to 4% of the population), and NVI and CIII individuals used for ingestion experiments.

Growth

Diet had significant effects on the cephalothorax length of CI (ANOVA: $F_c = 8.58$; $F_{theo(4;139;0.001)} = 4.90$), CII (ANOVA: $F_c = 6.95$; $F_{theo(4;145;0.001)} = 4.89$), CIII (ANOVA: $F_c = 4.45$; $F_{theo(4;145;0.01)} = 3.45$), CV male (ANOVA: $F_c = 6.37$; $F_{theo(4;132;0.001)} = 4.91$) and female (ANOVA: $F_c = 6.18$; $F_{theo(4;117;0.001)} = 4.96$) stages. Dry weight increased exponentially over time with all diets. Specific growth rate, *g* (slopes in Table 5), was significantly lower with the *Thalassiosira weissflogii* (4.5% d^{-1}) diet than with the others (9 to 15% body wt d^{-1}) diets. Whatever the diet offered, the dry weights measured in this study are among the highest in the lit-

Table 5. *Centropages typicus.* Linear model relating ln(mean dry weight) (µg ind.$^{-1}$) to time. Specific growth rate (*g*) given by slope. All regressions are significant at $p < 0.05$. Slopes did not differ significantly ($p > 0.05$) from each other except for the *T. weissflogii* treatment

Development stage	Diet	Slope	R
NIII-NVI	*Isochrysis galbana*	0.0966	0.99
CI-CV	*Hymenomonas elongata*	0.1480	0.93
CI-CV	*Thalassiosira weissflogii*	0.0446	0.85
CI-CV	*Strombidium sulcatum*	0.1262	0.79
CI-CV	*H. elongata* + *S. sulcatum*	0.1249	0.97
CI-CV	*T. weissflogii* + *S. sulcatum*	0.0932	0.79

Table 6. *Centropages typicus.* Summary of length and dry weight of the various development stages. –: no data. Full specific names as in Table 5

Stage	T(°C)	Diet	Dry weight (µg)	Cephalothorax length (µm)	Source
CVI female	–	*In situ* patchiness	39.9[a]	–	Dagg & Grill (1980)
CVI female	8	*In situ* patchiness	50.8 ± 0.6	2030[d]	Smith & Lane (1985)
CVI female	11	*In situ* patchiness	43.3 ± 3.0	1920[d]	Smith & Lane (1985)
CVI female	13	*In situ* patchiness	47.0 ± 2.3	1880[d]	Smith & Lane (1985)
CVI female	20	*In situ* patchiness	23.2 ± 0.5	1640[d]	Smith & Lane (1985)
CVI female	–	*In situ* patchiness	47.3 (ranging from 10 to 98)	ranging from 976 to 1260	Razouls & Razouls (1976)
CVI female	15	0.5 to 6 µg chl *a* l^{-1}	16.25–28.75[a,b]	1020–1120	Davis & Alatalo (1992)
CVI	16.5–17.5	Excess of *Oxyrrhis marina*	26[c]	–	Fryd et al. (1991)
CVI female	15	T. weissflogii + S. sulcatum	66.45	1119	This study
CVI female	15	*H. elongata* + *S. sulcatum*	55.14	1093	This study
CVI female	15	*S. sulcatum*	52.67	1098	This study
CVI female	15	*H. elongata*	31.40	1095	This study
CVI female	15	*T. weissflogii*	29.14	1068	This study
CVI male	–	*In situ* patchiness	47.1 (ranging from 10 to 110)	ranging from 961 to 1188	Razouls & Razouls (1976)
CVI male	15	0.5 to 6 µg chl *a* l^{-1}	13.75–21.25[a,b]	1000–1090	Davis & Alatalo (1992)
CVI male	15	*H. elongata* + *S. sulcatum*	57.18	1051	This study
CVI male	15	*T. weissflogii* + *S. sulcatum*	45.42	1069	This study
CVI male	15	*H. elongata*	42.26	1037	This study
CVI male	15	*S. sulcatum*	39.33	1039	This study
CVI male	15	*T. weissflogii*	22.37	1017	This study
CV female	15	0.5 to 6 µg chl *a* l^{-1}	7.5–8.75[a,b]	880–910	Davis & Alatalo (1992)
CV female	15	*H. elongata* + *S. sulcatum*	44.81	898	This study
CV female	15	*H. elongata*	34.68	879	This study
CV female	15	*T. weissflogii* + *S. sulcatum*	32.99	880	This study
CV female	15	*S. sulcatum*	31.08	839	This study
CV female	15	*T. weissflogii*	15.76	832	This study
CV male	15	0.5 to 6 µg chl *a* l^{-1}	6.75–10[a,b]	840–890	Davis & Alatalo (1992)
CV	16.5–17.5	Excess of *Oxyrrhis marina*	16[c]	–	Fryd et al. (1991)
CV male	15	*H. elongata* + *S. sulcatum*	33.63	874	This study
CV male	15	*H. elongata*	28.72	883	This study
CV male	15	*T. weissflogii* + *S. sulcatum*	25.26	866	This study
CV male	15	*S. sulcatum*	21.70	829	This study
CV male	15	*T. weissflogii*	13.62	817	This study
CIV	15	0.5 to 6 µg chl *a* l^{-1}	2.5–3.75[a,b]	600–700	Davis & Alatalo (1992)
CIV	16.5–17.5	Excess of *Oxyrrhis marina*	7.8[c]	–	Fryd et al. (1991)
CIV	15	*S. sulcatum*	30.11	684	This study
CIV	15	*T. weissflogii* + *S. sulcatum*	30.06	665	This study
CIV	15	*H. elongata* + *S. sulcatum*	21.73	676	This study
CIV	15	*T. weissflogii*	13.29	665	This study
CIV	15	*H. elongata*	11.32	696	This study
CIII	15	0.5 to 6 µg chl *a* l^{-1}	2.5[a,b]	500–530	Davis & Alatalo (1992)
CIII	16.5–17.5	Excess of *Oxyrrhis marina*	4.2[c]	–	Fryd et al. (1991)
CIII	15	*T. weissflogii* + *S. sulcatum*	24.50	519	This study
CIII	15	*S. sulcatum*	18.58	500	This study
CIII	15	*H. elongata* + *S. sulcatum*	14.85	489	This study
CIII	15	*T. weissflogii*	10.57	528	This study
CIII	15	*H. elongata*	8.07	529	This study
CII	15	0.5 to 6 µg chl *a* l^{-1}	1.25–1.75[a,b]	400–420	Davis & Alatalo (1992)
CII	16.5–17.5	Excess of *Oxyrrhis marina*	2.4[c]	–	Fryd et al. (1991)
CII	15	*T. weissflogii* + *S. sulcatum*	15.00	402	This study
CII	15	*S. sulcatum*	8.12	390	This study
CII	15	*T. weissflogii*	7.67	428	This study
CII	15	*H. elongata* + *S. sulcatum*	7.12	376	This study
CII	15	*H. elongata*	5.60	407	This study

Table 6 (continued)

Stage	T(°C)	Diet	Dry weight (µg)	Cephalothorax length (µm)	Source
CI	15	0.5 to 6 µg chl *a* l^{-1}	0.75[a,b]	300–320	Davis & Alatalo (1992)
CI	16.5–17.5	Excess of *Oxyrrhis marina*	1.4[c]	–	Fryd et al. (1991)
CI	15	*H. elongata* + *S. sulcatum*	7.77	323	This study
CI	15	*T. weissflogii* + *S. sulcatum*	6.93	329	This study
CI	15	*T. weissflogii*	5.58	353	This study
CI	15	*H. elongata*	5.46	341	This study
CI	15	*S. sulcatum*	4.91	320	This study
NVI	16.5–17.5	Excess of *Rhodomonos baltica*	1.05[c]		Fryd et al. (1991)
NVI	15	*I. galbana*	3.31	277[d]	This study
NV	16.5–17.5	Excess of *Rhodomonos baltica*	0.70[c]		Fryd et al. (1991)
NV	15	*I. galbana*	2.82	247[d]	This study
NIV	16.5–17.5	Excess of *Rhodomonos baltica*	0.50[c]	–	Fryd et al. (1991)
NIV	15	*I. galbana*	2.27	212[d]	This study
NIII	16.5–17.5	Excess of *Rhodomonos baltica*	0.35[c]	–	Fryd et al. (1991)
NIII	15	*I. galbana*	1.94	174[d]	This study
NII	16.5–17.5	Excess of *Rhodomonos baltica*	0.22[c]	–	Fryd et al. (1991)
NII	15	*I. galbana*	1.61	129[d]	This study

[a]Carbon values (cw, µg) were converted to dry weights (DW) using ratio: cw/DW = 0.376 (Gorsky et al. 1988)
[b]For copepodites, with $L > 0.4$ mm, W (µg) = 0.06 exp (4.612 L)
[c]Calculated from length-weight relations of Klein Breteler et al. (1982)
[d]Total length

erature for *Centropages typicus* development stages (Table 6). Length-weight relationships are shown in Fig. 2. The correlation coefficients between dry weight and cephalothorax length ranged between 0.926 and 0.988, with no significant difference among diets (ANCOVA: $F_c = 0.086$; $F_{theo(4;2;0.1\%)} = 199$).

Ingestion rate

For Stage NVI fed *Isochrysis galbana*, ingestion rate was 0.48 ± 0.25 µg C $µg^{-1}$ copepod C d^{-1}. Ingestion rates of CIII (Figure 3) varied among diets (ANOVA: $F_c = 10.72$; $F_{theo(4;9;0.005)} = 7.96$). Among the pure diets,

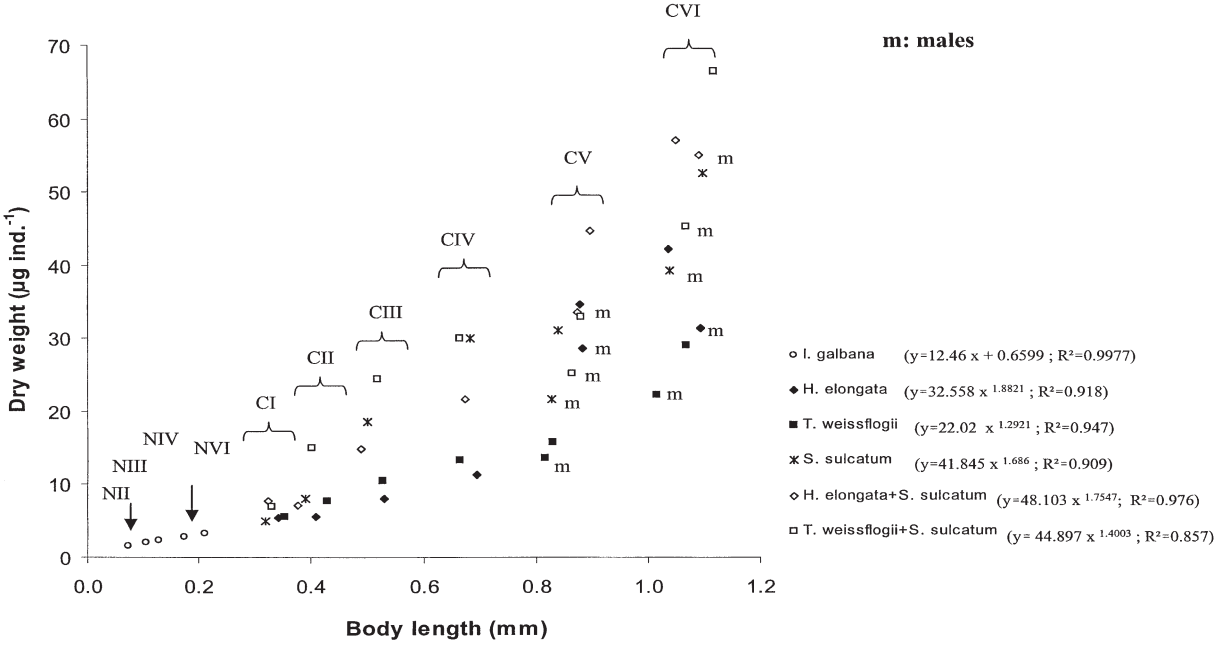

Fig. 2. *Centropages typicus.* Length-weight relationship of development stages of feed different diets

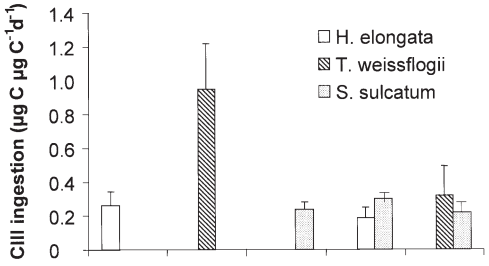

Fig. 3. *Centropages typicus.* Ingestion rates (µg C µg C^{-1} d^{-1}) of CIII stages fed different diets. Values are means ± SD

Thalassiosira weissflogii was ingested at the highest rate (Tukey's HSD: $p < 0.05$). For the mixed diets, a preliminary experiment showed negligible grazing impact of the ciliate *Strombidium sulcatum* on either *Hymenomonas elongata* or *T. weissflogii*. The total ingestion rates with the mixed diet were higher than the ingestion rates with each prey type offered alone, except for *T. weissflogii*. This means that CIII stages attained a higher ingestion rate in terms of carbon on mixed diets than when fed *H. elongata* or *S. sulcatum* alone, even though the concentrations offered were at saturation level.

Ingestion-dry weight ratios are presented in Table 7. The highest ingestion rate, 5.95 µg C ind.$^{-1}$ d^{-1} for *Thalassiosira weissflogii* + *Strombidium sulcatum* diet, was recorded for the heaviest individuals (9.80 µg C). Nevertheless, the highest ratio was displayed by copepods fed *T. weissflogii*. The ratio ingestion/dry weight varied strongly with the diet: ingestion of *T. weissflogii* represented 106% of the carbon weight for the CIII stage, whereas *Hymenomonas elongata* and *S. sulcatum* fed singly represented percentages lower than 30%. For *Isochrysis galbana* in the NVI stage, the value was 48.5%.

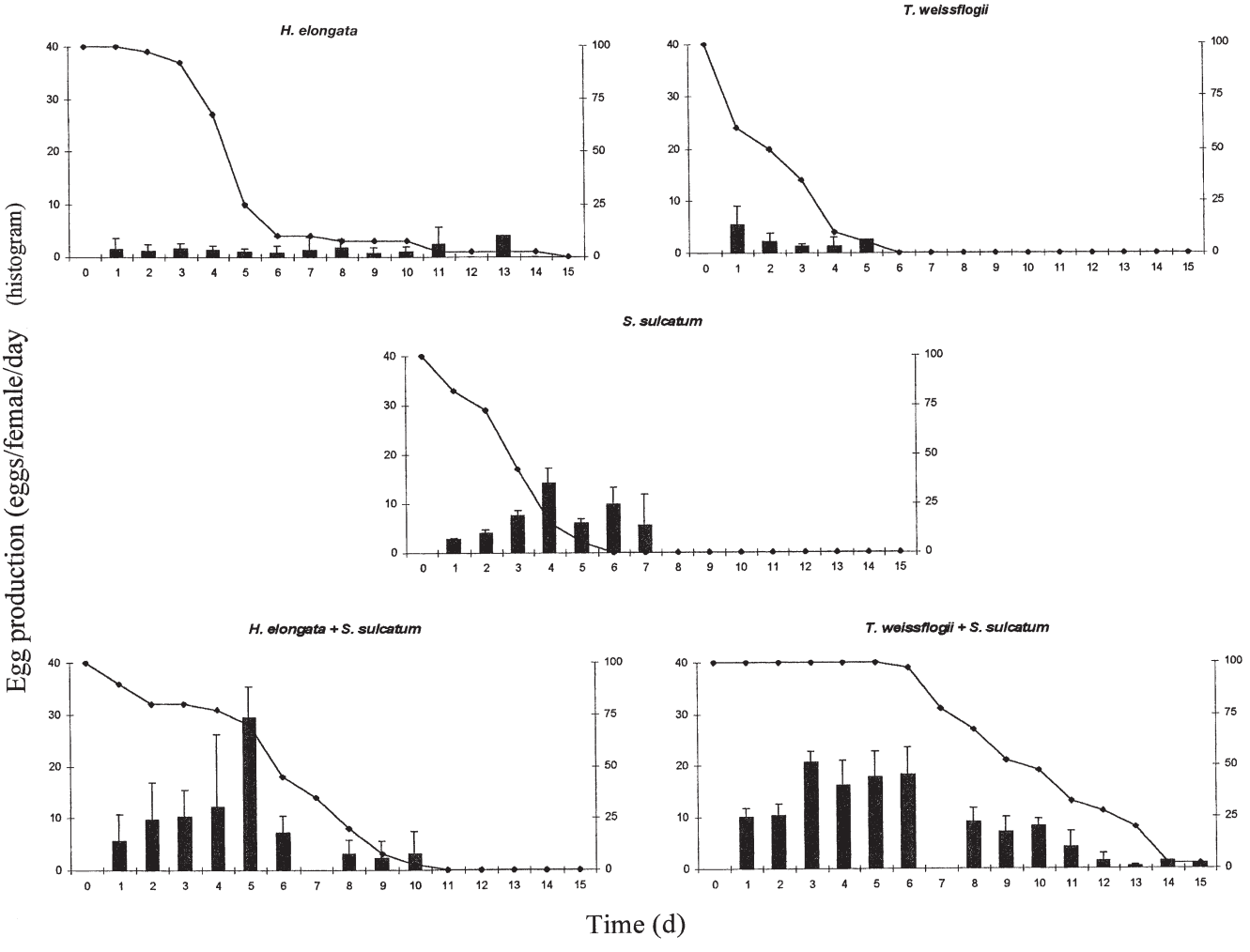

Fig. 4. *Centropages typicus.* Egg production rate and survival in the different cohorts (means + SD)

Female survival, egg production and hatching success

Maximum egg production rate was observed from Days 3 to 5 for females in the cohorts reared on the algal plus ciliate diets, and corresponded to the point at which females began dying (Fig. 4). The rates increased by 3- to 7-fold over those of cohorts fed algae alone. There were no obvious trends over time in egg production rates for cohorts reared on pure algal diets. The rate was significantly dependent on the diet offered (ANOVA: $F_c = 5.81$; $F_{theo(4;40;0.001)} = 4.37$).

When ciliates were included in the diet, female survival increased above those on pure algal or ciliate diets. The highest survival rates (in terms of longevity and percentage of females) were obtained for females reared on mixed (algae plus ciliate) diets. Indeed, 50% of the females died after 2 and 4.5 d on *Thalassiosira weissflogii* and *Hymenomonas elongata* diets respectively and after 5.85 and 9.5 d for *T. weissflogii* + *Strombidium sulcatum* and *H. elongata* + *S. sulcatum* diets.

On the fifth day, maximum egg production rate, which was on average 29 eggs female^{-1} d^{-1}, was reached by females grazing on *Hymenomonas elongata* + *Strombidium sulcatum*. Maximum fecundy (total number of eggs produced by a female during the observation time) was low on pure algal diets (<20 eggs female^{-1}) (Tukey's HSD: $p < 0.05$), but reached 50, 82 and 125 eggs female^{-1} on *S. sulcatum*, *H. elongata* + *S. sulcatum* and *Thalassiosira weissflogii* + *S. sulcatum* diets, respectively (Tukey's HSD: $p < 0.05$).

No significant difference was observed between the hatching success of eggs from the different cultures (ANOVA: $F_c = 2.23$; $F_{theo(4;39;0.05)} = 2.61$). For the ciliate diet, egg hatching success was 100% in ≤3 d regardless of female age (Fig. 5). For the other diets, hatching success ranged from 50 to 100% for *Hymenomonas elongata* diet, 40 to 100% for *Thalassiosira weissflogii* alone, 90 to 100% for *H. elongata* + *Strombidium sulcatum* and 15 to 100% for *T. weissflogii* + *S. sulcatum*. Time to 50% hatching was also very variable, and in general was longer than 2 d. There were no overall trends in the relationship between hatching success and diet or female survival.

Faecal pellet production

Faecal pellet production was not correlated with egg production for any food source nor with females' age (Fig. 6). No significant difference was noted between faecal pellet production of copepods on different diets (ANOVA: $F_c = 1.15$; $F_{theo\ (4;45;0.05)} = 2.58$). Nevertheless, the highest average faecal pellet production was observed for the diet containing *Thalassiosira weissflogii* mixed with *Strombidium sulcatum* (~23 pellets ind.$^{-1}$ d^{-1}), whereas highest peak faecal pellet production was found for the *Hymenomonas elongata* + *S. sulcatum* diet (~30 pellets ind.$^{-1}$ d^{-1}).

Table 7. *Centropages typicus.* Weight-specific ingestion (%) in terms of carbon for Stages NVI and CIII fed different diets. Ingestion results are from cell counts

Stage	Diet (replicates)	Ingestion I (µg C ind.$^{-1}$ d^{-1})	Dry wt P (µg C)	I/P (%)
NVI	*Isochrysis galbana* (8)	0.64 ± 0.34	1.32 ± 0.47	48.5
CIII	*Hymenomonas elongata* (3)	0.94 ± 0.29	3.23 ± 1.06	29.1
CIII	*Thalassiosira weissflogii* (3)	4.50 ± 1.25	4.23 ± 1.71	106.4
CIII	*S. sulcatum* (3)	1.95 ± 0.24	7.43 ± 2.23	26.2
CIII	*H. elongata* + *S. sulcatum* (3)	3.25 ± 0.59	5.94 ± 1.84	54.7
CIII	*T. weissflogii* + *S. sulcatum* (3)	5.95 ± 2.39	9.80 ± 3.69	60.7

DISCUSSION

Stage duration

Stage durations of *Centropages typicus* in this study ranged from 31.79 to 44.63% for nauplii and from 55.37 to 68.21% for copepodids. Landry (1983) explained the long duration of the first feeding stage by the need to recuperate weight loss during the non-feeding instars, and the duration of the CV instar by physiological changes in preparation for maturity.

The total development time varied from 25.9 to 36.4 d depending on diet (Table 4). These values are consistent (within any one diet) with development times of *Centropages typicus* at 15°C obtained for cultures by others authors: 25.82 d at 16000 cells ml^{-1} of *Hymenomonas elongata* (Carlotti & Nival 1992), 33.0 d at 4600 cells ml^{-1} of *Thalassiosira weissflogii* (Smith & Lane 1987). In our mixed diets, *T. weissflogii* supplemented by the ciliate *Strombidium sulcatum* decreased the development time of the copepods compared to the pure *T. weissflogi* diet, but this was not the case for *H. elongata*, which proved to be a good diet for development without ciliate addition.

Mortality rates

Diet did not significantly affect copepodid mortality rates (ANOVA: Table 4). The values obtained herein comprised the mortality rate of organisms plus the loss to daily sampling which varied with volume sampled (1% d^{-1} at the beginning of the experiment, rising to

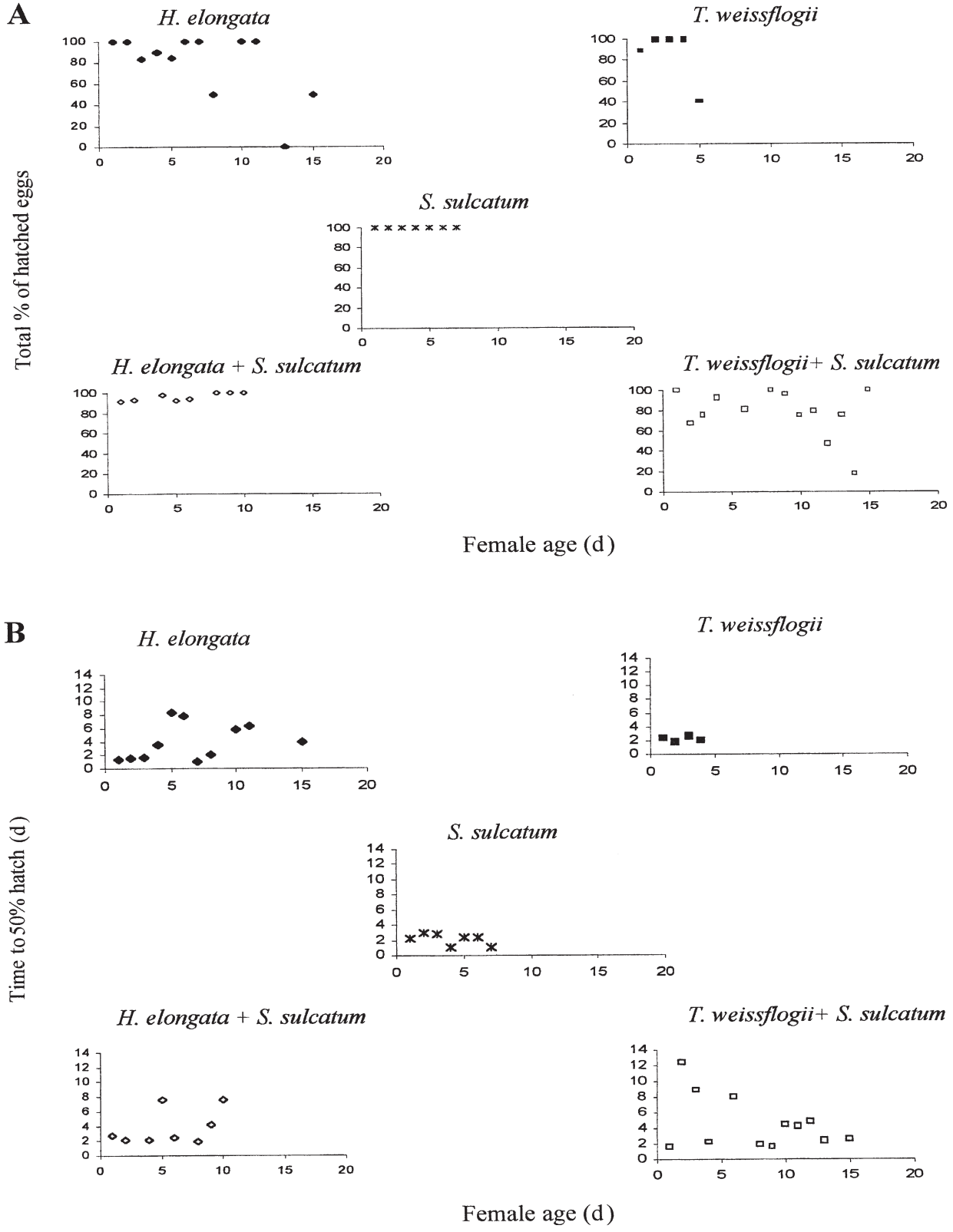

Fig. 5. *Centropages typicus.* Total percentage of (A) hatched eggs and (B) time to 50% hatch, as a function of age of reproductive females and their diet

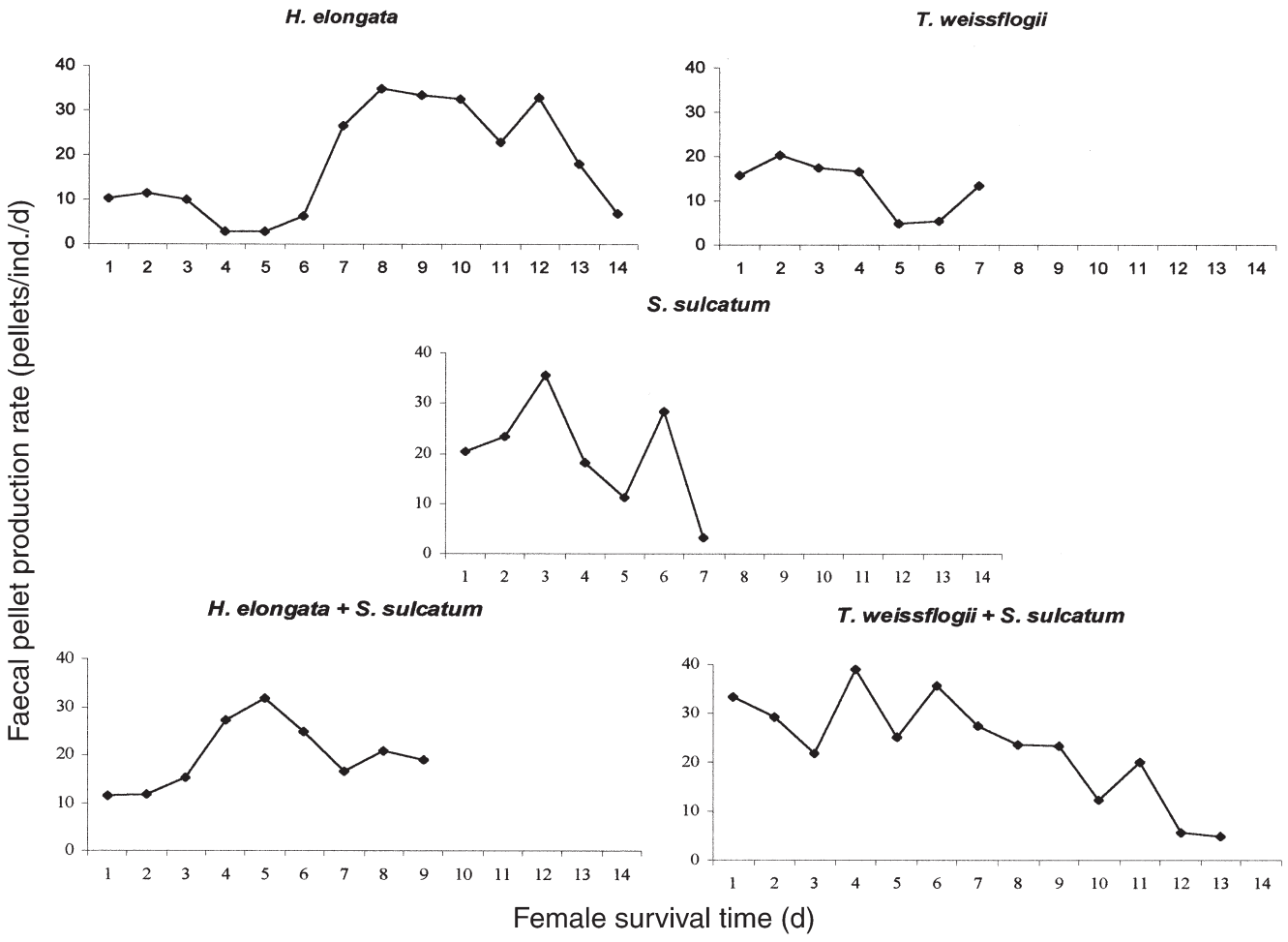

Fig. 6. *Centropages typicus.* Faecal pellet production rate as a function of female survival time (d) for the different diets

4 % d^{-1} at the end of the experiment). These values are in the range of mortality rates obtained for small copepods such as *Pseudocalanus newmani* by Ohman & Wood (1995, see their Fig. 3).

Female longevity

Survival of females reared on *Thalassiosira weissflogii* was particularly short (~2 d), in agreement with observations by Ianora & Poulet (1993) of wild female *Temora stylifera*: longevity was, on average, lower when *T. stylifera* were reared on the diatom *T. rotula* than on the dinoflagellate *Prorocentrum minimum*. The lifespan of female *Centropages typicus* fed *Hymenomonas elongata* was longer in the study of Carlotti et al. (1997) than in the present study. They report 50 % female mortality at 15 and 20°C after 22.25 and 15.5 d, respectively. The explanation for this difference may be methodological, since the females chosen for our experiments were not freshly moulted females, but females taken from mesocosms in which 50 % of the population had reached the adult stage (i.e. 5 d after the appearance of first females). The results of the present study must therefore be considered to represent minimum values for longevity.

Sex ratio

Many studies have related sex ratio to various factors such as temperature, season and population density (Mauchline 1998). The impact of food quality on the sex ratio of copepod cohorts raised in the laboratory has been considered, but without reaching any clear conclusion. Results from a laboratory culture of *Calanus helgolandicus* suggested that both food concentration and phytoplankton species composition may be important in sex determination (Paffenhöffer 1970), but in a study by Arnott et al. (1986), neither food concentration

nor food quality had an effect on the sex ratio of the calanoid copepod *Gladioferens pectinatus*. Our results show that *Centropages typicus* reared on *Thalassiosira weissflogii* skewed towards males; this is consistent with the rapid decrease of females in the egg production experiments with this diet (see Fig. 4). For the other diets, the sex ratio was close to 1.

Dry weight and length

Length and weight of *Centropages typicus* have been reported to be dependent on temperature and food concentration (see Mauchline 1998 for review). As far as we know, our study is the first to consider the effect of food quality on size, weight and development time of *C. typicus* simultaneously.

Our results highlight 3 major points: (1) A significant impact of diet on weight, for each stage, the highest weights being 2 to 3 times higher than the lowest ones. Comparable weight differences within *Centropages typicus* adults have already been shown by Smith & Lane (1985, their Table 2) in their laboratory study on egg production and development. (2) A significant (ANOVA) impact of diet on stage length for all instars except CIV and CVI. The correlation between body length and diet in a limited number of instars supports this hypothesis, since it suggests that the food offered was more suitable for some stages than for others. For example, algal diets induced the highest lengths for CI, CII and CIII stages, whereas mixed diets led to longer CV males and females (Fig. 2). (3) No significant difference between the length-weight relationships established for each food source (Fig. 2). The reason why length-weight relationships do not appear to be correlated with food quality may be changes in food requirements as individuals develop from copepodids to adults. There was a large difference in dry weights within the same stage for the different diets as well as a strong overlapping of weight ranges of successive stages. For example, the difference in CIII weight between individuals fed *Thalassiosira weissflogii* and those fed different diets suggests that food quality affects growth rate (weight and length) more than development rate (stage duration). In a study of the effect of food quality on the development of *Calanus helgolandicus* nauplii, Rey et al. (2001) reported that the food source which results in the shortest development time is not the food source which achieves the highest weights. This result is supported by the present study, in which single diets of the algae *Hymenomonas elongata* and *T. weissflogii* both led to the lowest adult weights (Table 4; Fig. 2). Conversely, mixed diets induced the highest weights, and *Strombidium sulcatum* alone produced intermediate values.

Ingestion rate

Centropages typicus has been shown to feed well on both algae (Smith & Lane 1985, 1987, Guerrero et al. 1997, Bonnet 1998, Caparroy 1998), and on the ciliate *Strombidium sulcatum* (Wiadnyana & Rassoulzadegan 1989, Caparroy et al. 1998).

The specific ingestion rates of adult females fed an optimal concentration of *Hymenomonas elongata* (Bonnet 1998) and fed *Strombidium sulcatum* (Caparroy 1998) were both 0.4 d^{-1}, a rate reported in other studies on *Centropages typicus* (see Mauchline 1998). In comparison, the specific ingestion rates of CIII fed the same food types (see Fig. 3) in the present study were around 0.27 d^{-1}. Specific ingestion rates are usually presumed to decrease with increasing weight, and thus with increasing stage (Paffenhöfer 1971); this was not the case in our study. We therefore presume that our CIII stage was not fed at optimum concentrations. The specific ingestion rate of CIII on *Thalassiosira weissflogii* (0.95 d^{-1}) does seem a realistic value, comparable to those obtained for the CIII stage of calanoid copepods (Mauchline 1998).

Kleppel (1993) showed that requirements vary, with food nutritional requirements changing ontogenetically through the copepodid to adult stages. Copepodite stages devote all resources to growth, whereas adults place greater priority on reproduction. Jónasdóttir et al. (1995) and Müller-Navarra (1995a) suggested that the polyunsaturated fatty acids, eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), are essential compounds, which can limit zooplankton productivity. In general, EPA occurs in significant amounts in diatoms, whereas DHA is abundant in dinoflagellates (Klein Breteler et al. 1999). Indeed, sterol availability influences survival and egg production. Copepods rely on dietary sterols to meet their metabolic requirements, since they lack biosynthetic capacity to synthesize sterols; this could explain the high ingestion rate of CIII fed *T. weissflogii* in our study.

Prey characteristics

Prey size also influences ingestion rate (Berggreen et al. 1988, Hansen et al. 1994). Hansen et al. (1994) calculated that the predator/prey size ratio for optimal selectivity is 18 ± 4 for nauplii and 18 ± 3 for copepodites.

Applying these ratios to the nauplii and copepodite sizes in our experiments results in optimum selectivities of particles between 5.8 and 15.4 µm and between 18.5 and 60.8 µm, respectively. The size of *Isochrysis galbana* (see Table 2) its within the opti-

mum range for nauplii. The sizes of *Thalassiosira weissflogii* and *Hymenomonas elongata* are below the optimal range of copepodid and adult selectivity. Thus we conclude that only the largest cells in our cultures were available as food. This could explain why the optimal threshold lay at cell concentrations (and biomass concentrations ≥800 µg C l^{-1}) much higher than the highest phytoplankton concentrations (in terms of carbon) observed *in situ*. Because of the large range of size changes in copepod stages, the size of prey offered is a major problem. Based on the Hansen et al. (1994) ratio, *S. sulcatum* is slightly too large for the copepodites; however, *S. sulcatum* is known to be successfully caught through ambush capture by *Centropages typicus* (Caparroy et al. 1998). Development times were not shorter when *S. sulcatum* was offered alone. However, compared with pure algal diets, mixed diets produced the highest final weights and sizes, probably because of the large prey spectrum available during development.

Selectivity could also involve cell carbon, nitrogen and protein composition. Cowles et al. (1988) have shown that copepods maximize the ingestion of nitrogen. In the present study, the 2 algae offered are of almost the same size (*Hymenomonas elongata* ~13 µm; *Thalassiosira weissflogii* ~12 µm); however *T. weissflogii* contains 1.68 times more nitrogen per cell than *H. elongata*. This could explain the high grazing rates on *T. weissflogii*, even though the copepods did not grow faster on this diet. The high N content and ingestion rate of *T. weissflogii* suggest that N was not a limiting nutrient for development and growth. The C/N ratio demand of an animal depends on its own C/N ratio (Urabe & Watanabe 1992); however, in her *in situ* study on *Centropages typicus*, Razouls (1977) showed that C/N ratios remained constant throughout the different stages, including the adult stages.

No correlation could be found in the present study between the C/N ratio of the food offered and the rate of copepod development. For instance, whereas the C/N ratios of both *Hymenomonas elongata* and *Thalassiosira weissflogii* were higher than that of *Strombidium sulcatum*, development time on the *S. sulcatum* diet lay between those of the 2 algal treatments. Therefore, the C/N ratio does not appear to be an adequate indicator of the effect of food quality on development. Indeed, the C/N ratio cannot be used to define the quality of a food source without first knowing the availability to and the efficiency of assimilation of carbon and nitrogen compounds by the copepods (Tang & Dam 1999). Furthermore, recent studies have shown that growth and egg production in crustaceans are more dependent on dietary polyunsaturated fatty acids than on the elemental composition of the food (Jónasdóttir et al. 1995, Müller-Navarra 1995a,b).

Egg production

The effects of microzooplankton food on the fecundity of copepods have rarely been examined apart from the studies of Williamson & Butler (1986) and Stoecker & Egloff (1987). Stoecker & Egloff have shown that inclusion of tintinnids in the diet of *Acartia tonsa* can increase egg production by ~25% compared with a pure algal diet. In our study, addition of *Strombidium sulcatum* to the algal diet of *Centropages typicus* resulted in an increase in the egg production rate by 3- to 7-fold, indicating a high food quality of the ciliate (Durbin et al. 1983, Stoecker & Egloff 1987). Kleppel (1992) strongly suggested that the link between feeding and egg production may be what is eaten rather than how much. Heinle et al. (1977) pointed out that copepods, although showing some selectivity in grazing, tend to feed on a rather wide variety of food and proposed that protozoans are an important food source in the copepod diet as they enhance egg production. Dam et al. (1994) showed that heterotrophic feeding was responsible for 50% of *in situ Acartia tonsa* egg production in Long Island Sound. Klein Breteler et al. (1999) showed that *Temora longicornis* and *Pseudocalanus elongatus* could not be raised on a diet of the chlorophycean *Dunaliella* sp., which contained all essential amino acids but was deficient in highly unsaturated fatty acids and sterols. However, when the heterotrophic dinoflagellate *Oxyrrhis marina* grown on *Dunaliella* sp. was fed to *T. longicornis* and *P. elongatus*, both copepod species rapidly developed to maturity (Klein Breteler et al. 1999). Microzooplankton (ciliates and heterotrophic dinoflagellates) generally have a lower C/N ratio than phytoplankton, and may contain other chemical constituents such as proteins, amino acids and fatty acids essential for copepod egg production (Stoecker & Capuzzo 1990).

Nevertheless, Ederington et al. (1995) showed that *Acartia tonsa* egg production was 10-fold lower for ciliate-fed copepods than for diatom-fed copepods. The ciliate *Pleuronema* sp. did not contain a measurable amount of the polyunsaturated fatty acids 20:5 or 22:6, which have been suggested to be essential to the growth and development of marine animals (Enright et al. 1986), whereas the diatom *Thalassiosira weissflogii* did. Therefore, in our study, the high egg production on the ciliate (*Strombidium sulcatum*) diet may have been achieved because this ciliate contains at least some fatty acids and sterols, or because the copepod *Centropages typicus* converted them at low rates from other lipids. A few studies have also reported a negative impact of diatoms on egg production and hatching success (Poulet et al. 1994, Miralto et al. 1999), which could explain the low egg production with the *T. weissflogii* diet in our study.

Hatching success

Our study did not reveal any strong correlation between diet or female age and hatching success. Previous work has shown that hatching success is mainly related to temperature (Smith & Lane 1985) or female fecundity (Guisande & Harris 1995); but the effects of food quantity and quality are less clear (Smith & Lane 1985, Ianora et al. 1995, Miralto et al. 1995, Guerrero et al. 1997).

Hatching success in our study was lower than other published values. For example, Guerrero et al. (1997) found a 90 ± 8% hatching success after 72 h for *Centropages typicus* feeding on *Hymenomonas elongata*. Smith & Lane (1987) reported that 12% of eggs from *C. typicus* raised on *Thalassiosira weissflogii* did not hatch after more than 72 h. They did not give any explanation for this observation, but their *in situ* data did not support the hypothesis of the production of resting eggs. Production of resting eggs has been reported for *C. typicus* (Lindley 1990) and for most of the Centropagidae (reviews: Uye 1985, Marcus & Lutz 1998). Carlotti et al. (1997) described 2 kinds of eggs produced by *C. typicus*, with or without spines, specifying that the latter never hatched and that some of the eggs with spines also could not hatch. In their experiments (their Fig. 2), more than 61% of eggs did not hatch, suggesting that resting eggs are produced. The low hatching success in our study could be due to the production of resting eggs.

Ban (1992) suggested that conditions under which nauplii develop determine whether the resultant adults produce diapause eggs. Further studies have discussed the contentious issue of whether delays in hatching rates are due to food quality (Ianora et al. 1995, Jónasdóttir & Kiørboe 1996, Tang et al. 1998). Tang et al. (1998) showed that copepod eggs can delay hatching for up to 11 d (mainly in response to a decrease in temperature), without necessarily being 'resting eggs'. Nevertheless, in our laboratory study, because of the similarity in hatching success and in hatching time between the different diets, and because 15.5% of the egg production had a total hatching success of <75%, and 64.3% of the eggs required >3 d to hatch, whatever the diet, we believe that the low hatching success and long hatching time in our study resulted from the production of resting eggs rather than from any effect of food quality.

Concluding remarks

Using mainly experimental results on adults, the most recent compilation of data on zooplankton nutrition (Reports of GLOBEC Process Studies Working Group, Roscoff, France) has underlined the importance of food quality to various zooplanktonic species. The present study highlights the need to examine the effect of food quality on the complete life cycle (i.e. the responses of different stages), since this cannot be generalised from adult data alone. To our knowledge, this study is one of the most complete to date, examining both growth and development simultaneously under different food conditions. Three major aspects should be borne in mind in future studies: (1) Weight-length relationships should be viewed with caution, since high variability in weight has been observed within the same stage of development dependant on food source. (2) Although mixed algae-ciliate diets seem to be the best food source for egg production, female survival and individual weight, the best results for growth, survival, ingestion, egg production rates, etc. were not always obtained for one and the same diet. (3) Optimal food concentration should not only be defined from ingestion rate, growth (weight), and development as in our study, but also using new approaches such as the RNA/DNA ratio, enzyme activities, etc. Since copepods change in size and behaviour during development, an approach based on determining optimal food concentrations for each development stage should be used.

Acknowledgements. The research work was supported by the Programme Réseau Diversité Marine (1998–2000) and the programme PNEC-ART2 (1998–1999) granted to F.C. D.B. was supported by the European project MTPII-MATER financed within the framework of the European Commission's MAST RTD programme under contract MAS3-CT96-0051 granted to F.C. We greatly appreciate the technical help of Vanessa Briano, and are grateful to Dr M. Koski, Dr R. P. Harris, Dr G. Tarling and S. Nival as well as the referees for their constructive comments on the manuscript.

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Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

Submitted: September 1, 2000; Accepted: April 5, 2001
Proofs received from author(s): November 30, 2001