

Seasonal cycles of egg production of two planktonic copepods, *Centropages typicus* and *Temora stylifera*, in the north-western Mediterranean Sea

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Reproduction of the dominant copepods Centropages typicus and Temora stylifera was studied at a permanent station in the Ligurian Sea (north-western Mediterranean). Seasonal patterns of egg production, clutch size, egg size and female prosome length were followed from January 1998 to December 1999. Female carbon content and weight-specific egg production were compared in autumn 1998 and spring 1999. Reproductive patterns of C. typicus and T. stylifera were very similar, indicating that reproduction was affected by the same environmental factors. Reproductive activity was highest in autumn in both species and years. A second peak of egg production was observed in early summer, which was less intense in 1999 after a bloom of salps. Egg production rates reached maximal values of 33.5 and 33.3 eggs female⁻¹ day⁻¹ and annual means of 10.8 and 11.7 eggs female⁻¹ day⁻¹ in Centropages and Temora, respectively. Maximal weight-specific egg production was 0.21 day⁻¹ in both species in November 1998, when female carbon contents were 6.7 (C. typicus) and 12.0 µg (T. stylifera). No statistical relationship between egg production and food availability or temperature was detected. Reproductive activity did not reflect the seasonal abundance patterns, with C. typicus dominating in spring and T. stylifera in autumn.

INTRODUCTION

The reproductive biology of copepods plays a key role in seasonal population oscillations and therefore determines, among other things, annual production (Kjørboe *et al.*, 1988; Franz *et al.*, 1989; Ianora and Buttino, 1990; Ianora *et al.*, 1992; Halsband and Hirche, 2001). Reproduction is affected by various environmental factors, basically by temperature and food availability (Dagg, 1978; Landry, 1978; Uye, 1981; Abou Debs and Nival, 1983; Smith and Lane, 1985; Huntley and Lopez, 1992; Hirche *et al.*, 1997; Saiz *et al.*, 1999). The interactions of these partly opposing factors are difficult to understand. Food can be limiting either quantitatively or qualitatively in terms of cell size, nutrient content, etc. (Runge, 1984; Beckman and Peterson, 1986; Kjørboe *et al.*, 1988; Jónasdóttir, 1994). Moreover, food availability is difficult to define in complex natural environments (Jónasdóttir *et al.*, 1995; Saiz *et al.*, 1999). Temperature has direct and indirect effects on egg

production. On the one hand, spawning intervals become shorter with increasing temperature (Runge, 1984), since physiological processes like maturation of oocytes are faster (Razouls, 1975; Hirche *et al.*, 1997). On the other hand, temperature is inversely correlated with body size and thus affects the reproductive potential of females, especially in populations with several successive generations and a wide range of *in situ* temperatures (Landry, 1978; Ambler, 1985; Kjørboe *et al.*, 1988; Hirche, 1992; Ban, 1994; Halsband and Hirche, 2001).

While in more boreal waters a few studies on seasonal reproduction patterns of copepods are available (Kjørboe and Nielsen, 1994; Halsband and Hirche, 2001), knowledge is scarce for warm-temperate seas, which represent a large part of the world oceans. Although the Mediterranean can function as an exemplary representative of warm-temperate ecosystems [(Saiz *et al.*, 1999) and references therein], only few studies were conducted on annual cycles of egg production (Ianora and Buttino, 1990;

Ianora *et al.*, 1992). In the north-western Mediterranean, the calanoid copepods *Centropages typicus* and *Temora stylifera* dominate the zooplankton. They account for between 10 and 50% (*C. typicus*) and 5 and 25% (*T. stylifera*) of total copepod numbers (Seguin, 1981; Ianora *et al.*, 1989; Ianora and Buttino, 1990). The two species show different seasonal distribution patterns: *C. typicus* is a temperate species indigenous to the temperate Atlantic, the North Sea and the Mediterranean, while *T. stylifera* prefers the warm waters of the Mediterranean and further south (Rose, 1933). In the north-western Mediterranean, *C. typicus* generally peaks in April, preceding *T. stylifera*, which is most abundant from September to November (Gilat *et al.*, 1965; S. Nival, personal communication). Here we present complete annual cycles of *in situ* egg production of *C. typicus* and *T. stylifera* in relation to body size, food concentration and temperature in the Ligurian Sea. Such long-term observations in the field are necessary to detect how reproduction is controlled by temperature and food availability. Furthermore, the aim was to understand whether the seasonal succession of *Centropages* and *Temora* is reflected in changes in their seasonal reproductive activity.

METHOD

Sampling

Plankton were collected at sampling site 'Point B' (43°41'10"N; 7°19'00"E) at the entrance of the Bay of Villefranche-sur-Mer (France) in the north-western Mediterranean (Ligurian Sea; Figure 1). Water depths rapidly reach 100 m at the entrance of the bay and fall further down to 2000 m at the level of the geological structure called the 'canyon of Villefranche' (Nival and Corre,

1976; Étienne *et al.*, 1991). For this reason, conditions of the open sea can be found near the coast.

From November 1997 to December 1999, collection was conducted on 182 days in all months, except in August when sampling was interrupted in both years. Plankton were sampled by vertical tows from 80 m depth to the surface with a plankton net (type Superhomogène, 280 µm mesh size). The plankton were brought to the laboratory within 1 h and adult females were sorted for incubation in experiments.

During a period of high salp abundance (*Salpa fusiformis*) in March/April 1999, the net was clogged and copepods probably suffered from the sampling procedure. The animals found were rarely vigorous enough to be incubated; therefore, results for egg production from this period might be underestimated due to stressed animals.

Temperature (°C) and chlorophyll (Chl) *a* content (mg m⁻³) were measured once a week at 10, 20, 30, 50 and 75 m depth from water samples taken with a 5 l Niskin bottle [for details, see (Étienne *et al.*, 1991)]. The sampling was part of the programme 'Point B' of ESA 7076 (Courtesy of S. Dallot, Marine Station of Villefranche) and the results presented below in the subsections on hydrography belong to the service of observation 'Rade de Villefranche' and SOMLIT (web page: <http://www.obs-vlfr.fr/RADE>). For the statistical analysis, we used the mean temperature of the water column (since the values of different layers produced no better results) and the maximal Chl *a* values, which mostly occurred in 30 or 50 m depth.

Egg production

Egg production measurements were conducted in cold rooms at ambient seawater temperature with natural daylight provided through a window. To obtain representative values of egg production rates of small calanoid copepods, a high number of females must be incubated in order to cover the range of individual variability. In our study, we chose cell wells (Corning®) with volumes of 5 ml, because a high number of females could be processed in a short time. Five to 54 females, if available, were incubated individually for 24 h in cell wells filled with 3–5 ml of filtered sea water (0.45 µm). The wells were checked for eggs 2–3 times per day and eggs or nauplii were removed. Empty egg shells were included in the counts in order to account for cannibalized eggs eaten by the females. Control intervals were shorter than the spawning intervals to distinguish single clutches and avoid any egg loss due to cannibalism. It has been demonstrated that incubation in small volumes does not affect egg production (Schmidt *et al.*, 1998; Niehoff *et al.*, 1999; Harris *et al.*, 2000). Incubation in filtered sea water is discussed controversially in the literature. While Tester and Turner (Tester and

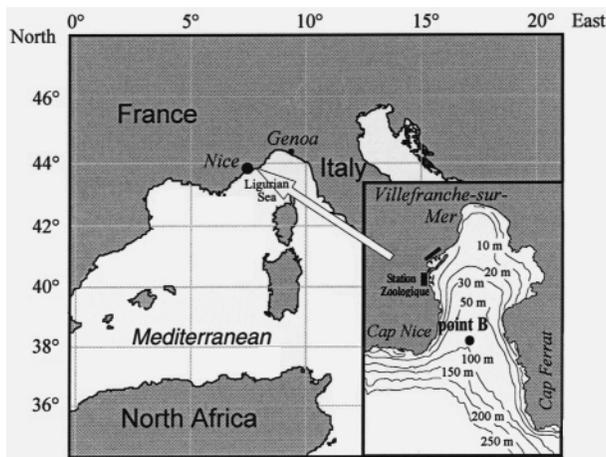


Fig. 1. The sampling station 'Point B' in the NW Mediterranean (43°41'10"N; 7°19'00"E).

Turner, 1990) showed that food conditions in short-term incubations had no effect on reproduction, Saiz *et al.* (Saiz *et al.*, 1997) found enhanced rates obtained from incubations in pre-screened *in situ* water and enriched food media compared to filtered sea water, especially at higher temperatures. However, since Laabir *et al.* (Laabir *et al.*, 1995) and Hirche *et al.* (Hirche *et al.*, 1997) confirmed that egg production rates for the first 24 h of incubation reflect the feeding history of the females in the field prior to capture, we think that our results are not greatly biased, but might only be slightly underestimated.

Egg production rates (EPR) were calculated as the mean number of eggs produced per female and day, including all incubated females. A corrected EPR (CEPR) was calculated, excluding all females that did not lay eggs within the incubation time (24 h). This rate was used for linear regressions and is mentioned in parentheses in the text (Table I).

Clutch size is given by the mean number of eggs per clutch calculated from all clutches of one experiment. The number of spawning females is given as the percentage of females that laid eggs during the incubation time of 24 h.

Eggs from *in situ* experiments were incubated in filtered sea water to determine embryonic development times. Hatching was controlled every 12–24 h over several days to determine hatching success.

Prosome length and egg size

After incubation, females and eggs were preserved in 4% buffered formalin. Prosome length (PL) and egg diameter were measured from preserved material using a video image digitizing system (Scion Image 1.6). PL measurements were available from January to July and October to December 1998, as well as from March to May and October to December 1999. From February to July 1998, 7–102 females were pooled monthly. Later on, 2–48 females were measured per incubation date.

For diameter measurements, 39–50 *C. typicus* eggs were pooled monthly in February, April and May 1998. From mid-November to mid-December 1998, as well as from the end of April to the end of May 1999, daily means are available with 13–55 eggs measured per date. Egg diameter of *T. stylifera* was measured in January, February and April 1998 from monthly pooled samples containing 26–50 eggs, and from October to December 1998 from daily samples with 28–56 eggs.

Carbon content

In November/December 1998 for both species and for *C. typicus* also in April/May 1999, occasionally 5–10 females from egg production experiments were frozen in silver caps for later analysis of carbon content. Individual body carbon was determined with the high-temperature

combustion method described by Salonen (Salonen, 1979) and Tanskanen (Tanskanen, 1994).

Egg carbon was estimated from egg diameters assuming a volume to carbon conversion of $0.14 \times 10^{-6} \mu\text{g C } \mu\text{m}^{-3}$ (Kiørboe *et al.*, 1985).

A weight-specific egg production rate (SEPR; day^{-1}) was calculated for the dates where body carbon data were available.

Statistics

Correlations between reproduction and environmental factors were tested by linear regressions. Correspondence of the reproduction parameters EPR, CEPR and clutch size of the investigated species was tested with a Spearman rank correlation test (since EPR was not normally distributed). Differences between the monthly means of egg diameters were tested with ANOVA analysis and Bonferroni–Dunn post hoc tests.

RESULTS

Hydrography

‘Point B’ is situated between Cap Ferrat and Cap of Nice (Figure 1). A cyclonic circulation in the Gulf of Genoa creates the Liguro–Provençal current, which strains along the coast from east to west before the Bay of Villefranche (Nival and Corre, 1976). The water column started to stratify at the end of April after a period of mixed water in winter. A distinct thermocline was established at 15–30 m depth in June and July. From August to October, the thermocline started to descend until the upper water layer was completely mixed in November and December. Surface temperature ranged from 13.5°C in winter to 25.8°C in summer during stratification. Deep-water layers below 50 m remained around 14°C all year round (Figure 2).

Temporal Chl *a* variations were nearly identical in both years. The subsurface Chl maximum occurred at 30–50 m depth (Figure 2). A single extraordinary peak was recorded in July 1998 with 3.78 mg m^{-3} at 30 m depth. In 1999, a weak phytoplankton bloom occurred in March 1999 with peak values of 1.22 mg Chl m^{-3} . This peak was followed by a bloom of salps causing a decline of Chl maxima down to 0.31 mg Chl m^{-3} at the end of April. The microplankton community showed three peaks in both years in May, August/September and November, respectively (F. Gomez, personal communication). Diatoms dominated in spring and autumn, whereas dinoflagellates were abundant in summer. Ciliates were distributed similarly to diatoms: abundant in July and from November to January with a major peak in November 1999.

Table I: Summary of reproduction parameters of *C. typicus* and *T. stylifera* from field studies

Max. EPR	Max. CEPR	Max. ind. EPR	Max. SEPR (day ⁻¹)	Max. mean clutch size	Max. ind. clutch size	Mean annual EPR	Mean PL (µm)	Mean fem. carbon (µgC)	Mean egg diameter (µm)	Mean egg carbon (µgC)	Season	Location	Reference
<i>C. typicus</i>													
33.5	40.3	83	0.21	30.5	72	10.8	1021	6.7	74.3	0.030	Whole year	Ligurian Sea (M)	This study
35.4		186		81.0	81	8.7	1110				Sep-Oct	German Bight (NS)	Halsband and Hirche (in press)
36.0							917-988	5.0	73.5		June	Catalan Sea (M)	Saiz <i>et al.</i> 1999
90.0	102.0	157				58.5					Aug-Sep	Kattegat (NS)	Kjørboe and Nielsen 1994
≈100.0											Whole year	Gulf of Naples (M)	Ianora <i>et al.</i> 1992
116.0		120	0.32								Whole year	Gulf of Naples (M)	Ianora and Buttino 1990
		163									August	Skagerrak (NS)	Petersen <i>et al.</i> 1991
230.0	180.0										Whole year	Gulf of Naples (M)	Ianora and Scotto di Carlo 1988
76.0			0.06								Spring	New York Bight (A)	Dagg 1978
8.0		29									Autumn	New York Bight (A)	Smith and Lane 1987
36.5			0.09		122						July	New York Bight (A)	Smith and Lane 1985
	49.0	106									August	Kosterfjorden (NS)	Tiselius <i>et al.</i> 1987
75.0											Spring	Gulf of Lion (M)	Razouls 1982
40.0/41.7		97/10					1028/1345					Gulf of Lion (M)	Razouls 1975
												Gulf of Lion (M)/ Channel (NS)	Le Ruyet-Person <i>et al.</i> 1975
<i>T. stylifera</i>													
33.3	65.0	92	0.21	48.0	64	11.7	969	12.0	77.7	0.034	Whole year	Ligurian Sea (M)	This study
12.5							977-1011	11.6	73.8		June	Catalan Sea (M)	Saiz <i>et al.</i> 1999
50.0											Whole year	Gulf of Naples (M)	Ianora <i>et al.</i> 1995
105.0						50.9					Whole year	Gulf of Naples (M)	Ianora and Poulet 1993
		140			45						Whole year	Gulf of Naples (M)	Ianora <i>et al.</i> 1989
	37.0	79			184				80.5	0.059	Laboratory	Ligurian Sea (M)	Abou Debs and Nival 1983
63.0												Gulf of Lion (M)	S. Razouls 1982
25.0		69									Autumn	Gulf of Lion (M)	S. Razouls 1975
							1003					Gulf of Lion (M)	Le Ruyet-Person <i>et al.</i> 1975

EPR = egg production rate; CEPR = corrected egg production rate; SEPR = weight-specific egg production rate; PL = prosome length; M = Mediterranean; A = Atlantic; NS = North Sea.

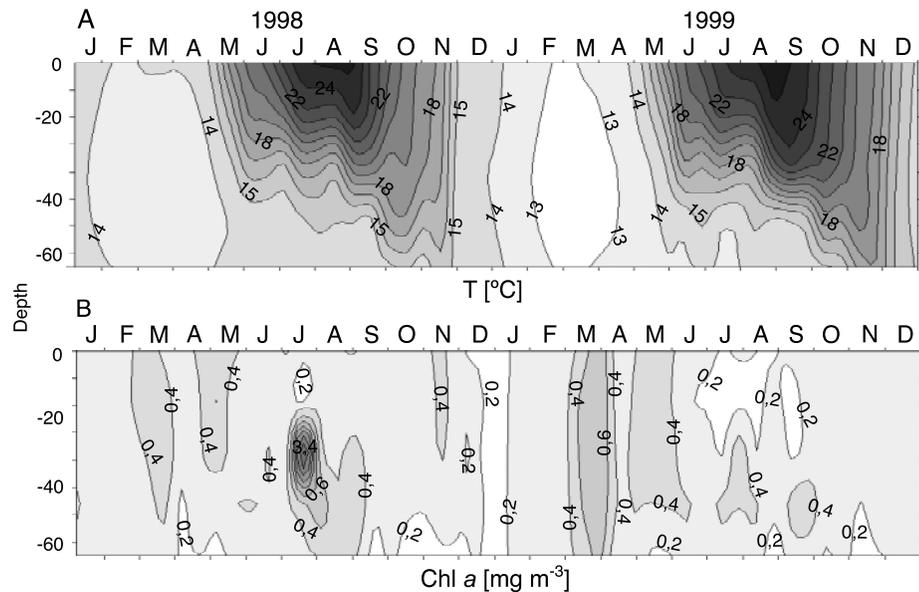


Fig. 2. Seasonal (A) temperature (°C) and (B) chlorophyll *a* (mg m⁻³) distribution at 'Point B' 1998 and 1999.

Seasonal cycles of egg production

Centropages typicus

The seasonal cycle of egg production of *C. typicus* is presented in Figure 3. In autumn 1997, *C. typicus* was rare, but reproduction rates were high, exceeding 20 eggs female⁻¹ day⁻¹. In contrast, reproductive activity was low in spring and summer 1998 with egg production rates ranging from <5 to 15 eggs female⁻¹ day⁻¹. In July 1998, reproduction became more important, increasing up to 26.0 (CEPR 32.9) eggs female⁻¹ day⁻¹. Clutches contained on average up to 28 eggs at that time. Females reached maximal egg production rates in December 1998 with 33.5 (CEPR 40.3) eggs female⁻¹ day⁻¹. The highest individual rate was 83 eggs female⁻¹ day⁻¹. Maximal mean clutch size was 30.5 eggs clutch⁻¹ with the biggest individual clutch containing 63 eggs. In spring 1999, egg production rates did not exceed 18 eggs female⁻¹ day⁻¹. During a massive occurrence of salps, egg production rates decreased down to nearly zero. In late spring, egg production recovered with rates around 20 eggs female⁻¹ day⁻¹. In autumn 1999, egg production reached a new peak with 30.5 (CEPR 36.0) eggs female⁻¹ day⁻¹ (Figure 3). The biggest clutches in 1999 contained on average 26.5 eggs with an individual maximum of 72 eggs clutch⁻¹ (Table I). The percentage of spawning females varied considerably (Figure 4); it was lowest in May with 25% (1998) and 29% (1999). The highest numbers of reproducing females were recorded in January (77%), October (88%) and

December 1998 (80%). In 1999, females were most reproductive in January (69%), July (78%) and October (74%). On an annual average, the number of spawning females was 55% in 1998 and 54% in 1999. Females usually produced 1 clutch day⁻¹, but 2–3 clutches day⁻¹ at times of high egg production. Annual mean egg production rates of *C. typicus* were 10.6 eggs female⁻¹ day⁻¹ in 1998 and 11.1 eggs female⁻¹ day⁻¹ in 1999; mean clutch sizes were 16.4 and 15.2 eggs clutch⁻¹, respectively. Hatching success was measured in June, November and December 1998, and from March to May 1999. In June 1998, mean hatching success was 83%; in November and December, 91 and 100% of all incubated eggs hatched, respectively. In spring 1999, mean hatching success decreased to 94% in March, 87% in April and 71% in May. On 18 May, only 6% of the incubated eggs were viable (Figure 5).

Individual female PL ranged from 850 to 1277 µm (Figure 6). The biggest females were found in January 1998 with a mean PL of 1160 µm, probably belonging to the population of the preceding year (they were therefore excluded from the regressions). The smallest females were recorded in July 1998 and at the end of May 1999 with minima of 894 and 890 µm, respectively. In autumn, mean PL increased up to 1064 and 1070 µm in December 1998 and 1999, respectively.

Females contained between 4.3 µg C (March 1999) and 10.0 µg C (November 1998), with a mean of 6.7 µg C (Figure 7). Individual egg diameters were in the range between 63.8 and 83.9 µm (Figure 8). Monthly and daily

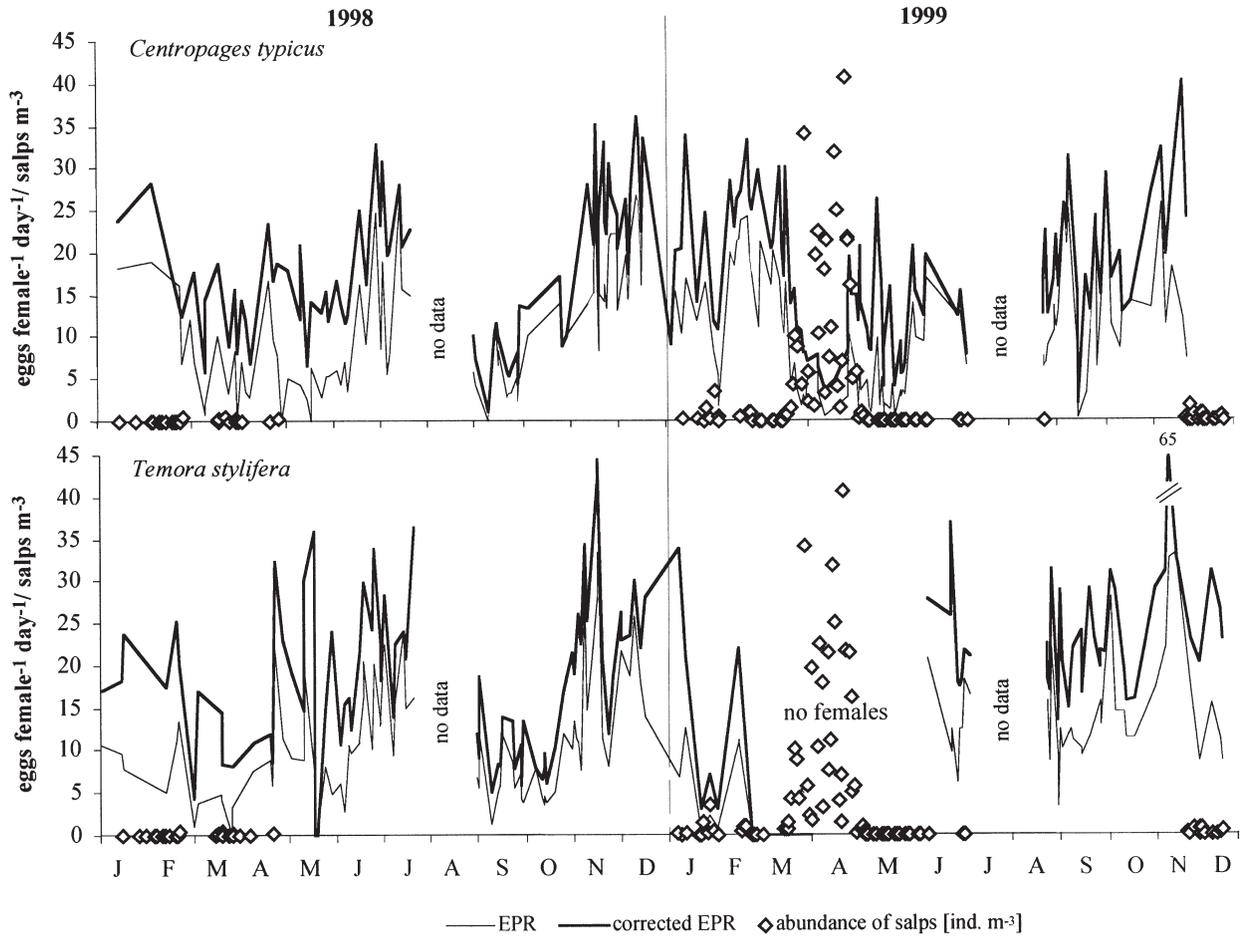


Fig. 3. Seasonal cycles of egg production rates (thin line) and corrected egg production rates (thick line) of *C. typicus* and *T. stylifera* and abundance (ind. m⁻³) of *Salpa fusiformis* (◇).

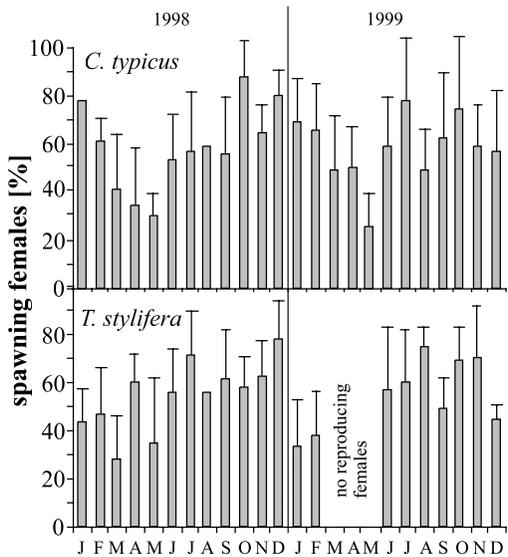


Fig. 4. Mean percentage of spawning females in 24 h incubations (vertical bars = standard deviation).

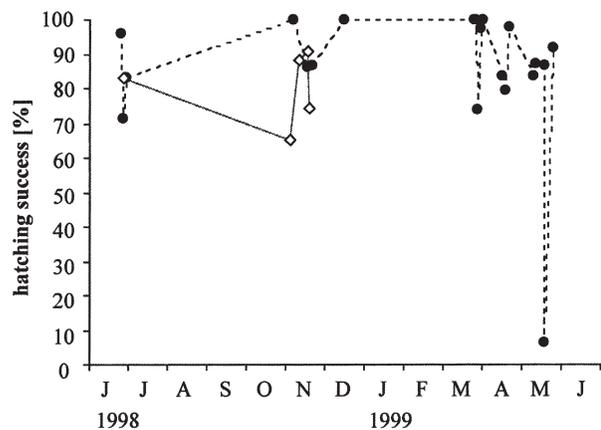


Fig. 5. Seasonal fluctuations in hatching success (%) of *C. typicus* (●) and *T. stylifera* (◇).

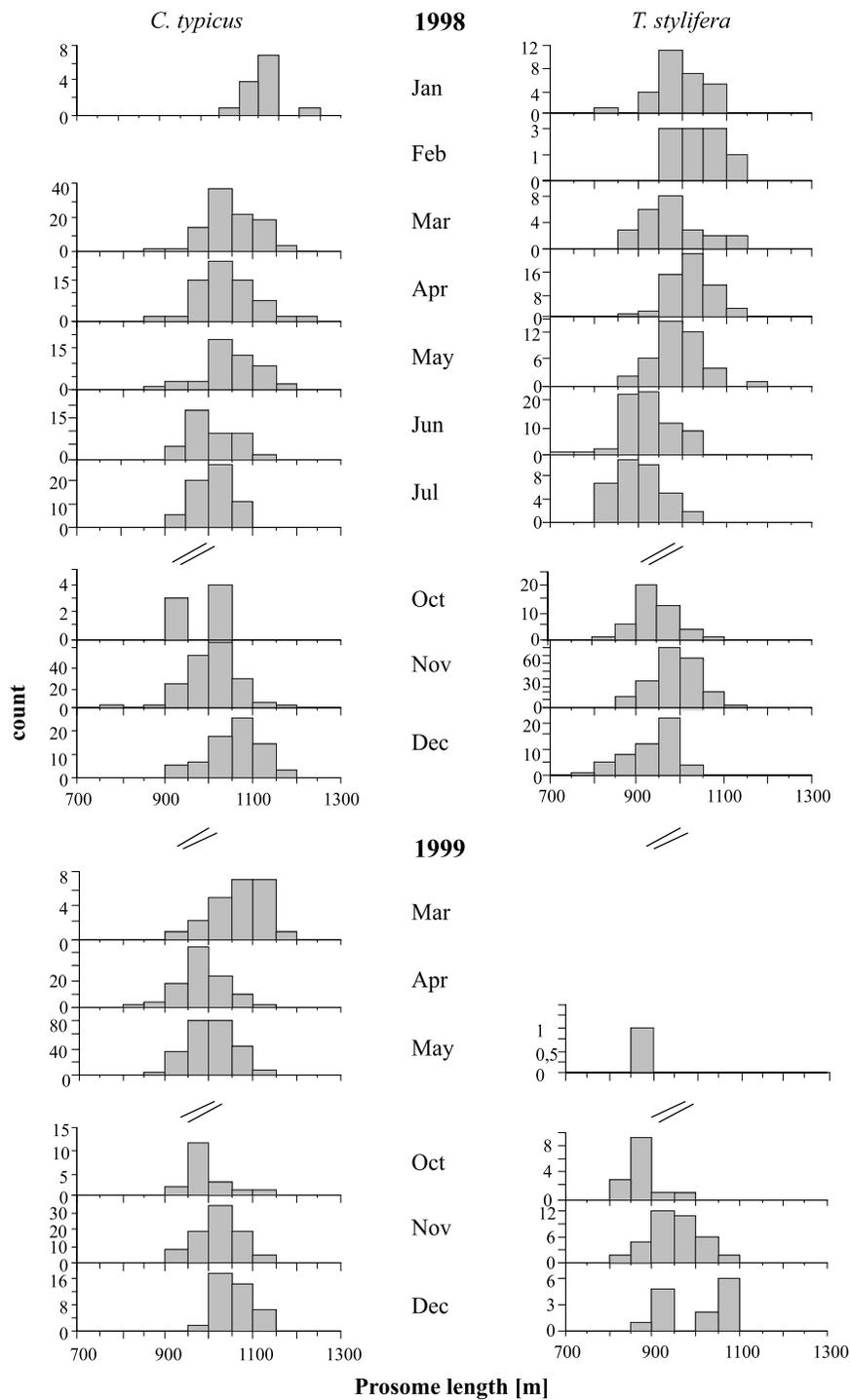


Fig. 6. Seasonal variation of size spectra of female prosome length.

means were relatively constant with an overall mean of 73.6 μm . In April 1999, they were significantly greater than in all other months observed (ANOVA, $P < 0.0001$). Moreover, we observed that the spines covering the egg shells were longer in autumn (up to 38 μm) than in spring

(5–18 μm). Estimated egg carbon ranged from 0.019 to 0.043 $\mu\text{g C egg}^{-1}$, the monthly means varied between 0.027 and 0.034 $\mu\text{g C egg}^{-1}$.

Individual weight-specific egg production rates ranged from 0.01 to 0.21 day^{-1} . Monthly means were 0.12

Table II: Determination coefficients (r^2) between egg production rate (EPR), corrected egg production rate (CEPR, including only spawning females), clutch size and weight specific egg production rate (SEPR) and prosome length (PL), temperature (T) and chlorophyll a (Chl a)

	<i>Centropages typicus</i>	<i>Temora stylifera</i>
EPR <i>C.typicus/T. stylifera</i>		***
CEPR <i>C.typicus/T. stylifera</i>		***
Clutch size <i>C.typicus/T. stylifera</i>		***
CEPR/female carbon	$r^2 = 0.48^*$	n.s.
SEPR/female carbon	$r^2 = 0.71^{**}$	n.s.
Egg carbon/female carbon	n.s.	n.s.
PL/T	n.s.	n.s.
CEPR/T	n.s.	n.s.
SEPR/T	n.s.	n.s.
Clutch size/T	n.s.	n.s.
CEPR/PL	n.s.	n.s.
SEPR/PL	$r^2 = 0.50^{**}$	n.s.
Clutch size/PL	$r^2 = 0.31^*$	n.s.
PL/Chl a	n.s.	n.s.
CEPR/Chl a	n.s.	n.s.
SEPR/Chl a	n.s.	n.s.
Clutch size/Chl a	n.s.	n.s.

EPR, CEPR and clutch size of *C. typicus* and *T. stylifera* were compared with a Spearman rank correlation
 Significance levels: * $P < 0.01$; ** $P < 0.001$; *** $P < 0.0001$; n.s.=not significant.

(November 1998), 0.09 (December 1998), 0.04 (March 1999), 0.06 (April 1999) and 0.08 day⁻¹ (May 1999).

Temora stylifera

Annual patterns of egg production rates were similar for *T. stylifera* (Figure 3). Egg production was decreasing from November 1997 to April 1998. In June and July 1998, between 9.6 (CEPR 12.0) and 24.0 (CEPR 36.5) eggs female⁻¹ day⁻¹ were produced; clutch size peaked at 29.2 eggs clutch⁻¹. After decreasing down to low rates in summer, egg production peaked again in November and December 1998. The maximal mean egg production rate was 33.3 (CEPR 44.4) eggs female⁻¹ day⁻¹, the most productive female produced 92 eggs day⁻¹. In winter 1998/99, egg production decreased and completely ceased in March when the salps appeared. Females

remained absent until May. In May and June, only few females were found and production rates were moderate. Egg production increased again in autumn 1999 and peaked in November with a mean of 33.0 eggs female⁻¹ day⁻¹ and an individual maximum of 65 eggs day⁻¹ (Figure 3; Table I).

The percentage of spawning females in 1998 ranged between 28% in March and 78% in December (Figure 4). In spring 1999, females produced no eggs in March and April, and in May no *Temora* female was found in the samples. The percentage of spawning females peaked in August and November with 75 and 70%, respectively (Figure 4). The mean number of spawning females was 56% in 1998 and only 50% in 1999. As in *Centropages*, females produced mostly one clutch per day, but up to 3 clutches day⁻¹ when reproductive activity was high. The

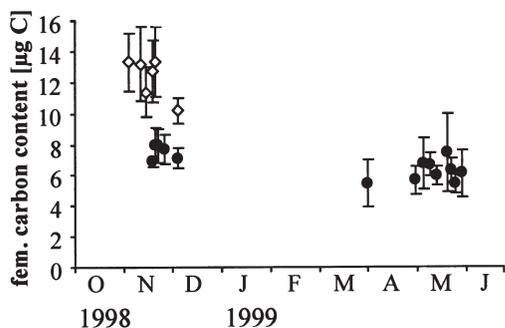


Fig. 7. Seasonal variation of female carbon content ($\mu\text{g C}$). Vertical bars indicate standard deviation. ●, *C. typicus*, ◇, *T. stylifera*.

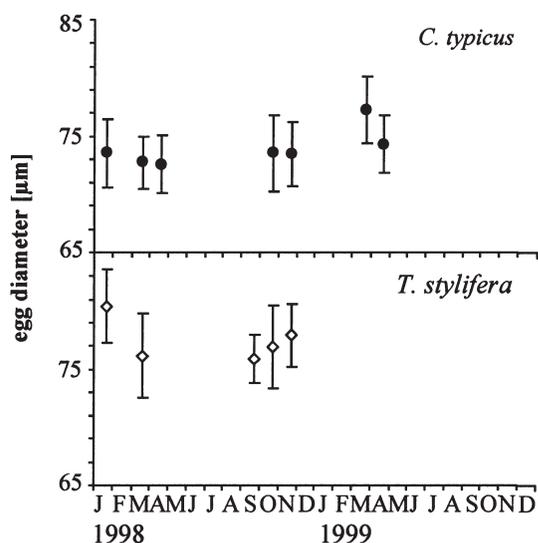


Fig. 8. Seasonal variation of egg diameters (μm). Vertical bars indicate standard deviation.

annual means of EPR were 11.1 (1998) and 12.2 eggs female⁻¹ day⁻¹ (1999). Mean annual clutch size was 16.5 eggs clutch⁻¹ (1998) and 20.6 eggs clutch⁻¹ (1999). Hatching success was 83% in June 1998 and ranged from 65 to 91% in November 1998 (Figure 5).

Individual PL varied between 747 and 1167 μm (Figure 6). The biggest females occurred in February and November 1998 with mean values of 1040 and 1013 μm , respectively, and in November 1999 with 1041 μm .

The carbon content of adult females was in the range 8.4–17.6 $\mu\text{g C female}^{-1}$ (Figure 7), with a mean of 12.4 $\mu\text{g C female}^{-1}$ (Table I). The eggs of *T. stylifera* were on average slightly bigger than those of *C. typicus*. Diameters ranged from 67.7 to 87.2 μm (Figure 8), with a mean of 77.4 μm . Two groups of eggs were distinguished statistically (ANOVA/Bonferroni–Dunn post hoc test, $P < 0.0001$): eggs were bigger in January and February 1998

than later in the year (April and October to December 1998). Estimated egg carbon was 0.023–0.049 $\mu\text{g C egg}^{-1}$, monthly means were in the range of 0.032–0.038 $\mu\text{g C egg}^{-1}$. Data of individual weight-specific egg production rates of *T. stylifera* were available only in November and December 1998, ranging from 0.01 to 0.21 day⁻¹ with a monthly mean of 0.1 day⁻¹.

Comparison of species

Generally, egg production was highly variable over the course of time, often changing considerably from day to day; therefore, the more striking it was how similar the cycles of both species were (Figure 3). Phases of high reproductive activity as well as periods of low egg production occurred simultaneously. EPR, CEPR and clutch size were related between both species at a high significance level (Table II).

In 1999, the annual cycle of 1998 was generally repeated, but the peaks were less intense in spring despite higher Chl concentrations in March. The bloom of salps in spring 1999 had a greater impact on *Temora*, which ceased egg production completely and disappeared from the samples until June. *Centropages* also decreased reproduction but could recover more rapidly and started egg production at high rates in mid-April. After its absence during the salp bloom, *T. stylifera* returned to high egg production rates in June and July. From September on, both species intensified their egg production until the autumnal peak in November.

Mean annual production rates of 11–12 eggs female⁻¹ day⁻¹ and maximal weight-specific rates of 0.21 were identical for *Centropages* and *Temora*. Also, the mean number of spawning females was ~55% in both species and years.

Effects of intrinsic and environmental factors

Both CEPR and SEPR were significantly related to female carbon content in *C. typicus* (Table II). In contrast, no relationship could be found either between female body carbon and PL, or between egg carbon and female carbon. Data for *T. stylifera* were probably too few to give any statistically relevant result. A temperature effect could not be detected. Although PL varied on an annual basis with small females in summer and the biggest ones in winter (Figure 4), regression of length versus *in situ* mean temperature produced no significant result. Egg production and clutch size showed no relationship with temperature either (Table II), even when the temperatures corresponding to the deep Chl maximum (30 and 50 m depth) were used in the analysis instead of the mean temperature. Egg production of *T. stylifera* seemed to have an optimum between 17 and 18°C rather than following a

linear regression. Prosome length only affected the reproduction of *C. typicus* significantly. CEPR and clutch size increased with female PL (Table II), while egg production and clutch size of *T. stylifera* were independent of PL. Chlorophyll did not correlate with any of the reproduction parameters (Table II).

DISCUSSION

While reproductive activity is often restricted to certain seasons in boreal regions (Ianora, 1998; Halsband and Hirche, 2001), in the Mediterranean Sea *C. typicus* and *T. stylifera* breed continuously in the Gulf of Marseille (Gaudy, 1971), the Gulf of Lion (Razouls, 1975), the Gulf of Naples (Ianora and Buttino, 1990; Ianora *et al.*, 1992) and the Ligurian Sea (present study). Maximal egg production rates of *C. typicus* and *T. stylifera* in the Mediterranean and adjacent seas were highly variable, depending on region and season (Table I). At 'Point B', we found maximal egg production rates of 33.3 and 33.5 eggs female⁻¹ day⁻¹ for *C. typicus* and *T. stylifera*, respectively. In the Catalan Sea, maximal egg production rates of *C. typicus* (36 eggs female⁻¹ day⁻¹) in June were comparable with our results from early summer 1998, while maximal production rates of *T. stylifera* were only 12.5 eggs female⁻¹ day⁻¹ there (Saiz *et al.*, 1999). In contrast, in the Gulf of Lion, *C. typicus* produced between 49 and 79 eggs female⁻¹ day⁻¹, and the egg production rate of *T. stylifera* ranged from 37 to 63 eggs female⁻¹ day⁻¹ (Razouls, 1975, 1982). Even higher maximal egg production rates were observed in the Gulf of Naples with ~100 eggs female⁻¹ day⁻¹ for both *C. typicus* and *T. stylifera* (Ianora and Buttino, 1990; Ianora and Poulet, 1993). In our study, the annual means of egg production rates were 5 times lower than in the Gulf of Naples with 10.8 (*C. typicus*) and 11.7 eggs female⁻¹ day⁻¹ (*T. stylifera*), compared to 58.5 and 50.9 eggs females⁻¹ day⁻¹, respectively (Ianora and Buttino, 1990; Ianora *et al.*, 1992). Thus, the Gulf of Naples and the Gulf of Lion appear more productive than the Ligurian and the Catalan Sea, probably due to nutrient input from the coast. The latter two represent more oceanic sites, where food limitation is reflected by comparably low Chl concentrations. Indeed, Chl concentrations were 2–5 times higher in the Gulf of Naples (maximum 7 mg m⁻³) than at 'Point B' (maximum 1.2 mg m⁻³).

In more northern regions, PL of the two genera is up to 100–200 µm greater than that of their counterparts in the Mediterranean (Table I), and hence their reproductive potential is higher. Indeed, several authors reported much higher egg production rates of *C. typicus* in the North Atlantic and the North Sea, such as 116 eggs female⁻¹ day⁻¹ in the Skagerrak (Peterson *et al.*, 1991), 90 eggs female⁻¹ day⁻¹ in the Kattegat (Kjørboe and Nielsen,

1994), 76 eggs female⁻¹ day⁻¹ in the New York Bight (Smith and Lane, 1987) and even 230 eggs female⁻¹ day⁻¹ in the same area in spring (Dagg, 1978). However, in other regions of the North Sea, maximal egg production rates were the same as in the Mediterranean. At Helgoland Island, *C. typicus* produced a maximum of 33.3 eggs female⁻¹ day⁻¹ (Halsband and Hirche, 2001). Tiselius *et al.* reported comparable rates of 36.5 eggs female⁻¹ day⁻¹ for *C. typicus* from Kosterfjorden in August (Tiselius *et al.*, 1987). Le Ruyet-Person *et al.* compared the English Channel and the Gulf of Lion, and found that egg production of *C. typicus* was the same in both regions with 41.7 and 40.0 eggs female⁻¹ day⁻¹, respectively (Le Ruyet-Person *et al.*, 1975).

The carbon content of females and egg diameters were the same as in the Catalan Sea (Saiz *et al.*, 1999). Weight-specific egg production rates ranged between 0.01 and 0.21 in both species and matched the values reported for the Atlantic and the North Sea (Table II). However, information on seasonal variation of weight-specific production in the Mediterranean is still lacking in the literature.

Chlorophyll was a poor indicator for egg production on the annual time scale. Like Ianora and Scotto di Carlo (Ianora and Scotto di Carlo, 1988), we found no correlation between reproduction and Chl either. Laboratory experiments showed that food selection and prey switching enable copepods to mount a complex behavioural response in order to cope with strong food limitation (Poulet and Marsot, 1980; Kjørboe *et al.*, 1996). Furthermore, copepods often prefer microzooplankton as a food source relative to diatoms; it seems to be more efficient for reproduction than phytoplankton. Thus, egg production and growth were significantly enhanced in the laboratory when copepods grazed on ciliates rather than algae (Stoecker and Egloff, 1987; Wiadnyana and Rassoulzadegan, 1989; Kleppel *et al.*, 1991; Fessenden and Cowles, 1994). In the field, Wiadnyana found copepod biomass to be related to microzooplankton biomass in the Ligurian Sea and concluded that microzooplankton were of seasonally varying importance as copepod food (Wiadnyana, 1992). At 'Point B', *Centropages* and *Temora* may have switched between algal and heterotrophic nutrition depending on the actual conditions, since the reproductive maxima coincided with a microzooplankton peak in November (F. Gomez, personal communication).

Surface temperature at 'Point B' ranged from 13.5 to 25.8°C during both years. However, no significant relationship between egg production and temperature was detected (Table II). If *C. typicus* and *T. stylifera* performed a diurnal migration cycle as in other regions of the Mediterranean, descending to the deep Chl maximum during the daytime and coming up to the

surface at night (Pagano *et al.*, 1993; Saiz *et al.*, 1999), they encountered a wide range of temperatures (15–26°C) during summer stratification. Thus, interactions between temperature and reproduction are expected to be complex. In boreal regions, temperature affects egg production on the seasonal time scale via body size: females are biggest in the cold season and thus are capable of producing bigger clutches than in summer (Landry, 1978; Ambler, 1985; Kiørboe *et al.*, 1988; Hirche, 1992; Ban, 1994; Halsband and Hirche, 2001). In fact, CEPR and clutch size of *C. typicus* were significantly related to body size (Table II). However, body size may depend either on temperature or food (Mullin and Brooks, 1970; Runge, 1984). In our study, PL varied on an annual basis with big females in late autumn and small females in summer, but without any significant correlation with temperature. In 1999, *Centropages* females were already smallest in April, probably due to strong food limitation during the salp bloom in this year.

Reproduction is an important factor in population dynamics. However, in our study, seasonal distribution did not reflect egg production rates. Despite parallel seasonal reproduction patterns of *C. typicus* and *T. stylifera*, abundance peaks occurred at different times of the year. *Centropages* copepodites usually peaked in April, while the abundance maximum of *Temora* occurred in late summer and autumn, and with much smaller numbers of individuals (S. Nival, personal communication). The development of the *Centropages* population therefore followed the reproduction peak in autumn, whereas recruitment of *Temora* seemed to profit from the summer reproduction peak. This mismatch might be explained by differences in physiology, predation pressure and/or feeding behaviour. Since *C. typicus* is a common species of the temperate Atlantic, the North Sea and the Mediterranean, and *T. stylifera* is a more warm-loving species distributed in the Mediterranean and further south (Rose, 1933), species-specific temperature preferences, other than for reproduction, are likely to be one reason for these distribution patterns. Temperature adaptations of hatching and development might enhance survival at high (*T. stylifera*) and low (*C. typicus*) temperature, respectively. For instance, the variations in length of the tegumental spines of *C. typicus* eggs, which were longer in autumn than in spring, can be considered as a temperature adaptation [(Carlotti *et al.*, 1997) and references therein]. When embryonic development times increase due to autumnal cooling, the enhanced buoyancy of eggs with longer spines will extend sinking time and enable nauplii to hatch, while *Temora* eggs might be lost to the sediment. Furthermore, predation pressure on reproducing females and immature stages might be crucial for differences in population development *in situ* (Landry, 1978; Kimmerer

and McKinnon, 1989; Ianora and Poulet, 1993; Ohman *et al.*, 1996; Saiz *et al.*, 1999). Different predation pressure might result, for instance, from different specific behaviour patterns, like swimming and/or escape behaviour (Paffenhöfer *et al.*, 1996; Paffenhöfer, 1998). Swimming behaviour of *Temora* and *Centropages* copepodites is quite different and therefore could induce different responses of predators (Tiselius and Jonsson, 1990; Hwang, 1991; Fields and Yen, 1997). The specific response to food competition might also play an important role for copepod fitness, especially in oligotrophic environments. The salp bloom gives an example for the impact of food competitors on copepod reproduction. Salps are known to clear phytoplankton from the water column efficiently (Andersen, 1985; Braconnot *et al.*, 1988). Hence, egg production rates of *C. typicus* decreased dramatically. *Temora stylifera* was affected much more strongly and disappeared completely from the samples after having ceased reproduction. *Centropages* was obviously more resistant towards this competition and could maintain its population better during the salp bloom than *Temora*, which was completely displaced from the area.

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