ELSEVIER

Journal of Experimental Marine Biology and Ecology
271 (2002) 121–153

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

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Temperature impact on reproduction and development of congener copepod populations

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Received 31 July 2001; received in revised form 20 January 2002; accepted 24 January 2002

Abstract

The goal of this study was to relate the temperature response of all developmental stages and reproductive biology of two congener copepod pairs inhabiting different biogeographic regions to their geographic distribution patterns. Survival of adult females and egg production, embryonic development and hatching success of the genera *Centropages* and *Temora* from two stations, in the North Sea and the Mediterranean, were studied in laboratory experiments in a temperature range from 2 to 35 °C. Postembryonic development was determined from cohorts raised at temperatures between 10 and 20 °C with surplus food. Tolerance limits and optima of female survival, reproduction and development distinguished the northern species *Centropages hamatus* and *Temora longicornis* from the southern *T. stylifera*, while *C. typicus*, which is found in both regions, was intermediate. Thus, thermal preferences could in part explain distribution patterns of these species. While *C. hamatus* and the two *Temora* species showed distinct temperature ranges, *C. typicus* was able to tolerate different temperature conditions, resulting in its wide distribution range from the subarctic to the tropics. However, the thermal range of a species did not necessarily correlate with the optimal temperatures in the experiments. Optima of egg production and stage development were surprisingly low in *T. stylifera*, which has a mere southern distribution.

Keywords: *Centropages*; Development; Distribution; Reproduction; *Temora*; Temperature response

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0022-0981/02/$ - see front matter
PII: S0022-0981(02)00025-4

1. Introduction

Biogeography has raised interest recently within the context of biodiversity and climate change. While there exists a large body of literature on geographic distributions, little is known on the factors controlling it (Pörtner, 2001). Congener pairs appear most appropriate to study tolerance limits and optima of life history traits with regard to their significance for distribution patterns, as they are morphologically very similar.

Distribution patterns of congener copepod species often differ considerably either on a spatial or temporal scale. Spatial separation of species can occur (1) horizontally, e.g. by geographical latitudes (Conover, 1988; Jashnov, 1970) or hydrographic features (Planque and Fromentin, 1996) as shown for *Calanus* sp., (2) vertically like in *Calanus* and *Euchaeta* congeners (Williams, 1985; Roe, 1972), or (3) by topographic regions, e.g. shelf or off shore areas, observed for *Centropages* species (Grant, 1988). Temporal separation of species is observed as seasonal succession, like in *Acartia tonsa* and *A. hudsonica* (Sullivan and McManus, 1986).

In our study, we focused on pairs of *Centropages* (*Centropages typicus* and *C. hamatus*) and *Temora* (*Temora longicornis* and *T. stylifera*) congeners (Copepoda: Calanoida) occurring in the North Sea and the Mediterranean. These free-spawning species belong on the one hand to a boreal, cold-temperate community (*C. hamatus*, *T. longicornis*), while *T. stylifera* on the other hand is a southern, warm-temperate species. *C. typicus* is regarded as a common constituent of both the warm and the northern cold plankton and therefore is called a ''southern intermediate form'' (Colebrook, 1964). Their distributional ranges are summarized in Table 1. The southern boundary of *T. longicornis* coincides with the 20 °C isotherm in summer (Lindau, 2001), while *C. hamatus* persists as diapause eggs in the sediment to overwinter in the north and aestivate in the south during unfavourable temperature conditions in the water column (Marcus, 1989 and references therein). *C. typicus* seems relatively independent of temperature boundaries, since its distribution covers the Atlantic from the equatorial province to the subarctic province (van der Spoel and Heyman, 1983). *T. stylifera* occurs as far north as the 12.5 °C isotherm in winter (Lindau, 2001), but is occasionally advected to the English Channel by warm Atlantic currents from the south (A. John, personal communication). Morphologically, the congeners differ only slightly and their size ranges, assembled from different seasons and locations, largely overlap (Fig. 1).

In areas where these congener species coexist, like in the North Sea, their temporal distribution patterns differ considerably in the course of seasons. Whereas, *C. hamatus* occurs from April to September in coastal regions, *C. typicus* prefers the more saline and warmer waters of Atlantic origin and appears in the German Bight in the second half of the year (Fransz et al., 1991). Grant (1988) noticed a succession of *Centropages* congeners also in the Middle Atlantic Bight and assumed that it is based on the different temperature preferences of species. There, in a temperature range of 2–27 °C, *C. hamatus* occurred only in the cold period below 17 °C, while *C. typicus* was always present. He concluded that *C. hamatus* is a cold water species, while *C. typicus* shows a wide tolerance for temperature. In the warmer Mediterranean, *C. typicus* is the only representative of the two *Centropages* species considered here. *C. typicus* dominates the copepod community in spring (Gilat et al., 1965; S. Nival, personal communication), but can be

Table 1
Geographic distribution of *C. typicus*, *C. hamatus*, *Temora longicornis* and *T. stylifera* in the North Atlantic and adjacent seas

Species	Characteristics	Geographic distribution	References
C. typicus	southern-intermediate oceanic epipelagic	warm Atlantic surface waters	Krause et al., 1995
		Faroe-Shetland Channel	Jespersen, 1940
		Mediterranean	Rose, 1933
		Atlantic 6°S–62°N	Sars, 1928
		Iceland and Faroes	Scott, 1911
		Atlantic 36°–62°N	Giesbrecht, 1892
C. hamatus	cold-temperate neritic diapause eggs	North Sea and Baltic Sea to the fjords of Iceland	Krause et al., 1995
		western Spitsbergen, Barents Sea, White Sea, Kara Sea	Klekowski and Weslawski, 1990
		Newfoundland to Florida along the North American coast	Marcus, 1989 (and references therein)
		Middle Atlantic Bight	Grant, 1988
		White Sea	Pertzova, 1974
		41–66°N	Sars, 1928
		50–60°N	Giesbrecht, 1892
T. longicornis	cold-temperate neritic euryhaline epipelagic	coasts from Portugal to northern Norway	Krause et al., 1995
		western Spitsbergen, Barents Sea	Klekowski and Weslawski, 1990
		40–72°N	Sars, 1928
		50–60°N	Giesbrecht, 1892
T. stylifera	warm-temperate	occasionally English Channel	John, personal communication
		tropical Atlantic and Pacific, Mediterranean, Red Sea	Mori, 1964
		Mediterranean, temperate and warm Atlantic	Rose, 1957
		Atlantic 37°S–46°N	Giesbrecht, 1892

found reproducing almost during the whole year (Ianora and Buttino, 1990; Halsband-Lenk et al., 2001).

The two *Temora* species hardly overlap in their geographical distribution range (Fig. 1). In the North Sea, *T. longicornis* is abundant at any time of the year and females are able to reproduce during the whole seasonal cycle (Halsband and Hirche, 2001). *T. stylifera* is a predominant copepod in the NW Mediterranean, which occurs in high numbers mainly during late summer and autumn (Gilat et al., 1965; S. Nival, personal communication), while females are potentially able to lay eggs throughout the year (Halsband-Lenk et al., 2001).

The geographical distribution and life cycles of these four species suggests that temperature is an important factor in their seasonal and regional abundance patterns. Temperature has traditionally been assumed to be a basic factor, ruling the physical environment (viscosity, etc.), limiting physiological processes (e.g. oxygen delivery within the organism) and biochemical reactions (e.g. enzyme activity), and finally determining growth and developmental rates (reviewed in Kinne, 1963). So far, it is hardly known which phase of the copepod life cycle is most sensitive to temperature limitation. Limitation might occur in the development of specific stages, e.g. nauplii (Pedersen and

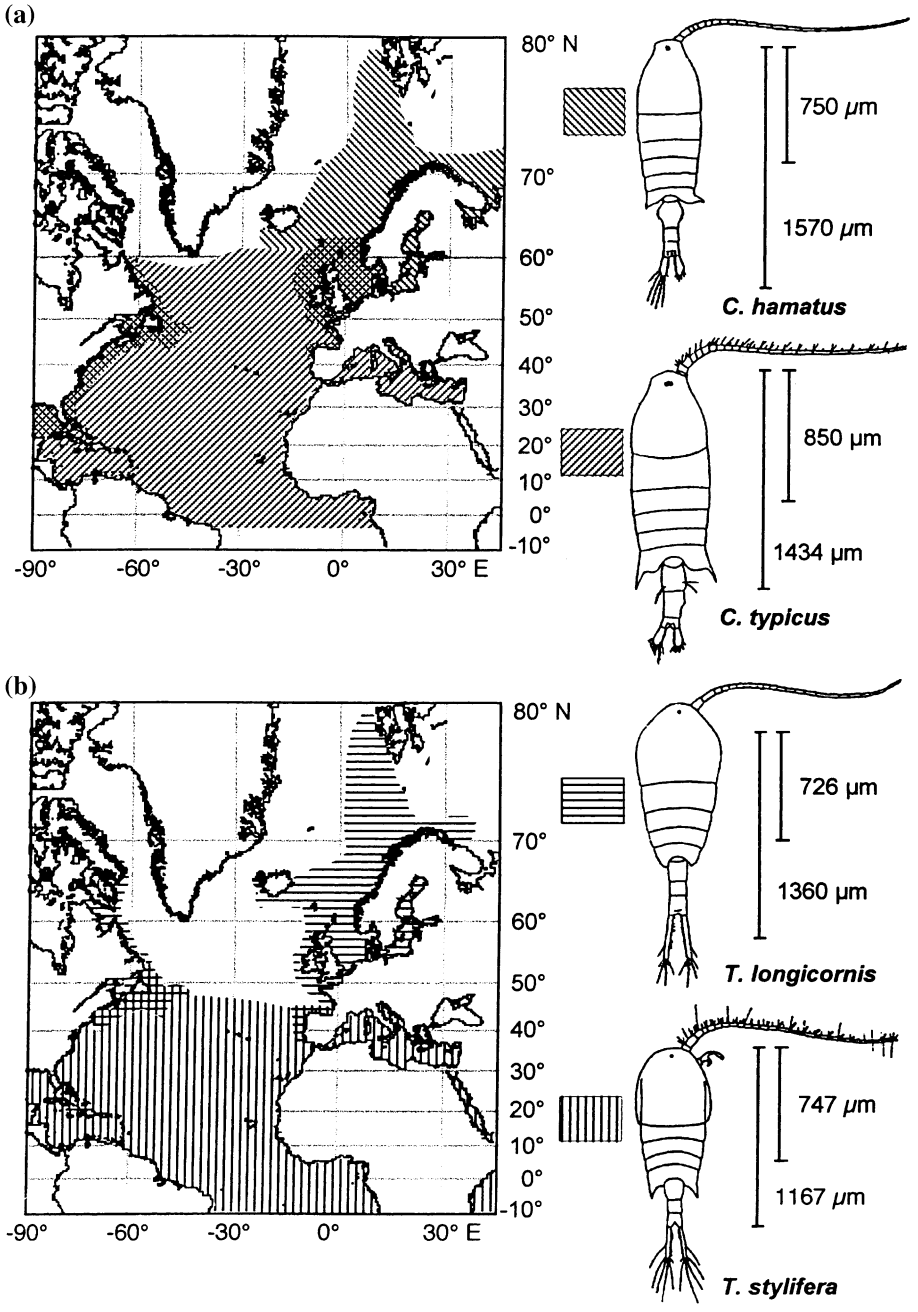


Fig. 1. Habit (after Rose, 1957; modified), range of prosome length in situ (Halsband-Lenk, partly unpublished) and geographical distribution in the Atlantic and adjacent seas of (a) *C. typicus* and *C. hamatus*, (b) *T. longicornis* and *T. stylifera*.

Tande, 1992), or in reproductive biology. Earlier demographic studies concerned either egg development (Corkett, 1972; McLaren et al., 1969; McLaren, 1966), nauplii development (Corkett and McLaren, 1970) or generation time as a whole (McLaren, 1978), but rarely the different developmental stages. Most experimental studies were conducted in the natural temperature range of a species' habitat, without considering extreme temperatures (e.g. Abou-Debs and Nival, 1983).

Here, we tried to detect temperature limitation in all developmental stages and in reproductive biology. Laboratory experiments were conducted at Helgoland Island (SE North Sea) and in Villefranche-sur-Mer (NW Mediterranean) to compare the temperature responses of *Centropages* and *Temora* congeners in regard to different temperature regimes. Female thermal tolerance, egg production and development times were recorded in a temperature range from 2 to 35 °C. Rearing experiments were conducted in mesocosms at different temperatures to compare stage duration, generation time and mortality rates in congener populations.

2. Material and methods

2.1. Sampling

Plankton was collected at the sampling sites "Kabeltonne" (54°11′ 3″ N, 7°54′ 0″ E) at Helgoland Roads in the south-eastern North Sea with a Calcofi net (280 μm mesh size) and "Point B" (43°41′ 10″ N, 7°19′ 00″ E) at the entrance of the Bay of Villefranche-sur-Mer in the north-western Mediterranean using a net of the type "Superhomogène" (280 μm mesh size). These stations are of a similar longitude position, but represent two different climatic regions due to the different latitudes: the boreal North Sea with an annual surface temperature range from 0 to 20 °C, and the warm-temperate Mediterranean Sea, where surface temperatures vary between 13 and 26 °C (Fig. 2).

Specimens of *C. typicus*, *C. hamatus* and *T. longicornis* from Helgoland Roads (indexed $_{NS}$ further on) were collected in summer 1999, when surface temperature ranged

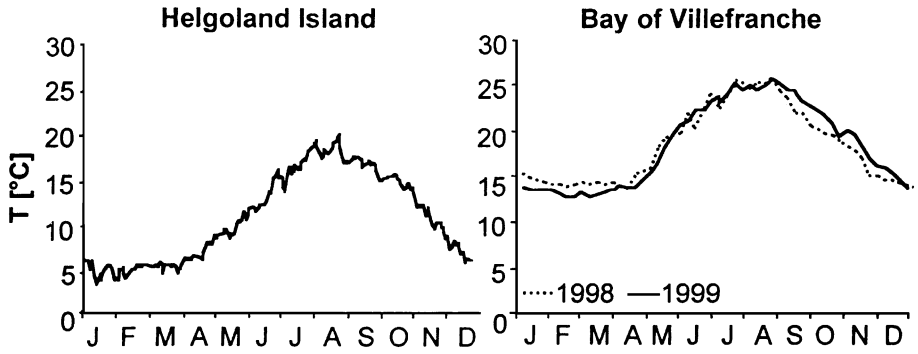


Fig. 2. Seasonal cycle of surface temperature in the North Sea (Helgoland Roads) in 1999 and in the Mediterranean (Bay of Villefranche) in 1998 and 1999.

between 14 and 19 °C. Experiments with *C. typicus* and *T. stylifera* in the Mediterranean (indexed $_{Med}$) were carried out in autumn 1998 at surface temperatures around 17 °C. They were repeated for *C. typicus*$_{Med}$ in March and May 1999, when in situ temperature was around 15 °C. The plankton was brought to the laboratory within 1 h and adult females were sorted for incubation. Experiments were conducted in temperature-controlled cold rooms at 15 and 20 °C ($\pm$ 0.5 °C), all other incubations were carried out in water bathes ($T \pm 0.2$ °C). The light cycle was 12 h dimmed light/12 h darkness.

2.2. Survival of adult females and egg production

Survival of adult females and egg production rates were measured during periods of high reproductive activity in the field (autumn 1998 in Villefranche, summer 1999 at Helgoland Island). In order to analyse seasonal variations, experiments were repeated in spring with *C. typicus* in the Mediterranean. About 12–45 females were kept individually in small glasses of approximately 15 ml for 5 days. Before incubations started, the animals were adapted to the experimental temperature during 24 h by cooling (or warming) in steps of 5 °C in water baths. Filtered seawater (0.45 μm) enriched with 15,000 cells ml^{-1} ($\approx$ 4 μg C ml^{-1}) of the flagellate *Hymenomonas elongata* was offered as food. The dishes were checked for dead animals, eggs and faecal pellets twice a day, and eggs and pellets were removed. Egg cannibalism was accounted for by including empty egg shells in the counts. Individuals that died before the end of the experiment or laid no eggs were discarded. Viable individuals were preserved in 4% buffered formalin for later measurements of prosome length.

Females from the North Sea were incubated at 2, 5, 7.5 (except *C. hamatus*), 10, 12.5 (except *C. typicus*), 15, 20, 22.5 (except *C. hamatus*), 25, 30 and 35 °C. Experimental temperatures for specimens from the Mediterranean were 2, 5, 7.5, 8, 10, 15, 20, 22.5 (except *T. stylifera*), 25, 30 and 35 °C. Additional data were available for *T. longicornis*, incubated at 0 °C in March 1996 with *Dunalliella tertiolecta* as food.

Egg production was expressed as mean egg production rate of all egg-laying females during 5 days (eggs female^{-1} day^{-1}) and as cumulative egg production over 5 days of incubation (eggs female^{-1}). Since all females of *T. stylifera* died at 20 °C within the incubation time of 5 days, egg production in this case was calculated for all females that survived until day 4.5.

Mean female carbon was measured by the high-temperature combustion method (Salonen, 1979; Tanskanen, 1994) from individuals sampled between September 1995 and June 1996, and in summer 1999 (North Sea), and in autumn 1998 and spring 1999 (Mediterranean, see Halsband-Lenk et al., 2001). Mean egg carbon was estimated from egg diameter with a volume to carbon conversion of 0.14×10^{-6} μg C μm^{-3} (Kiørbœ et al., 1985). Mean female carbon and mean egg carbon were used to calculate a weight specific egg production rate (SEPR).

2.3. Prosome length

Prosome length of preserved females from the incubations was measured with a digitizing video system (Scion Image 1.6®). Differences in size between experiments were tested with ANOVA and Scheffe's post hoc tests.

2.4. Embryonic development

Eggs were obtained from freshly captured females incubated 24 h in filtered seawater at 15 °C. Embryonic development times were determined from 2 to 30 °C in summer 1999 for all North Sea species. Complementary results for eggs of *T. longicornis*, incubated from 0 to 16 °C in March and June 1996 were included. Development times in the Mediterranean were recorded from 2 to 30 °C in June 1998, March and May 1999 for *C. typicus* and in November 1998 for both *C. typicus* and *T. stylifera*. Hatching was controlled three times a day until the first nauplii appeared. Then nauplii were counted every 1–2 h (except overnight) until all eggs had hatched or no more development occurred. Development times are defined as the time needed by 50% of all viable nauplii to hatch (median development times).

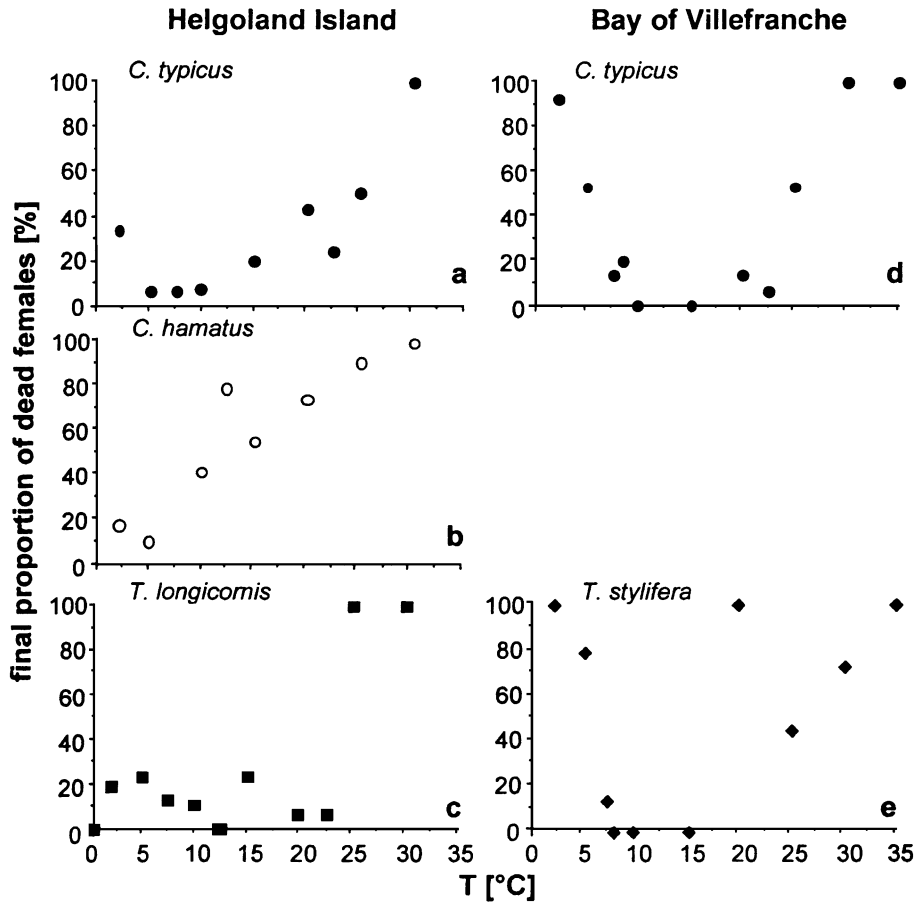


Fig. 3. Total mortality of adult females after 5 days of incubation at different temperatures.

The temperature response of embryonic development is described by Bělehrádek's function of the form $D = a(T - \alpha)^b$, with b assumed as constant (-2.05) for all species (McLaren et al., 1969). Differences between seasons were compared by ANCOVA analysis, after ln-transformation of development times.

2.5. Post-embryonic development

In the North Sea, cohorts of all three species were raised at 15 and 20 °C and *C. typicus* additionally at 10 °C in summer 1999. In the Mediterranean, *C. typicus* was cultured at 12, 15 and 18 °C in spring 1998, *T. stylifera* at 10, 15 and 20 °C in autumn 1998. For initiation of cultures, around 200 freshly captured females and 50 males were kept in Plexiglas cylinders, closed at the bottom with gauze of 280 μm, and immersed in a 5-l beaker filled with filtered seawater (0.45 μm). To induce high spawning rates, the culture was enriched with 15,000 cells ml^{-1} of *H. elongata* and the beaker softly oxygenated with air. Spawned eggs fell through the mesh and were collected at the bottom of the beaker. After a spawning period of 24–48 h, the adults were removed and sampling started.

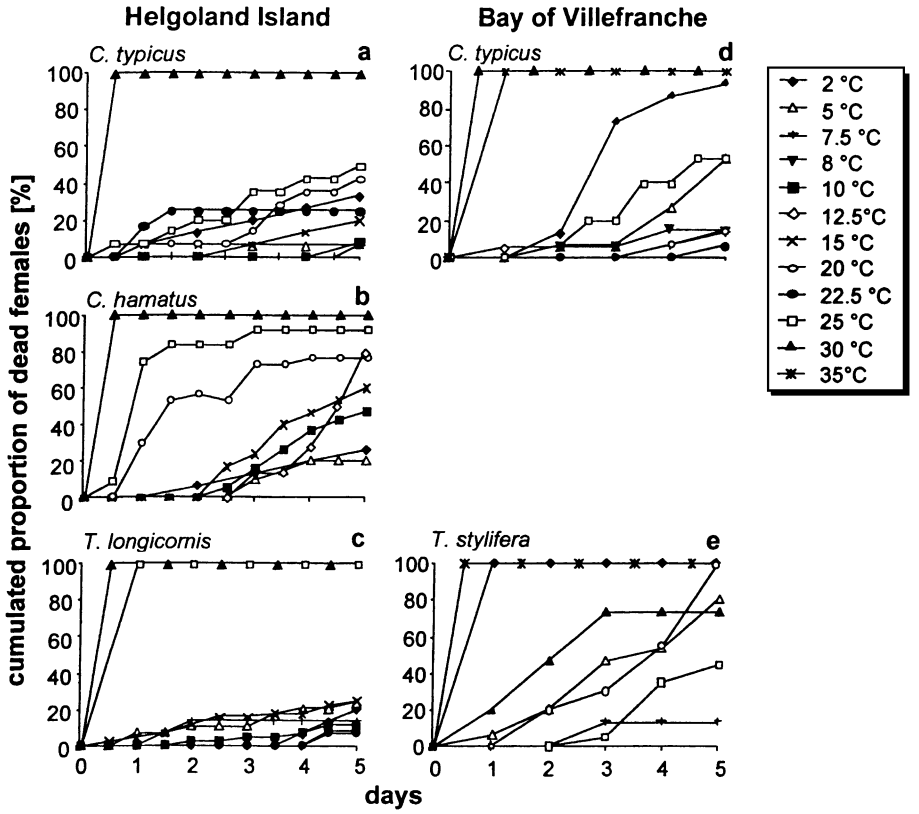


Fig. 4. Cumulative proportions of dead females incubated 5 days at different temperatures.

Since the size spectra of ingested particles changes within the development of the copepods, around 100,000 cells ml^{-1} of *Isochrysis galbana* were added after removal of the adults. The size of these algae (4–7 μm) corresponds best to the food size spectra of the youngest nauplii stages (Nival and Nival, 1976). When the first N3 appeared, *I. galbana* progressively was exchanged by *H. elongata* (15 μm) to ≈10,000 cells ml^{-1} (≈2.6 μg C ml^{-1}). Every day a subsample of 1–4% was taken to estimate the abundance of the larval stages and control food concentration.

Development time was defined as the time when 50% of the population had completed molting to a given stage, calculated with the help of least square regressions. Stage duration then was calculated as the interval between the development time to a given stage and the time to the subsequent stage (Landry, 1983). Females and males were not distinguished, since they appeared simultaneously. Mortality rates were estimated from the slope of linear regressions of logarithmic transformed population abundances, after correction of population size for mortality due to sampling (Aksnes et al., 1997). Two

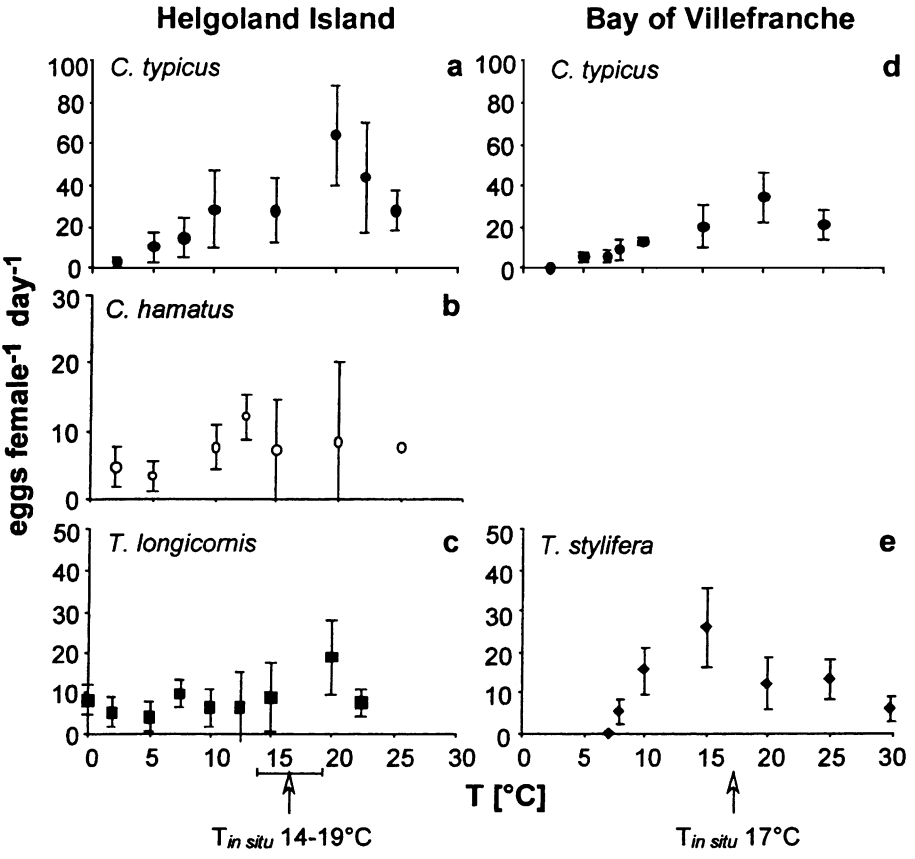


Fig. 5. Temperature impact on egg production rates. Vertical bars indicate standard deviation.

regressions per population were calculated, one from egg to CI, the other from CI to 50% adulthood. In some experiments, the cohorts suddenly broke down for unknown reasons so that populations did not reach adulthood (Table 3). In those cases, stage duration was estimated only for all instars available.

3. Results

3.1. Thermal impact on survival, reproduction and development

3.1.1. Female thermal tolerance (FTT)

FTT followed an optimum curve in *C. typicus*$_{NS+Med}$ and *T. stylifera* with increased mortality at temperatures higher and lower than the optimum (Fig. 3). Mortality of *C. hamatus* increased linearly with temperature (12.5 °C excluded), while no clear pattern was found in *T. longicornis*.

The cumulated numbers of dead females during the 5 days of observations are presented in Fig. 4 for the four species and for the different temperatures of incubation. In general, two patterns were observed: (1) hyperbolic curves with a very high mortality of

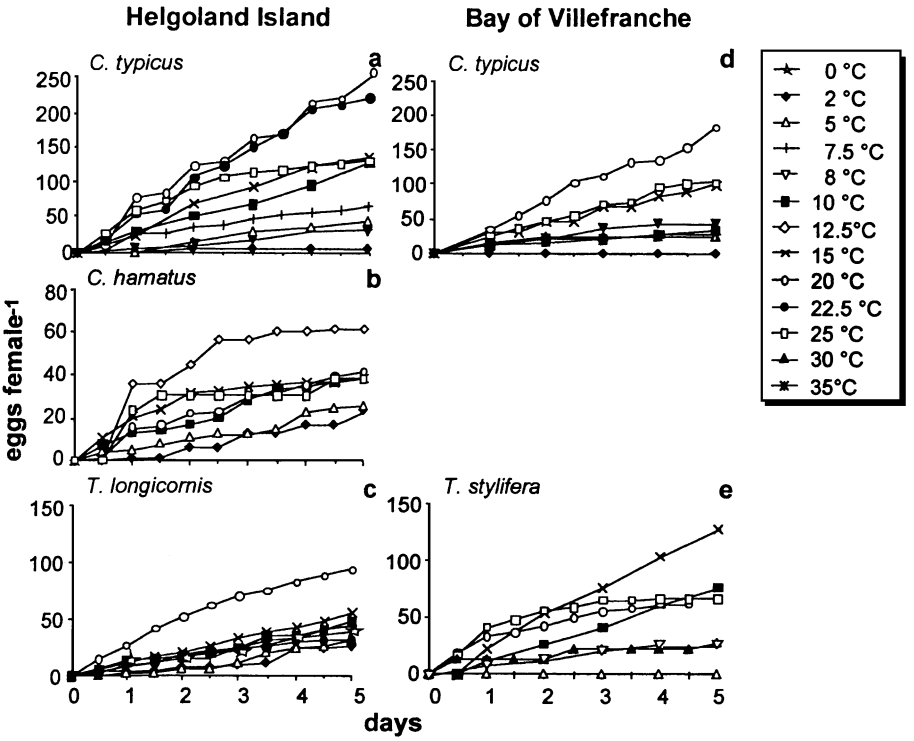


Fig. 6. Cumulative egg production during 5 days at different temperatures.

females during the first days followed by a constant proportion of survivors, (2) a constant death rate, or (3) the proportion of dead females increasing with age. For all species, pattern (1) was recorded at the highest temperatures, i.e. 25 and 30 °C for *T. longicornis*, 30 °C for *C. typicus*$_{NS}$ and *C. hamatus*, 30 and 35 °C for *C. typicus*$_{Med}$ and *T. stylifera*. The same type of response was observed in *C. typicus*$_{NS}$ at 22.5 °C and in *C. hamatus* at 25 °C, and to a less degree, at 20 °C. Pattern (2) was observed at all other temperatures in *C. typicus*$_{NS}$ and *T. longicornis.* Mortality of *T. stylifera* reached 100% at 20 °C due to constant death rate. Pattern (3) occurred in *C. typicus*$_{Med}$ at all temperatures from 2 to 25 °C, in *C. hamatus* at 12.5 °C and in *T. stylifera* at 25 °C.

3.1.2. Reproductive thermal response (RTR)

RTR generally showed an optimum curve (Fig. 5). Optimal temperature was around 20 °C for *C. typicus*$_{NS+Med}$ and for *T. longicornis*, whereas *C. hamatus* spawned most eggs at 12.5 °C and *T. stylifera* at 15 °C. Egg production rate over 5 days mostly was constant (Fig. 6), other in cases reproduction stopped after a few days (*C. typicus*$_{NS}$ at 25 °C, *C. hamatus* at 12.5, 15 and 25 °C, *T. stylifera* at 25 and 30 °C). Weight specific production

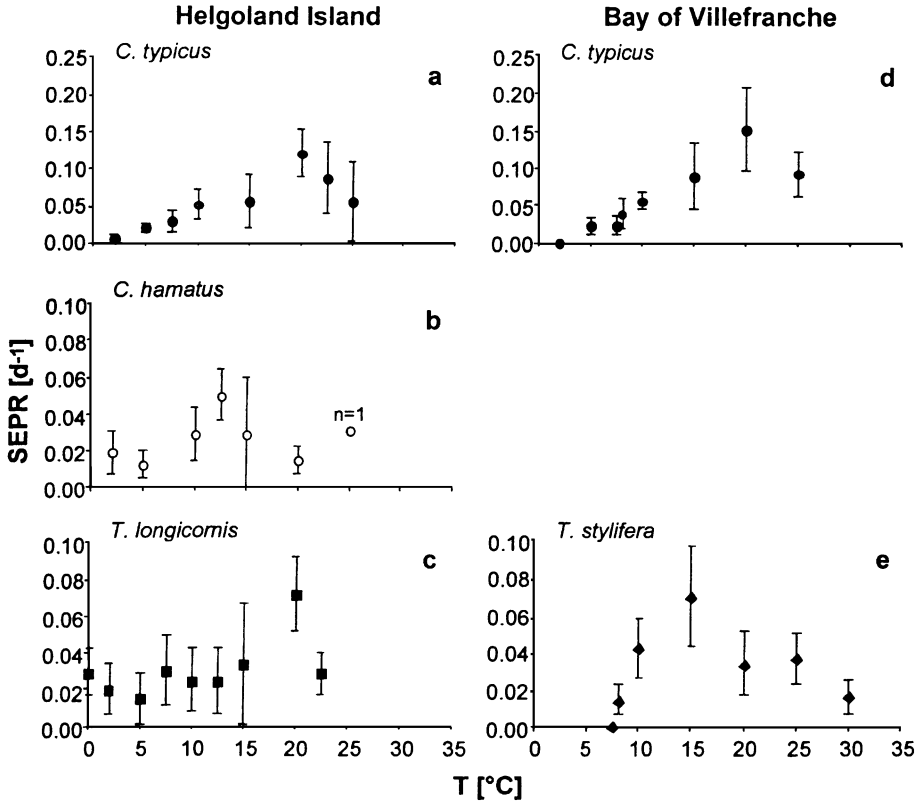


Fig. 7. Temperature impact on weight specific egg production. Vertical bars indicate standard deviation.

rates (SEPR) were in the same range for all species except *C. typicus* and varied between 6% and 7.5% day^{-1} at the optimal temperatures (Fig. 7b,c,e). Both *C. typicus* populations had higher specific production reaching $11\%_{NS}$ and $16\%_{Med}$ at the optimum, respectively (Fig. 7a,d).

3.1.3. Prosome length of females

Prosome length of females used in our experiments showed little variability within species (Fig. 8) in comparison to the range of prosome length compiled from different seasons and locations (see Fig. 1). Prosome length of *C. typicus*$_{NS}$ ranged from 971.1 to 1415.9 μm with a mean of 1158.9 ± 83.6 μm. Specimens of *C. typicus*$_{Med}$ were smaller, ranging from 921.8 to 1174.0 μm with a mean of 1036.7 ± 61.5 μm. Body size of *C. hamatus* was between 793.1 and 1146.8 μm, with a mean of 944.6 ± 79.5 μm. *T. longicornis* and *T. stylifera* females had a similar mean prosome length of 951.1 ± 71.3 and 965.7 ± 47.9 μm, respectively. The size range of *T. longicornis* from 774.3 to 1212.6 μm (mean 951.1 ± 71.3 μm) was broader than that of *T. stylifera* with 876.8–1073.7 μm (mean 965.7 ± 47.9 μm). Size differences between experiments were not significant in a

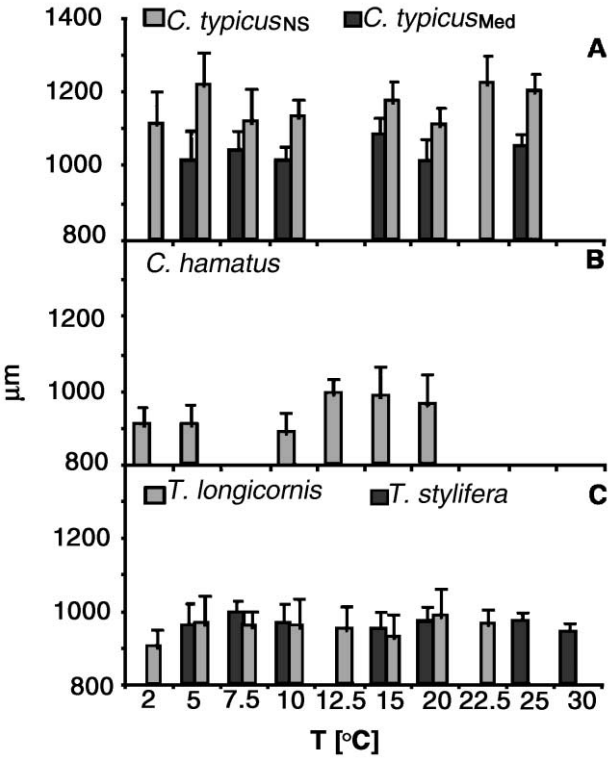


Fig. 8. Prosome length of females incubated in experiments. Vertical bars indicate standard deviation.

given population, except in *C. typicus*$_{Med}$ and *C. hamatus*. In both cases, females were greater at 15 °C than at 10 °C ($p < 0.0001$).

3.1.4. Embryonic thermal response (ETR) and hatching success

Temperature impact on embryonic duration is presented in Fig. 9. At all temperatures where eggs were produced hatching was also possible, except in *T. stylifera* at 30 °C and *C. typicus*$_{Med}$ at 2 °C. Embryonic development times decreased with increasing temperature following Bělehrádek functions in all species (Table 2). In few cases (Fig. 9b,d), embryonic duration increased at higher temperatures, as at 25 °C in *C. hamatus* and at 28 °C in *C. typicus*$_{Med}$. Hatching success was maximum or very high at any temperature situation in *C. typicus*$_{NS}$ and *T. longicornis* (Fig. 10). In *C. typicus*$_{Med}$, more than 70% of nauplii hatched at all temperatures. A more variable proportion of viable nauplii was observed in *C. hamatus* ranging from 34% to 89%. In *T. stylifera*, survival of eggs increased linearly with temperature from 52% at 10 °C to 90% at 20 and 25 °C.

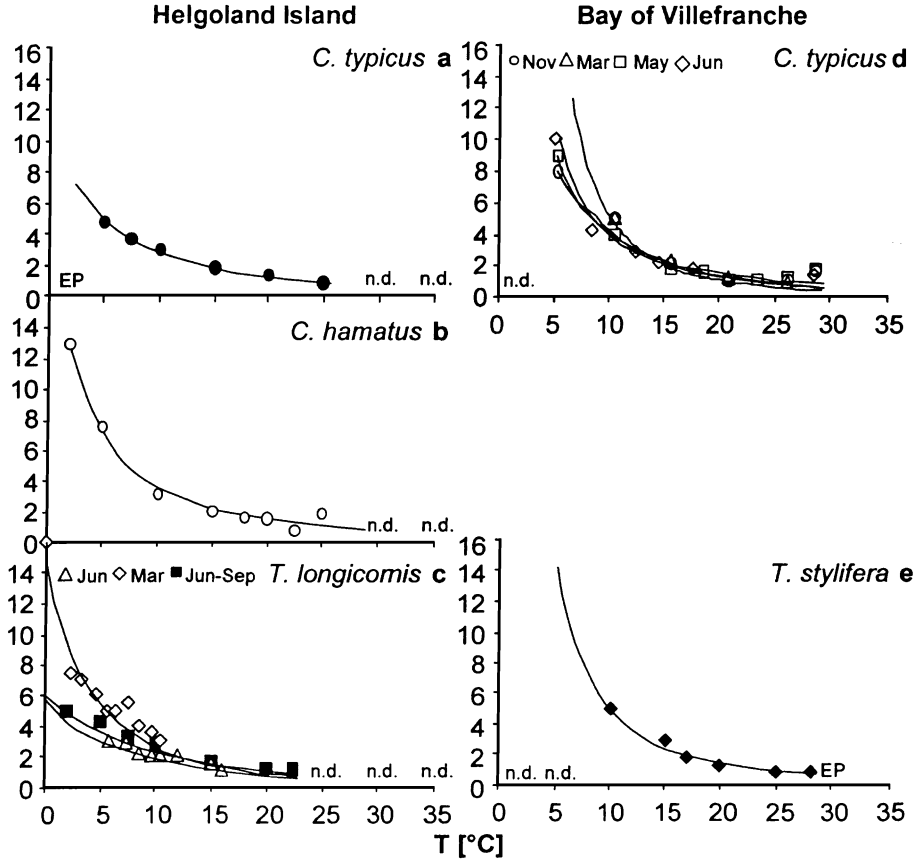


Fig. 9. Embryonic development times fitted with Belehrádek curves. n.d. = no development, EP = egg production observed.

Table 2
Belehrádek functions of embryonic development at different temperatures

	Species	Equation	References
Northern Atlantic/North Sea	*C. typicus*		
	Jul–Sep	$D = 1535.3(T + 11.6)^{-2.05}$	this study
		$D = 1068(T + 9.37)^{-2.05}$	McLaren et al., 1989
	C. hamatus		
	Jul–Sep	$D = 1148.9(T + 6.9)^{-2.05}$	this study
	T. longicornis		
	Jul–Sep	$D = 2469.5(T + 18.2)^{-2.05}$	this study
	Mar	$D = 1121.7(T + 8.1)^{-2.05}$	this study
	Jun	$D = 1474.9(T + 14.7)^{-2.05}$	this study
		$D = 1346.0(T + 10.4)^{-2.05}$	Corkett and McLaren, 1970
Mediterranean Sea	*C. typicus*		
	Nov	$D = 1579.0(T + 8.0)^{-2.05}$	this study
	Mar	$D = 586.7(T + 0.3)^{-2.05}$	this study
	May	$D = 1059.5(T + 5.3)^{-2.05}$	this study
	Jun	$D = 1113.3(T + 5.0)^{-2.05}$	this study
	T. stylifera		
	Nov	$D = 791.0(T + 1.8)^{-2.05}$	this study
	Autumn	$D = 3.5(T - 12.0)^{-0.50}$	Abou-Debs and Nival, 1983
	Spring	$D = 45.4(T + 0.5)^{-1.14}$	Abou-Debs and Nival, 1983

3.1.5. Post-embryonic development and mortality rates

The proportions of the population having completed a given moult versus time during cultivation at different temperatures and resulting linear regressions are presented in Figs. 11–13. Stage durations and mortality rates are summarized in Table 3. Naupliar and copepodite development, as well as generation times, are compared in Table 4.

For better comparison, stage durations are presented graphically on Fig. 14. Egg duration was higher than or equal to naupliar stages in all *Centropages* populations; late copepodites showed the slowest development (Fig. 14a–e). In the *Temora* species, naupliar durations were similar to copepodite durations, except when mortality stopped development (Fig. 14f–h).

3.2. Comparison of the two C. typicus populations and the congener pairs

3.2.1. C. typicus in the North Sea and the Mediterranean

FTT differed between the two *C. typicus* populations in the North Sea and the Mediterranean (Table 5). While mortality rates of females were similar at upper temperatures, they were higher in the Mediterranean at the lower temperature range. Optimal survival occurred at 5–10 °C in the North Sea, but at 10–15 °C in the Mediterranean (Fig. 4a,d).

In contrast to FTT, RTR was very similar in the two populations, except at 2 °C, where *C. typicus*$_{NS}$ produced eggs, whereas *C. typicus*$_{Med}$ did not (Fig. 6a,d). At the optimum (20 °C), the larger *C. typicus*$_{NS}$ females produced more eggs (54.5 eggs female^{-1} day^{-1}) than the smaller *C. typicus*$_{Med}$ (34.1 eggs female^{-1} day^{-1}). On a weight-specific base,

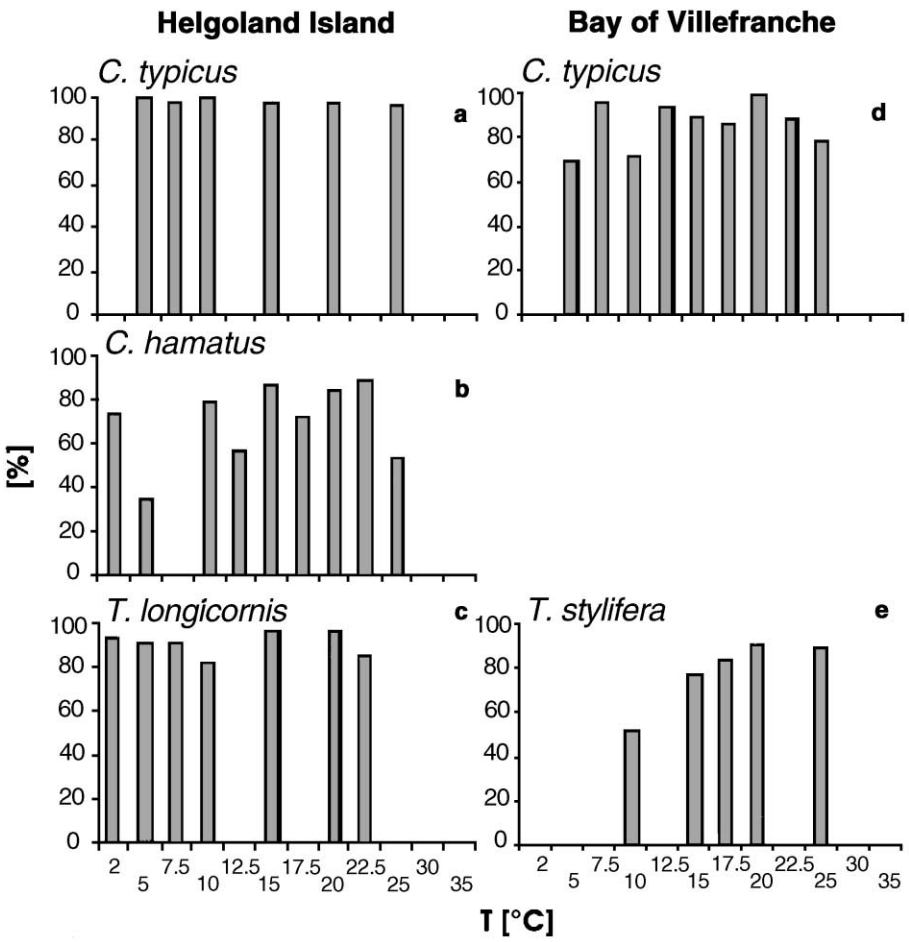
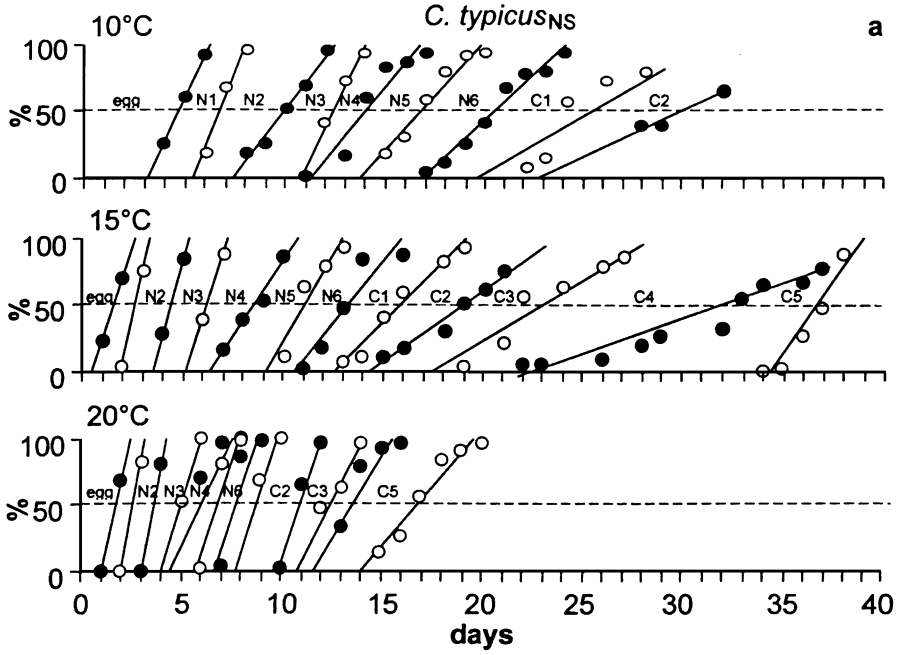


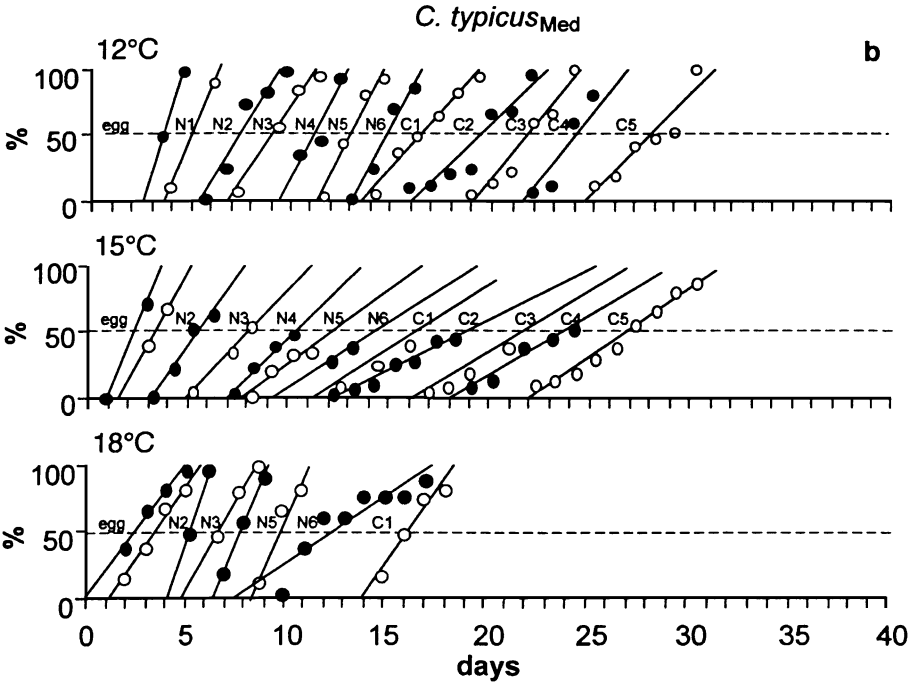
Fig. 10. Hatching success of eggs incubated at different temperatures.

egg production was similar in both populations with a slightly higher maximum of *C. typicus*$_{Med}$ (Fig. 7a,d).

Complementary experiments with *C. typicus*$_{Med}$ (Fig. 15) showed very similar RTR in November, March and May, indicating independence from season. Optimum temperature of egg production remained invariable at 20 °C, only the magnitude of egg production varied seasonally, while body size was almost constant. Likely, the seasonal variability of ETR was not significant (Fig. 9d).

The lower temperature limit of embryonic development was 5 °C in both populations, although females were able to produce eggs at 2 °C in the North Sea. At the upper temperature range, embryonic duration was shortest at 25 °C at both stations. At 28 °C, hatching was retarded in Mediterranean eggs; no data were available for the North Sea (Fig. 9a,d).


C. typicus NS
a
10°C
15°C
20°C
100
%
50
0
egg
N1
N2
N3
N4
N5
N6
C1
C2
C3
C4
C5
0
5
10
15
20
25
30
35
40
days


C. typicus Med
b
12°C
15°C
18°C
100
%
50
0
egg
N1
N2
N3
N4
N5
N6
C1
C2
C3
C4
C5
0
5
10
15
20
25
30
35
40
days

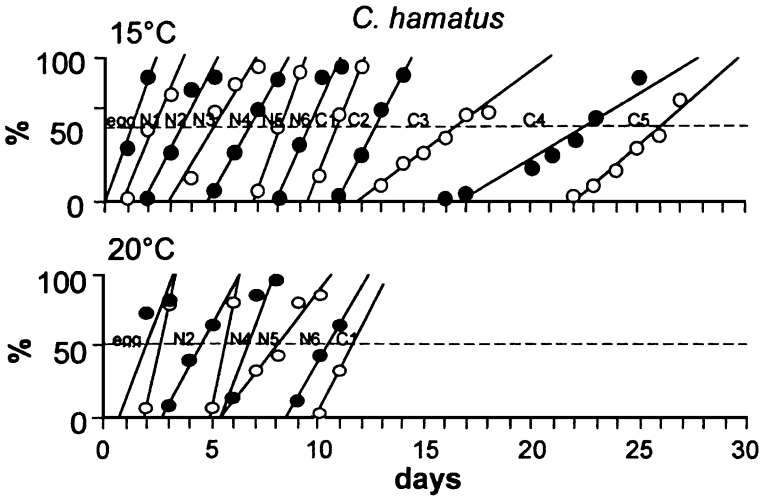


Fig. 12. *C. hamatus*. Stage composition in cohorts reared at different temperatures. For annotations see Fig. 11.

Instars of *C. typicus*$_{Med}$ tended to develop more rapidly than those of *C. typicus*$_{NS}$ at 12 and 15 °C (Fig. 14a–c, Table 5), but not at 18 °C when the culture broke down (Fig. 14c). At 15 and at 12 °C, the generation time of *C. typicus*$_{Med}$ was shorter than that of *C. typicus*$_{NS}$ at 15 °C (Table 4). Equiproportional development was found in *C. typicus*$_{Med}$ at 12 and 15 °C and to a less degree in *C. typicus*$_{NS}$, where proportions of all stages except CV were greater at 20 °C than at 15 °C. Relative stage duration compared between study sites showed no equiproportionality (Table 6). Mortality rates of nauplii$_{NS}$ were lowest at 15 °C with 0.014 day^{-1}, increasing both at 10 and 18 °C to 0.086 and 0.088 day^{-1}, respectively (Table 3). The opposite occurred for copepodites$_{NS}$, which had higher mortality rates at 15 °C (0.116 day^{-1}) than at 20 °C (0.012 day^{-1}). Mortality rates of nauplii$_{Med}$ and copepodites$_{Med}$ were very similar and decreased constantly with increasing temperature from 0.1 day^{-1} at 12 °C to 0.001 day^{-1} at 18 °C (Table 3).

3.2.2. C. typicus and C. hamatus in the North Sea

FTT differed between both congeners (Table 5). *C. typicus* was more sensitive to low temperatures. In *C. hamatus*, in contrast, mortality was much higher at any temperature >5 °C.

The temperature range of egg production was the same in both species (2–25 °C), but optima were different. *C. typicus* had highest egg production rates at 20 °C (54 eggs female^{-1} day^{-1}), *C. hamatus* at 12.5 °C (12.1 eggs female^{-1} day^{-1}) with high standard deviations at 15 and 20 °C (Fig. 6a,b).

Fig. 11. *C. typicus*. Stage composition in cohorts reared at different temperatures. Symbols show cumulative percentage of the population having completed a given moult versus time. Open and closed circles alternate for adjacent stages. Indices $_{NS}$ and $_{Med}$ = North Sea and Mediterranean.

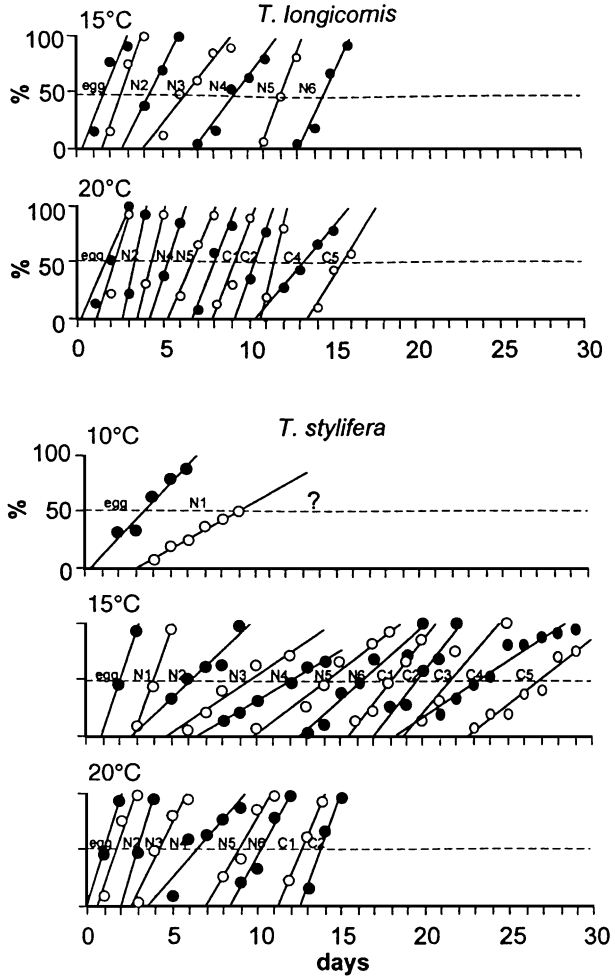


Fig. 13. *T. longicornis* and *T. stylifera*. Stage composition in cohorts reared at different temperatures. For annotations see Fig. 11.

Egg development times between congeners were nearly the same between 10 and 20 °C. At lower temperatures, *C. typicus* eggs had shorter development times. Embryos of *C. typicus* developed most quickly at 25 °C, those of *C. hamatus* at 22.5 °C with a prolonged development at 25 °C (Fig. 9a,b). Hatching success was more variable in *C. hamatus* (Fig. 10a,b).

Stage development showed similar patterns in both species with short stage durations in nauplii and slowest development in late copepodites (Fig. 14b,d). Nauplii of *C. hamatus* developed more rapidly (9.4 days) than nauplii of *C. typicus* (13.2 days) at 15 °C from egg to CI, respectively (Table 4). At 20 °C, development of eggs, NII and NVI of *C. hamatus* was retarded as compared to 15 °C and thus was slower than in *C. typicus* (Fig. 14c,e).

Table 3
Stage durations (day) and mortality rates (day^{-1}) of *C. typicus*, *C. hamatus*, *T. longicornis* and *T. stylifera* at different temperatures

	North Sea							Mediterranean					
	C. typicus			*C. hamatus*		*T. longicornis*		*C. typicus*			*T. stylifera*		
	10 °C	15 °C	20 °C	15 °C	20 °C	15 °C	20 °C	12 °C	15 °C	18 °C	10 °C	15 °C	20 °C
Instar													
Egg	4.70	1.54	0.72	1.21	1.93	1.69	1.75	3.28	2.32	1.56	3.47	1.94	1.05
NI	2.04	1.08	0.89	1.04	0.66	0.98	0.50	1.48	1.39	0.92	5.35	1.60	0.67
NII	3.12	1.74	1.02	1.26	1.83	1.68	1.13	2.55	2.24	1.51		2.30	1.30
NIII	2.50	1.82	1.36	1.50	1.16	2.08	0.93	0.97	2.06	1.03		2.81	1.18
NIV	1.58	2.30	1.02	1.60	1.05	2.79	0.92	1.28	1.65	1.80		1.66	2.20
NV	2.76	2.57	0.79	1.43	1.27	2.86	1.46	1.69	1.52	2.04		1.54	2.47
NVI	3.79	2.14	0.95	1.35	2.46	2.65	1.27	2.63	1.71	2.39		1.70	1.28
CI	4.87	2.59	1.15	1.50	1.25		1.14	2.71	2.30	4.00		1.70	2.51
CII	4.08	3.22	1.00	1.73			1.21	1.69	2.68			1.44	1.04
CIII		3.98	2.56	4.06			1.15	2.86	2.78			2.76	
CIV		9.43	1.13	5.31			1.67	2.65	2.52			2.11	
CV		4.41	3.27	4.05			2.31	3.48	3.80			2.65	
Mortality (day^{-1})													
Egg–CI	0.050	0.030	0.012	0.038	0.165	0.150	0.172	0.101	0.034	0.001		0.092	0.339
CI–adult		0.172	0.012	0.045			0.103	0.102	0.055			−0.020	

Development times were equiproportional in both congeners at 15 °C (Table 6). Mortality rates of nauplii and copepodites were the same in *C. hamatus*, while copepodites of *C. typicus* suffered much higher mortality than nauplii (Table 3). Mortality increased considerably from 15 to 20 °C both in *C. hamatus* and *C. typicus* nauplii (Table 3).

3.2.3. T. longicornis (North Sea) and T. stylifera (Mediterranean)

The two *Temora* species considered here showed quite different FTT (Table 5). *T. stylifera* females stayed alive and maintained reproduction up to 30 °C (Figs. 5e and 6e), whereas *T. longicornis* could not withstand temperatures above 22.5 °C (Fig. 4c). Optimal survival of *T. stylifera* occurred at 10 and 15 °C, while 2 and 5 °C were lethal. The mortality observed at 20 °C can be considered as suspect (Fig. 4e). *T. longicornis* showed low mortality between 0 and 22.5 °C without any clear optimum (Fig. 4c).

RTR also differed between the *Temora* congeners. Egg production of *T. longicornis* ranged between 5 and 10 eggs female^{-1} day^{-1} from 0 to 15 °C, peaked at 20 °C with 18.8 eggs female^{-1} day^{-1} and decreased sharply at 22.5 °C (Fig. 6c). In contrast, *T.*

Notes to Table 4:
NS = North Sea, M = Mediterranean, A = Atlantic.
I.g. = *Isochrysis galbana*, H.e. = *Hymenomonas elongata*, T.s. = *Tetraselmis suecica*, D.t. = *Dunalliella tertiolecta*, T.w. = *Thalassiosira weissflogii*, T.r. = *Thalassiosira rotula*, R.b. = *Rodomonas baltica*, R.sp. = *Rhodomonas* sp., O.m. = *Oxyrrhis marina*.

Table 4
Egg production rates (EPR) and development times of *C. typicus*, *C. hamatus*, *T. longicornis* and *T. stylifera*

Species		*T* [°C]	Food	EPR	Egg–CI [day]	CI–adult [day]	Generation time [day]	Definition	Reference
C. typicus	NS	2	I.g./H.e.	2.9					this study
	NS	5	I.g./H.e.	10.3					this study
	M	5	I.g./H.e.	5.0					this study
	NS	7.5	I.g./H.e.	15.8					this study
	M	8	I.g./H.e.						this study
	NS	10	I.g./H.e.	28.7	19.9			egg–adult	this study
									this study
	A	10	T.w.		23.0	26.0	49.0	egg–adult	Smith and Lane, 1985
	M	12	I.g./H.e.		13.9	13.4	27.3	egg–adult	this study
	NS	15	I.g./H.e.	27.8	13.2	23.6	36.8	egg–adult	this study
	M	15	I.g./H.e.	20.0	12.9	14.1	27.0	egg–adult	this study
	NS	17	R.b./O.m.		5.8 NII–CI	8.9	14.6	NII–adult	Fryd et al., 1991
	M	18	I.g./H.e.		11.3			egg–adult	this study
	A	18–19	mixed		9–11	10–12	19–23	egg–adult	Lawson and Grice, 1970
	M	18–20	in situ		8.0	20.0	28.0	egg–adult	Gaudy, 1976
	NS	20	I.g./H.e.	64.7	7.3	9.1	15.9	egg–adult	this study
	M	20	I.g./H.e.	34.1					this study
	M	20	T.s.				25.0	egg–maturity	Le Ruyet-Person et al., 1975
	NS	22.5	I.g./H.e.	44.3					this study
	NS	25	I.g./H.e.	28.1					this study
	M	25	I.g./H.e.	20.7					this study
C. hamatus	NS	2	I.g./H.e.	4.6					this study
	NS	5	I.g./H.e.	3.3					this study
	NS	10	I.g./H.e.	7.6					this study
		≈7–10	in situ				≈25	egg–adult	McLaren, 1978
		≈10–14	in situ				≈20	egg–adult	McLaren, 1978
	NS	12.5	I.g./H.e.	12.1					this study
	NS	15	I.g./H.e.	7.1	9.4	16.7	26.0	egg–adult	this study
	NS	17	R.b./O.m.		7.3 NII–CI	8.8	16.1	NII–adult	Fryd et al., 1991
	NS	20	I.g./H.e.	8.3	10.4			egg–adult	this study
	NS	20	T.s.				22.0	egg–maturity	Le Ruyet-Person et al., 1975
	NS	25	I.g./H.e.	7.6					this study

T. longicornis	NS	0	D.t.	8.5					this study
	NS	2	I.g./H.e.	5.3					this study
	A	≈2–8	in situ				62.0	egg–adult	Peterson and Kimmerer, 1995
	A	4.1	I.g.	4.7					Corkett and Zilioux, 1975
	NS	5	O.m., R.sp., I.g.		30.1	31.1	61.2	egg–adult	Klein-Breteler and Gonzales, 1986
	NS	5	I.g./H.e.	3.9					this study
		8.5	in situ				39	egg–adult	McLaren, 1978
	A	≈8–15	in situ				≈30	egg–adult	Peterson and Kimmerer, 1995
		9.5	I.g.	7.6					Corkett and Zilioux, 1975
	NS	10	I.g./H.e.	6.5					this study
	NS	10	O.m., R.sp., I.g.		13.7	16.4	30.0	egg–adult	Klein-Breteler and Gonzales, 1986
		10–13	in situ				35	egg–adult	McLaren, 1978
	NS	12.5	T.r.		13.1		28.2	egg–adult	Harris and Paffenhöfer, 1976
	NS	15	I.g./H.e.	8.8	14.7			egg–adult	this study
	NS	15	O.m., R.sp., I.g.		8.8	11.7	20.5	egg–adult	Klein-Breteler and Gonzales, 1986
		15.4	I.g.	17.3					Corkett and Zilioux, 1975
	NS	20	I.g./H.e.	18.8	8.0	7.5	15.4	egg–adult	this study
	NS	20	T.s.				21.0	egg–maturity	Le Ruyet-Person et al., 1975
	NS	20	O.m., R.sp., I.g.		7.8	8.9	16.6	egg–adult	Klein-Breteler and Gonzales, 1986
	NS	22.5	I.g./H.e.	7.5					this study
T. stylifera	M	8	I.g./H.e.	5.3					this study
	M	10	I.g./H.e.	15.3					this study
	M	15	I.g./H.e.	25.7	16.37	10.49	26.86	egg–adult	this study
	M	16	H.e.	40.0					Abou Debs and Nival, 1983
	M	16–17	H.e.			16.00			Abou Debs, 1979
	M	18	mixed		9.00	12.00	21.00	egg–adult	Nassogne, 1972
	M	20	I.g./H.e.	12.3	10.15			egg–adult	this study
	M	22	H.e.		8.00	9.94 C2–ad			Carlotti and Nival, 1991
	M	25	I.g./H.e.	13.4					this study
	M	30	I.g./H.e.	5.8					this study

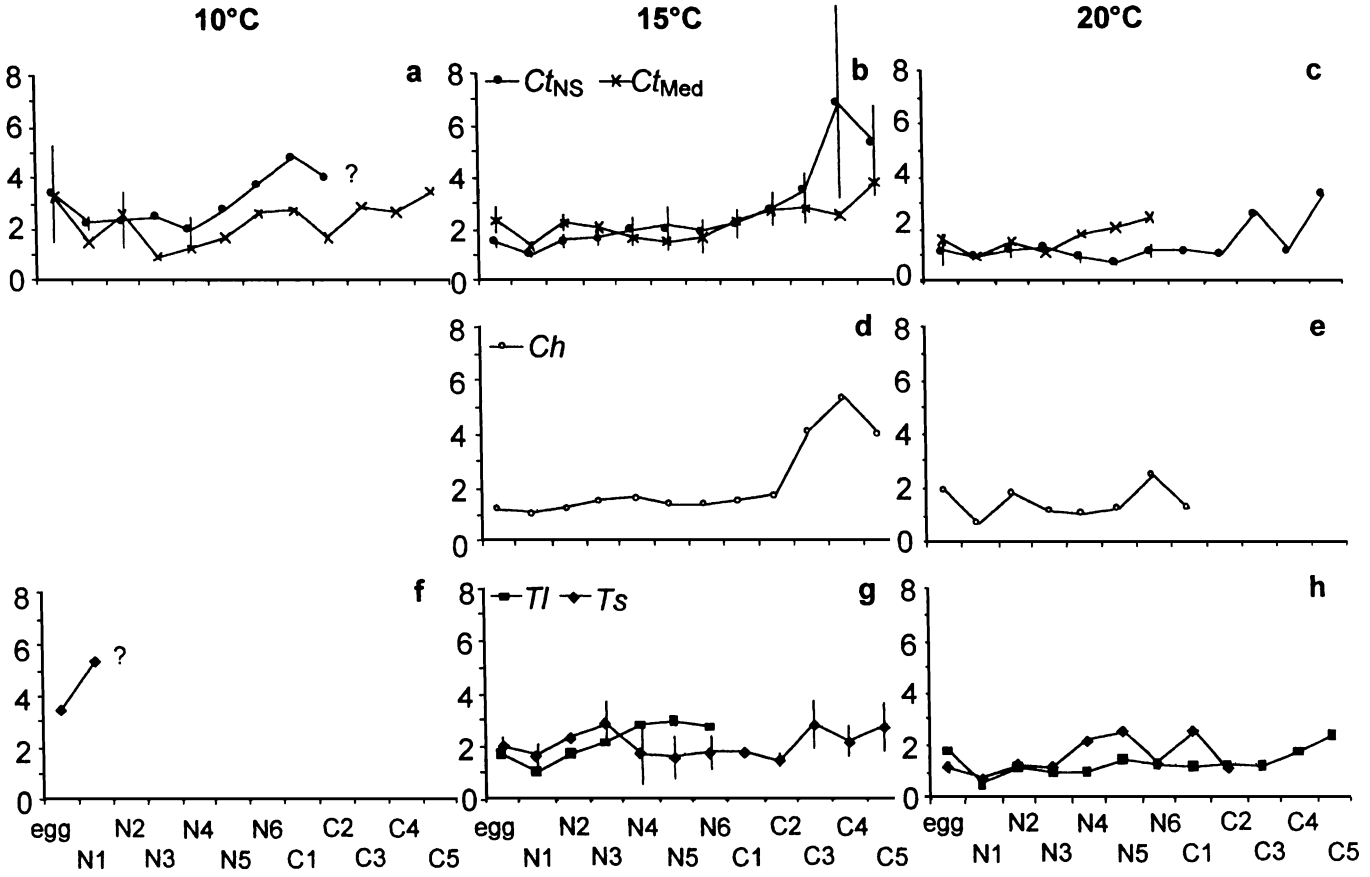


Fig. 14. Stage durations of developmental instars from rearing experiments.

Table 5
Synthesis of results from incubations in a temperature gradient from 0 to 35 °C

Species	FTT		RTR		ETR	
	Lethal (°C)	Optimum (°C)	Range (°C)	Optimum (°C)	Range (°C)	Optimum (°C)
C. typicus$_{NS}$	30	5–10	2–25	20	5–25	25
C. hamatus	25	5	2–25	12.5	2–25	22.5
C. typicus$_{Med}$	2/30	10–15	5–25	20	5–28	25
T. longicornis	25	2–22.5	0–22.5	20	0–22.5	22.5
T. stylifera	2/30	10–15	8–30	15	10–28	28

Female thermal tolerance (FTT), reproductive thermal response (RTR) and embryonic thermal response (ETR).

stylifera produced no eggs below 8 °C; the optimum occurred at 15 °C with 25.7 eggs female^{-1} day^{-1}, at higher temperatures the egg production rates declined (Fig. 6e).

ETR showed different tolerance limits for *T. longicornis* (0–22.5 °C) and *T. stylifera* (10–28 °C; Table 5). The Belehrádek function of *T. stylifera* had a similar curvilinearity as that of *T. longicornis* in March, but was displaced towards higher temperatures (Fig. 9c,e). Cold temperatures inhibited development of *T. stylifera* embryos. No nauplii hatched below 10 °C and the proportion of viable eggs increased with temperature from 10 to 20 °C and slightly decreased at 25 °C (Fig. 10e). In contrast, hatching success of *T. longicornis* was high at all temperatures between 2 and 22.5 °C, but no eggs developed beyond this limit (Fig. 10c).

A seasonal comparison of ETR was available for *T. longicornis* (Fig. 9c). Eggs developed relatively quickly at low temperatures in summer, but slower in winter. In March 1996, embryos needed more time to hatch at a given temperature than in June 1996 ($p < 0.0001$), and than from June to September 1999 ($p < 0.0001$). The difference was less significant between June 1996 and June to September 1999 ($p < 0.01$).

Stage durations of nauplii were slightly shorter in *T. longicornis* than in *T. stylifera* at 15 and 20 °C (Table 3). Development times of *T. longicornis* decreased from 15 to 20 °C, while NIV, NV and CI of *T. stylifera* developed more quickly at 15 °C than at 20 °C (Fig. 14f–h). At 10 °C, no development was observed beyond NI in *T. stylifera* (Fig. 14f). Relative development times of both congeners were equiproportional (Table 6). Mortality rates of *T. longicornis* were 0.150 and 0.172 day^{-1} for nauplii at 15 and 20 °C,

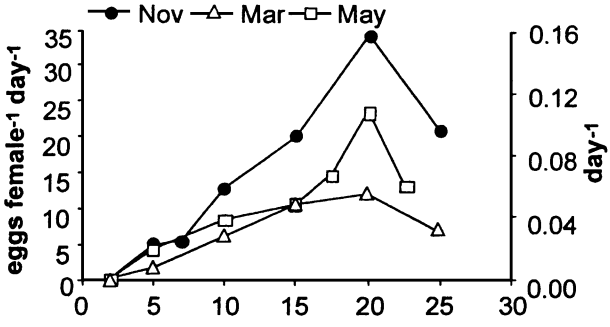


Fig. 15. Seasonal variation of egg production of *C. typicus* in the Mediterranean.

Table 6
Proportion of total development time (egg-laying to adult) spent in each stage (= cumulative median development time/generation time)

	Ct$_{NS}$	*Ct*$_{NS}$	*Ct*$_{Med}$	*Ct*$_{Med}$	*Ch*	*Tl*	*Ts*
	15 °C	20 °C	12 °C	15 °C	15 °C	20 °C	15 °C
NI	0.04	0.05	0.12	0.09	0.05	0.11	0.09
NII	0.07	0.10	0.17	0.14	0.09	0.15	0.14
NIII	0.12	0.17	0.27	0.22	0.13	0.22	0.22
NIV	0.17	0.25	0.30	0.30	0.19	0.28	0.30
NV	0.23	0.32	0.35	0.36	0.25	0.34	0.36
NVI	0.30	0.37	0.41	0.41	0.31	0.43	0.41
CI	0.36	0.43	0.51	0.48	0.36	0.52	0.48
CII	0.43	0.50	0.61	0.56	0.42	0.59	0.56
CIII	0.51	0.56	0.67	0.66	0.48	0.67	0.66
CIV	0.62	0.72	0.78	0.76	0.64	0.74	0.76
CV	0.88	0.79	0.87	0.86	0.84	0.85	0.86
Adult	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Ct = *C. typicus*, *Ch* = *C. hamatus*, *Tl* = *T. longicornis*, *Ts* = *T. stylifera*.

respectively, and 0.103 day^{-1} for copepodites at 20 °C (Table 3). *T. stylifera* had very high death rates in nauplii at 20 °C (0.339 day^{-1}) prior to collapse of the culture and thus were considered as artefact. At 15 °C, nauplii mortality was 0.092 day^{-1}. Negative mortality was observed in copepodites (Table 3), due to the sampling technique, i.e. a misrepresentation of specimens in the subsamples, which is attributed to inefficient mixing of the culture before sampling.

4. Discussion

4.1. General responses of life history traits

Temperature affected all phases of the copepod life cycle considered here. Like in many poikilotherms, temperature response was not fixed but showed a suite of adaptational mechanisms. Response patterns to varying temperatures were (1) optimum curves of survival and reproduction over a wide range of temperatures, (2) Belehrádek functions of embryonic development and (3) equiproportional development of instars. These responses often varied between congener species and locations.

4.1.1. Thermal tolerance limits

The thermal ranges were rather similar in all parameters considered (Table 5). However, in some cases, a slight decrease of tolerance was observed in subsequent life phases, e.g. in *T. stylifera* whose temperature range was wider for female survival than for reproduction and even narrower for embryonic development.

Heat death occurred in all species, except *T. stylifera*, at 30 °C or below, indicating that this temperature represents a threshold beyond which a selective measure is necessary to ascertain survival, e.g. the production of heat shock proteins reported for various marine

organisms (Burdon, 1987; Hofmann, 1999). Depression of development rate (i.e. increasing development time) as an expression of physiological inefficiency at the upper end of a species' thermal range has been reported for embryos of *A. clausi*, *T. stylifera* and *C. chierchiae* (Landry, 1975; Bernard, 1971). We also observed prolonged embryonic duration at 25 °C or above, both in the North Sea (*C. hamatus*) and in the Mediterranean (*C. typicus*).

Cold death occurred below 5 °C in warm-acclimated individuals of the Mediterranean. The lower temperature limit of the boreal species was missed during this study and may be around the freezing point of seawater.

4.1.2. Optimum curves

Survival and reproduction rate are optimum functions of temperature under saturating food conditions, increasing up to the optimum and decreasing beyond (Corkett and Zilioux, 1975; Uye, 1981; Kimoto et al., 1986). All species investigated followed this pattern, with differences in tolerance limits and optimal temperatures (Table 5). The optima of reproduction differed between the congeners *C. typicus* and *C. hamatus*, while intraspecific variability was restricted to a shift in the lower tolerance limit of *C. typicus* from different locations. The *Temora* congeners clearly distinguished in their optima and tolerance limits. *T. longicornis* showed increasing egg production rates between between 0 and 20 °C, matching the values reported by Corkett and Zilioux (1975) (Table 4). *T. stylifera*, in contrast, showed highest reproductive activity at 15 °C with declining rates at higher and lower temperatures according to Abou-Debs and Nival (1983) (Table 4).

4.1.3. Belehrádek curves

Belehrádek's function $D = a(T - \alpha)^b$ has been widely used in the literature to describe the temperature response of development. In our study, embryonic development followed Belehrádek functions in all species studied (Table 2). The constant b is assumed to be -2.05 for all copepod species (McLaren et al., 1969; Landry, 1975; Ambler, 1985) and therefore was also used in our equations. The curve of *C. typicus*$_{NS}$ corresponded to that of *C. typicus*$_{Med}$ in autumn, while the equation derived by McLaren et al. (1989) from Atlantic specimens matched best with our equation from May (Table 2). Abou-Debs and Nival (1983) presented to equations for *T. stylifera* embryos from spring and autumn. Our curve from November matched their values at temperatures >15 °C, but did not confirm the very high "biological zero" they suggest for the development of offspring of warm-acclimated parents.

Embryonic development time has been primarily attributed to egg size both on a seasonal and latitudinal scale (Corkett, 1972; Lonsdale and Levinton, 1985), with larger eggs from larger females having lower metabolic rates than smaller eggs due to lower oxygen diffusion rates. During our study, egg-size was almost constant throughout the study period in all species (Halsband-Lenk, unpublished). Therefore, parental influences due to acclimation (Landry, 1975) and heredity (Fujisawa, 1995) seem more likely to influence ETR in this case.

A fast embryonic development seems advantageous to reduce predation pressure on motionless eggs, which increases with the time needed until hatching (Ohman, 1986). Moreover, a long non-swimming phase denotes a high risk of loss below the euphotic zone

or to the sediment in shallow shelf regions. Thus, short embryonic duration at low temperature was observed in embryos of *T. longicornis* and *C. typicus*$_{NS}$. *C. hamatus*, in contrast, has established other adaptations to low temperature, switching from the production of subitanous eggs to diapause eggs in fall (Grice and Marcus, 1981).

4.1.4. Equiproportional development

The thermal response of post-embryonic development followed the patterns described by Landry (1983): the first non-feeding stage (NI) developed quickly, while the first feeding stage (NII) was prolonged. Thereafter, development in some experiments approximated isochronal development (e.g. *C. hamatus* at 15 °C and *T. longicornis* at 20 °C). The late copepodites CIV (*C. typicus*$_{NS}$ and *C. hamatus*) or CV (*C. typicus*$_{Med}$, *T. stylifera*, *T. longicornis*) again had increased stage durations, probably due to formation of reproductive products prior to adulthood (Fryd et al., 1991). Equiproportional development as defined by Corkett and McLaren (1984) means that the relative proportion of the generation time spent in each stage is the same regardless temperature. *C. typicus* was reported to follow this rule (Fryd et al., 1991), and we found equiproportional development both in *C. typicus*$_{NS}$ and *C. typicus*$_{Med}$ (Table 6). Relative development times did not match in *C. typicus* populations from different locations, but those of the congeners *C. typicus*$_{NS}$ and *C. hamatus* and of *T. longicornis* and *T. stylifera* were very close (Table 6).

Literature and our results showed shortest generation time at 20 °C for all species investigated (Klein Breteler et al., 1994; Klein Breteler and Gonzales, 1986). However, we found that stage duration did not consistently decrease with increasing temperature. This might indicate thermal stress of some specific developmental stages at high temperatures in the boreal populations *C. hamatus* and *T. longicornis*, but also in both Mediterranean populations.

Generation time at a given temperature was similar for all species (Table 4) and fell in the range of the temperature function presented by Huntley and Lopez (1992, Fig. 3).

4.2. Adaptational responses

4.2.1. Seasonal variations

Seasonal variations in the temperature response of reproduction, investigated here for *C. typicus*$_{Med}$, were restricted to the absolute number of eggs produced, reflecting different reproductive potential of females in different seasons, while RTR remained constant. The same was observed for *T. stylifera* (Abou-Debs and Nival, 1983), which produced more eggs in March than in October at three experimental temperatures, while the optimum remained at 16 °C. The variations in absolute egg numbers might be due to different age structure of the population (proportion of spent females), different nutritional state and/or body size of females (Uye, 1981).

T. longicornis embryos showed seasonal alterations of ETR. Eggs laid in March 1996 during a cold winter developed more slowly at a given temperature than in summer. Many authors observed shorter egg development times in eggs of warm-acclimated parents (Ambler, 1985; Tester, 1982), while Landry (1975) observed the opposite: cold-acclimated eggs of *A. clausi* hatched faster at a given temperature than their counterparts

in summer. He concluded that enhanced metabolic rates are an acclimation response of cold-adapted embryos to high temperatures. Abou-Debs and Nival (1983) found much slower development at low temperatures in eggs produced in autumn than in spring and concluded that warm acclimated embryos have a much higher ''biological zero'', while those produced in cold spring matched the development times of Atlantic species. Hart and McLaren (1978) emphasized the opposing effects of long-term (seasonal) and short-term acclimation responses suggesting that seasonal temperature compensation is overridden by size effects and heredity of embryonic duration in the field. Besides adaptation effects, both geographical and seasonal differences in ETR might additionally reflect varying nutritional investment of females in the yolk of their eggs, depending on the quantity and quality of available food (Lonsdale and Levinton, 1985; Jónasdóttir, 1994).

4.2.2. Regional variations

The Belehrádek curves of cold-acclimated North Sea embryos were displaced by about 5° towards lower temperatures in relation to the curves of their Mediterranean congeners (Fig. 9). Post-embryonic stages of *C. typicus* tended to develop more quickly in the Mediterranean than in the North Sea at all temperatures investigated (Fig. 14), suggesting an influence of body size as postulated by Vidal (1980), who stated that smaller individuals have shorter stage durations than larger ones.

4.3. Geographic distribution and thermal response

When our results are compared with field data, a mismatch between RTR in the laboratory and reproduction peaks in the field became apparent. While the temperature optima of egg-laying differed considerably between *C. hamatus* and *T. longicornis* in our experiments, in the North Sea their reproduction peaks occurred simultaneously in spring at 5–10 °C in situ temperature (van Rijswijk et al., 1989; Halsband and Hirche, 2001). Egg production rate was controlled by body size which in turn was related to temperature (Halsband and Hirche, 2001). Analogously, in the Bay of Villefranche in situ reproduction peaks of *C. typicus*$_{\mathrm{Med}}$ and *T. stylifera* coincided in autumn when females were largest (Halsband-Lenk et al., 2001), while temperature optima in the laboratory were different. There, body size appeared to be less influenced by temperature, eventually due to the narrow annual temperature range. This was different from *C. typicus* in the Gulf of Naples, where maximal egg production rates were recorded in spring (Ianora and Buttino, 1990). Possibly, autumn temperatures are still too high in that shallower region to favour high reproduction rates in this species.

However, specific temperature preferences of individuals seem to be overridden by body size-related reproductive potential at sea. Body size is negatively related to temperature and consequently, the bigger specimens of *C. typicus*$_{\mathrm{NS}}$ produced more eggs per day than their smaller counterparts in the Mediterranean, constant egg size provided. Accordingly, similar sized females produced similar numbers of eggs, like *T. longicornis* and *T. stylifera*. Weight specific egg production eliminated size differences and was similar among congeners. The values were lower than those reviewed by Kiørbœ and Sabatini (1995).

4.3.1. Centropages sp.

The comparison of *C. typicus* in two different temperature regimes shows that the species is eurytherm and could shift its tolerance range dynamically to the temperature window of a specific environment. Thus, this species is most independent of temperature and could establish a wide distribution in the North and Middle Atlantic and adjacent seas. The shift of tolerance towards lower temperatures in the North Sea indicates adaptation and temperature compensation. In how far this shift is genetically fixed, as described for benthic organisms and insects with populations along a latitudinal temperature gradient (Hummel et al., 1997; Dahlhoff and Rank, 2000), needs further investigation.

Regarding the congeners in the North Sea, they showed distinct FTT in our experiments, with *C. typicus* favouring intermediate and *C. hamatus* low temperatures. The optima of RTR were congruent with the temperature ranges they encounter during their successive reproduction periods in the North Sea. Both *C. typicus* and *C. hamatus* disappear regularly from the water column in winter, but overwintering strategies are different. *C. hamatus* produces resting eggs, which persist unfavourable conditions in the sediment (Lindley, 1990; Marcus, 1996). *C. typicus* depends on a recurring input from the Atlantic with the inflow of relatively warm water (Fransz et al., 1991) and thus probably overwinters in more temperate regions like the English Channel (Le-Ruyet Person et al., 1975). Thus, the latitudinal and seasonal distribution patterns of both congeners reflect clearly the temperature limits of their survival and reproduction as revealed during our experiments. While *C. typicus* occurs in waters from the subarctic to the tropics, *C. hamatus* needs to outlast too cold and too warm conditions outside the water column (Fig. 1).

4.3.2. Temora sp.

The differences of thermal tolerance between these congeners confirmed the classification as a cold-temperate (*T. longicornis*) and a warm-temperate species (*T. stylifera*) and hence their geographic distribution. *T. longicornis* tolerated the whole temperature range found in the North Sea as expected from its perennial occurrence there. The fact that it could not withstand temperatures >22.5 °C, explains its absence from warmer environments and its restriction to the northern hemisphere with a southern boundary coinciding with the 20 °C isotherm of the Atlantic in summer (Lindau, 2001).

T. stylifera, in contrast, was the only species that could survive temperatures >25 °C, at least in the adult stage, and is accordingly distributed in lower latitudes. Limitation to the north corresponded to the 10 °C isotherm in winter (Lindau, 2001), representing probably the northern margin of reproductive success, while its occurrence in the English Channel seems more likely a result of advection. However, the thermal optimum of FTT and RTR at 10–15 °C (Table 5) seemed at first sight surprisingly low, since *T. stylifera* is considered as a warm-temperate species (Table 1). On the other hand, Abou-Debs and Nival (1983) also found an optimum of RTR at 16 °C and declining egg production rates towards the temperature extremes of their Mediterranean habitat (13 and 23 °C). In fact, *T. stylifera* reproduces mainly during autumnal cooling in the western Mediterranean (Halsband-Lenk et al., 2001). Similar to FTT and RTR, development of some instars was favoured at 15 °C. At 10 °C, no development was possible in culture. Assuming that population development takes place in autumn following the reproduction peak, the preference of a low autumnal

temperature matched the species' life strategy in situ. Although the limits of temperature tolerance would allow survival and development at higher temperatures, *T. stylifera* tended to prefer intermediate temperatures in the Mediterranean, possibly to avoid resource competition with other copepods (Razouls, 1974). Consequently, thermal tolerance was not necessarily correlated with the optimum.

4.4. Conclusion

Despite intraspecific variability, the temperature responses recorded in this study were related to the geographical distribution of the species investigated, with the most northerly species having the lowest minimal temperatures and vice versa. Thus, our results indicate that thermal tolerance of survival, reproduction and development may at least partly determine horizontal and seasonal distribution patterns of these species. Beside temperature, other aspects could be decisive, e.g. other abiotic factors, such as salinity (Gaudy et al., 2000), or biotic factors, e.g. behaviour or ontogeny. Moreover, our results were obtained using mono-algal food cultures, so that the variations in food quantity and quality could possibly modify growth and reproduction rates in the field. Behavioural traits like migration, swimming and escape behaviour may determine mortality patterns (Ohman, 1990) and thus temporal distribution of species, while different life cycle strategies (e.g. undergoing diapause or not) can be responsible for seasonal succession of species.

In a given environment, interactions between species lead to extinction of less adapted species and dominance of better adapted ones, resulting in a specific spatial and temporal species composition. A shift in temperature, either on a latitudinal or a seasonal scale, will modify these interactions and result in a changed combination of species, e.g. as result of climatic changes like global warming. An assessment of the impact of such long-term changes on the zooplankton communities requires more information on how populations respond to critical temperatures, both from an ecological and physiological approach.

Acknowledgements

C.H.L. was supported by a grant of the French Government (CROUS No. 12478) and within the framework of the PROCOPE Project No. 98179 of DAAD (Germany) and APAPE (France) granted to H.J.H. and F.C. The research work was supported by the programme PNEC-ART2 (1998–1999) and the programme Réseau Diversité Marine (1998–2000) granted to F.C. **[RW]**

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