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Aus dem

ALFRED-WEGENER-INSTITUT FÜR POLAR- UND MEERESFORSCHUNG

Bremerhaven

Temperature impact on reproduction and development of congener marine copepods – a key to distribution patterns?

Claudia HALSBAND-LENK

geb. am 9. März 1971 in Bochum

Vom Fachbereich 7 – Biologie, Geo- und Umweltwissenschaften – der Universität Oldenburg zur Erlangung des Grades einer Doktorin der Naturwissenschaften (Dr. rer. nat.) angenommene Dissertation

Erstreferent: Prof. H.K. Schminke

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If children took a moment to look at copepods,
they would forget about dinosaurs!

Mark D. Ohman
Scripps Institute of Oceanography
University of California, San Diego, USA

CONTENTS

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ABBREVIATIONS

CEPR	Corrected egg production rate [eggs female^{-1} day^{-1}]
Chl_a	Chlorophyll a [µg l^{-1}]
CI – CVI	Copepodite stages I – V (1-6 in Figs.)
EPR	Egg production rate [eggs female^{-1} day^{-1}]
ETR	Embryonic thermal response
FTT	Female thermal tolerance
NI – NVI	Naupliar stages I – VI (1 – 6 in Figs.)
PL	Prosome length [µm]
PPC	Particulate phytoplankton carbon [µg l^{-1}]
RTR	Reproductive thermal response
T	Temperature [°C]

SUMMARY

The present study investigated the annual life cycles of four free-spawning copepod species, thereof two congener pairs, which differentiate in their geographical and/or seasonal distribution patterns. These pairs are *Temora longicornis* and *T. stylifera*, as well as *Centropages hamatus* and *C. typicus*, respectively. The boreal *T. longicornis* occurs farthermost north and has hardly any overlap with its warm-temperate congener *T. stylifera*, which has a southern distribution. The two *Centropages* species represent a homologous pair, with the cold-temperate *C. hamatus* and the southern-intermediate *C. typicus*. The distribution patterns of these species let assume that temperature is a major factor for copepod population dynamics and distribution. Two sampling stations were chosen with respect to the different temperature regimes prevailing there, (1) Helgoland Roads in the southern North Sea, where *T. longicornis*, *C. hamatus* and *C. typicus* at times co-occur and (2) the Bay of Villefranche-sur-Mer in the north-western Mediterranean Sea, where *T. stylifera* and *C. typicus* are present year round, but with successive abundance peaks.

A field study focused mainly on the reproductive strategies of these species. Prosome length, egg production rate, clutch size, number of spawning females and their carbon content were determined *in situ* and related to temperature and phytoplankton concentration at both stations under identical experimental conditions over several years.

In the laboratory, survival of adult females and their egg production, embryonic development and hatching success were studied in a temperature range from 2 to 35°C. Stage development was determined from cohorts raised at temperatures between 10 and 20°C with surplus food.

The results have shown that temperature plays a central role in the life cycles of small calanoid copepods in mid-latitudes. In the North Sea, *T. longicornis* was always present, while *C. hamatus* was absent from the water column from November to April. Both species are known to overwinter as resting eggs in the sediment. The presence of *C. typicus* was irregular in that region at its northern distribution margin, underlying high interannual variability and depending on advection and favourable conditions. The timing of maximum reproductive activity was similar between species and was recorded in April/May, except in *C. typicus*

when it arrived only later in the year. Significant correlations were obtained between clutch size, and thus egg production rate, and prosome length, which in turn was inversely correlated with temperature. It is therefore concluded that temperature controlled egg production via its effect on body size at Helgoland Roads and that food probably was not limiting.

In contrast, oligotrophy governed copepod life in the Mediterranean, where egg production rates were considerably lower, but continuous throughout the year in both *T. stylifera* and *C. typicus*. However, no statistical relationship between reproduction and food availability or temperature was detected. Egg production of *C. typicus* was correlated only with female prosome length.

The laboratory experiments strengthened the assumption of a strong temperature dependence of life cycles and distribution patterns, which seems to be one important source of the observed interannual and regional variability. The thermal ranges were similar in all life phases considered, although in some cases a decrease of tolerance was observed in subsequent phases, e.g. a wider temperature range of female survival than for reproduction and embryonic development. Optima of egg production generally were at higher temperatures than optima of survival. Nevertheless, tolerance limits and optima of female survival, reproduction and development distinguished the northern species *T. longicornis* and *C. hamatus* from the southern *T. stylifera*, while *C. typicus*, which is found in both regions, was intermediate. Thus, thermal preferences can in part explain distribution patterns of these species. While the two *Temora* species and *C. hamatus* 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: thermal optima of egg production and stage development were surprisingly low in *T. stylifera*, which has a mere southern distribution.

RÉSUMÉ

La présente étude a analysé les cycles annuels de vie de quatre copépodes qui pondent leurs œufs directement dans le milieu, dont deux paires congénériques qui se distinguent par leur répartition géographique ou saisonnière. Ces paires sont *Temora longicornis* et *T. stylifera*, ainsi que *Centropages hamatus* et *C. typicus*, respectivement. L'espèce boréale *T. longicornis* se trouve le plus au nord et n'a presque pas de coïncidence avec son pendant tempéré-chaud *T. stylifera*, qui a une répartition méridionale. Les deux espèces de *Centropages* représentent une paire homologue, avec l'espèce tempérée-froide *C. hamatus* et celle méridionale-intermédiaire *C. typicus*. La manière dont se répartissent ces espèces laisse supposer que la température est un facteur principal pour la dynamique des populations de copépodes et leur distribution. Deux stations d'échantillonnage ont été choisies en raison de leurs régimes thermiques différents, (1) la rade d'Helgoland au sud de la Mer du Nord, où *T. longicornis*, *C. hamatus* et *C. typicus* apparaissent temporairement ensembles et (2) la baie de Villefranche-sur-Mer, où *T. stylifera* et *C. typicus* sont présents toute l'année, mais avec des pics d'abondance successifs.

Une étude *in situ* a porté surtout sur les stratégies reproductives des espèces. La longueur du prosome, la production d'œufs, la taille des couvées, le nombre des femelles qui pondent et leur contenu en carbone ont été déterminés en fonction de la température et de la concentration en phytoplancton aux deux stations dans des conditions expérimentales identiques pendant plusieurs années.

En laboratoire, la survie des femelles et leur reproduction, le développement embryonnaire et les taux d'éclosion ont été étudiés dans une gamme de température de 2 à 35°C. Le développement des stades a été examiné par l'élevage de cohortes à des températures de 10 à 20°C dans des conditions de nourriture non limitantes.

Les résultats ont montré que la température joue un rôle primordial dans les cycles de vie des petits copépodes aux latitudes moyennes. En Mer du Nord, *T. longicornis* était constamment présent, tandis que *C. hamatus* était absent de la colonne d'eau de novembre à avril. Tous les deux sont connus pour hiverner dans les sédiments à l'état d'œufs de durée. La présence de *C. typicus* était irrégulière dans cette région à la limite nord de répartition de l'espèce, soumise à une forte

variabilité interannuelle et dépendant de l'advection et de conditions favorables. La période d'activité reproductive maximale était similaire entre les espèces et a été observée en avril/mai, sauf pour *C. typicus* qui arrivait plus tard dans l'année. Des corrélations significatives ont été obtenues entre la taille des couvées, et donc le taux de ponte, et la longueur du prosome, qui, de son côté, était inversement liée à la température. C'est pourquoi on peut conclure que la température a contrôlé la production d'œufs via son effet sur la taille des femelles dans la rade d'Helgoland et que la nourriture probablement n'était pas limitée.

En revanche, la vie des copépodes en Méditerranée était soumise à l'oligotrophie du milieu. La ponte était considérablement plus basse, mais continue toute l'année pour les deux espèces *T. stylifera* et *C. typicus*. Cependant, aucune relation statistique n'a pu être détectée entre la reproduction et la nourriture ou la température, la ponte de *C. typicus* n'étant corrélée qu'avec la taille des femelles.

Les expériences en laboratoire ont renforcé la supposition que les cycles de vie dépendent fortement de la répartition de la température, qui semble une source importante de variabilités interannuelles et régionales. Les gammes thermiques étaient assez similaires dans les phases de vie considérées, bien que parfois une diminution de tolérance ait été observée dans des phases de vie consécutives, p.ex. une tolérance plus grande en ce qui concerne la survie que dans la reproduction ou le développement embryonnaire. Les optima de la reproduction avaient généralement lieu à des températures plus élevées que les optima de survie. Néanmoins, les limites de tolérance et les optima de survie des femelles, la reproduction et le développement ont distingué les espèces du nord *T. longicornis* et *C. hamatus* de l'espèce du sud *T. stylifera*, tandis que *C. typicus*, qu'on trouve dans les deux régions, était intermédiaire. Par conséquent, les préférences thermiques pouvaient en partie expliquer la répartition de ces espèces. Tandis que les deux espèces de *Temora* et *C. hamatus* ont montré des gammes de températures distinctes, *C. typicus* a pu tolérer des conditions thermiques différentes, ce qui explique l'étendue de sa distribution du subarctique aux régions tropicales. De toute façon, la gamme thermique d'une espèce n'était pas forcément liée aux optima dans les expériences en laboratoire: Les optima thermiques de la ponte et du développement étaient étonnamment basses chez *T. stylifera*, qui se rencontre seulement dans le sud.

ZUSAMMENFASSUNG

Die vorliegende Arbeit untersucht die annuellen Lebenszyklen von vier Copepodenarten, die ihre Eier frei ins Wasser ablegen, davon jeweils zwei Artenpaare desselben Genus, die sich in ihrer geographischen oder saisonalen Verteilung unterscheiden. Diese Paare sind einerseits *Temora longicornis* und *T. stylifera*, und andererseits *Centropages hamatus* und *C. typicus*. Die boreale Art *T. longicornis* kommt am weitesten nördlich vor und überschneidet sich kaum mit ihrem warm-gemäßigten Gegenstück *T. stylifera*, das eine südliche Verbreitung besitzt. Die beiden *Centropages*-Arten repräsentieren ein homologes Paar, mit dem kalt-gemäßigten *C. hamatus* und dem südlich-intermediären *C. typicus*. Die Verteilungsmuster dieser Arten lassen vermuten, daß die Temperatur ein entscheidender Faktor für die Populationsdynamik und Verteilung von Copepoden ist. Zwei Probennahmestationen wurden hinsichtlich ihrer Temperaturspektren ausgewählt, (1) die Helgoländer Reede in der südlichen Nordsee, wo *T. longicornis*, *C. hamatus* und *C. typicus* zeitweilig koexistieren und (2) die Bucht von Villefranche-sur-Mer im nordwestlichen Mittelmeer, wo *T. stylifera* und *C. typicus* ganzjährig vertreten sind, allerdings mit saisonal unterschiedlichen Abundanzmaxima.

Eine Feldstudie konzentrierte sich hauptsächlich auf die Reproduktionsstrategien dieser Arten. An beiden Stationen wurden Prosomalängen, Eiproduktionsraten, Gelegegrößen, die Anzahl eierlegender Weibchen und ihr Kohlenstoffgehalt *in situ* unter identischen experimentellen Bedingungen über mehrere Jahre bestimmt und mit der Temperatur und der Futterverfügbarkeit korreliert.

Im Labor wurden Überlebensraten von Weibchen und ihre Eiproduktion, die Embryonalentwicklung und der Schlupferfolg von Gelegen in einem Temperaturgradienten von 2 bis 35°C untersucht. Die Stadienentwicklung wurde anhand von Aufzuchtexperimenten bei Temperaturen zwischen 10 und 20°C und überschüssigem Futterangebot bestimmt.

Die Ergebnisse haben gezeigt, daß die Temperatur in den Lebenszyklen kleiner calanoider Copepoden mittlerer Breiten eine zentrale Rolle spielt. In der Nordsee war *T. longicornis* zu jeder Zeit präsent, während *C. hamatus* von November bis April nicht in der Wassersäule zu finden war. Beide Arten sind dafür bekannt, daß sie im Sediment in Form von Dauereiern überwintern können. Das Vorkommen der Art *C. typicus* war in dieser Region, am nördlichen Rand ihres

Verbreitungsgebietes, starken interannuellen Schwankungen unterworfen und hing von Advektion und für die Art günstigen Bedingungen ab. Das zeitliche Auftreten der maximalen Reproduktionsaktivität war ähnlich unter den Arten, außer bei *C. typicus*, wenn die Art erst später im Jahr auftrat. Es wurden signifikante Korrelationen zwischen der Gelegegröße, und damit auch der Eiproduktionsrate, und der Prosomalänge gefunden, die ihrerseits umgekehrt mit der Temperatur korreliert war. Daraus kann geschlossen werden, daß die Temperatur in der Helgoländer Reede die Eiproduktion über ihren Effekt auf die Körpergröße kontrolliert, wohingegen das Futter anscheinend nicht limitierend war.

Im Gegensatz dazu wurde das Leben der Copepoden im Mittelmeer von der dort herrschenden Oligotrophie beherrscht. Die Eiproduktion war geringer, lief aber sowohl bei *T. stylifera* als auch bei *C. typicus* ganzjährig ab. Dennoch wurde weder zwischen Reproduktion und Futterverfügbarkeit noch zwischen Reproduktion und Temperatur ein signifikanter Zusammenhang ermittelt. Die Eiproduktion von *C. typicus* war einzig mit der Prosomalänge der Weibchen korreliert.

Die Laborexperimente bekräftigten die Annahme einer starken Abhängigkeit der Lebenszyklen und Verteilungsmuster von der Temperatur, die eine wichtige Quelle der beobachteten interannuellen und regionalen Variabilität zu sein scheint. Die Toleranzgrenzen der betrachteten Lebensphasen waren ähnlich, auch wenn in einigen Fällen eine Abnahme der Toleranz in aufeinanderfolgenden Phasen zu beobachten war, z.B. eine höhere Toleranz der Weibchen als der Reproduktion und der Embryonalentwicklung. Die Optima der Eiproduktion lagen im allgemeinen bei höheren Temperaturen als die der Vitalität der Weibchen. Nichtsdestoweniger unterschieden die Toleranzgrenzen und Optima von Weibchenvitalität, Reproduktion und Entwicklung die nördlichen Arten *T. longicornis* und *C. hamatus* von der südlichen Art *T. stylifera*, während *C. typicus*, der in beiden Regionen vorkommt, eine Mittelstellung einnahm. Somit können Temperaturpräferenzen die Verteilungsmuster dieser Arten zum Teil erklären. Während die beiden *Temora*-Arten und *C. hamatus* distinkte Temperaturspektren zeigten, war *C. typicus* in der Lage unterschiedliche Temperaturbedingungen zu tolerieren, die in der weiten Verbreitung von der Subarktis bis in die Tropen resultiert. Das Temperaturspektrum einer Art hing jedoch nicht zwangsläufig mit den Optima der Experimente zusammen: Die Optima der Eiproduktion und der Stadienentwicklung von *T. stylifera* waren überraschend niedrig angesichts der rein südlichen Verbreitung dieser Art.

1 INTRODUCTION

1.1 General overview of temperature effects on marine poikilotherms

The temperature range of the world oceans is relatively narrow, from –2° to 43°C including shallow coastal and brackish estuarine areas. In contrast, in terrestrial ecosystems temperatures may reach -68°C near the poles to 65°C in deserts (KINNE 1963). The annual and daily variations of temperature in the ocean are smallest in the tropics, increase with latitude and decrease again towards the poles. Variability also decreases with depth to more or less stable abyssal temperatures around 4°C (SVERDRUP *et al.* 1964).

For the life of marine invertebrates, temperature is a major environmental entity, affecting both the physico-chemical characteristics of their habitat (e.g. viscosity, dissolved gases, osmotic pressure, etc.) and various biological processes. Temperature represents a unit for molecular motion and determines the rate of biochemical reactions and thus of metabolism, particularly in poikilotherms. Besides absolute temperature values, changes in temperature at various temporal scales can play a role for population dynamics. Daily or seasonal temperature fluctuations, which – possibly correlated with other factors (photoperiod, food availability) – may be a precondition for normal completion of life cycles. The biological effects of a given temperature pattern may differ between populations of the same species, between different life stages or sexes and may reflect the temperature history of the individual. Moreover, present and past effects of other factors (e.g. salinity, oxygen supply) may interact with temperature responses.

Animals may react directly to a change in temperature or show adaptation, i.e. genetic or non-genetic adjustments to thermal alterations that increase their survival, reproductive and competitive capacity. Resistance adaptations comprise cold and heat acclimation to temperature extremes (SCHLIEPER 1966), while capacity adaptations imply modifications of metabolism, reproduction or development within the tolerance range (KINNE 1970).

From a phylogenetic point of view, individual variations of thermal responses represent a source for selection and may ensure population survival under increasing environmental stress or dispersal of individuals to new habitats, and thus speciation.

1.1.1 Functional responses

1.1.1.1 Tolerance

Stenotherm invertebrates tend to inhabit the open ocean, while eurytherm species can be found in coastal or brackish waters where wide temperature variations occur (KINNE 1963). Thermal tolerance is species specific, but can gradually change during ontogeny (SULKIN & MCKEEN 1994). Since oligocellular stages usually have less capacities for adjustments than advanced stages, gametes and embryos have the smallest and most specific thermal tolerance. On the other hand, resting eggs and spores can withstand great fluctuations of environmental conditions. Endurance limits may also be a function of age, nutritive state, environmental history or season (KINNE 1970).

Cold death follows a depletion of life-supporting functions such as motility, respiratory movements, muscular strength and parasitic resistance and usually are caused by disintegration of physiological processes, often preceding direct cell damages, e.g. by ice crystals. Animals often die some time (days, weeks) after exposure to the critical minimal temperature. Heat death, in contrast, often occurs more immediately, not far above the upper temperature limit of the distribution range of a given species. Heat death is mainly induced by insufficient oxygen supply, protein denaturation, increased permeability of membranes and finally release of toxic waste products from damaged cells (KINNE 1970).

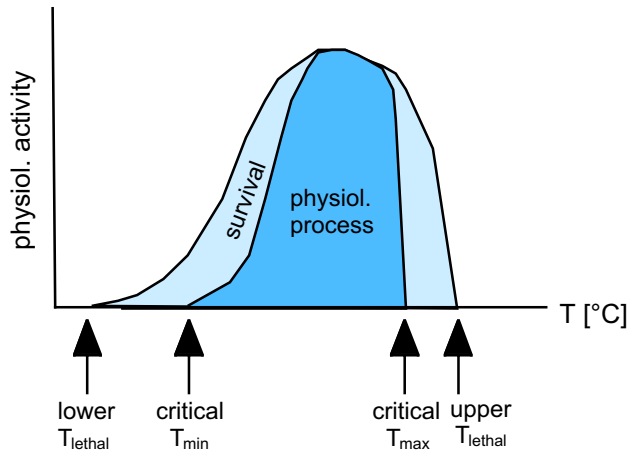


Fig. 1.1: Functional temperature response of marine poikilotherms. T=temperature

1.1.1.2 Metabolism and activity

Metabolism comprises all processes, which use and convert material and energy for maintenance, growth, reproduction and repair, while activity is the result of the integrated metabolism and involves respiration, locomotion, fighting, courting and mating. Both aspects interact, since a change in metabolism will affect activity and vice versa. The rates of metabolism and activity generally increase with increasing temperature until they suddenly decrease near the critical maximal temperature (Fig. 1.1). Different functions may have different temperature ranges; for example growth and reproduction (see below) often require narrower thermal windows than maintenance of basic physiological performance.

Oxygen consumption is a function of temperature and body size (KRÜGER 1964). At extreme temperatures, the capacity for oxygen delivery within organs, tissues and fluids seems to limit the thermal tolerance of marine organisms (PÖRTNER 2001). It has been observed that respiration rates are higher in cold acclimated animals than in warm acclimated ones at a given temperature, suggesting metabolic cold adaptation (FARMANFARMAIAN & GIESE 1963, SCHOLANDER *et al.* 1953). Nevertheless, CLARKE (1991) has discussed critically temperature compensation of respiration (see chapter 1.1.3).

Ingestion rate increases, while time needed for food conversion decreases with increasing temperature (PAFFENHÖFER 1968). At low winter temperatures, many species tolerate starvation for several months (KINNE 1963 and references therein). On a physiological basis, temperature may influence the activity of digestive enzymes (DAVIS & CALABRESE 1964, KOLODZIEJSKA & SIKORSKI 1996, KLINGER *et al.* 1997).

In poikilotherms, growth is an exponential function of temperature under saturated feeding conditions. According to HUNTLEY & LOPEZ (1992), temperature explains more than 90% of variance in growth rate of marine copepods, independently of species and body weight, via its effect on metabolic activity. Beside metabolic rate, temperature also affects the efficiency of material and energy conversion (CONOVER 1964).

Activity can be altered by temperature both at the individual level, e.g. the frequency of movements, and at the population level, e.g. as a trigger for the alternation of dormant and active life stages (DAHMS 1995).

1.1.1.3 Reproduction

Thermal requirements for reproduction often are restricted to a quite narrow temperature window separating the vegetative from the reproductive temperature range and may additionally differ between gonad growth, gamete maturation, spawning and embryonic development (KINNE 1970, SEWELL & YOUNG 1999). Reproduction usually competes with body growth. The regulation of both processes is controlled by hormones and cytochemical mechanisms, which in turn are influenced by temperature (CHANG 1991). In contrast to continuously spawning forms, many species only spawn in specific seasons. Reproduction then is induced either when a specific temperature threshold is reached or when temperature changes. The final trigger for spawning – favourable temperature conditions given – often are additional factors, such as photoperiod (CEBALLOS-VAZQUEZ *et al.* 2000), food availability (HIRCHE 1996) or pheromones (MILLER 1989, HARDEGE & BENTLEY 1997).

A variety of seasonal spawning patterns have been described: continuous spawning throughout the year, at certain intervals or single spawning events triggered by various impulses (GIESE 1959). Gonad growth and gamete maturation are controlled by temperature, but may also depend on food and light. Maturation of gametes may be completed long before spawning starts (SCHELTEMA 1967), which is initiated as soon as the threshold temperature is reached. The frequency of spawning events can increase with increasing temperature, while clutch sizes often decline due to reduction of body size at elevated temperatures (APELT 1969, RUNGE 1984, HIRCHE 1992). While spawning generally is related to the warm season in temperate and higher latitudes, it may also be induced by decreasing temperature in cold water species (CRISP 1957). Species with different reproductive temperature preferences can live in the same habitat, where they have consecutive spawning periods in winter, spring and summer (RUNNSTRÖM 1927). Embryonic development rate is highly temperature dependent, but rather independent of experimental handling (LANDRY 1975). Therefore, embryonic duration has been frequently used as a measure of temperature response (e.g. CORKETT 1972, MORIYASU & LANTEIGNE 1998, STANWELL-SMITH & PECK 1998, WARNKE 1999). However, egg development times have been discussed to depend additionally on parental temperature history and acclimation effects (LANDRY 1975, HART & MCLAREN 1978).

1.1.1.4 Distribution

The geographical distribution of species depends on historical, abiotic and biotic factors. Primarily, a species disperses from its place of origin to other regions and habitats, where it has to establish itself permanently. This implies that the physical environment is adequate and interactions with other organisms (food availability, competition, predation) allow to maintain an autochthonous population. With increasing complexity and differentiation of organisms, their behaviour becomes progressively important for their distribution patterns, extending their potentialities beyond their physiological capacities (KINNE 1963). On the other hand, advancing specialization may lead to complex relationships among organisms and thus to their dependence on each other, e.g. in predator-prey or symbiotic relations.

The most significant effect of temperature on distribution is the exclusion of species from areas with unfavourable temperature conditions. Extremes that occur occasionally may thereby be of greater importance than the intermediate normal temperature range. Direct and indirect temperature effects may concern growth rates, life span, reproductive output and inter- and intraspecific interactions (KINNE 1970).

Latitudinal distribution patterns are most obvious in north-south direction and appear largely temperature controlled (WELCH *et al.* 1995, WELCH *et al.* 1998). Thereby, summer and winter conditions are important determinants for distribution limits, rather than the overall latitudinal gradient; i.e. distribution may be limited either by lowest winter temperatures towards the poles and/or highest summer temperatures towards the equator (HUTCHINS 1947). Other horizontal patterns might result from cold or warm currents representing almost impermeable barriers, or horizontal migrations, e.g. to warmer waters in winter (KINNE 1970).

Vertical distribution may be affected by temperature first of all by exclusion of organisms from unfavourable temperature layers, but also as result of active migration within a vertical temperature gradient or as consequence of hydrological characteristics like thermoclines or vertical water movements like upwelling (KINNE 1970). Especially for plankton organisms the physical traits of the water column, which are in turn temperature-driven, are of vital importance. A temperature increase provokes a decrease in viscosity and highly affects the buoyancy of

floating organisms. Thus, sinking velocity is crucial for the loss of epipelagic individuals below the euphotic zone (SVERDRUP *et al.* 1964).

1.1.2 Structural responses

It has often been observed that body size increases with increasing latitude and thus with decreasing temperature as well on the individual level as in congeners and higher taxonomic groups (SVERDRUP *et al.* 1964, WIMPENNY 1941). Slow growth rates at low temperature result in larger individuals with a prolonged growing period, late attainment of maturity and long life span. Moreover, a reduced surface to volume ratio appears physiologically advantageous in cold habitats (KINNE 1963). Variations in body size were also observed on a seasonal scale in marine copepods of temperate seas, with large animals developing in cold spring waters and smallest individuals occurring in summer (DEEVEY 1960, HIRCHE 1992, RICCARDI & MARIOTTO 2000).

Differential growth of appendages or dermal differentiations, such as number and length of cilia, spines or other appendages, modifies the shape of organisms and can enhance their buoyancy at increasing summer temperatures and resulting decreased viscosity of water in order to retard sinking (KINNE 1970).

1.1.3 Adaptation

Adaptation is the evolutionary adjustment of organisms to the environment (CLARKE 1991). Temperature adaptations comprise the various functional and structural adjustments described above, which may be genetically fixed (genetic adaptation) or environmentally induced (non-genetic adaptation) and concern either tolerance limits (resistance adaptation) or variations in performance within the tolerated range (capacity adaptation). Adaptations cannot always be clearly distinguished from mere responses, but they generally represent advantageous adjustments (i.e. they enhance survival, reproduction and/or competition capacity) and persist beyond their instantaneous utility (KINNE 1963).

Since selection acts on genetic variations, genetic adaptation represents a basic mechanism of evolution and is a prerequisite to endure abiotic or biotic changes over long time periods (KINNE 1963). Genetic adaptation to temperature has been documented in related taxa present along a latitudinal temperature

gradient, having very similar activity and metabolic rates in arctic, temperate and tropical habitats (THORSON 1958). In turn, SCHOLANDER *et al.* (1953) showed that arctic poikilotherms exhibit much higher respiration rates at a given intermediate temperature than their tropical counterparts and concluded that arctic organisms evolved genetic adaptations of their basal metabolism to life in the cold. However, more recent studies found no confirmation for metabolic cold adaptation (HIRCHE 1984, LONSDALE & LEVINTON 1985). CLARKE (1991) regarded this interpretation with caution, since complex physiological performances such as respiration represent a summation of processes, which may react differently to temperature. Additionally, this author emphasized that the "expected" rate always depends on the comparative organism and the mode of extrapolation.

Adjustments within the genetic range of individuals have been defined by PROSSER (1958) as acclimation, meaning the adaptation to a single factor (e.g. in laboratory experiments), and acclimatization, i.e. adaptation to multifactorial, complex changes (e.g. to climatic change). Non-genetic adaptations occur at three scales, (1) the acute response, immediately (seconds to minutes) after a temperature change, (2) the stabilization phase (minutes to hours) which gradually leads to a constant rate and (3) the new steady state (hours to weeks) at which a maximum of adjustment is reached (KINNE 1963). Direct responses include shock reactions, resulting in an over- or undershoot of metabolic rate or performance, gradual adjustments and direct adjustments without any measurable shock effect, e.g. in oxygen consumption (GRAINGER 1958). The length of the stabilization period may vary with species, age, developmental stage, and process considered. Finally, the results of acclimation can involve a shift of temperature limits towards either lower or higher temperatures relative to the original state, an alteration of temperature preference or of behavioural traits (KINNE 1970). For example, the lower lethal temperature of fishes could be influenced by different acclimation temperatures (DOUDOROFF 1942, CHUNG 2000, MORRITT & INGOLFSSON 2000).

1.2 Copepod distribution patterns – a result of temperature limitation?

1.2.1 Distribution patterns

Copepods are the most abundant organisms in aquatic ecosystems and hold, as principal consumers of the phytoplankton, an ecological key role as link

between primary production and higher trophic levels. They are an essential component in the understanding of fishery, since they represent the main nutrition component of commercially important fish species. Consequently, knowledge on copepod distribution patterns and population dynamics is elementary for modelling the marine food web and carbon flux.

Biogeography recently has raised interest within the context of biodiversity and climate change. Distribution patterns of congener copepod species often differ considerably either on a spatial or temporal scale. Spatial separation of species occurs latitudinally, as shown for *Calanus* species (JASHNOV 1970, CONOVER 1988, PLANQUE & FROMENTIN 1996), vertically in the water column like in *Euchaeta* and *Calanus* congeners (ROE 1972, WILLIAMS 1985), or by topographic regions, e.g. shelf or off shore areas, observed for *Centropages* species (GRANT 1988). Temporal separation has been noticed as seasonal succession in different regions and species, where "colder species" precede "warmer" ones (ERIKSSON 1973, FRANSZ & VAN ARKEL 1983, SULLIVAN & MCMANUS 1986). A large body of literature on geographic distribution is available by now, but which factors actually determine distribution?

Temperature limitation is assumed to be one primary determinant for distributional patterns. Temperature may limit oxygen delivery within the organism (PÖRTNER 2001), or rule cell-biochemistry, e.g. enzyme activity (PATARNELLO & BATTAGLIA 1992), production of anti-freeze substances or heat shock proteins (GODDARD *et al.* 1999, HOFMANN 1999, CLEGG *et al.* 2000). However, other environmental factors could also be crucial for distribution, e.g. salinity gradients in coastal regions influenced by freshwater input (JEFFRIES 1962, GAUDY *et al.* 2000). Beside physiology, interactions with other organisms, like competition for resources (food, space, mating partners etc), predation and parasitism govern distribution. Behavioural traits like migration, swimming and escape behaviour may determine mortality patterns (OHMAN 1990) and thus temporal distribution of species. Ontogenetic faculties, like the ability to undergo diapause, may cause seasonal succession of species as a part of their life history strategies (UYE 1985).

1.2.2 Distribution of congener species

Congener species 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. CONOVER (1988) compared the distribution patterns of several *Calanus* species in the northern hemisphere, which are characterized by a latitudinal gradient and thus by temperature limits: the arctic species *C. glacialis* JASCHOV and *C. hyperboreus* KRØYER have almost coincident distribution patterns in the Arctic Ocean and enter the Atlantic Ocean only marginally in the northeast. *C. finmarchicus* (GUNNERUS) roughly follows the North Atlantic drift from the east coast of the U.S. to the northeast of the Atlantic Ocean up to 80°N, where it frequently co-occurs with *C. glacialis* in zones of mixed Arctic and Atlantic waters. *C. helgolandicus* has its center of origin in the Mediterranean Sea, from where it spreads to Bay of Biscay, the English Channel, the North Sea and the southern coast of Norway. In the northern areas, *C. helgolandicus* often is associated with *C. finmarchicus*.

In the Atlantic, the North Sea and the Mediterranean, the genera *Temora* and *Centropages* (Copepoda: Calanoida) occur with several species. The present work focused on congener pairs of cold-temperate and warm-temperate representatives of these genera. Such pairs are *T. longicornis* (MÜLLER) and *T. stylifera* DANA, as well as *C. hamatus* (LILLJEBORG) and *C. typicus* KRØYER, respectively. These free-spawning species clearly differentiate in their distribution patterns, either spatially (Fig. 1.2) or seasonally. Tab. 1.1 presents the latitudinal distribution patterns in the Atlantic and adjacent seas, summarized from various references. *T. longicornis* occurs farthermost north from 40°N to 72°N, including the North Sea and western Spitsbergen, and has hardly any overlap with its congener *T. stylifera*, which is distributed from 37°S to 46°N including the Mediterranean and the Red Sea. *C. hamatus* was found between 41°N and 66°N including the North Sea, White Sea and Kara Sea and along the coasts of Norway and Spitsbergen. *C. typicus* has been observed between 6°S and 62°N, including the Mediterranean Sea and the North Sea.

The southern boundary of the northern *T. longicornis* seems to coincide with the 20°C isotherm in summer (LINDAU 2001) (Fig. 1.3), 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 & HEYMAN 1983). *T. stylifera* occurs as far north as the 12.5°C isotherm in winter (LINDAU 2001) (Fig. 1.3), but is occasionally brought to the English Channel by warm Atlantic currents from the south (A. John, pers. communication).

Tab. 1.1: Geographic distribution of *Temora longicornis, T. stylifera, Centropages hamatus* and *C. typicus* in the North Atlantic and adjacent seas

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

T. longicornis is present all year round in the neritic waters of the North Sea with a maximum in summer (FRANSZ *et al.* 1989) and has its reproductive maximum in the cold spring period between 5 and 10°C (VAN RIJSWIJK *et al.* 1989). *T. stylifera* is present throughout the seasonal cycle in the NW Mediterranean with abundance peaks in late summer and autumn (GILAT *et al.* 1965, S. NIVAL pers. comm.).

In areas where the *Centropages* species coexist, their temporal and spatial distribution patterns differ considerably in the course of seasons (GRANT 1988). In the North Sea, *C. hamatus* occurs from April to September in coastal regions, whereas *C. typicus* prefers the more saline and warmer waters of Atlantic origin and is abundant there in the second half of the year (RAE & REES 1947, FRANSZ *et al.* 1991).

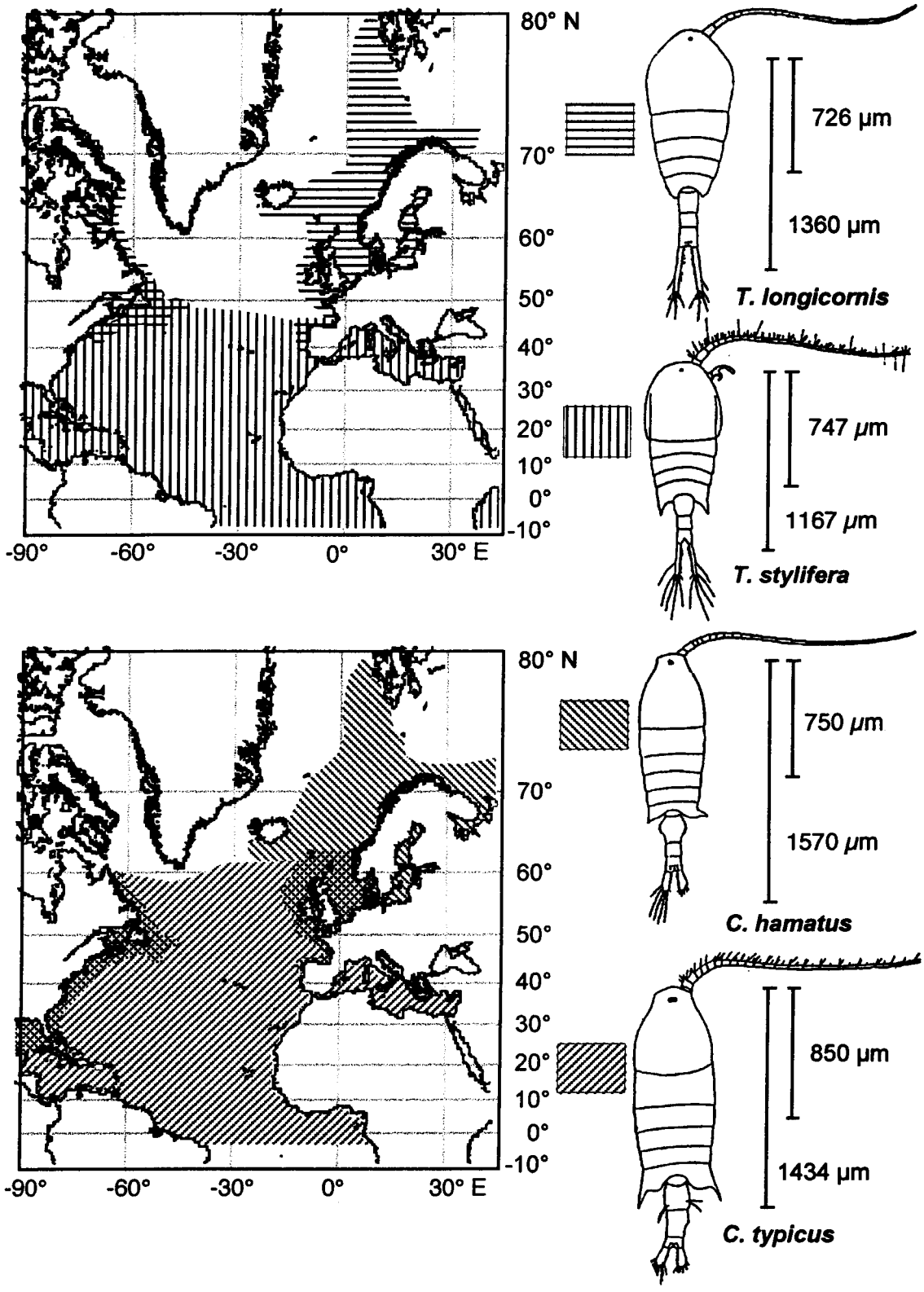
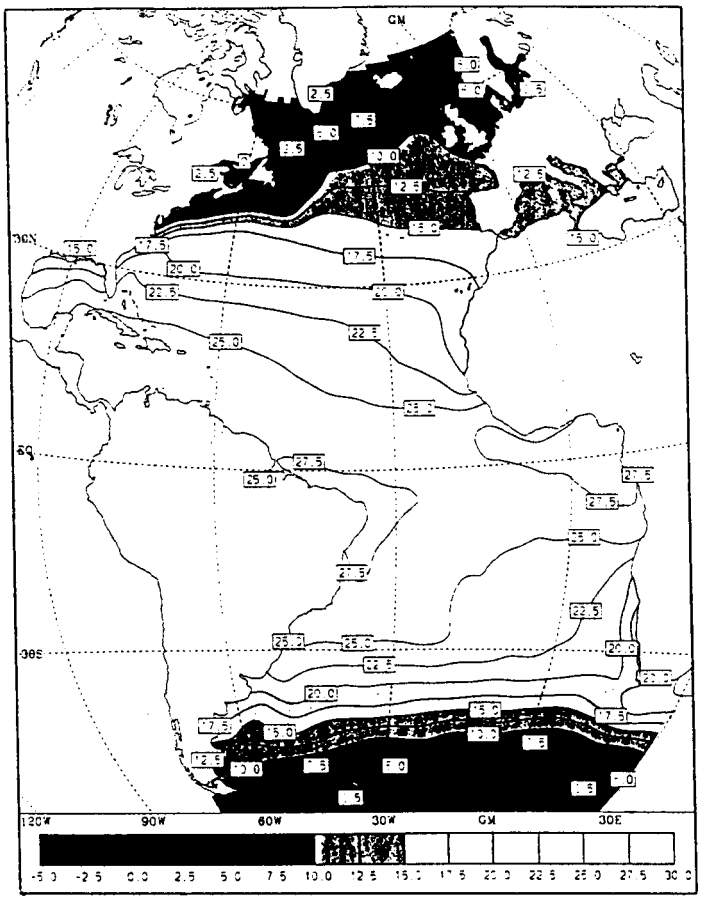
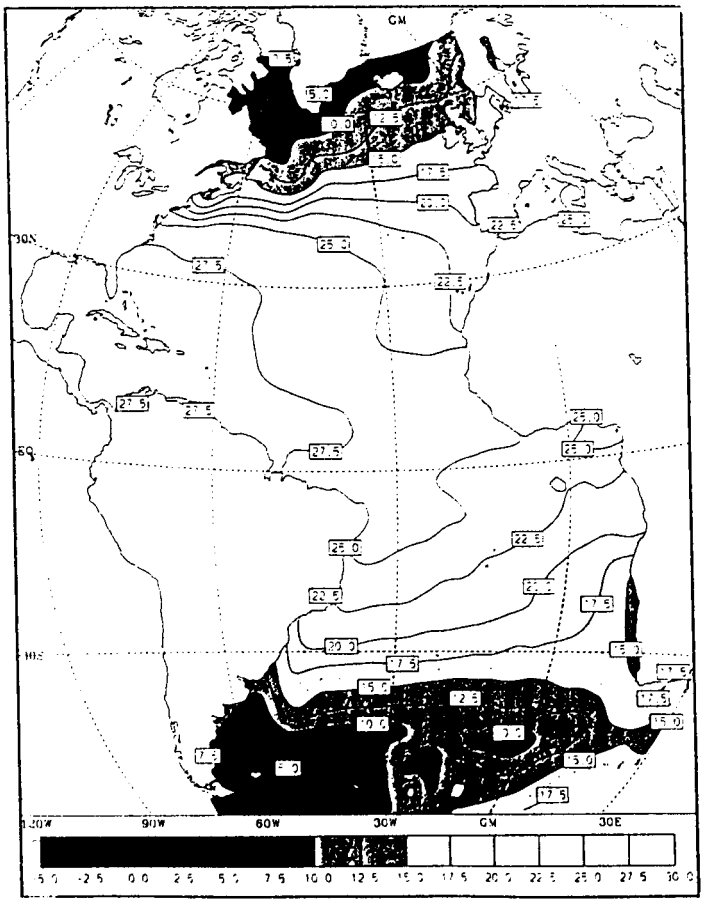


Fig. 1.2: Distribution patterns of *Temora longicornis*, *T. stylifera*, *Centropages hamatus* and *C. typicus* in the Atlantic and adjacent seas (drawings after ROSE 1933, modified) and ranges of prosome length [µm]



February



August

Fig. 1.3: Sea surface temperature [°C] in the northern Atlantic in February and August (LINDAU 2001, modified)

Both species disappear from the water column in winter in order to avoid the unfavourable season, demanding appropriate overwintering strategies, such as production of resting eggs. GRANT (1988) assumed that this succession, which he noticed also in the Middle Atlantic Bight, is based on the different temperature preferences of congener 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. GRANT concluded that *C. hamatus* is a cold water species, while *C. typicus* shows a wide tolerance for temperature.

C. typicus has another center of distribution in the Mediterranean Sea, where it occurs all year round (IANORA & BUTTINO 1990). In this warmer region, the species dominates the plankton community in spring (GILAT *et al.* 1965, S. NIVAL pers. comm.). Females can be found reproducing almost during the whole year (IANORA & BUTTINO 1990).

1.3 Thesis outline

The present work was conceived to answer the question, if temperature is the main driving force of seasonal and geographic copepod distribution patterns. Closely related congener species with different latitudinal distribution centers or different seasonal abundance patterns are ideal objects to study thermal tolerance and its significance for distribution patterns. Information on temperature responses on the individual or population level is an essential prerequisite for studies regarding the cellular and physiological processes standing behind.

Two pairs of congeners were chosen for this study, which distinguish either on a latitudinal or a seasonal scale: (1) *Temora longicornis* and *T. stylifera*, as representatives of a northern and a southern distributed species which hardly overlap, and (2) *Centropages hamatus* and *C. typicus* showing a seasonal succession in the North Sea. Moreover, *C. typicus* has populations both in the North Sea and in the Mediterranean Sea and thus shows a wide distribution range.

So far, it is hardly known which phase of the copepod life cycle is most sensitive to temperature limitation. Demographic studies concern either egg development (CORKETT 1972, MCLAREN *et al.* 1969, M CLAREN 1966), nauplii development (CORKETT & MCLAREN 1970), or the whole generation time (MCLAREN, 1978), but rarely the different developmental stages, while a limitation might occur in specific stages, e.g. nauplii (PEDERSEN & TANDE 1992), or in

reproductive biology. Most experimental studies were conducted in the natural temperature range of a species' habitat, without considering extreme temperatures (e.g. ABOU-DEBS & NIVAL, 1983).

A combination of field studies and experiments under controlled laboratory conditions was carried out in order to clarify how the congener pairs of *Temora* and *Centropages*, living in divergent temperature conditions, differentiate in their temperature responses on different levels of their life cycle.

A field study has been conducted at Helgoland Island (SE North Sea) and in Villefranche-sur-Mer (NW Mediterranean) to compare the seasonal cycles of reproduction in a boreal and a warm-temperate ecosystem in regard to different temperature regimes (Fig. 1.4). In laboratory experiments, conducted in both regions under identical conditions and with the same methods, the temperature impact on survival, reproduction and development were compared between the congener pairs. The temperature responses then were related to the distribution patterns of the species. Survival of adult females and egg production, embryonic development and hatching success of *Temora* and *Centropages* congeners were studied in a temperature range from 2°C to 35°C. Since temperature history may play a role for the actual temperature response of individuals, these experiments were partly repeated in different seasons. Postembryonic development was determined from cohorts reared between 10°C and 20°C under controlled conditions in order to compare stage duration, mortality and generation time of northern and southern populations.

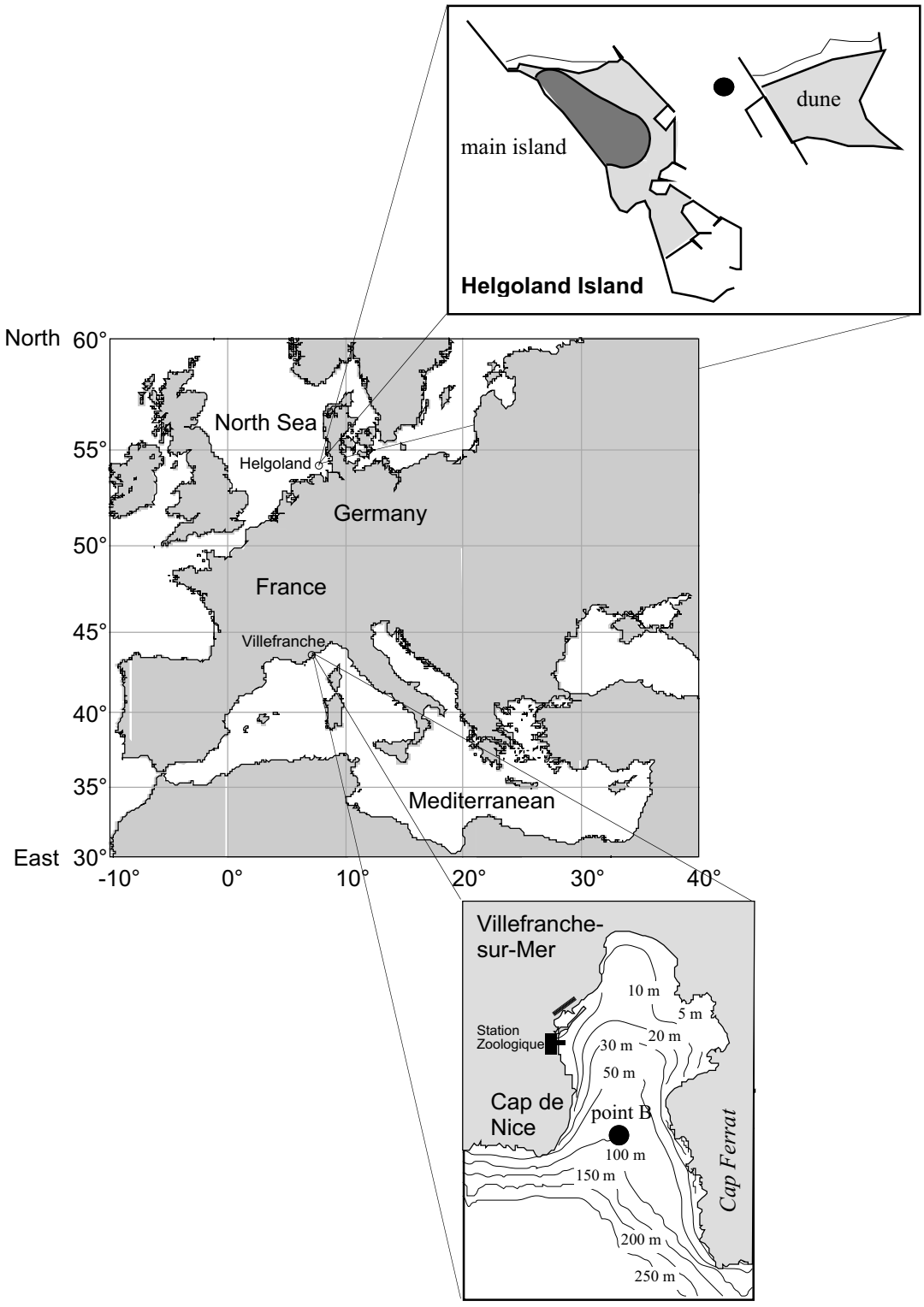


Fig. 1.4: Sampling stations in the southern North Sea (Helgoland Island) and in the north-western Mediterranean Sea (Villefranche-sur-Mer)

1.4 Study sites

1.4.1 Helgoland Island

As an adjacent sea of the NE Atlantic, the North Sea is a typical shelf sea covering an area of 575,000 km^2 with a mean water depth of 100 m (BANNER *et al.* 1980) and is surrounded by the coasts of Great Britain, Norway, Denmark, Germany, the Netherlands and France. Water masses of Atlantic origin reach the North Sea from the south through the English Channel and from the north between Shetland and Norway. These main streams (Fig. 1.5) fuse to several eddies which circulate anticlockwise and are well mixed from the bottom to the surface, except in the deep trough off Norway. Water of low salinity reaches the North Sea from the Baltic Sea via the Skagerrak. In the German Bight, great amounts of fresh water and nutrients enter the North Sea from the big rivers RHINE, ELBE and WESER.

Helgoland Island is situated in the German Bight ca. 70 km off the German coast and is influenced by all above mentioned water masses. The sampling station is located at Helgoland Roads, a 1 km wide channel between the main island characterized by a rocky underground, and the sandy dune, at a water depth of 10 m (Fig. 1.4).

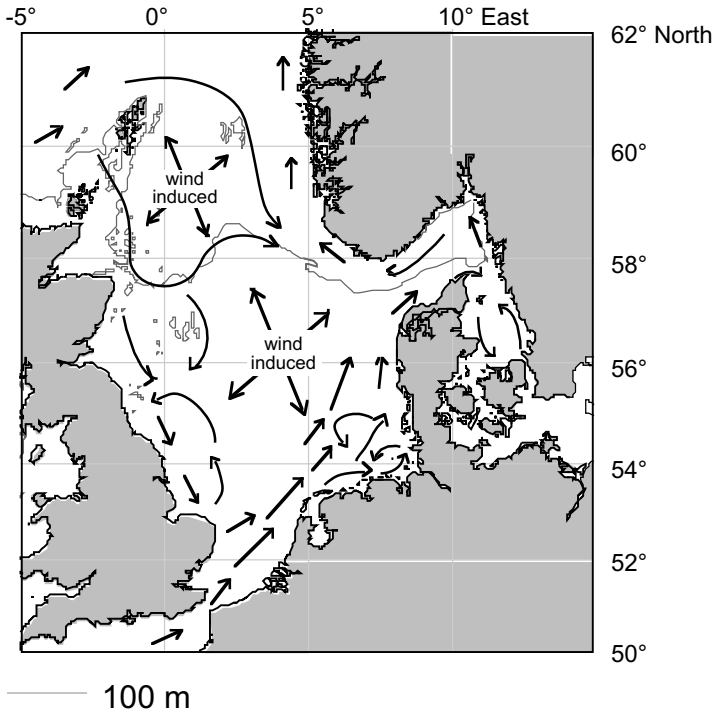


Fig. 1.5: Surface currents in the North Sea (after BANNER *et al.* 1980, modified)

1.4.2 Bay of Villefranche

The Bay of Villefranche is part of the Ligurian Sea, located in the north-western basin of the Mediterranean Sea, which covers an area of 200,000 km^2 (Fig. 1.6). Water depths reach 4000 m, providing more oceanic conditions as compared to the North Sea. Three watermasses can be distinguished: (1) the surface layer (0-200 m) is subject to the annual variations of sun radiation and exchange processes with the atmosphere. Winds and climate control the oceanographic conditions of this layer by evaporation and precipitation and cause the formation of dense waters. (2) Intermediate water (200-500 m) separates itself from the surface water by the 38.5 psu isohaline. (3) Deep waters show low variability with a temperature of 12.7°C and a salinity of 38.4 psu descending to 4000 m depth. An exchange of water with other parts of the Mediterranean is reduced to narrow deep openings, e.g. through the channels of Corsica, Majorca or the large chute between Menorca and south Corsica (BETHOUX & PRIEUR 1983).

The Bay of Villefranche is sheltered from wind between the “Cap Ferrat” and the “Cap de Nice” (Fig. 1.4). Water depths rapidly reach 100 m at the entrance of the Bay and fall further down to great depths of more than 2000 m in the “canyon of Villefranche”. A cyclonic circulation in the golf of Genoa creates the Liguro-Provençal current, passing the Bay from east to west (Fig. 1.6). Ascending currents from the deep provide a rich community of pelagic copepod species near the surface, simulating conditions of the open sea close to the shore (NIVAL & CORRE 1976). The sampling station “Point B” is situated at the entrance of the Bay at 80 m depth (Fig. 1.4).

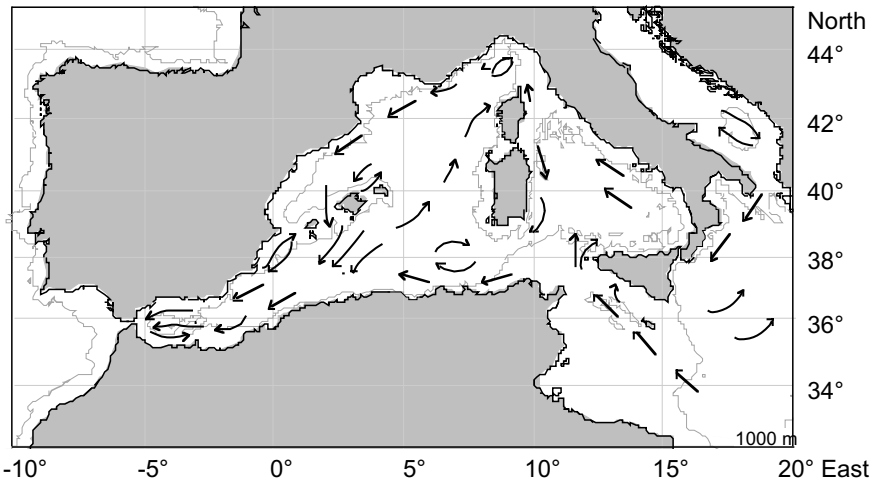


Fig. 1.6: Surface currents in the western Mediterraenan Sea (after OVCHINNIKOV 1966, modified)

2 MATERIAL AND METHODS

2.1 Field observations

2.1.1 Hydrography

2.1.1.1 North Sea

Temperature [°C], salinity [psu] and phytoplankton distribution [µg C l^{-1}] were measured 5 days a week from surface waters (data preliminary, courtesy of Helgoland Reede time series, partly unpublished; HICKEL *et al.* 1997, http://www.pangaea.de). Data were available for 1995, 1996, 1998, 1999 (phytoplankton only from 04.01. to 31.05.1999) and 2000 (phytoplankton from 03.04. to 31.12.2000). Total particulate phytoplankton carbon was estimated from cell counts as the sum of diatoms and flagellates. The group "flagellates" was a taxonomic conglomerate. The biomass was dominated by dinoflagellates, while nanoflagellates occurred in highest numbers (HICKEL *et al.* 1997).

2.1.1.2 Mediterranean

Temperature [°C] and chlorophyll$_a$ content [mg m^{-3}] were measured once a week in 1998 and 1999 at 10, 20, 30, 50 and 75 m depth from water samples collected with 5 L Niskin bottles (for details see ETIENNE *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 paragraph "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 chlorophyll *a* values, which mostly occurred in 30 or 50 m depth.

2.1.2 Plankton sampling

2.1.2.1 North Sea

Plankton was collected at Helgoland Roads (54°11.3'N, 7°54.0'E) in the years 1995, 1996, 1998, 1999 and 2000 (Fig. 1.4). In 1995, samples were taken during July, in mid August, between 20th September and 6th October, in the first

half of November and in the second week of December. From June to October 1999, sampling was conducted on almost all working days. Some more samples were available at the end of March/beginning April and in September 2000. Specimens of *T. longicornis* were found on 128 sampling dates, *C. hamatus* on 86 days and *C. typicus* on 83 days. Sampling was conducted in the morning by horizontal net tows (CALCOFI-net, 280 µm mesh size) for ca. 10 minutes at a water depth of 10 m. In general, the sampled volume was about 200 m^3. The samples were gently diluted into 10 L of unfiltered seawater and brought to the laboratory within one hour. Adult females were sorted under a binocular microscope for incubation in experiments. Three species were considered for this study: *Temora longicornis*, *Centropages hamatus* and *C. typicus*.

Abundance data were available once a month from vertical hauls from 10 m depth to the surface with a sample volume of 4.4 m^3 taken with a NANSEN-net. These samples were conducted from November 1995 to August 1996, usually at midmonth. Species were staged in 4 groups: adult females, adult males, C IV-V and C I-III.

2.1.2.2 Mediterranean

Plankton was collected at the 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) (Fig. 1.4). There, water depths rapidly reach 100 m and decrease to 2000 m at the level of the geological structure called “canyon of Villefranche” (NIVAL & CORRE 1976, ETIENNE *et al.* 1991). For this reason, conditions of the open sea can be found near the coast.

From November 1997 to December 1999, plankton sampling was conducted on 228 workdays in all months, except in August when sampling was interrupted in both years. Vertical tows from 80 m depth to the surface were taken with a plankton net (type SUPERHOMOGÈNE, 280 µm mesh size). The sampled water volume was around 160 m^3. The plankton was brought to the laboratory within one hour for further processing. The species considered were *Temora stylifera* and *Centropages typicus*. *C. typicus*, although morphologically belonging to the same species (K. SCHULZ pers. comm.), were smaller, lighter in colour and more delicate than their northern counterparts.

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 aggrieved animals.

Abundance data were available for 1998 (NIVAL & NIVAL, personal communication) for the group C IV to adult from samples taken every work day and pooled weekly for analysis.

2.1.3 Egg production

Egg production measurements were conducted in cold rooms at ambient seawater temperature with natural daylight provided through a window or an artificial cycle of 12 h light/darkness. 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 order to process a high number of females in a short time, multiwells (Corning®) with volumes of 5 ml were chosen as incubation chambers (Fig. 2.1).

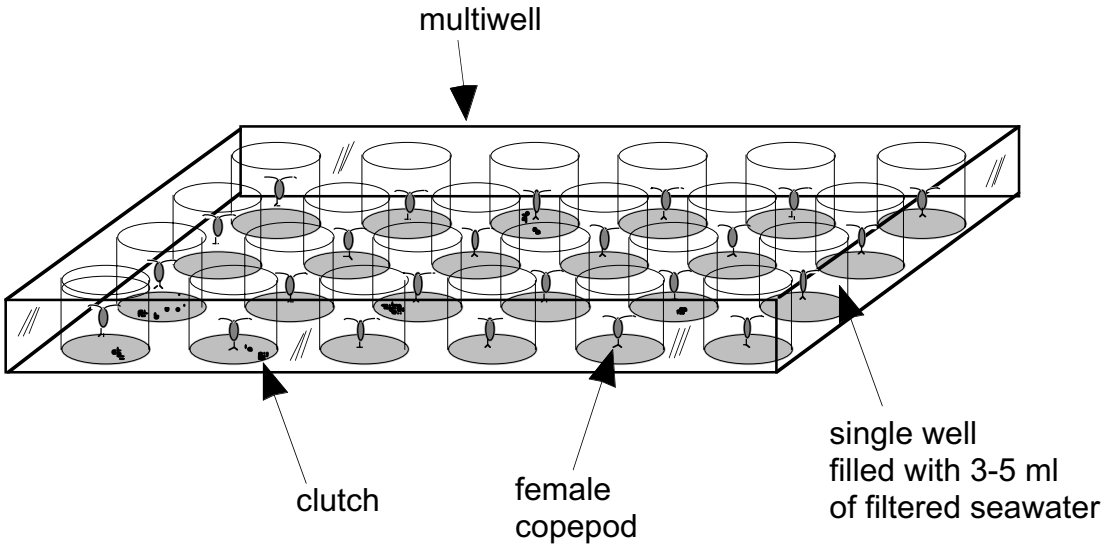


Fig. 2.1: Experimental arrangement for egg production measurements in multiwells

5 to 54 females, depending on availability, were incubated individually for 24 h in multiwells filled with 3-5 ml of filtered seawater (0.45 µm). The wells were checked for eggs after 4, 8, 18 and 24 h 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 fell short of the spawning intervals in order to distinguish single clutches and avoid egg loss due to cannibalism. It has been demonstrated that incubation in small volumes does not affect egg production (HALSBAND 1996, SCHMIDT *et al.* 1998, NIEHOFF *et al.* 1999, HARRIS *et al.* 2000). Incubation in filtered seawater is discussed controversially in the literature (HARRIS *et al.* 2000). While TESTER & TURNER (1990) showed that food conditions in short term incubations had no effect on reproduction, SAIZ *et al.* (1997) found enhanced rates obtained from incubations in pre-screened *in situ* water and enriched food media compared to filtered seawater, especially at higher temperatures. In contrast, LAABIR *et al.* (1995) and HIRCHE *et al.* (1997) confirmed that at ambient temperatures egg production rates of the first 24h of incubation reflect the feeding history of the females in the field prior to capture, so the results should not be greatly biased, but might only be slightly underestimated.

Egg production rates (EPR) were calculated as 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 (24h). This rate shows more or less the same seasonal pattern as the EPR, but is normally distributed and therefore was used for statistics.

All four species investigated are broadcast spawners and seldom produce single eggs, but batches of up to 100 eggs or more, defined as clutches. 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 seawater to determine embryonic development times. To determine hatching success, these clutches were controlled every 6 h and every hour as soon as the first nauplii occurred, except overnight when observations were interrupted for 12 h. Hatching was controlled over a maximum of 16 days, except when all nauplii had hatched before.

2.1.4 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 (NIH Image 1.6).

At Helgoland Island, the prosome length of 4 to 30 females was measured from July 1995 to July 1996 except in November 1995. Furthermore, 2 to 50 females were measured per species and incubation date in September 1998, from June to October 1999 and in April 2000. In 1996 samples of females and eggs were pooled monthly. Egg diameter was determined from September 1995 to June 1996 and in summer 1999 for 2-95 eggs per species and incubation date/month, respectively.

In Villefranche, prosome length measurements were available from January to July and from October to December 1998, as well as from March to May and from October to December 1999. From February to July 1998, 7 to 102 females were pooled monthly. Later on, 2 to 48 females were measured per incubation date. For egg size measurements, up to 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 were available. Egg diameter of *T. stylifera* was measured in January, February and April 1998 from monthly pooled samples containing 26 to 50 eggs and from October to December 1998 from daily samples with 28 to 56 eggs.

2.1.5 Carbon content and weight specific egg production

Carbon content of 67 (*C. typicus*), 56 (*C. hamatus*) and 134 (*T. longicornis*) females from egg production experiments was measured between July and October 1995, from February to April 1996 and from June to October 1999. In Villefranche, samples for carbon measurements were available in November and December 1998 for *C. typicus* and *T. stylifera* and for the former also from March to May 1999. 87 (*C. typicus*) and 59 (*T. stylifera*) females were analyzed. Mostly 5-10 females with high egg production rates were chosen for carbon analysis, while the others were used for length measurements.

Females 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 (1979) and TANSKANEN (1994). Egg carbon was estimated from egg diameters assuming a volume to carbon conversion of 0.14×10^{-6} µg C μm^{-3} (KIØRBØE *et al.*, 1985). A weight-specific egg production rate (SEPR [day^{-1}]) was calculated for the dates where carbon data were available. Since only a small proportion of reproducing females was used for carbon

analysis, SEPR will not represent mean values of the population like those of EPR including all incubated females.

2.1.6 Statistics

Relationships between reproduction parameters and environmental factors were tested by linear regressions. Correspondence of the reproduction parameters CEPR, clutch size and SEPR of the species investigated were tested with Spearman rank correlation tests. ANOVA analysis was used to detect differences (1) between monthly means of egg diameters, (2) in egg-laying during the day and at night and (3) in prosome length in laboratory experiments, followed by Bonferroni-Dunn Post-Hoc-Tests.

2.2 Laboratory observations on temperature effects

For better understanding of the text, the two populations of *Centropages typicus* will be indexed $_{NS}$ for “North Sea” and $_{Med}$ for “Mediterranean” in this section and in chapters 3.3 and 4.2.

2.2.1 Food media

Sterilized filtered sea water (0.45 µm) was enriched with “Guillard's F/2 water enrichment solution” (SIGMA) under sterile conditions and kept 12 h, then a few ml of existing algae cultures were added. The Erlenmeyer bottles were positioned in cold rooms at 15°C in front of neon lights and gently oxygenated with a pump. The growth of the “mother” cultures was followed for each species (Fig. 2.2).

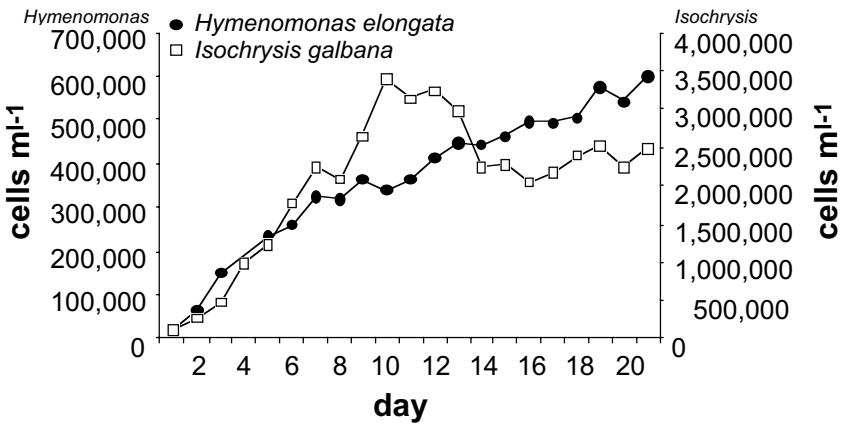


Fig. 2.2: Growth of algae cultures at 15°C

After ca. one week, when the cultures were dense enough, they were used as food either for the cohorts or egg production experiments. During the next 8-14 days the cultures still showed exponential growth and were taken as food. After 3 weeks the quality of the cells got worse, the cells became smaller and often agglomerated and were no longer utilized as food media.

Food concentration was determined in subsamples fixed with Lugol solution. Cell counts were conducted with the help of a LEMAUR cell (volume 0.01 ml) for *Hymenomonas elongata* and a MALASSEZ cell (volume $2.5*10^{-4}$ ml) for *Isochrysis galbana* under a microscope with a magnification of 35x and 100x, respectively.

2.2.2 Survival and egg production

Survival of adult females and egg production were measured during periods of high reproductive activity in the field, i.e. in autumn 1998 in Villefranche and in summer 1999 at Helgoland Island. For these experiments, 12 to 45 females were incubated individually in small beakers for 5 days after 1 day of adaptation to the experimental temperature. Filtered seawater (MILLIPORE filters, 0.45 µm) enriched with 15,000 cells ml^{-1} (≈ 4 µg C ml^{-1}) of the flagellate *Hymenomonas elongata* was offered as food. The algae solutions were shortly adapted to the experimental temperature 1 hour before application and were renewed every day. The beakers were checked twice a day for dead animals, eggs and faecal pellets. Eggs and pellets were removed. Egg cannibalism was accounted for by including empty egg shells in the counts, where one shell corresponds to one egg. Egg production is presented as the mean number of eggs produced per female and day, as well as cumulative egg production during the five-day-period. 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 prosome length measurements.

The results are summarized and defined as female thermal tolerance (FTT) and reproductive thermal response (RTR).

2.2.3 Embryonic development

Eggs were obtained from freshly captured females incubated 24 h in filtered seawater. Embryonic development times were determined at the experimental temperatures. Hatching was controlled three times a day until the first nauplii

appeared. Then nauplii were counted every 1-2 hours (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 eggs to hatch. The temperature response of embryonic development (ETR) is described by Belehrádek's function of the form $D=a(T-\alpha)^b$, with *b* assumed constant (-2.05) for all species (McLaren *et al.* 1969). Differences between seasons were compared by ANCOVA analysis, after ln-transformation of development times, and fitted with Microsoft Origin®.

2.2.4 Post-embryonic development

Cohorts were raised at 10°C (*C. typicus*$_{NS}$ and *T. stylifera*), 12°C (*C. typicus*$_{Med}$), 15°C (all species), 18°C (*C. typicus*$_{Med}$) and 20°C (all species). For initiation, around 200 freshly captured females and 50 males were kept in a Plexiglas cylinder, closed at the bottom with gauze of 280 µm, and diluted in a 5L beaker filled with 0.45 µm filtered seawater (Fig. 2.3).

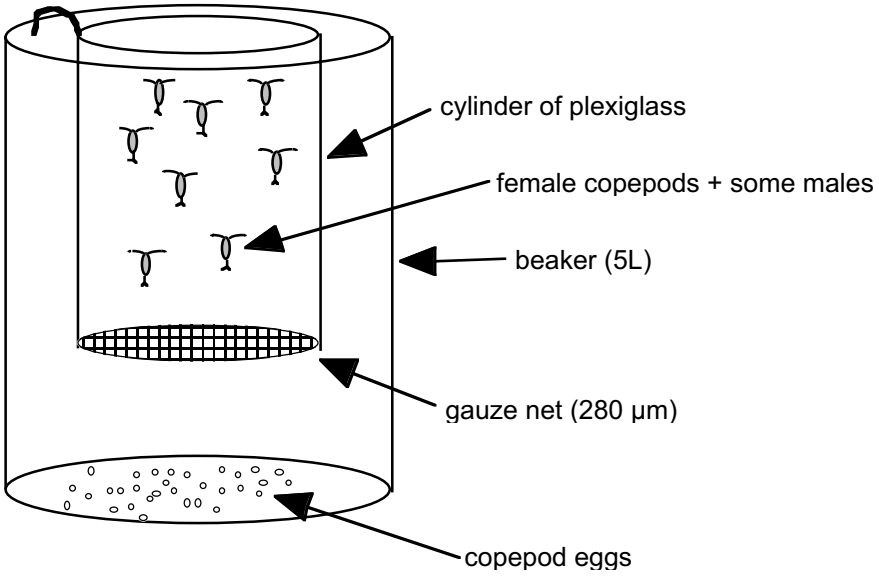


Fig.2.3: Experimental design for rearing experiments. Initiation of a cohort in a mesocosm of 5 L.

To induce high spawning rates, the culture was enriched with *H. elongata* (15,000 cells ml^{-1}) 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, adults were removed and sampling started.

Since the size spectra of ingestable particles change as copepods develop (Nival & Nival 1976, Berggreen *et al.* 1988), development of nauplii was

compared in a preliminary experiment with *H. elongata* (diameter ≈15 µm) and *I. galbana* (diameter 4 to 7 µm) as food source (Fig. 2.4).

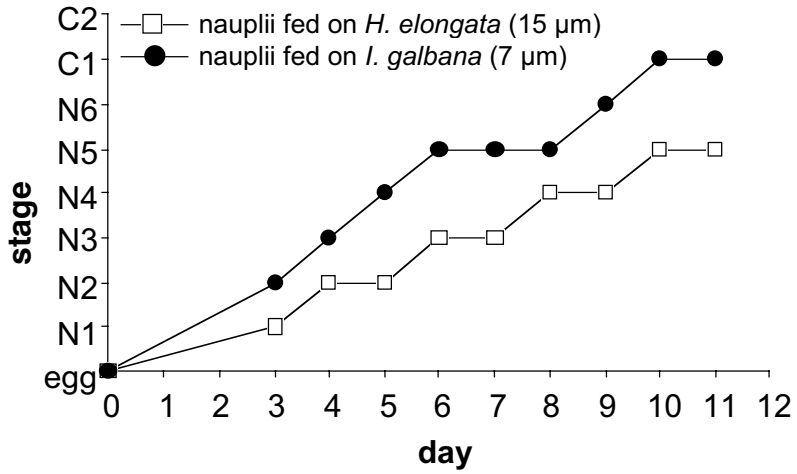


Fig. 2.4: Early development of nauplii on different diets (the most numerous instar was estimated qualitatively)

When *H. elongata* was offered, development was retarded compared to nauplii fed on *I. galbana*. The smaller size of *I. galbana* corresponded better to the food size spectra of the youngest nauplii stages. Therefore, around 100,000 cells ml^{-1} (≈ 2.6 µg C ml^{-1}) of *I. galbana* were added to the cultures after removal of the adults. When the first N3 appeared, *I. galbana* progressively was exchanged by *H. elongata*, and adjusted to 10,000 cells ml^{-1}. Every day a subsample of 1 to 4% of the total volume was taken to estimate the abundance of the larval stages and control food concentration.

Stage duration was calculated from median development times. 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 regressions per population were calculated, one from egg to C 1, the other from C 1 to 50% adulthood. In some experiments, the cohorts suddenly broke down for unknown reasons, so that populations did not reach adulthood. In those cases, stage duration was estimated for all instars available.

3 RESULTS

3.1 Hydrography

3.1.1 Helgoland Island

3.1.1.1 Temperature

The North Sea is subject to a typical boreal temperature cycle with distinct seasons. Maximum temperatures occurred in August and slightly differed between years with 20.2°C in 1995, 18.5°C in 1996, 17.6°C in 1998, 19.0°C in 1999 and 17.8°C in 2000 (Fig. 3.1A). The winter 1995/96 was the coldest during my sampling period with ice cover in the Wadden Sea and a minimum of -0.5°C in February. In the other years, minimal temperature ranged from 3.4 to 4.4°C (Fig. 3.1A). Due to shallow depth and strong currents between both parts of the island, the sampling station Helgoland Roads was never stratified.

3.1.1.2 Salinity

Salinity was highly influenced by river run off, mainly in spring and summer when values reached minima below 30 psu. In winter, an influence of Atlantic waters and cold dry winds from north-east enhanced evaporation and salinity increased up to 34 psu (Fig. 3.1B).

3.1.1.3 Phytoplankton

The North Sea and especially the German Bight is rich in nutrients due to eutrophication from coastal river run off (HICKEL *et al.* 1997). In consequence, particulate phytoplankton carbon concentrations (PPC=diatoms + flagellates) were high, with peaks of 343, 899, 302, 405 and 590 mg C m^{-3} in 1995, 1996, 1998 1999 and 2000, respectively (Fig. 3.1C).

There was great inter-annual variability in phytoplankton development at Helgoland Island. Phytoplankton blooms were usually characterized by high diatom abundance in spring, as observed in early May 1995. In 1996, a very strong diatom bloom, consisting mainly of the large *Coscinodiscus wailesii* (diameter >250 µm), started in January during a period of high atmospheric pressure reaching its maximum in early April.

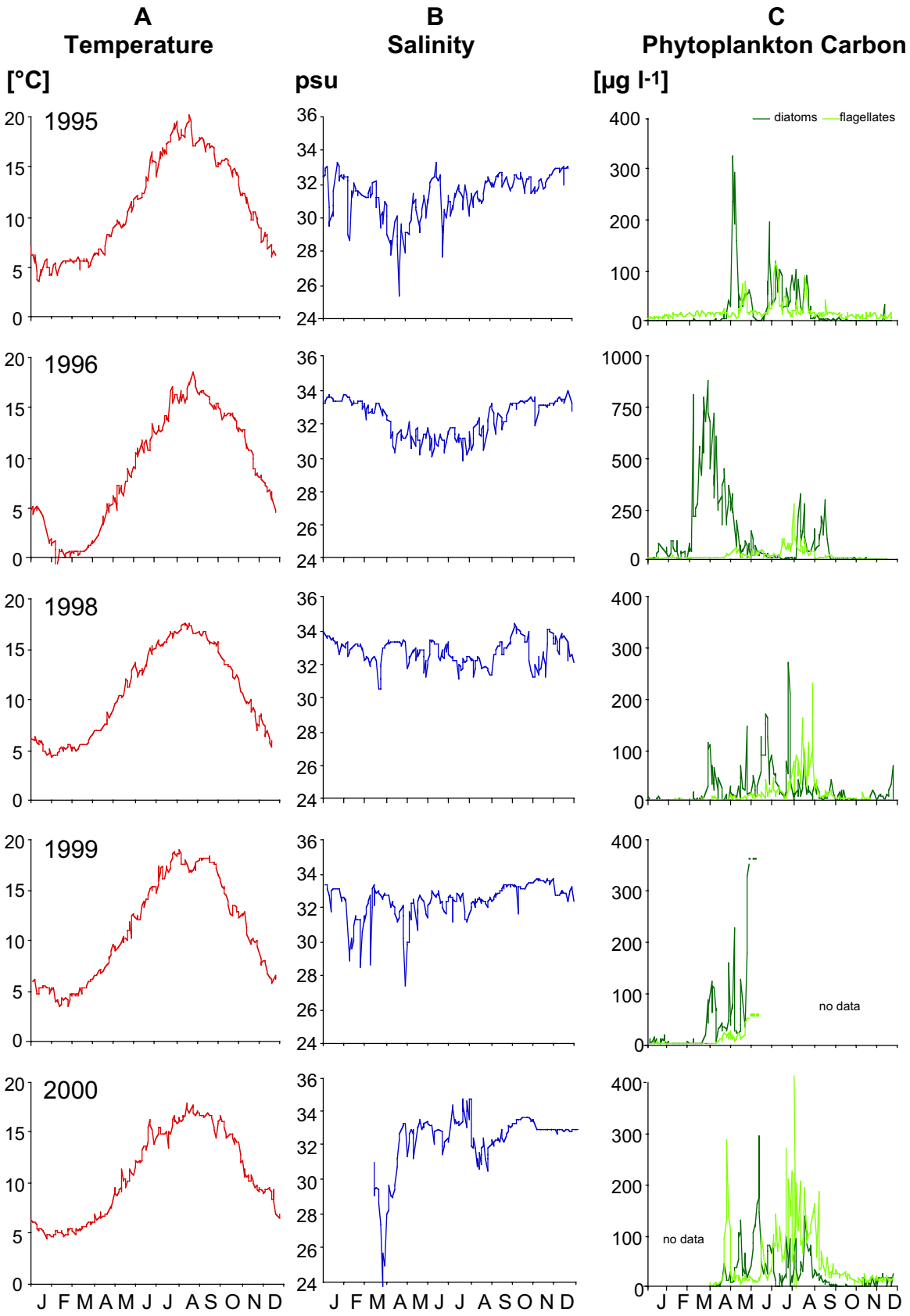


Fig. 3.1: Hydrography at Helgoland Roads 1995-2000. A Surface temperature [°C], B Salinity [psu], C Phytoplankton carbon (diatoms and flagellates, note scale in 1996!) [µg l^{-1}]

For 1999, phytoplankton data were available from January to May only. During this period diatoms peaked in early April and May. The dominating species were the large diatom *C. wailesii*, *Thalassiosira* sp. and *Gyrodinium* sp. In these years, flagellates played a minor role in phytoplankton dynamics with maximal values in summer (Fig. 3.1C).

1998 and 2000 were exceptions from this pattern. In these two years, the spring bloom was less intense than the summer peak; diatom maxima occurred later, in late July 1998 and in June 2000, respectively. Additionally, high flagellate abundances were observed from August to September 1998, in April 2000 and from July to September 2000, respectively.

Lowest phytoplankton concentrations (0.2-4.0 mg C m^{-3}) were recorded in autumn (November 1995, December 1996) and winter (January 1998 and 1999).

3.1.2 Bay of Villefranche

3.1.2.1 Temperature

The Bay of Villefranche showed an annual thermal cycle with strong summer stratification in both years investigated. The water column started to stratify in May after a period of mixed water in winter (Fig. 3.2A). A distinct thermocline was established in 15-30 m depth in June and July. From August to October, the thermocline started to descend to depth 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 at around 14°C all year round (Fig. 3.2B).

3.1.2.2 Salinity

In 1998, salinity tended to be lower than in 1999. Maxima in both years occurred in August and September when evaporation was high. In spring (May and June), lowest salinity was observed near the surface due to precipitation. In 1999, a second minimum was recorded in November (Fig. 3.2C). In general, salinity in the Bay of Villefranche was higher and more stable than in the North Sea, ranging from 37.2 to 38.4 psu (Fig. 3.2D).

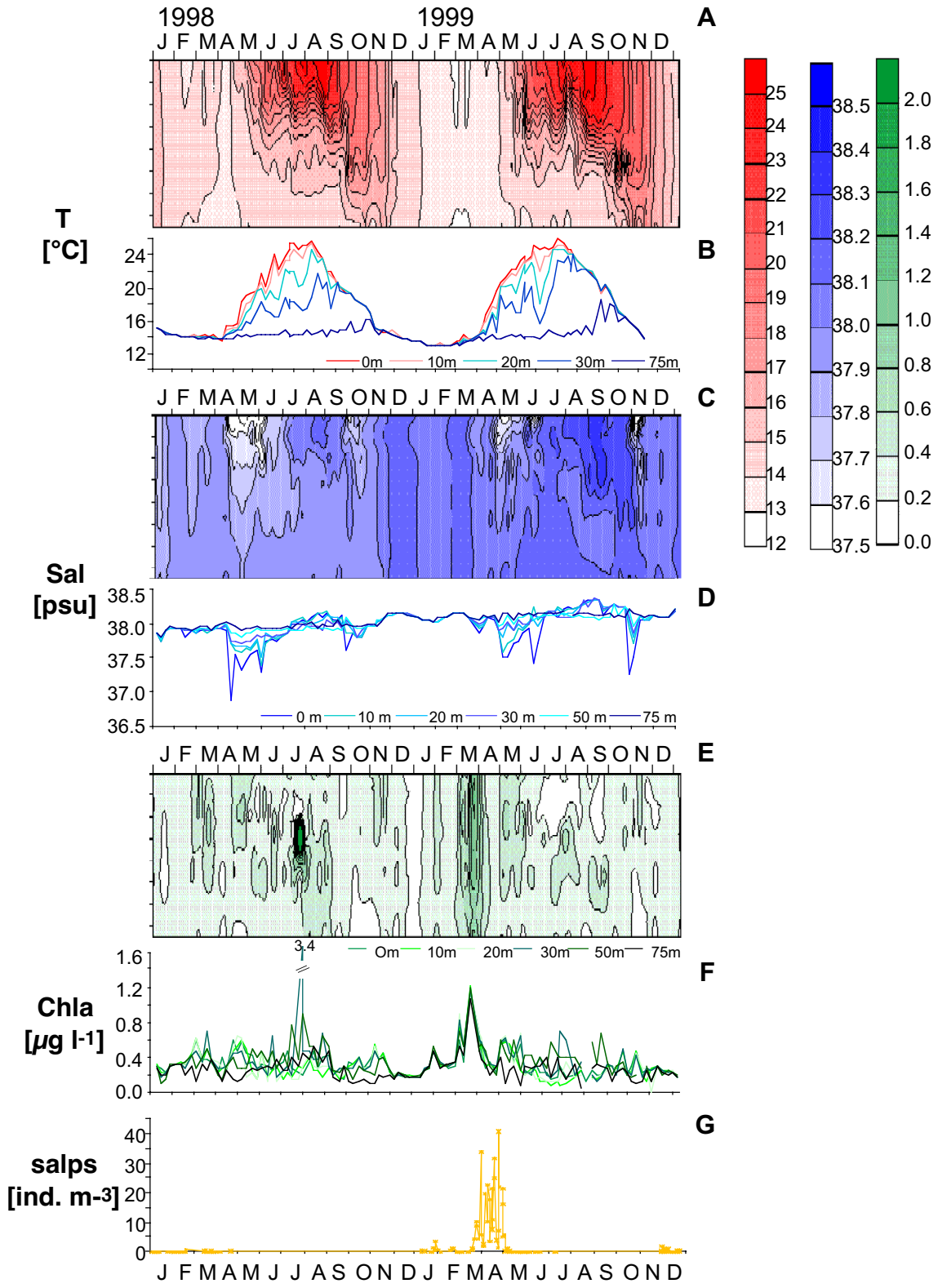


Fig. 3.2: Hydrography in the Bay of Villefranche. A Profile of temperature [°C], B Annual temperature cycle at different depths, C Profile of salinity [psu], D Annual salinity cycle at different depths, E Chlorophyll$_a$ profile [µg l^{-1}], F Annual chlorophyll$_a$ cycles at different depths, G Density of salps [ind. m^{-3}] (courtesy of S. DALLOT, Marine Station of Villefranche-sur-Mer)

3.1.2.3 Phytoplankton

The annual cycle of chlorophyll$_a$ was nearly identical in 1998 and 1999 with a weak phytoplankton bloom in spring. A subsurface chlorophyll maximum usually occurred in 30 to 50 m depth (Fig. 3.2E). A single extraordinary peak was recorded in July 1998 with 3.78 mg m^{-3} in 30 m depth (Fig. 3.2F). In 1999, the phytoplankton bloom in March reached peak values of 1.22 mg chlorophyll m^{-3}. This peak was followed by a bloom of salps inducing a decline of chlorophyll maxima down to 0.31 mg chlorophyll m^{-3} at the end of April.

The microplankton community showed three peaks in both years in May, August/September and November, respectively. Diatoms dominated in spring and autumn, dinoflagellates were abundant in summer. Ciliates were similarly distributed as diatoms, abundant in July and from November to January with a major peak in November 1999 (F. Gomez, personal communication). In comparison to the North Sea, the NW Mediterranean is strongly oligotrophic. Phytoplankton concentrations were up to 25 times lower than at Helgoland Island, assuming a conversion factor from PPC to Chl_a of 40, suitable for diatoms (RIEMANN *et al.* (1989) report Carbon: Chl_a ratios between 27 and 67).

3.1.2.4 Density of Salps

While salps were rare in 1998, a strong bloom of these highly efficient filter feeders was observed in March and April 1999 (Fig. 3.2G). Individual numbers reached values of 40 ind. m^{-3} in late April (DALLOT pers. comm.), since the salps showed a tendency to concentrate in the Bay.

3.2 Reproduction cycles in the North Sea and the Mediterranean and their interannual variability

3.2.1 North Sea Populations

Periods of EPR measurements are indicated at the top of the figures. Most data were available for EPR, clutch size and prosome length, while carbon content and SEPR were determined only between July and October 1995, from February to April 1996 and from June to October 1999 from few females with high egg production rates (cf. chapter 2.1.5). Monthly abundance data were available only from November 1995 to August 1996 (cf. chapter 2.1.2.1).

3.2.1.1 *Temora longicornis*

Temora longicornis was found at Helgoland Roads on all sampling dates (Fig. 3.3). In winter, the number of individuals was small, but all groups of stages were found. The population showed several peaks in the first half of 1996 and abundance of young copepodites peaked in July (Fig. 3.4B).

Fig. 3.3: *Temora longicornis* (female) from Helgoland Roads.

Body size of female *T. longicornis* varied seasonally, while interannual variability was small. Individual extremes of prosome length were 726 and 1360 µm. Largest females were found in April 1996 and April 2000, while body size decreased during summer with the smallest specimens in October 1995, August 1996 and August 1999. In September 1999, prosome length slightly increased after the summer minimum (Fig. 3.4C).

Carbon content of females decreased from July to September 1995 and increased in October. In spring 1996 female weight increased to the maximum of 26.7 µg C. In summer 1999, female carbon content showed little variation and was lower than in summer 1995 with the minimum of 6.7 µg C recorded in July 1999 (Fig. 3.4D).

Reproduction of *T. longicornis* continued throughout the year. Egg production rates showed a pronounced annual cycle, with peak values at the end of April and, to a less degree, in summer (Fig. 3.4E).

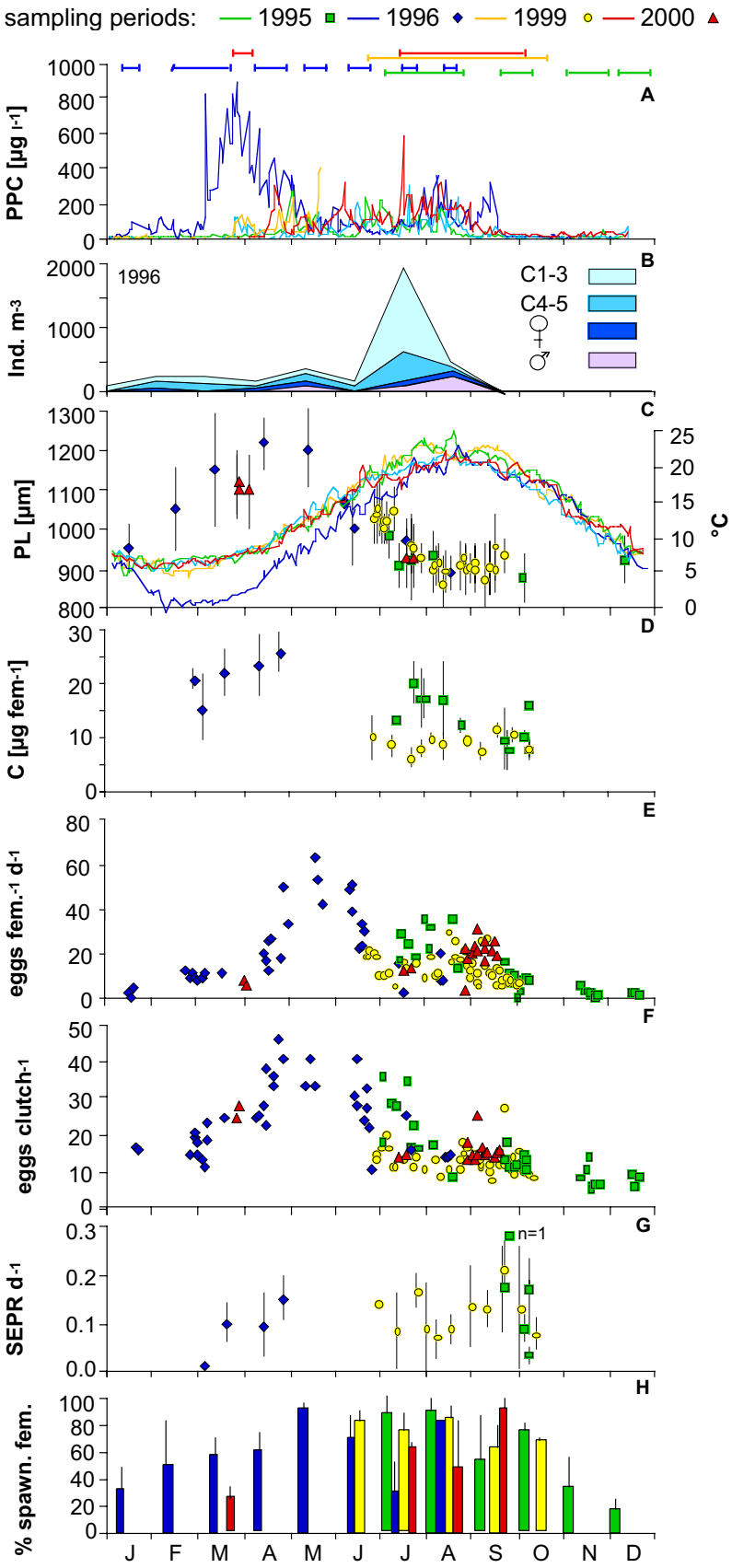


Fig. 3.4: *Temora longicornis* at Helgoland Roads. **A** PPC (diatoms+flagellates) [µg l^{-1}], **B** Cumulated stage abundance from November 1995 to July 1996 [ind. m^{-3}], **C** PL [µm] and temperature [°C] cycles, **D** Female carbon content [µg], **E** EPR [eggs $female^{-1}$ day^{-1}], **F** Clutch size [eggs $clutch^{-1}$], **G** SEPR [day^{-1}], **H** Proportion of spawning females [%]

In July and August 1995, egg production rates varied between 20 and 40 eggs female^{-1}d^{-1}. In September, females reduced their reproductive activity to less than 10 eggs female^{-1}d^{-1} and the rates remained low during winter until the following spring. The highest daily mean rate was measured in May 1996 with 62.4 eggs female^{-1}d^{-1} (CEPR 66.0 eggs female^{-1}d^{-1}); the highest individual rate was 122 eggs female^{-1}d^{-1}. In 1999, egg production decreased during June, but recovered to more than 30 eggs female^{-1}d^{-1} in August. This pattern was repeated in September.

Egg production rates were higher in summer 1995 than in 1999. The values from late March and summer 2000 matched the results from previous years with a peak of 30 eggs female^{-1} day^{-1} in late August. Mean annual egg production rates were 11.7 eggs female^{-1} day^{-1} in 1995 (July to December), 21.8 in 1996 (January to August) and 13.5 eggs female day^{-1} in 1999 (June to October).

Clutch size was highly variable with a maximum of 73 eggs clutch^{-1} in April 1996. Maximum mean clutch size was 45.5 eggs clutch^{-1} and closely followed the seasonal cycle of egg production rate (Fig. 3.4F). In winter and spring, usually one clutch was produced per day, while in summer the number of clutches increased up to 3 clutches per day. Spawning took place mostly at night (Fig. 3.5), but the difference was significant only in summer ($p<0.01$).

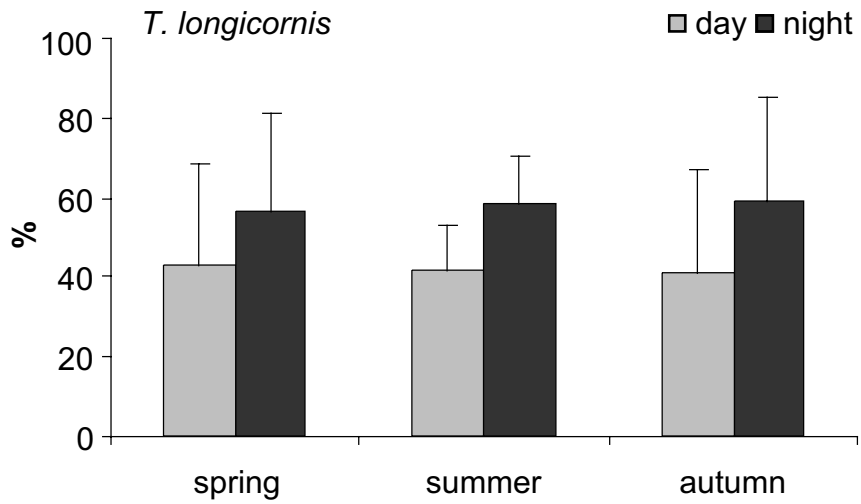


Fig. 3.5: *T. longicornis* at Helgoland Roads. Proportion of clutches produced during the day (8-18h) and during night (18-8h) in different seasons (data from various years)

Weight specific egg production rates (SEPR) were maximal in September 1995 and heavily decreased from 0.28 d^{-1} to 0.04 d^{-1} in October (Fig. 3.4G). In March 1996, SEPR was 0.1 d^{-1} and increased in late April to 0.15 d^{-1}. In 1999,

SEPR was variable ranging from 0.09 to 0.21 d^{-1} with two peaks in July and September.

Reproductive activity was lowest in December and January, when less than 20% of the females were spawning (Fig. 3.4H). Highest proportions of egg-laying females occurred from May to October, with highest percentages in May 1996 (94%), August 1995 (92 %) and September 2000 (93%). In 1996 and 2000, the proportion of egg-laying females was unusually low (<50%) in July and August, respectively.

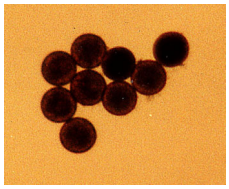


Fig. 3.6: Eggs of *T. longicornis*

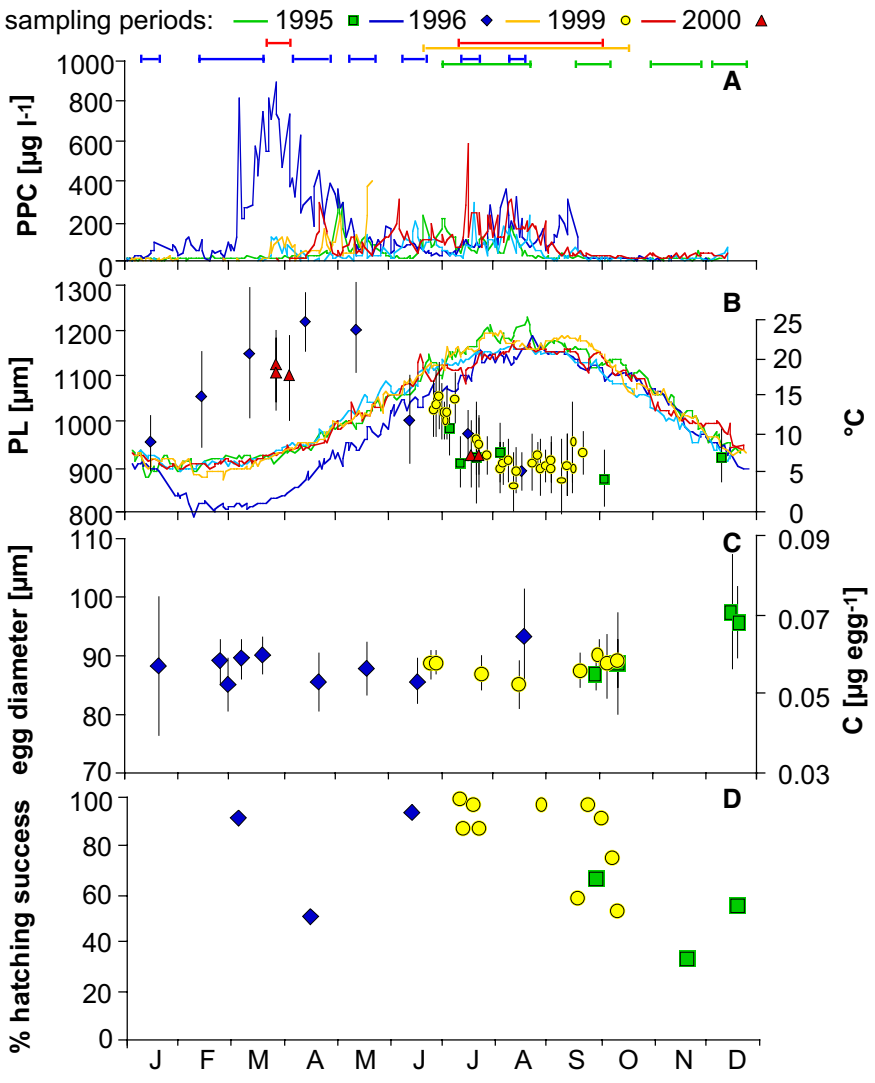


Fig. 3.7: *T. longicornis* at Helgoland Roads. **A** PPC [µg l^{-1}], **B** PL [µm] and temperature [°C] cycles, **C** Egg diameter [µm] and carbon content [µg], **D** Hatching success [%]

T. longicornis produced clutches of smooth eggs, which varied in colour from white to yellow or brownish and stuck together for some time after deposition (Fig. 3.6). Monthly mean egg diameter ranged from 85.3 to 95.6 µm with extremes of 79 and 101 µm (Fig. 3.7C). Eggs were significantly larger in December 1995 and August 1996 than in the other months (ANOVA/Bonferroni-Dunn Post-Hoc-Test, $p < 0.0001$). Mean carbon content was 0.028 to 0.098 µg C egg^{-1} (Fig. 3.7C). In autumn 1995, hatching success decreased from 66 to 33%, then increased to 55% in December. In March and June 1996, 92% and 94% of all incubated eggs developed to nauplii, respectively, while in April only 51% hatched. In summer 1999, high proportions of around 90% of the eggs hatched, decreasing to 53% in October (Fig. 3.7D).

3.2.1.2 *Centropages hamatus*

Females of *Centropages hamatus* (Fig. 3.8) were present from late March to November at Helgoland Roads and were always reproducing, except on two sampling dates in April 1996 when the reproductive period just had started. The species was most numerous from June to August with two peaks (Fig. 3.9B).

Fig. 3.8: *Centropages hamatus* (female) from Helgoland Roads

Prosome length varied in individual females by a factor of two from the minimum of 750 µm recorded in October 1995 to the maximum of 1570 µm observed in May 1996 (Fig. 3.9C). Female carbon content was higher in summer 1995, with around 12 µg C, than in summer 1999 with a minimum of 1.3 µg C in July. The biggest animal was found in May 1996 containing 20.8 µg C (Fig. 3.9D).

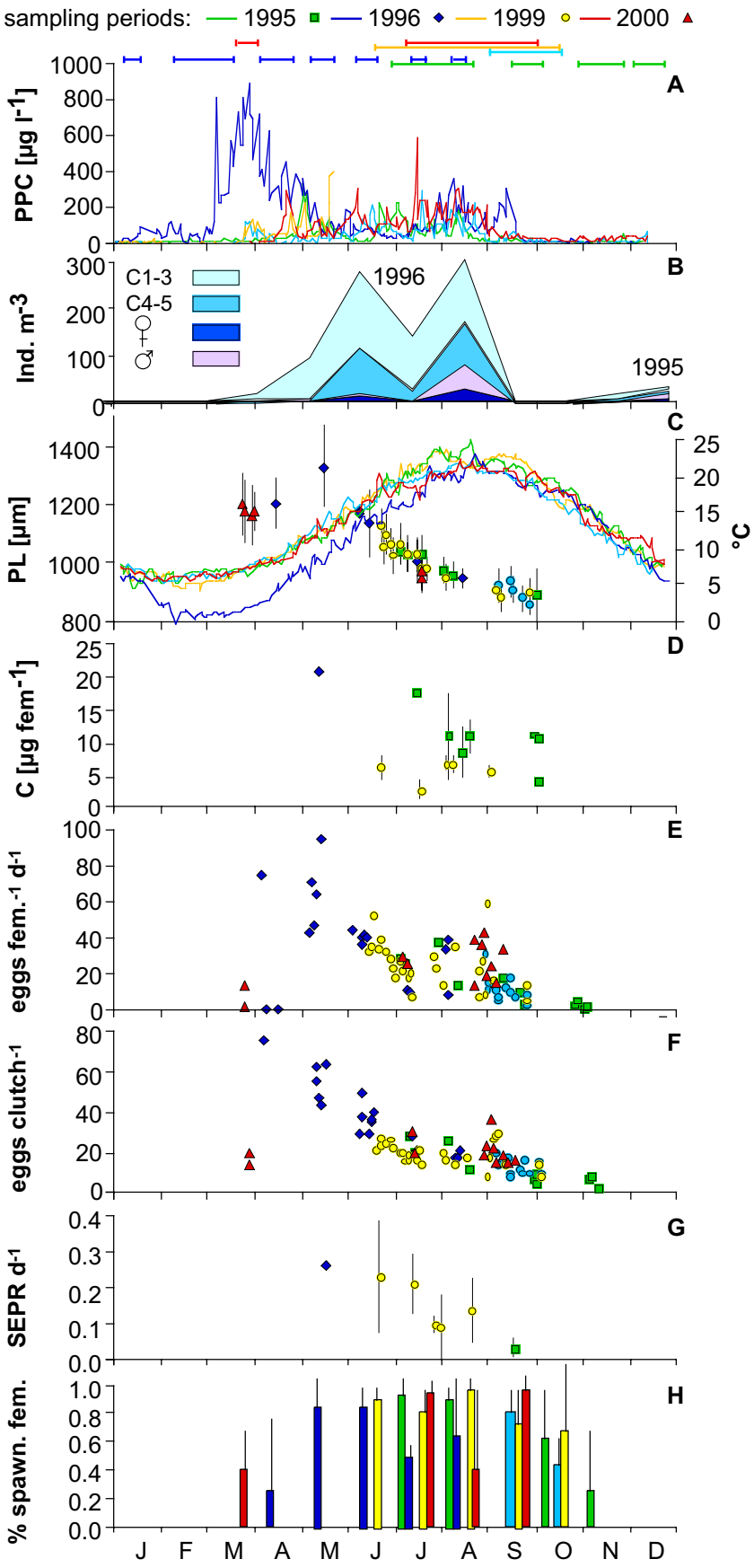


Fig. 3.9: *Centropages hamatus* at Helgoland Roads. **A** PPC (diatoms+flagellates) [µg l^{-1}], **B** Cumulated stage abundance from November 1995 to July 1996 [ind. m^{-3}], **C** PL [µm] and temperature [°C] cycles, **D** Female carbon content [µg], **E** EPR [eggs $female^{-1}$ day^{-1}], **F** Clutch size [eggs $clutch^{-1}$], **G** SEPR [day^{-1}], **H** Proportion of spawning females [%]

Reproduction patterns were quite similar between years (Fig. 3.9E). In summer 1995, egg production rates were intermediate and declined steadily until October. Thereafter, no females were caught until April 1996. After a period of low egg production, reproduction rates increased rapidly to the annual maximum of 95 eggs female^{-1} day^{-1} in May 1996. The individual maximum was 153 eggs day^{-1}. From June to July 1996, egg production decreased continuously, then had a second smaller peak in August and decreased again. In 1998, egg production rates fell from 30 eggs female^{-1} day^{-1}, when sampling started in early September, to 3 eggs female^{-1} day^{-1} in early October. In 1999, two peaks were observed in late June and in September with more than 50 eggs female^{-1} day^{-1}. After the first peak in June, reproduction decreased to less than 10 eggs female^{-1} day^{-1}, then increased and varied between 8 and 30 eggs female^{-1} day^{-1}. In August, egg production was intensified to the second maximum before it decreased to lower rates until the end of September. As a result, females seemed to have the highest spawning activity in spring, while smaller peaks could also occur during summer.

Overall mean egg production rates were 12.3 eggs female^{-1} day^{-1} in 1995 (July to November), 40.8 eggs female^{-1} day^{-1} in 1996 (April to August), 12.1 eggs female^{-1} day^{-1} in 1998 (September/October) and 24.9 eggs female^{-1} day^{-1} in 1999 (June to September).

Maximal clutch size (75 eggs clutch^{-1}) was reached in May 1996 and decreased steadily thereafter in all years (Fig. 3.9F). The annual pattern of clutch size was close to that of egg production rate.

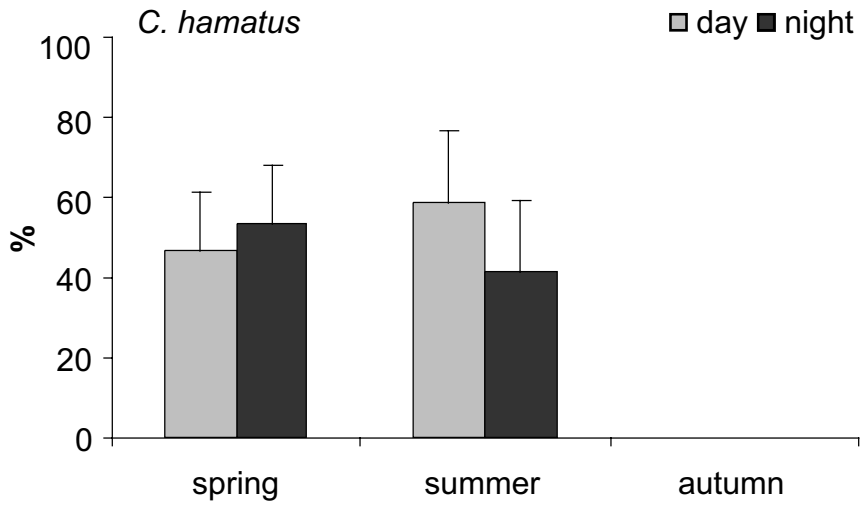


Fig. 3.10: *C. hamatus* at Helgoland Roads. Proportion of clutches produced during the day (8-18h) and during the night (18-8h) in different seasons (data from various years)

As shown in Fig. 3.10, no clear diurnal pattern was found in spawning activity. While the difference between day and night was not significant in spring, more clutches were produced during the day in summer (ANOVA, $p<0.001$).

Weight specific reproduction was maximal in May 1996 and June 1999 and continuously decreased later in the year (Fig. 3.9G). SEPR ranged from 0.031 d^{-1} in October 1995 to 0.264 d^{-1} in May 1996.

The monthly mean proportion of reproducing females over 5 years shows an optimum around 80% from May to September followed by a decrease in October and November. In March and April, an increasing trend may be assumed from the scarce data (Fig. 3.9H). Matching the observations in *T. longicornis*, low proportions of spawning females were observed in July 1996 and August 2000.

Fig. 3.11: Eggs of *C. hamatus*

C. hamatus produced eggs with spines of 25-35 µm length (Fig. 3.11). Egg diameter ranged from 68.0 to 92.1 µm with monthly means between 73.5 and 80.9 µm (Fig. 3.12C). Means were statistically different (cf. Annex 7.1). In August 1996, eggs were bigger than in the other months, in May 1996 they were bigger than in June 1996. In June 1996, eggs were significantly smaller than in June 1999 (ANOVA/ Bonferroni-Dunn Post-Hoc-Test $p<0.0001$). Carbon content of eggs was 0.023 to 0.057 µg C egg^{-1} (Fig. 3.12C). Hatching success was 63% and 74% in April and June 1996, respectively. In 1999, it ranged from 60 to 100% in June and July. In September, hatching rates showed a large variability between 14.7 and 100%, both between different years and within 1998 (Fig. 3.12D).

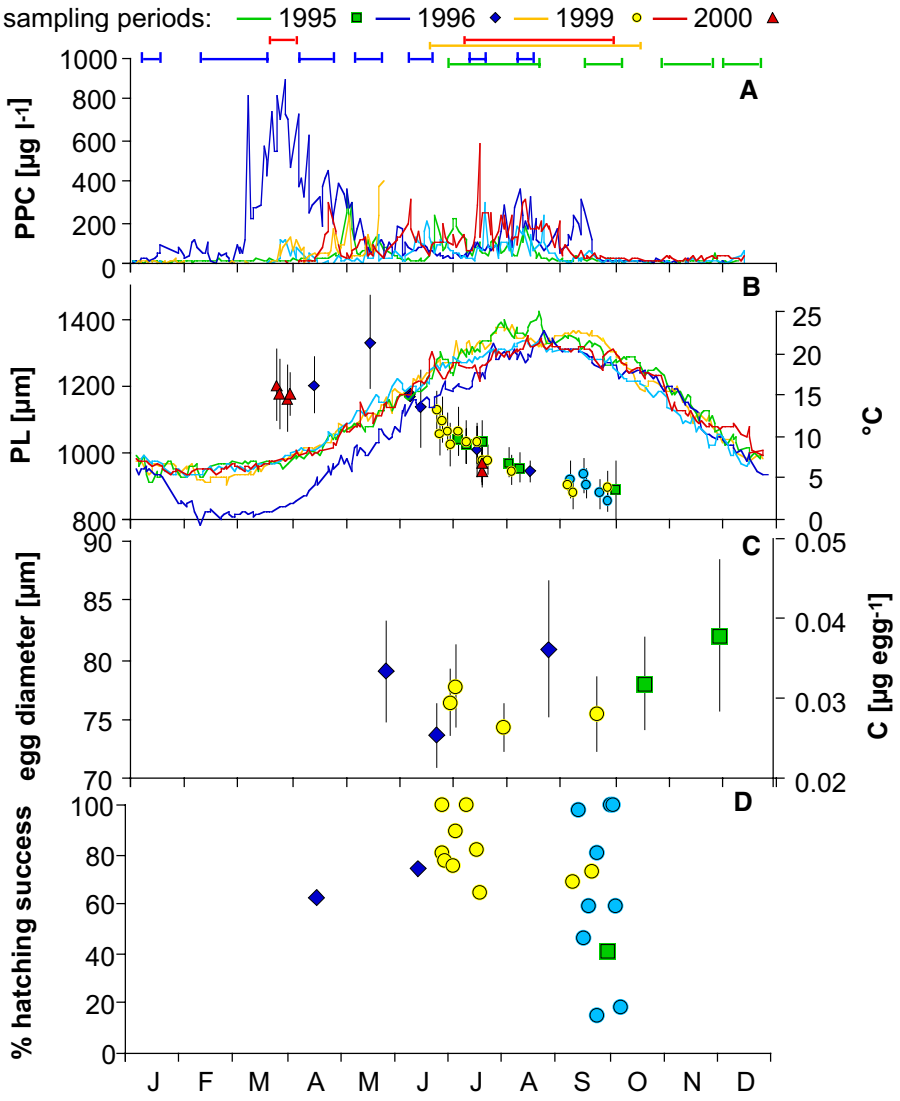


Fig. 3.12: *C. hamatus* at Helgoland Roads. PPC [µg l^{-1}], **B** PL [µm] and temperature [°C] cycles, **C** Egg diameter [µm] and carbon content [µg], **D** Hatching success [%]

3.2.1.3 *Centropages typicus*

The occurrence of *Centropages typicus* at Helgoland Roads (Fig. 3.13) showed great interannual variability. In 1995, no adults were observed before September; then they remained present until January (Fig. 3.14B). In spring 1996, females were missing in the samples until the end of sampling in August. The species was abundant throughout the study period from September to October 1998. In 1999, *C. typicus* was regularly found already from June to early October. In 2000, single individuals were recorded already in April. Abundance of *C. typicus* tended to correlate positively with salinity, since females appeared in September 1995 paralleling an increase in salinity above 30 psu. In contrast, *C. typicus* was absent in spring 1996 when salinity was relatively low, while single individuals

were found in April 2000 following a considerable increase in salinity (cf. Fig. 3.1B).

Fig. 3.13: *Centropages typicus* (female) from Helgoland Roads

Body size of *C. typicus* was consistent in the different years studied. Individual female length ranged from 900 to 1434 µm. They were largest in early April 2000 and smallest in December 1995 and January 1996 (Fig. 3.14C).

Carbon content of females varied from 12 to 18 µg C in September 1995. During summer 1999, female weight tended to increase ranging from 4.7 µg C in July to 18.7 µg C in early October (Fig. 3.14D).

The seasonal cycle of *C. typicus* was determined primarily by the presence and absence of females, which occurred in higher numbers usually in the second, warmer half of the year and disappeared again in winter. In 1995, *C. typicus* showed up in the samples only in September and females produced around 30 eggs female^{-1}d^{-1}. Reproduction heavily decreased until October and nearly ceased from November to January (Fig. 3.14E). In 1998, egg production rates were very similar to those from 1995, declining during September. In 1999, females with very high egg production rates were found already in June. The highest mean egg production rate was 101.3 eggs female^{-1}d^{-1} (CEPR 121.6 eggs female^{-1}d^{-1}) on 29th June (Fig. 3.14E). Reproduction decreased during July and raised again in August. Decreasing reproductive activity was observed in September, as in the other years. In April 2000, single individuals were caught with moderate egg production rates of about 20 eggs female^{-1}d^{-1}. Females were more abundant again in summer 2000 and reproduced actively with high rates at the end of July, a maximum of 80 eggs female^{-1}d^{-1} in early August and a strong decline to 20 eggs female^{-1}d^{-1} at the end of that month (Fig. 3.14E).

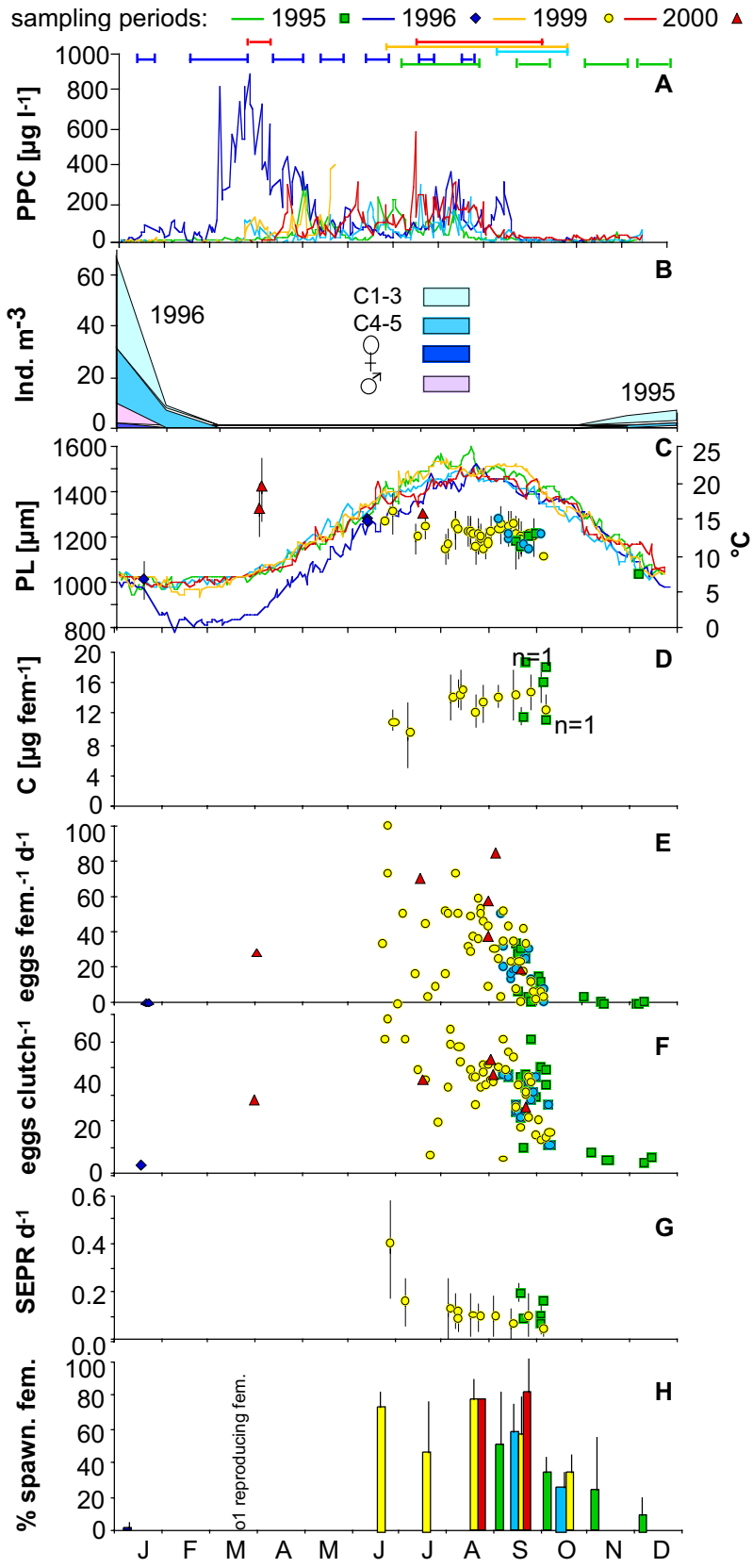


Fig. 3.14: *Centropages typicus* at Helgoland Roads. **A** PPC (diatoms+flagellates) [µg l^{-1}], **B** Cumulated stage abundance from November 1995 to July 1996 [ind. m^{-3}], **C** PL [µm] and temperature [°C] cycles, **D** Female carbon content [µg], **E** EPR [eggs $female^{-1}$ day^{-1}], **F** Clutch size [eggs $clutch^{-1}$], **G** SEPR [day^{-1}], **H** Proportion of spawning females [%]

Over the five years of sampling, *C. typicus* mainly spawned in summer with maxima between June and August and strongly declining rates in late summer and autumn, before females disappeared from the water column in winter. Overall mean egg production was 11.5 eggs female^{-1}d^{-1} in 1995 (September-December), 22.5 in 1998 (September/October) and 33.6 in 1999 (June-October).

Similar to *C. hamatus*, eggs were laid in big clutches, which stuck together several hours after spawning. Clutch size followed the same annual pattern as the egg production rate (Fig. 3.14F). The biggest single clutch contained 245 eggs. Like in *C. hamatus*, more clutches were produced during day-time in summer ($p<0.01$), whereas in autumn, when only a single clutch per day was produced, no significant pattern was found in autumn (Fig. 3.15).

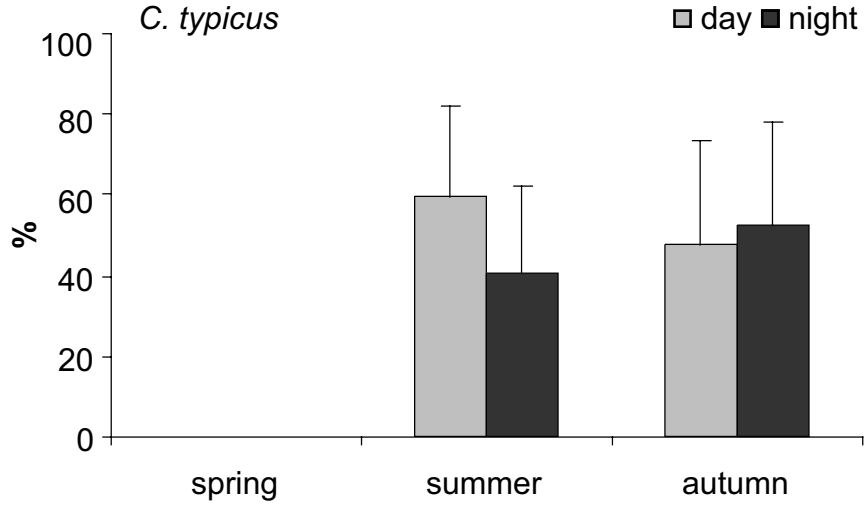


Fig. 3.15: *C. typicus* at Helgoland Roads. Proportion of clutches produced during the day (8-18h) and during night (18-8h) in different seasons (data from various years)

SEPR ranged from 0.006 to 0.531 d^{-1} on the individual level. The lowest monthly mean was recorded in October 1999 (0.055 d-1), the highest in June 1999 (0.413 d-1). Although carbon content of females slightly increased in summer 1999, SEPR declined in the course of time (Fig. 3.14G).

Not all females found were reproducing. The monthly mean percentage of spawning females was highest in August and September 2000 with around 80%. It varied from 35 to 79% in 1999. Lowest proportions were measured in 1995 and 1998, ranging from 10% in December to 60% in September (Fig. 3.14H).

C. typicus produced eggs covered with spines, which were morphologically similar to those of *C. hamatus* (Fig. 3.16), but with shorter spines (5-20 µm).

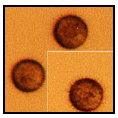


Fig. 3.16: Eggs of *C. typicus* from Helgoland Roads

Egg size varied with time (ANOVA/Bonferroni-Dunn Post-Hoc-Test $p<0.0001$) and ranged from 60.0 to 82.2 µm with monthly means between 69.8 and 76.5 µm (Fig. 3.17C). Eggs were significantly smaller in August and September 1999 than in the other months (cf. Annex 7.1). Estimated carbon content of eggs was 0.024-0.033 µg C egg^{-1} (Fig. 3.17C). Hatching success generally was high (mean 82-100%), except in September 1998, when some single clutches did not hatch at all (mean 64.9%) (Fig. 3.17D).

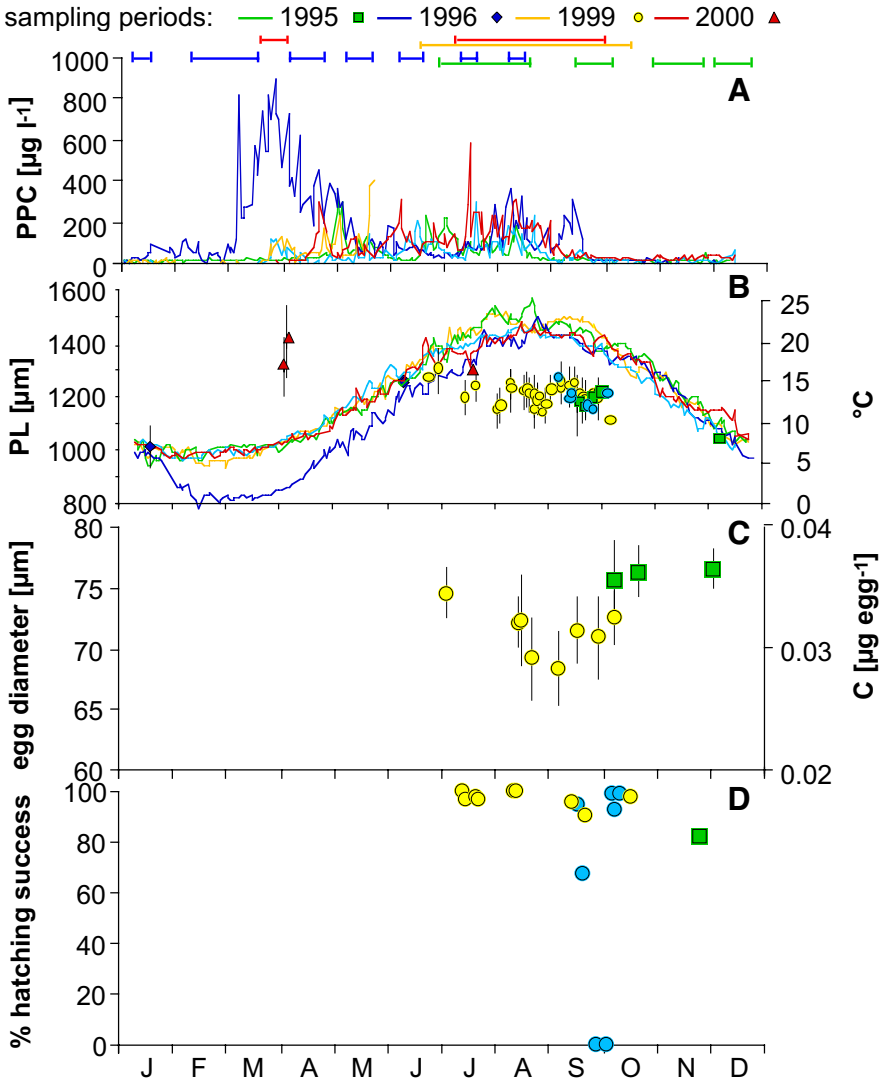


Fig. 3.17: *C. typicus* at Helgoland Roads. Phytoplankton carbon [µg l^{-1}], **B** PL [µm] and temperature [°C] cycles, **C** Egg diameter [µm] and carbon content [µg], **D** Hatching success [%]

3.2.2 Mediterranean populations

In the Mediterranean Sea, egg production measurements were conducted in all months from November 1997 to December 1999 except August. Samples for carbon measurements and SEPR were available in November and December 1998 and from March to May 1999 for *C. typicus* only. Abundance data were available only for 1998 (cf. chapter 2.1.2.2).

3.2.2.1 *Temora stylifera*

Abundance of *Temora stylifera* (no photo available) was low in the first half of the year increasing in August. Adult individuals and late copepodites were most frequent from August to November, then the population decreased rapidly (Fig. 3.18B).

Individual prosome length varied between 747 and 1167 µm. Largest females occurred in February and November 1998 with mean values of 1040 and 1013 µm, respectively, and in November 1999 with 1041 µm (Fig. 3.18C). Carbon content of adult females was in the range of 8.4 to 17.6 µg C female^{-1}, with a mean of 12.4 µg C female^{-1}, in autumn 1998 (Fig. 3.18D).

Egg production of *T. stylifera* decreased 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 (Fig. 3.18E). After dropping down to low rates (around 10 eggs female^{-1} day^{-1}) in late summer, egg production peaked again in November and December 1998. 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 salps appeared in the samples (Fig. 3.18F). Females remained absent until May, and thereafter only few females were found with moderate production rates until September. 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} (Fig. 3.18E). In autumn, egg production rates were somewhat lower in 1998 compared to 1999. Annual mean egg production rates were 11.1 in 1998 and 12.2 eggs female^{-1}day^{-1} in 1999, respectively.

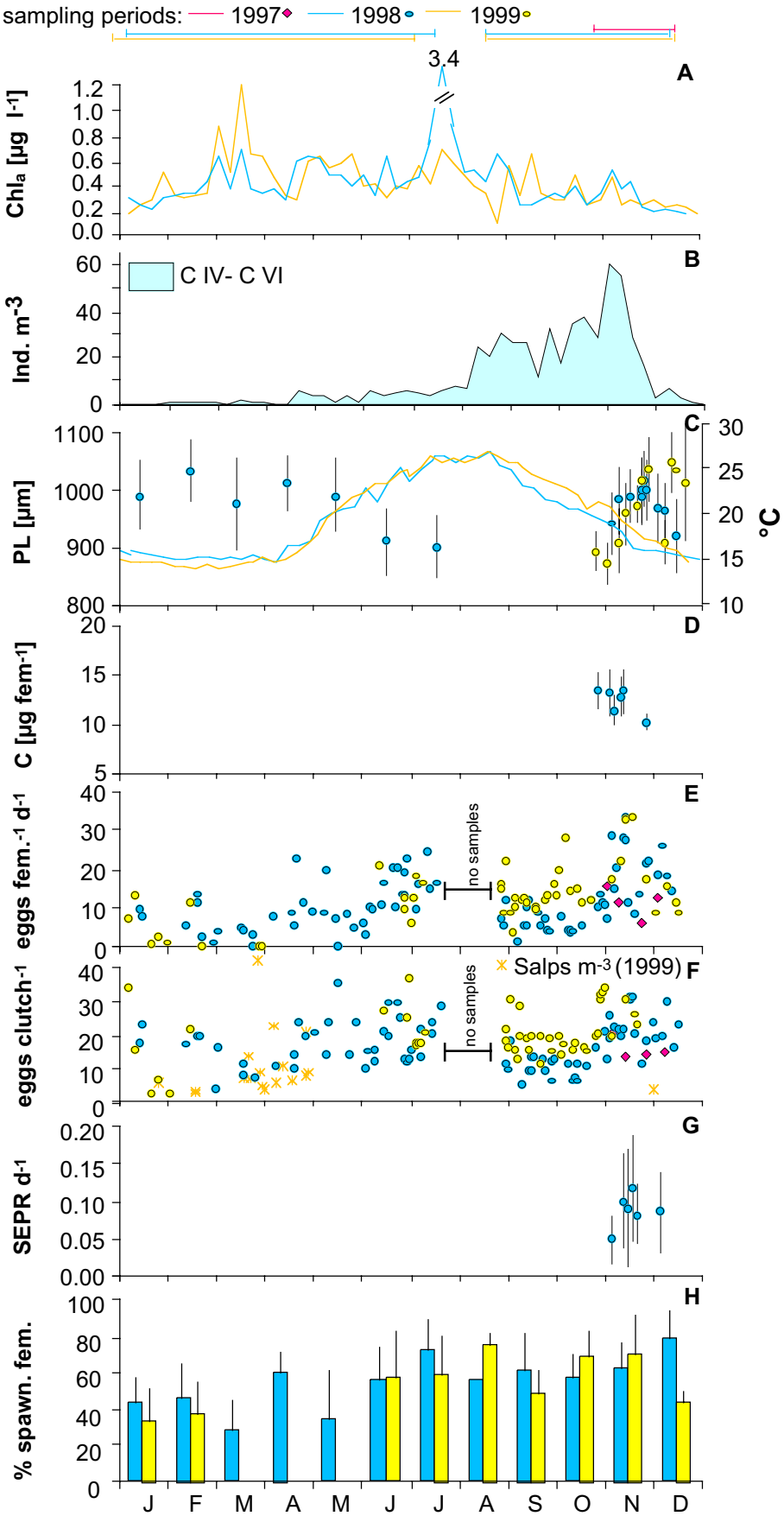


Fig. 3.18: *Temora stylifera* in Villefranche. **A** Chl$_a$ maximum [µg l^{-1}], **B** Abundance [ind. m^{-3}], **C** PL [µm] and mean T [°C], **D** Female carbon content [µg], **E** EPR [eggs fem.$^{-1}$ d^{-1}], **F** Clutch size [eggs clutch^{-1}] and salp density (ind. m^{-3}, 1999), **G** SEPR [day^{-1}], **H** Proportion of spawning females [%]

Females produced mostly one clutch per day, but up to 3 clutches day^{-1} when reproductive activity was high. Most clutches were produced during the night in all seasons ($p<0.0001$), except in winter (Fig. 3.19). Clutches contained more eggs in 1999 than in 1998, resulting in a lower annual mean clutch size of 16.5 eggs clutch^{-1} in 1998 as compared to 20.6 eggs clutch^{-1} in 1999. Mean clutch size peaked with 29.2 egg clutch^{-1} in November 1999 (Fig. 3.18F).

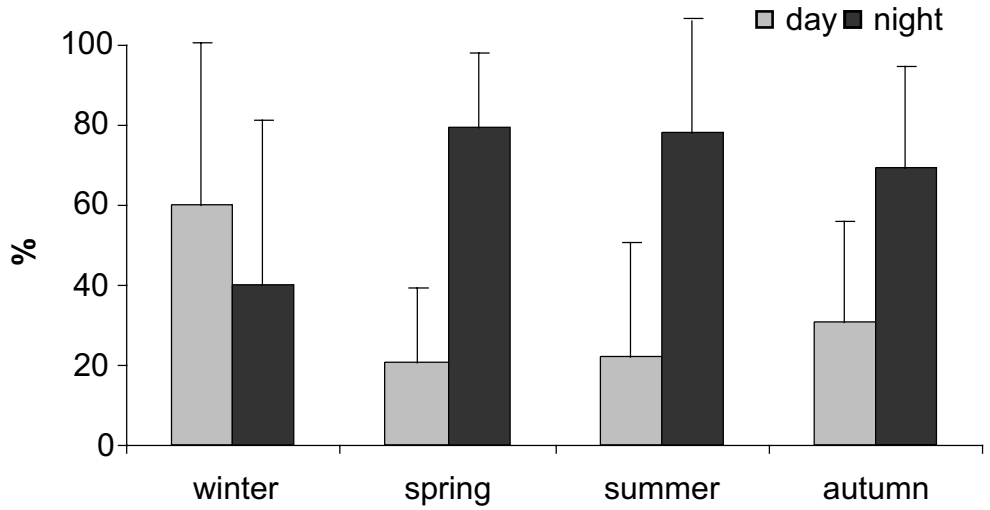


Fig. 3.19: *T. stylifera* in Villefranche. Proportion of clutches produced during the day and during the night in different seasons (data from various years)

Data of individual weight-specific egg production rates of *T. stylifera* in November and December 1998 ranged from 0.01 to 0.21 day^{-1} with a monthly mean of 0.10 day^{-1} in both months (Fig. 3.18G).

Percentage of spawning females ranged between 28% in March and 78% in December 1998. In 1999, females produced no eggs in March and April, while in May no females were found. The proportion of spawning females peaked in August and November with 75% and 70%, respectively (Fig. 3.18H).

The eggs of *T. stylifera* were smooth like those of *T. longicornis* (no photo available). Diameters ranged from 67.7 to 87.2 µm (Fig. 3.20C), with a mean of 77.4 µm. Two groups of eggs were distinguished (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 µg C egg^{-1}, monthly means were in the range of 0.032 to 0.038 µg C egg^{-1} (Fig. 3.20C). Hatching success was 83% in June 1998 and ranged from 65 to 91% in November 1998 (Fig. 3.20D).

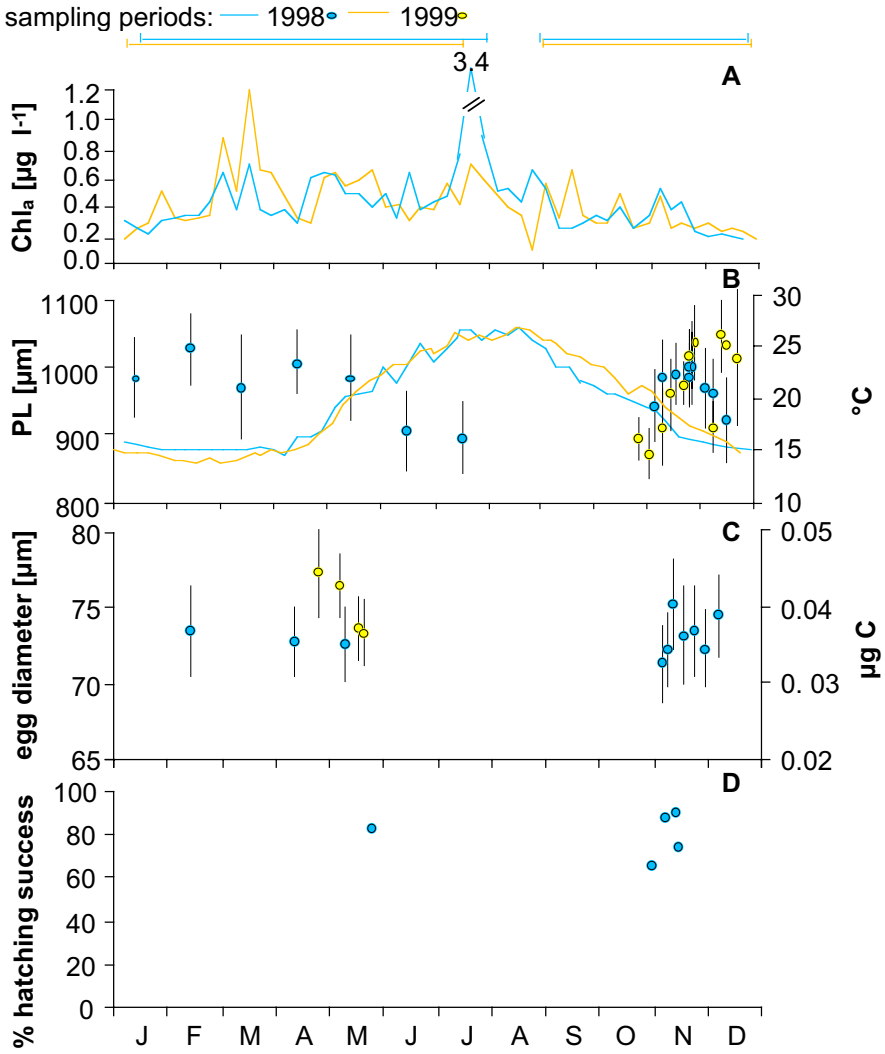


Fig. 3.20: *T. stylifera* in Villefranche. **A** Chl$_a$ maximum [µg l^{-1}], **B** PL [µm] and temperature [°C] cycles, **C** Egg diameter [µm] and carbon content [µg], **D** Hatching success [%]

3.2.2.2 *Centropages typicus*

In contrast to *T. stylifera*, *C. typicus* (Fig. 3.21) was found in highest numbers in spring, with a maximum in May 1998 (Fig. 3.22B). From June on, the number of individuals declined continuously to the end of the year.

Fig. 3.21: *Centropages typicus* (female) from the Bay of Villefranche

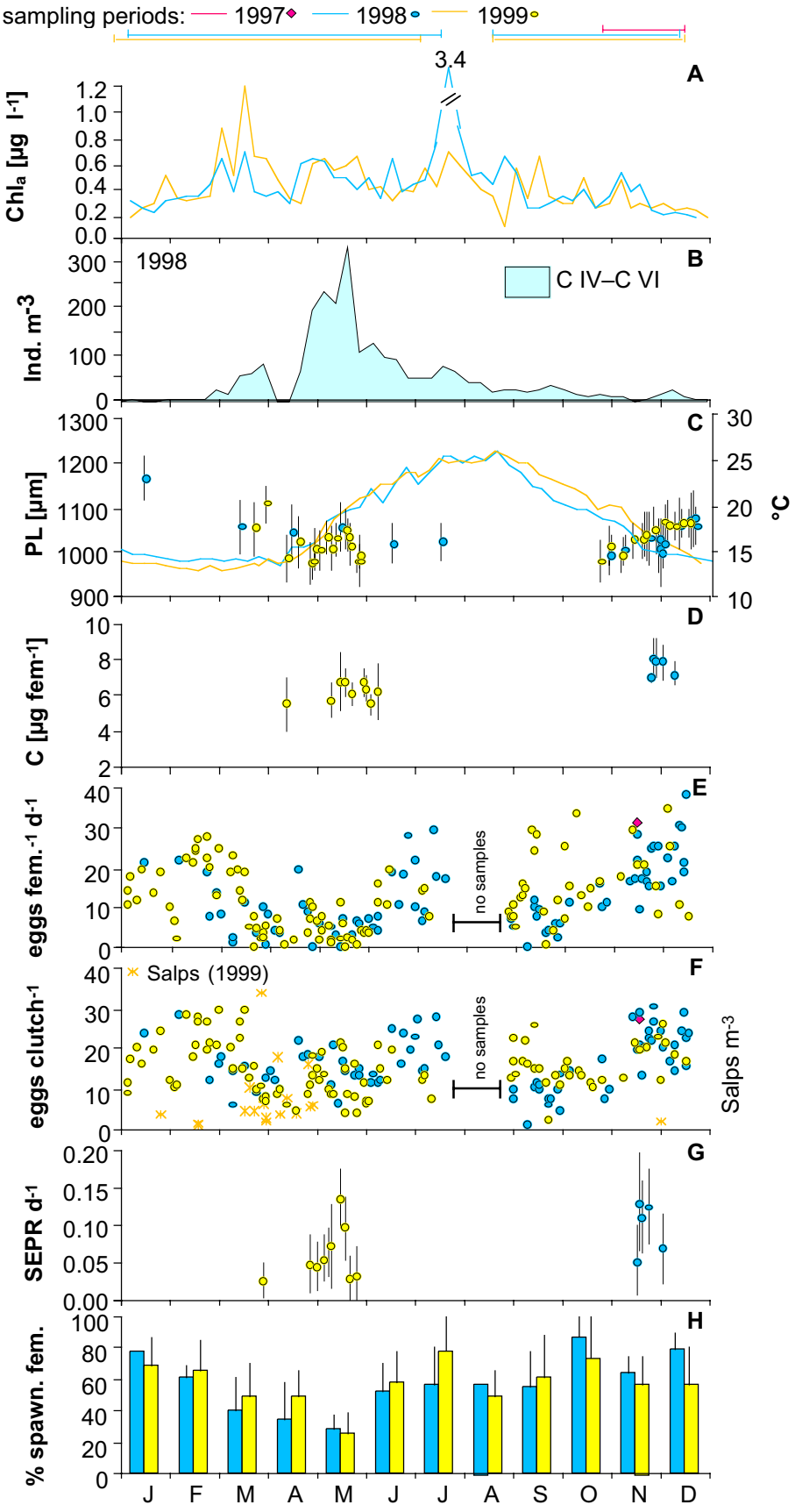


Fig. 3.22: *Centropages typicus* in Villefranche. **A** Chl$_a$ maximum [µg l^{-1}], **B** Abundance [ind. m^{-3}], **C** PL [µm] and mean T [°C], **D** Female carbon content [µg], **E** EPR [eggs fem.$^{-1}$ d^{-1}], **F** Clutch size [eggs clutch^{-1}] and salp density (ind. m^{-3}, 1999), **G** SEPR [day^{-1}], **H** Proportion of spawning females [%]

Individual female prosome length ranged from 850 to 1277 µm. Largest females were found in January 1998 with a mean prosome length of 1160 µm, probably belonging to the population of the preceding year (they therefore were excluded from the regressions). 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 prosome length increased up to 1064 and 1070 µm in December 1998 and 1999, respectively (Fig. 3.22C). Females contained between 4.3 µg C (March 1999) and 10.0 µg C (November 1998), with a mean of 6.7 µg C (Fig. 3.22D).

Annual patterns of egg production rates were similar as in *T. stylifera* (Fig. 3.22E). Adult females were rare in the samples in autumn 1997, but reproduction rates were relatively high, exceeding 20 eggs female^{-1}day^{-1}. In contrast, reproductive activity was low in spring and summer 1998 with egg production rates 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} (Fig. 3.22E). Average clutch size was up to 28 eggs clutch^{-1} at that time. Females reached maximal egg production rates in December 1998 with 33.5 eggs female^{-1} day^{-1} (CEPR 40.3 eggs female^{-1} day^{-1}). The highest individual rate was 83 eggs female^{-1} day^{-1}. In spring 1999, egg production rates did not exceed 18 eggs female^{-1} day^{-1}. During a massive occurrence of salps in March and April 1999, egg production rates dropped down close to zero. In late spring, they recovered with rates around 20 eggs female^{-1} day^{-1}. In autumn 1999, egg production reached another peak with 30.5 (CEPR 36.0) eggs female^{-1}day^{-1} (Fig. 3.22E). 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, respectively.

As in *T. stylifera*, females usually produced 1 clutch day^{-1}, but 2-3 clutches day^{-1} at times of high egg production, mostly at night in spring, summer and autumn ($p<0.0001$), and independent of daytime in winter (Fig. 3.23). Maximal mean clutch size in 1998 was 30.5 eggs clutch^{-1} with the biggest individual clutch containing 63 eggs in November. Biggest clutches in 1999 contained on the average 26.5 eggs with an individual maximum of 72 eggs clutch^{-1} in December (Fig. 3.22F).

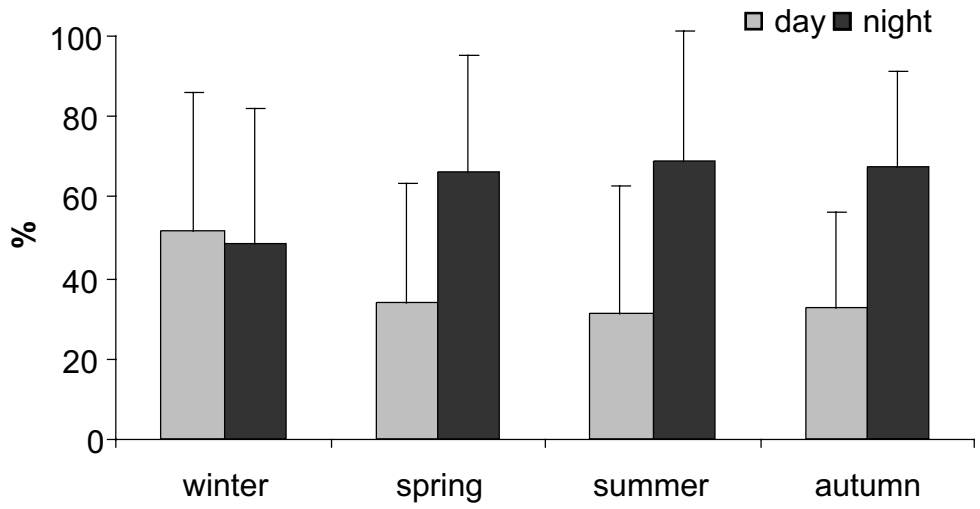


Fig. 3.23: *C. typicus* in Villefranche. Proportion of clutches produced during the day and during night in different seasons (data from various years)

Weight-specific egg production rates ranged from 0.01 to 0.21 day^{-1} in individuals. Monthly means were 0.12 d^{-1} in November 1998 and 0.09 d^{-1} in December 1998. In spring 1999, SEPR seemed to have a peak of 0.14 d^{-1} in May and to decrease thereafter, but this result was not observed in the egg production rates (Fig. 3.22E+G).

The percentage of spawning females showed a seasonal cycle with lowest values in May (25% in 1998; 29% in 1999). The highest numbers of reproducing females were recorded in autumn and winter 1998 with 77% in January, 88% in October and 80% in December. In 1999, females were most productive in January (69%), July (78%) and October (74%), respectively (Fig. 3.22H).

Eggs were morphologically identical to those in the North Sea. The spines covering the egg shells were longer in autumn (up to 38 µm) than in spring (5-18 µm). Egg diameters varied between 63.8 and 83.9 µm with monthly means ranging from 72.7 to 77.3 µm (Fig. 3.24C). In April 1999, eggs were significantly bigger than in all other months studied (ANOVA/Bonferroni-Dunn Post-Hoc-Test $p<0.0001$). Eggs from May 1999 were bigger than those from May 1998 (cf. Annex 7.1). Estimated egg carbon ranged from 0.019 to 0.043 µg C egg^{-1}, the monthly means varied between 0.027 and 0.034 µg C egg^{-1} (Fig. 3.24C).

Hatching success was measured in June, November and December 1998 and from March to May 1999. In June 1998 monthly 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 18th May, only 6% of the incubated eggs were viable (Fig. 3.24D).

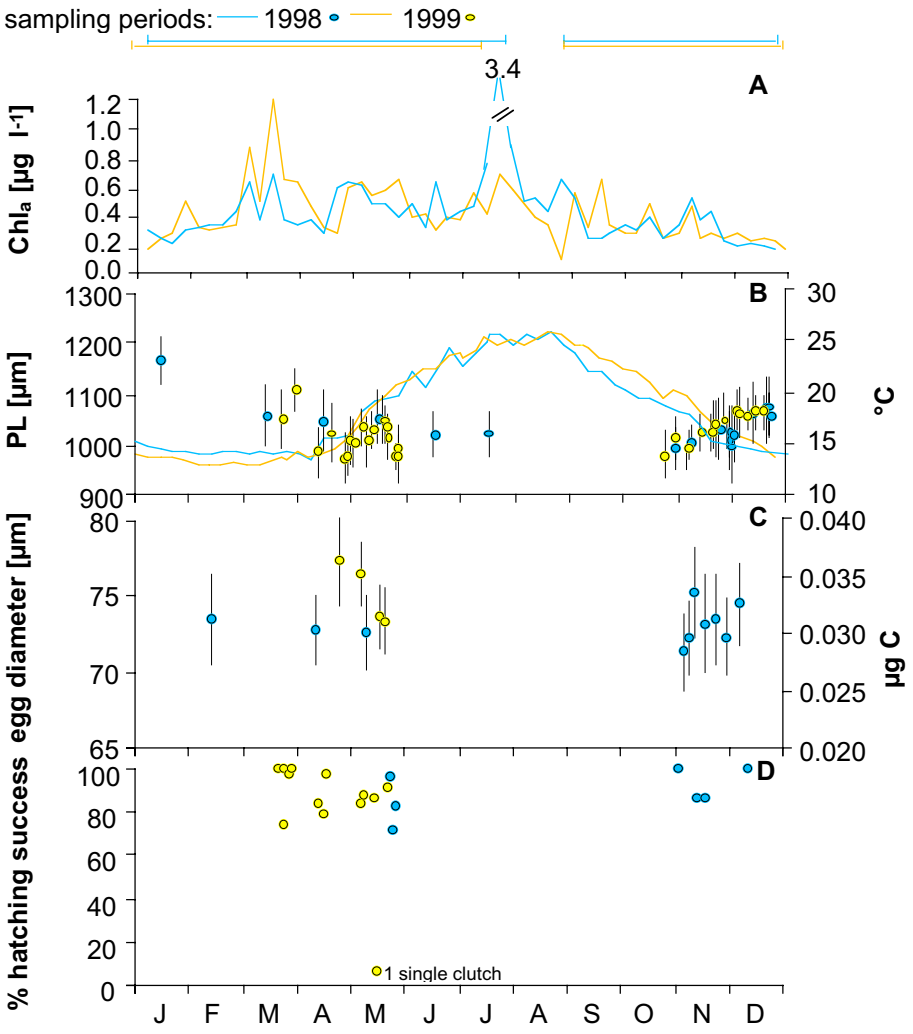


Fig. 3.24: *C. typicus* in Villefranche. **A** Chl$_a$ maximum [µg l^{-1}], **B** PL [µm] and temperature [°C] cycles, **C** Egg diameter [µm] and carbon content [µg], **D** Hatching success [%]

3.2.3 Annual patterns of reproduction in relation to environmental parameters and inter-site variability

In the North Sea, egg production followed a pronounced seasonal cycle with the main reproductive period in spring (*T. longicornis*, *C. hamatus*) and summer (*C. typicus*). In winter egg production was low in *T. longicornis*. Adult females of *C. hamatus* and *C. typicus* were absent. Egg production rates of *T. longicornis* and *C. hamatus* peaked simultaneously in May and were significantly correlated with each other (Tab. 3.1). The seasonal variability of clutch size and egg production rate followed closely seasonal changes in body size (Figs. 3.4, 3.9). The maxima

and minima of length were lagging behind the respective minima and maxima of temperature, which is explained by the fact that adult body size is the result of the temperature conditions during larval development (HART & MCLAREN 1978). Consequently, in a phase of temperature increase (spring) the specimens grew at lower temperatures than those recorded at collection of adult females, during cooling phases they grew at higher temperatures (autumn). The increase in temperature paralleled an increase in egg production rate only during spring, while thereafter egg production rate decreased with further increasing temperature.

C. typicus seemed to be an exception from this pattern. CEPR did not correlate with any other species, since spawning activity peaked later in the year at high summer temperatures. The temperature-size relationship was, however, also valid for *C. typicus*, since single individuals caught in April 2000 were largest.

Tab. 3.1: Spearman rank correlations of CEPR, clutch size and SEPR of *Temora longicornis*, *Centropages hamatus*, *C. typicus* and *T. stylifera*. ***=p<0.0001, n.s.=not significant, – = not enough data to compute

		North Sea	
	CEPR	Clutch size	SEPR
T. longicornis/C. hamatus	***	***	n.s.
T. longicornis/C. typicus	n.s.	n.s.	n.s.
C.hamatus/C. typicus	n.s.	n.s.	n.s.

		Mediterranean	
	CEPR	Clutch size	SEPR
T. stylifera/C. typicus	***	***	–

Egg production rates in the Mediterranean were low, but continuous, in contrast to the patterns in the North Sea (Figs. 3.18, 3.22). Oscillations in reproductive activity were less intense and egg production peaked in autumn instead of spring. As in *T. longicornis* and *C. hamatus* at Helgoland, the cycles of *C. typicus* and *T. stylifera* likewise were remarkably parallel in Villefranche (Figs. 3.18, 3.22). CEPR and clutch size were related between both species on a high significance level, indicating that a common factor controlled their spawning activity (Tab. 3.1).

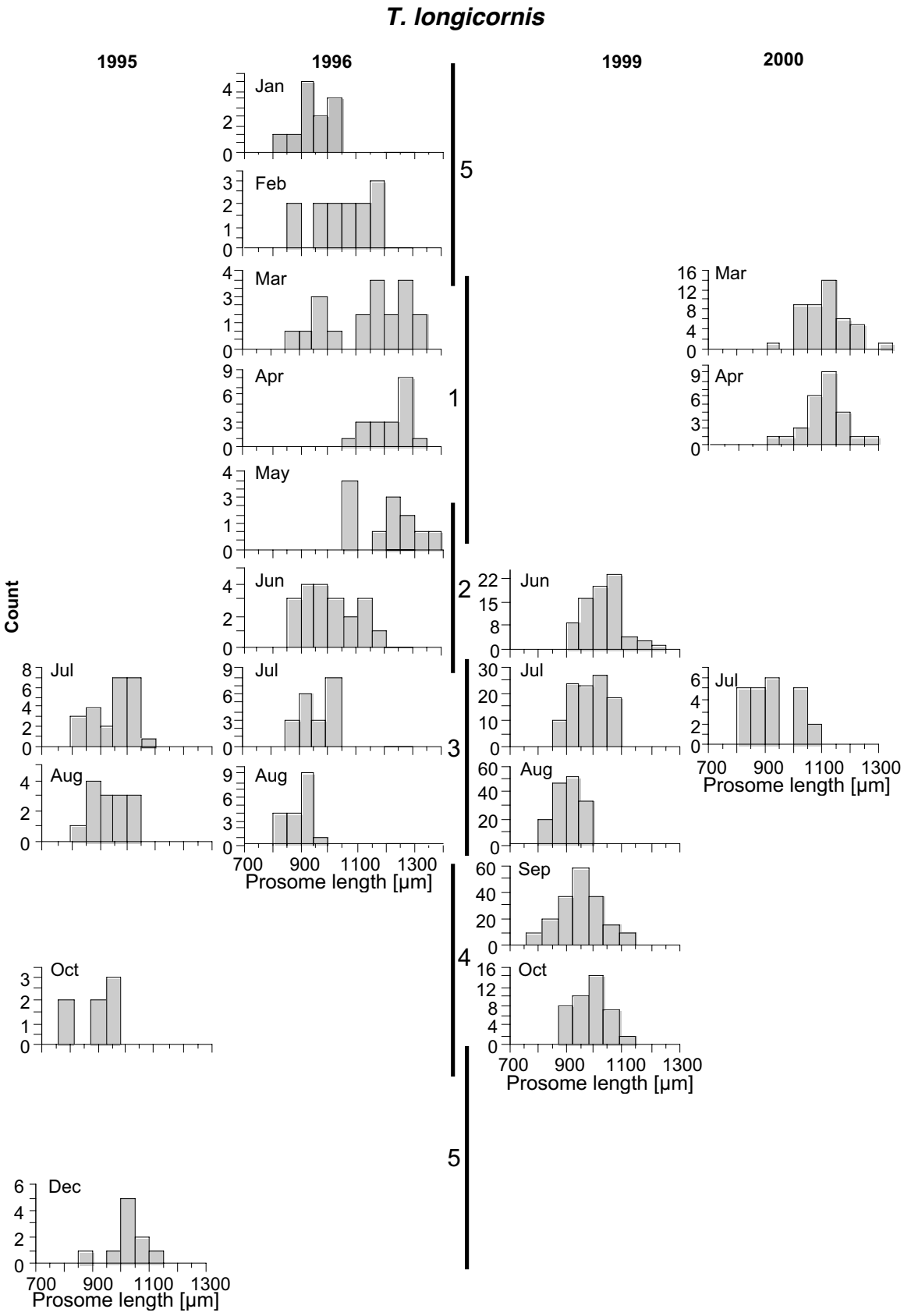


Fig. 3.25 Prosome length frequency distribution [µm] of *T. longicornis* at Helgoland Roads and estimated generation times (vertical bars)

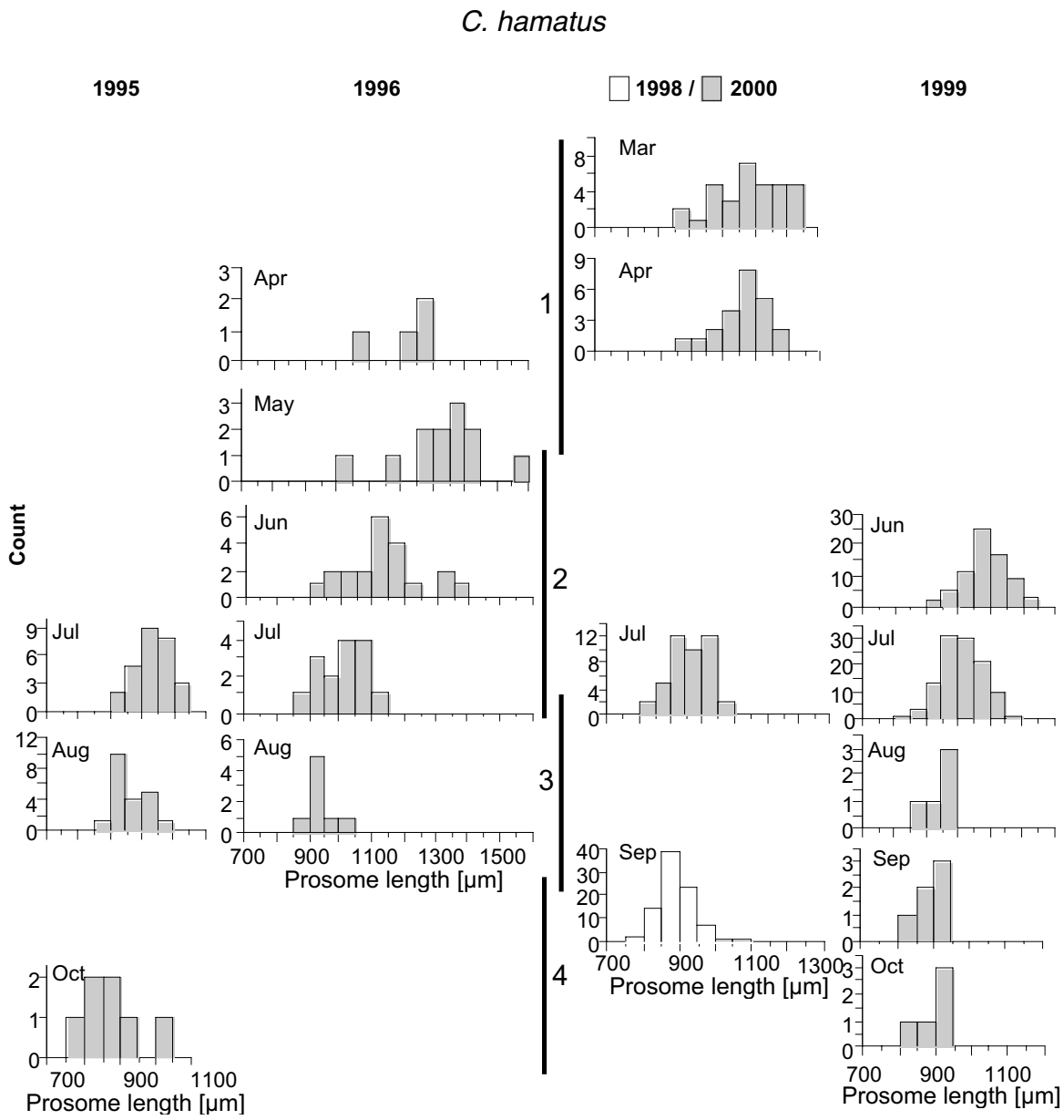


Fig. 3.26 Prosome length frequency distribution [µm] of *C. hamatus* at Helgoland Roads and estimated generation times (vertical bars)

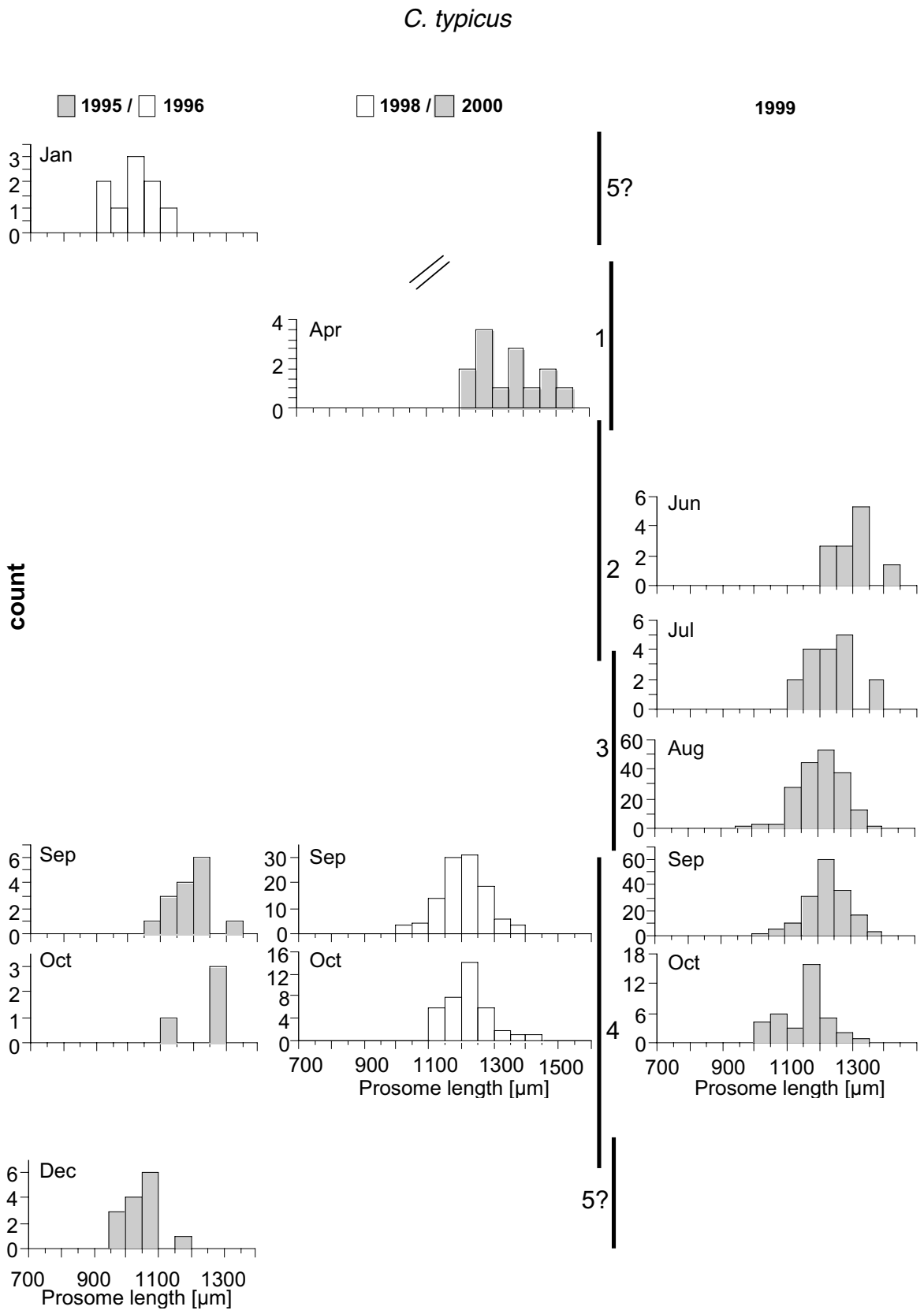


Fig. 3.27 Prosome length frequency distribution [µm] of *C. typicus* at Helgoland Roads and estimated generation times (vertical bars)

Variations of prosome length showed a strong seasonal cycle with up to twofold larger females in spring than in autumn in the boreal species (Figs. 3.25-3.27). In the Mediterranean populations, prosome length also changed with season, but the size-range between smallest and largest animals was <10% (Fig. 3.28). Difference in size between northern and southern *C. typicus* was on the average 18.4%, while *T. longicornis* was 4.7% larger than *T. stylifera*.

Female carbon content followed the patterns of body size. *T. longicornis* had highest carbon contents of all species observed, followed by *C. hamatus and C. typicus* (Tab. 4.2). In the Mediterranean, carbon content of *C. typicus* was half that of the boreal specimens and slightly higher in autumn than in spring. Data for *T. stylifera* were restricted to autumn only, when females contained approximately half the carbon of the congener *T. longicornis* females. *C. hamatus* was similar in size as *T. longicornis,* while carbon content was slightly lower. *T. longicornis* laid the biggest eggs, followed by *C. hamatus* and *T. stylifera*. Eggs of *C. typicus* were smallest, but slightly bigger in the Mediterranean than in the North Sea (Tab. 4.2). Maximal SEPR were 2 times higher in the North Sea than in the Mediterranean. Comparing both regions, differences in size and carbon content were much more pronounced between the two *C. typicus* populations than between *T. longicornis* and *T. stylifera* .

In the North Sea, clear differences were observed in the timing of maximal reproductive activity of the three species and phytoplankton development. Egg production and clutch size of *T. longicornis* increased before the spring diatom increase and reached their maximum one month after the phytoplankton peak (Fig. 3.4). Females of *C. hamatus* grew up to adults during the bloom and reached highest egg production rates after the bloom as *T. longicornis* (Fig. 3.9). Since *C. typicus* females mainly occurred at Helgoland in summer, their reproduction was completely decoupled from the diatom spring bloom. They only could profit from increasing non-diatom phytoplankton in summer (Fig. 3.14).

In the Bay of Villefranche no comparable phytoplankton bloom occurred, oligotrophic conditions prevailed during the whole year and chlorophyll concentration was always low. Small chlorophyll peaks in spring and summer had no obvious effect on egg production rates.

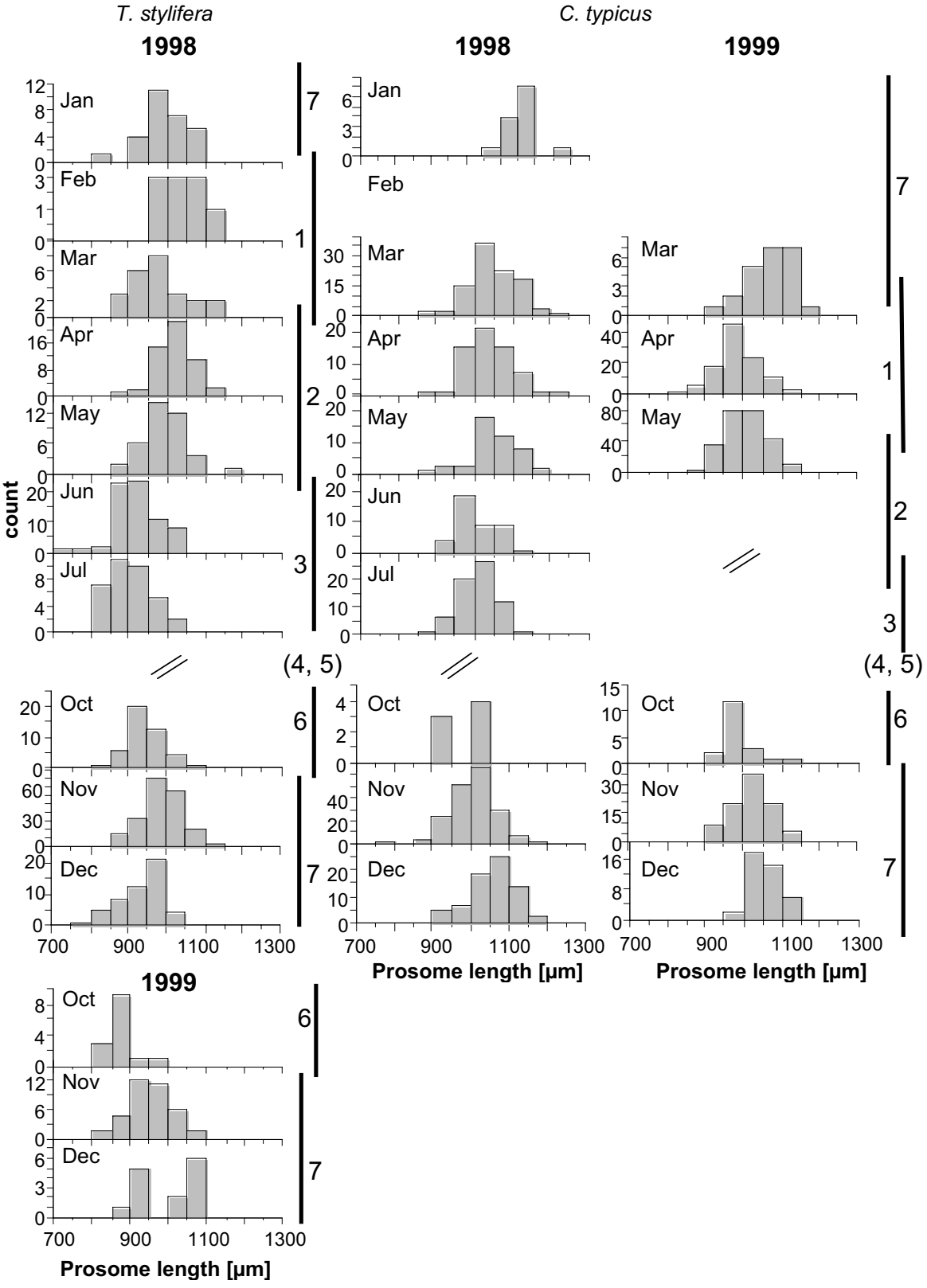


Fig. 3.28 Prosome length frequency distribution [µm] of *T. stylifera* and *C. typicus* in the Bay of Villefranche and estimated generation times (vertical bars)

At Helgoland Island, interannual variability in reproductive patterns was higher than in Villefranche, depending on timing of adult female appearance. *C. typicus* females showed up only in September 1995, while reproducing females were found already in June 1999 and single individuals in April 2000. However, the principal patterns of egg production were the same in all years, driven by the temperature-dependent changes in body size.

In Villefranche, the annual cycle of 1998 generally was repeated in 1999, but the reproduction peaks were less intense in spring despite higher chlorophyll concentrations in March. The bloom of salps in spring 1999 had a great impact on egg production. Apparently, *T. stylifera* suffered from the invasion of these food competitors, and ceased egg production completely before it disappeared from the samples until June. *C. typicus* also decreased reproduction but could recover more rapidly afterwards and restarted 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.

In Tab. 3.2, the determination coefficients of linear regressions between temperature, prosome length, female carbon content, phytoplankton components and reproductive parameters are presented. Regression analysis showed highly significant inverse relationships between temperature and body size in all North Sea species, but not in the Mediterranean populations. Inverse correlations were also significant between clutch size and temperature for both *C. hamatus* and *T. longicornis,* and between egg production rate and temperature for *C. hamatus*. Highly significant relationships were found between clutch size/egg production rate and prosome length in *T. longicornis* and *C. hamatus*, but not in *C. typicus* (Tab. 3.2). Since reproduction and body size were also influenced by food availability, some highly significant relationships were found between phytoplankton carbon, prosome length and clutch size in *T. longicornis* and *C. hamatus* (Tab. 3.2).

In Villefranche, a temperature effect could not be detected. Although prosome length varied on an annual basis with small females in summer and biggest ones in winter (Fig. 3.28), regression of length versus *in situ* mean temperature (0-75 m) produced no significant result. Egg production and clutch size showed no relationship with temperature either (Tab. 3.2), even when the

temperature of the deep chlorophyll maximum (30 and 50 m depth) was used in the analysis instead of the mean of the water column. Egg production of *T. stylifera* seemed to have an optimum between 17 and 18 °C rather than following a linear relationship with temperature (cf. Annex 7.2).

Tab. 3.2: Determination coefficients (r^2) between temperature at collection [°C], food availability (chlorophyll$_a$=Chl$_a$ [µg l^{-1}] or phytoplankton carbon=PPC [µg l^{-1}], diatom carbon [µg l^{-1}], flagellate-carbon [µg l^{-1}]) and prosome length=PL [µm], corrected egg production rate=CEPR, specific egg production rate=SEPR, clutch size, female carbon and egg carbon. Significance levels: n.s.=not significant, *=p<0.01, **=p<0.001, ***=p<0.0001; number of observations in parenthesis.

	North Sea			Mediterranean	
parameter	*T. longicornis*	*C. hamatus*	*C. typicus*	*T. stylifera*	*C. typicus*
PL/T	0.63*** (76)	0.74*** (52)	n.s. (50)	n.s. (21)	n.s. (38)
CEPR/T	n.s. (126)	0.25*** (79)	n.s. (83)	n.s. (92)	n.s. (179)
SEPR/T	n.s. (16)	n.s. (5)	n.s. (16)	n.s. (5)	n.s. (14)
clutch size/T	0.20*** (126)	0.42*** (78)	n.s. (78)	n.s. (92)	n.s. (180)
fem. carbon/T	0.46** (24)	n.s. (12)	n.s. (16)	n.s. (5)	n.s. (14)
CEPR/PL	0.27*** (78)	0.55*** (48)	n.s. (48)	n.s. (21)	0.26** (38)
SEPR/PL	n.s. (10)	n.s. (4)	n.s. (12)	n.s. (4)	n.s. (7)
clutch size/PL	0.41*** (78)	0.65*** (47)	n.s. (47)	n.s. (21)	n.s. (38)
fem. carbon/PL	n.s. (18)	n.s. (9)	n.s. (12)	n.s. (4)	n.s. (7)
CEPR/fem. carbon	0.46** (24)	n.s. (12)	n.s. (16)	n.s. (6)	n.s. (14)
SEPR/fem. carbon	n.s. (16)	n.s. (5)	n.s. (16)	n.s. (6)	n.s. (14)
clutch size/fem. carbon	0.55*** (24)	n.s. (12)	n.s. (16)	n.s. (6)	n.s. (14)
egg carbon/fem. carbon	n.s. (11)	n.s. (5)	n.s. (16)	n.s. (6)	n.s. (14)
PL/diatom-C	0.39*** (52)	0.31** (33)	n.s. (20)	–	–
PL/non diatom-C	0.21** (52)	n.s. (33)	n.s. (20)	–	–
PL/PPC	0.29*** (52)	0.28* (33)	n.s. (20)	–	–
CEPR/diatom-C	0.17** (79)	n.s. (52)	n.s. (36)	–	–
CEPR/non diatom-C	n.s. (79)	n.s. (52)	n.s. (36)	–	–
CEPR/PPC	0.17** (79)	n.s. (52)	n.s. (36)	–	–
SEPR/diatom-C	n.s. (7)	–	n.s. (5)	–	–
SEPR/non diatom-C	n.s. (7)	–	n.s. (5)	–	–
SEPR/PPC	n.s. (7)	–	n.s. (5)	–	–
clutch size/diatom-C	0.31*** (79)	0.41*** (49)	n.s. (32)	–	–
clutch size/ non diatom-C	n.s. (79)	n.s. (49)	n.s. (32)	–	–
clutch size/PPC	0.29*** (79)	0.37*** (49)	n.s. (32)	–	–
fem. carbon/diatom-C	n.s. (13)	n.s. (7)	n.s. (5)	–	–
fem. carbon/non diatom-C	n.s. (13)	n.s. (7)	n.s. (5)	–	–
fem. carbon/PPC	n.s. (13)	n.s. (7)	n.s. (5)	–	–
PL/Chl$_a$	–	–	–	n.s. (9)	n.s. (15)
CEPR/Chl$_a$	–	–	–	n.s. (53)	n.s. (74)
SEPR/Chl$_a$	–	–	–	n.s. (3)	n.s. (6)
clutch size/Chl$_a$	–	–	–	n.s. (53)	n.s. (74)
fem. carbon/Chl$_a$	–	–	–	n.s. (3)	n.s. (6)

Prosome length only affected the reproduction of *C. typicus* significantly (Tab. 3.2): corrected egg production rate and clutch size increased with females body size (Tab. 3.2). Egg production and clutch size of *T. stylifera* seemed to be independent of prosome length, probably because data were too few to give any statistically relevant result. Neither CEPR nor SEPR were significantly related to

female carbon content in *C. typicus* (Tab. 3.2). Likewise, there was no relationship either between female body carbon and prosome length, or between egg carbon and female carbon. Chlorophyll$_a$ did not correlate with any of the reproduction parameters (Tab. 3.2).

3.3 Temperature impact on reproductive biology and development: laboratory observations

3.3.1 Temperature impact on survival, reproduction and development

3.3.1.1 Female thermal tolerance (FTT)

Female thermal tolerance followed an optimum curve in *T. stylifera* and both *C. typicus* populations (indexed $_{NS}$ and $_{Med}$ further on) with increased mortality at temperatures higher and lower than the optimum (Fig. 3.29C, D, E). Survival of *C. hamatus* (Fig. 3.29B) decreased linearly with temperature (12.5°C excluded), while no clear pattern was found in *T. longicornis* (Fig. 3.29A).

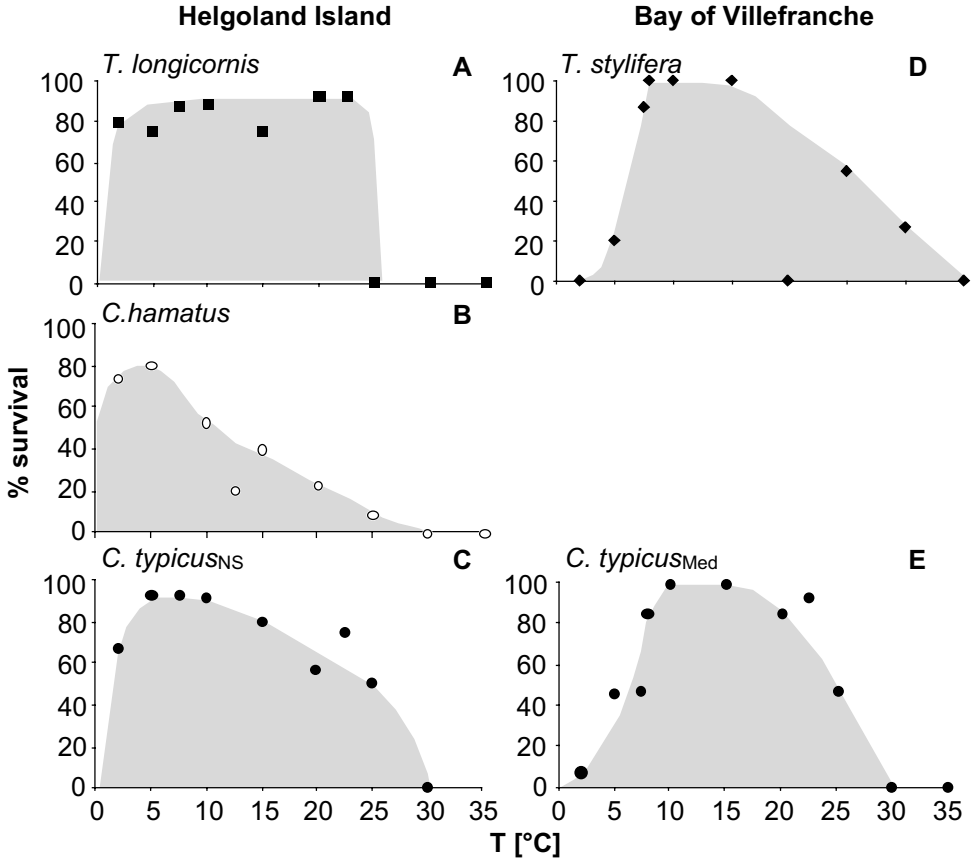


Fig. 3.29: Female thermal tolerance (FTT) of *Temora* and *Centropages* congeners from Helgoland Island and the Bay of Villefranche. Proportion of surviving females after 5 days of incubation

Proportions of surviving females during 5 days of observation are presented in Fig. 3.30 for all species and for a variety of temperatures. In general three patterns were observed: (1) hyperbolic curves with a very high mortality of females during the first days followed by a constant proportion of survivors, (2) a constant survival rate, or (3) the proportion of survivors decreasing with age. For all species pattern (1) was recorded at the highest temperatures, i.e. 25°C and 30°C for *T. longicornis*, 30°C for *C. typicus*$_{NS}$ and *C. hamatus*, 30°C and 35°C for *T. stylifera* and *C. typicus*$_{Med}$. 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 *T. longicornis* and *C. typicus*$_{NS}$. 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.

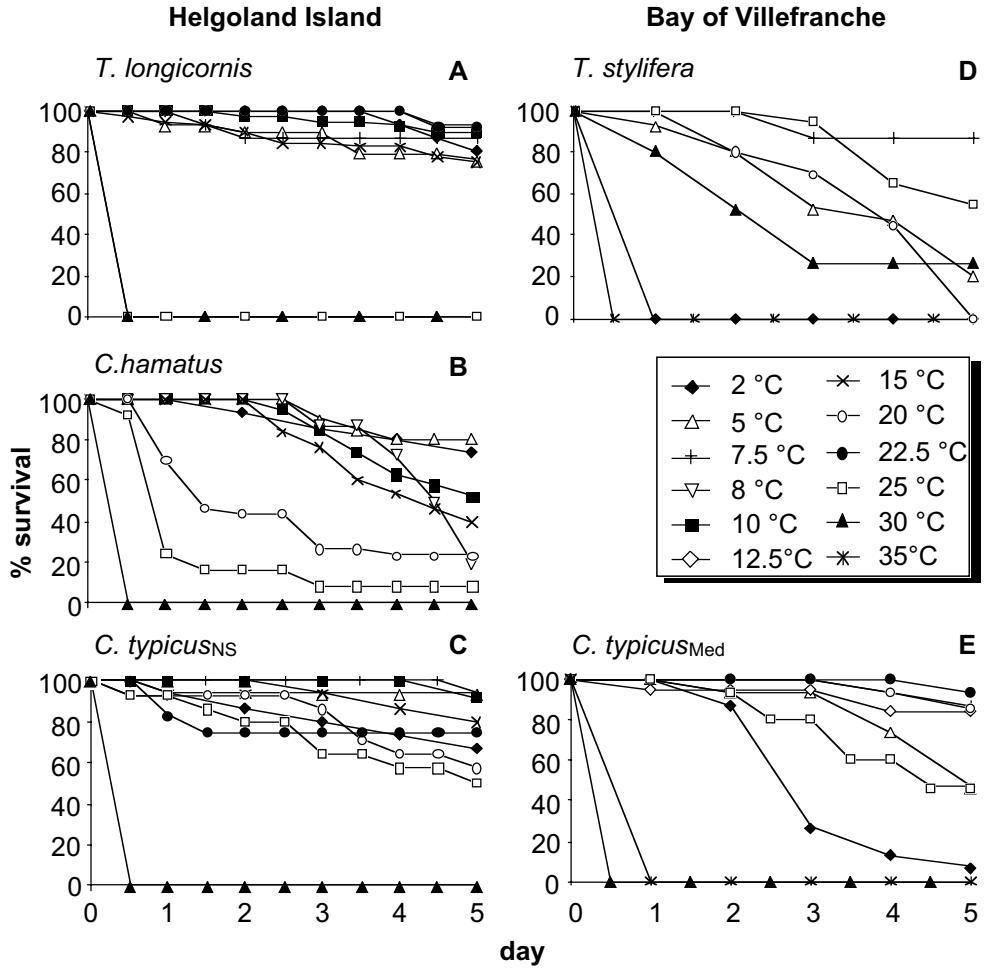


Fig. 3.30: Female thermal tolerance (FTT). Proportions of survivors during 5 days of incubation at different temperatures

3.3.1.2 Reproductive thermal response (RTR)

RTR generally showed an optimum curve. Optimal temperature was around 20°C for *T. longicornis* and *C. typicus*$_{NS+Med}$, whereas *C. hamatus* spawned most eggs at 12.5°C and *T. stylifera* at 15°C (Fig. 3.31).

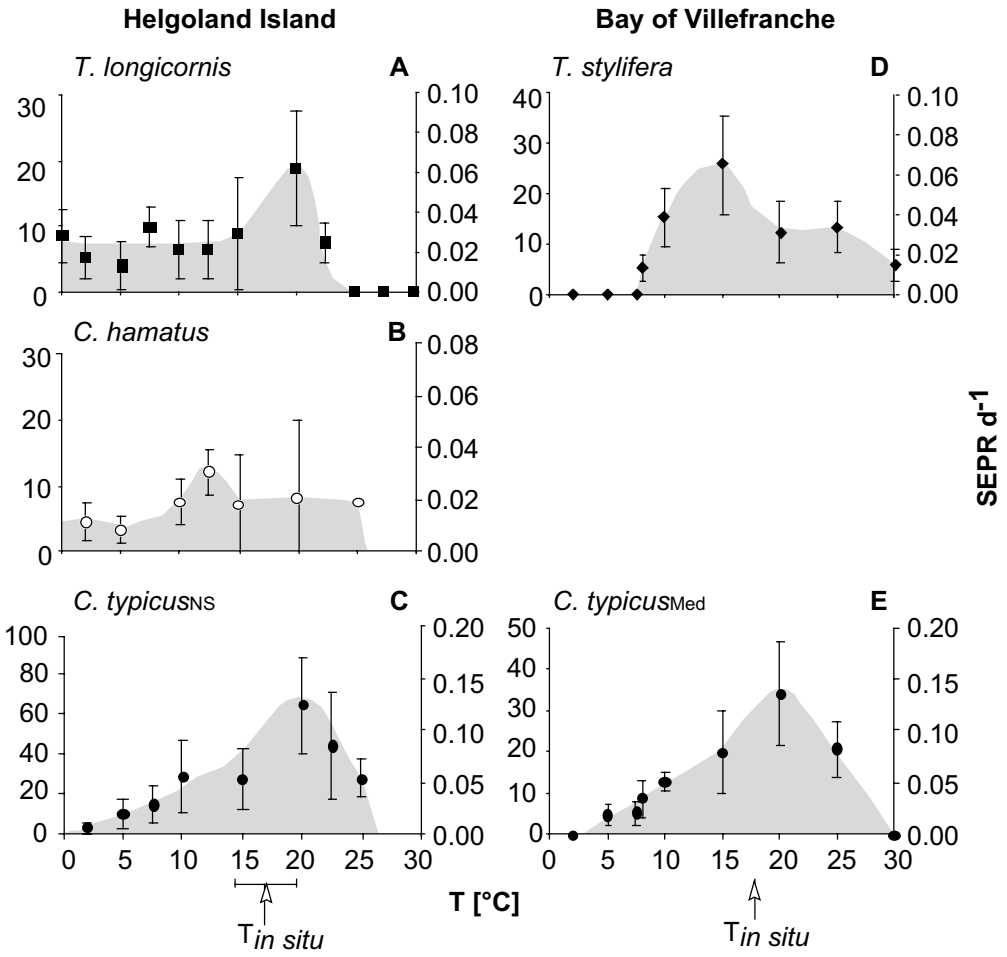


Fig. 3.31: Reproductive thermal response (RTR) of *Temora* and *Centropages* congeners from Helgoland Island and the Bay of Villferanche. Mean egg production rates from 5 days of incubation

Weight specific production rates (SEPR) were in the same range for all species except *C. typicus* and varied between 6 and 7.5% d^{-1} at the optimal temperatures (Figs. 3.31B, C, E). Both *C. typicus* populations had higher specific production reaching 11%$_{NS}$ and 16%$_{Med}$ at the optimum, respectively (Figs. 3.31A, D).

Egg production rate over 5 days was mostly constant (Fig. 3.32), except when reproduction stopped after a few days (*C. hamatus* at 12.5°C, 15°C and 25°C, *C. typicus*$_{NS}$ at 25°C, *T. stylifera* at 25°C and 30°C).

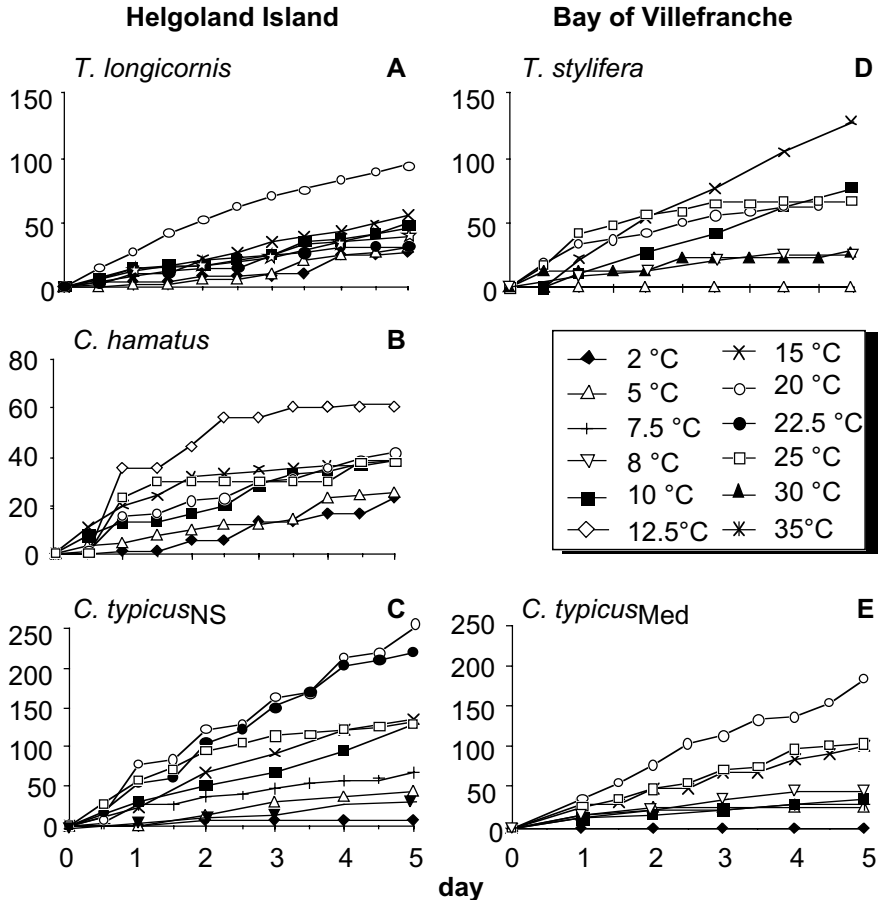


Fig. 3.32: Reproductive thermal response (RTR). Cumulated numbers of eggs laid during 5 days of incubation at different temperatures

3.3.1.3 Prosome length of females

Prosome length of females in my experiments showed little variability within species (Fig. 3.33) in comparison to the ranges of prosome length compiled from different seasons and locations (cf. Fig. 1.2). *T. longicornis* and *T. stylifera* females had a similar mean prosome length of 951.1 ± 71.3 µm 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 to 1073.7 µm (mean 965.7 ± 47.9 µm). Body size of *C. hamatus* was between 793.1 µm and 1146.8 µm, with a mean of 944.6 ± 79.5 µm. 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. Size differences between experiments were not significant in a given population, except in *C. typicus*$_{Med}$ and *C. hamatus*. In both cases, females were greater at 15°C than at 10°C ($p<0.0001$).

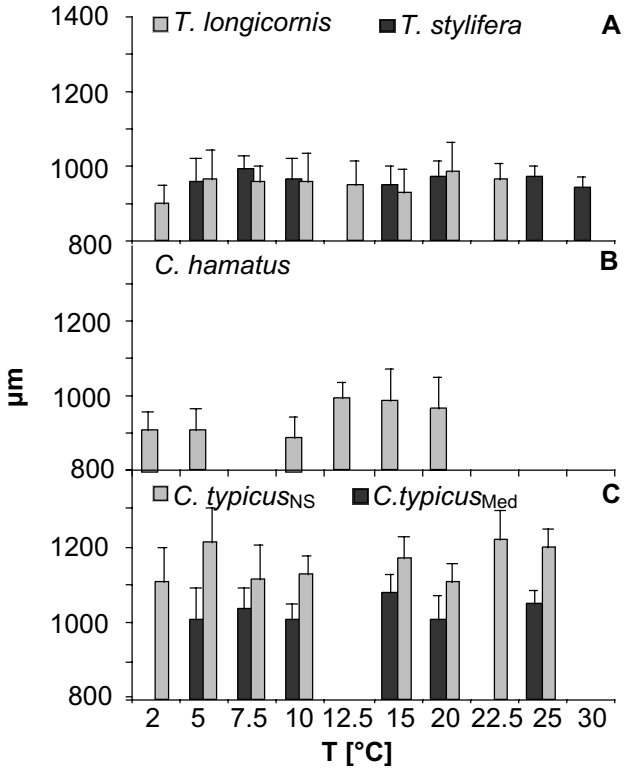


Fig. 3.33: Prosome length [µm] of females incubated in the temperature gradient

3.3.1.4 Embryonic thermal response (ETR) and hatching success

Temperature impact on embryonic duration is presented in Fig. 3.34. At all temperatures where eggs were produced, nauplii hatched, except in *T. stylifera* at 30°C and *C. typicus*$_{Med}$ at 2°C.

Embryonic development times decreased with increasing temperature following Belehrádek functions in all species (Tab. 4.3). In few cases, embryonic duration increased at higher temperatures, as at 25°C in *C. hamatus* and at 28°C in *C. typicus*$_{Med}$ (Fig. 3.34B, D). Hatching success was maximum or very high at any temperature situation in *T. longicornis* and *C. typicus*$_{NS}$ (Fig. 3.35A, C). 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% (Fig. 3.35B). In *T. stylifera*, survival of eggs increased linearly with temperature from 52% at 10°C to 100% at 20 and 25°C (Fig. 3.35E).

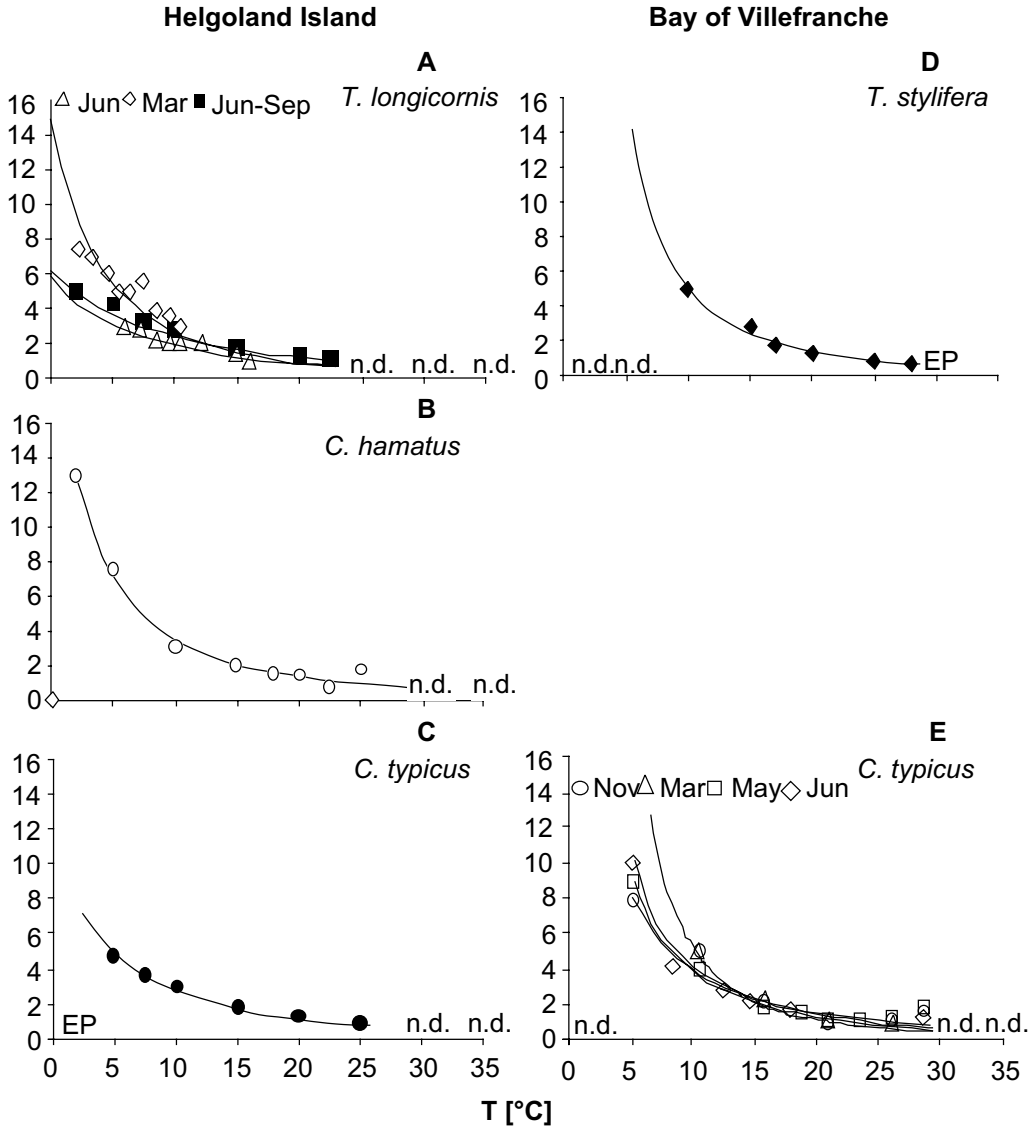


Fig. 3.34: Embryonic thermal response (ETR). Development times [days] fitted with Belehrádek curves. n.d.= no development, EP=no development, but egg production was observed

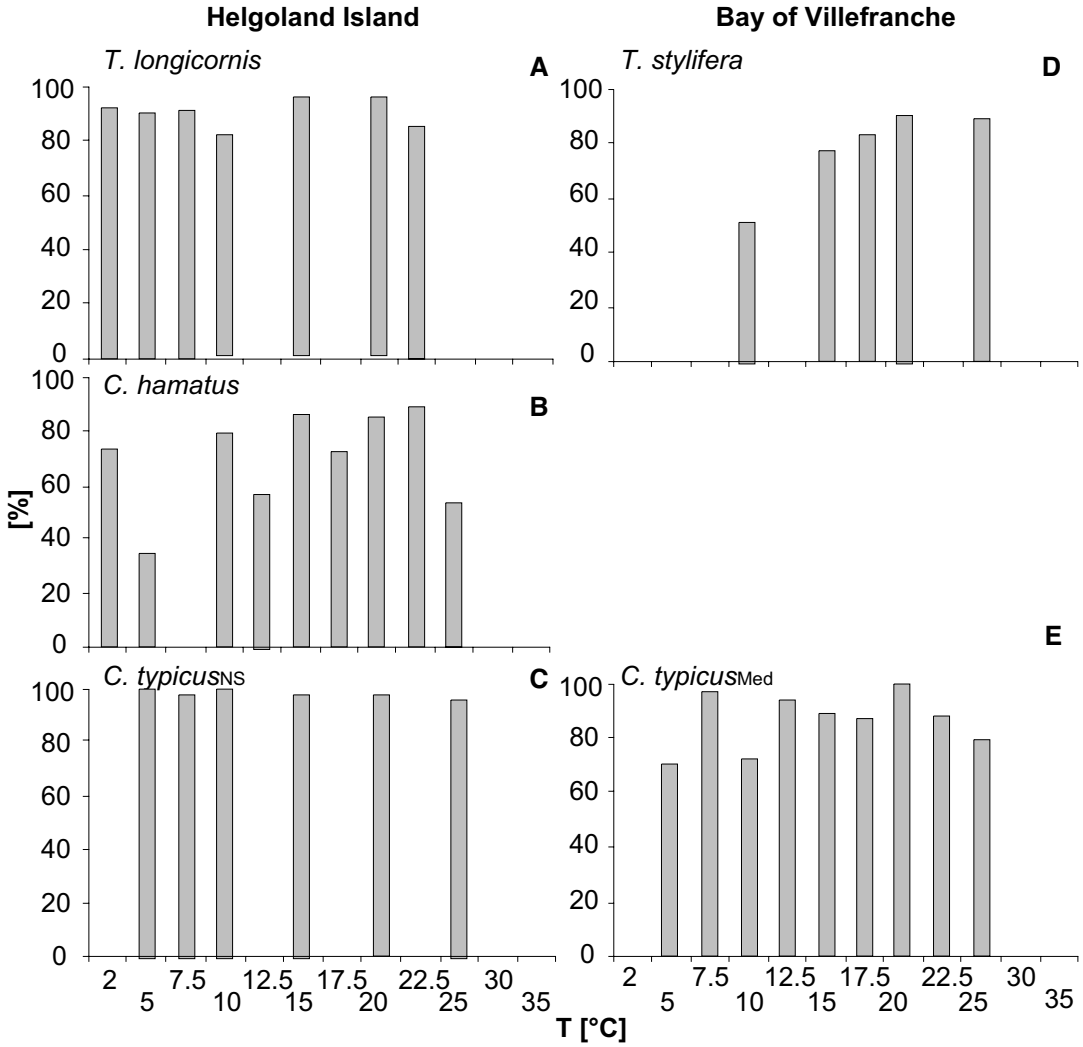


Fig. 3.35: Hatching success of eggs incubated at different temperatures

3.3.1.5 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 Fig. 3.36 (for details of population development cf. Annex 7.3). Stage durations and mortality rates are summarized in Tab. 3.3, proportions of total development time (egg-laying to adult) spent in each stage are compared in Tab. 3.4. Naupliar and copepodite development, as well as generation times, are presented together with data from the literature in Tab. 4.5. The generation times of *C. typicus*$_{NS}$ reared at 15 and 20°C provided the following equation:

log G=-0.0593 T [°C]+2.4011, with G = generation time.

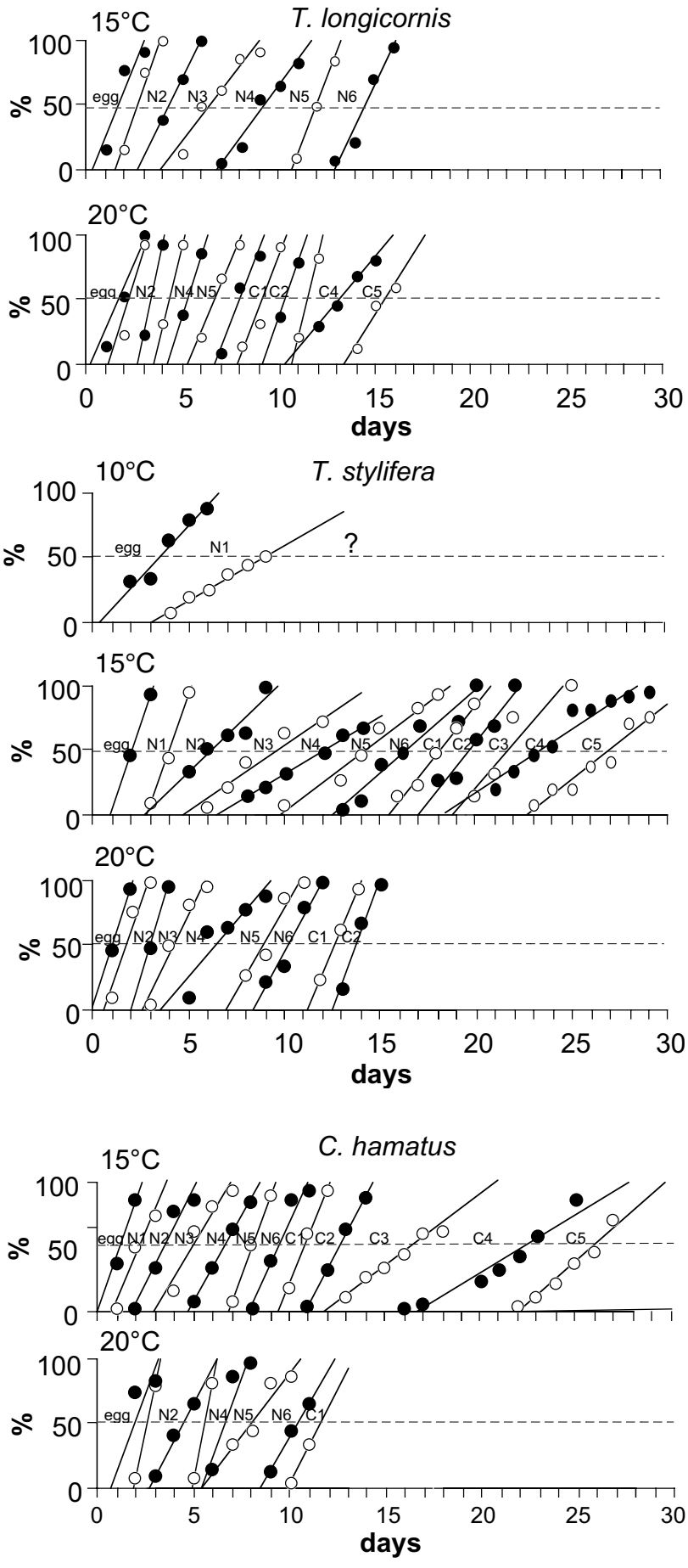


Fig. 3.36 Legend see next page

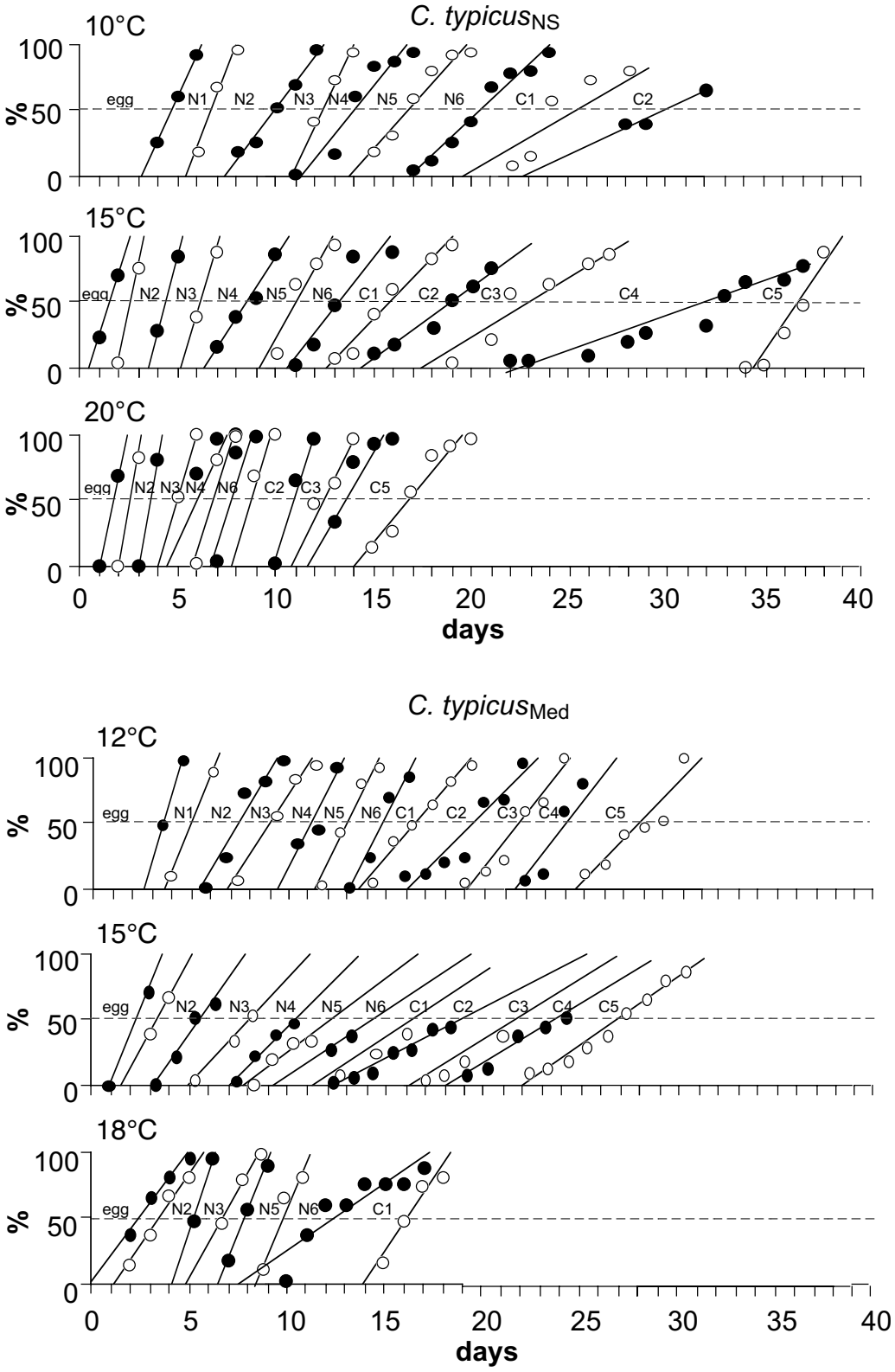


Fig. 3.36: Continued. Stage composition in cohorts reared at different temperatures. Symbols show cumulative percentage of the population having completed a given moult versus time. Open and closed circles alternate for subsequent stages

Tab. 3.3: Stage durations [d] and mortality rates [d^{-1}] of *Centropages typicus*, *C. hamatus*, *Temora longicornis* and *T. stylifera* at different temperatures.

	North Sea							Mediterranean					
	C. typicus			*C. hamatus*		*T. longicornis*		*C. typicus*			*T. stylifera*		
instar	**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**
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
N 1	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
N 2	3.12	1.74	1.02	1.26	1.83	1.68	1.13	2.55	2.24	1.51		2.30	1.30
N 3	2.50	1.82	1.36	1.50	1.16	2.08	0.93	0.97	2.06	1.03		2.81	1.18
N 4	1.58	2.30	1.02	1.60	1.05	2.79	0.92	1.28	1.65	1.80		1.66	2.20
N 5	2.76	2.57	0.79	1.43	1.27	2.86	1.46	1.69	1.52	2.04		1.54	2.47
N 6	3.79	2.14	0.95	1.35	2.46	2.65	1.27	2.63	1.71	2.39		1.70	1.28
C 1	4.87	2.59	1.15	1.50	1.25		1.14	2.71	2.30	4.00		1.70	2.51
C 2	4.08	3.22	1.00	1.73			1.21	1.69	2.68			1.44	1.04
C 3		3.98	2.56	4.06			1.15	2.86	2.78			2.76	
C 4		9.43	1.13	5.31			1.67	2.65	2.52			2.11	
C 5		4.41	3.27	4.05			2.31	3.48	3.80			2.65	
mortality [d^{-1}]													
egg-C I	0.050	0.030	0.012	0.038	0.165	0.150	0.172	0.101	0.034	0.001		0.092	0.339
C I-adult		0.172	0.012	0.045			0.103	0.102	0.055			-0.020	

For better comparison, stage durations are presented graphically on Fig. 3.37. Egg duration was higher than or equal to naupliar stages in all *Centropages* populations; late copepodites showed the slowest development (Figs. 3.37A-E). In the *Temora* species, naupliar durations were similar to copepodite durations, except when mortality stopped development (Figs. 3.37F-H).

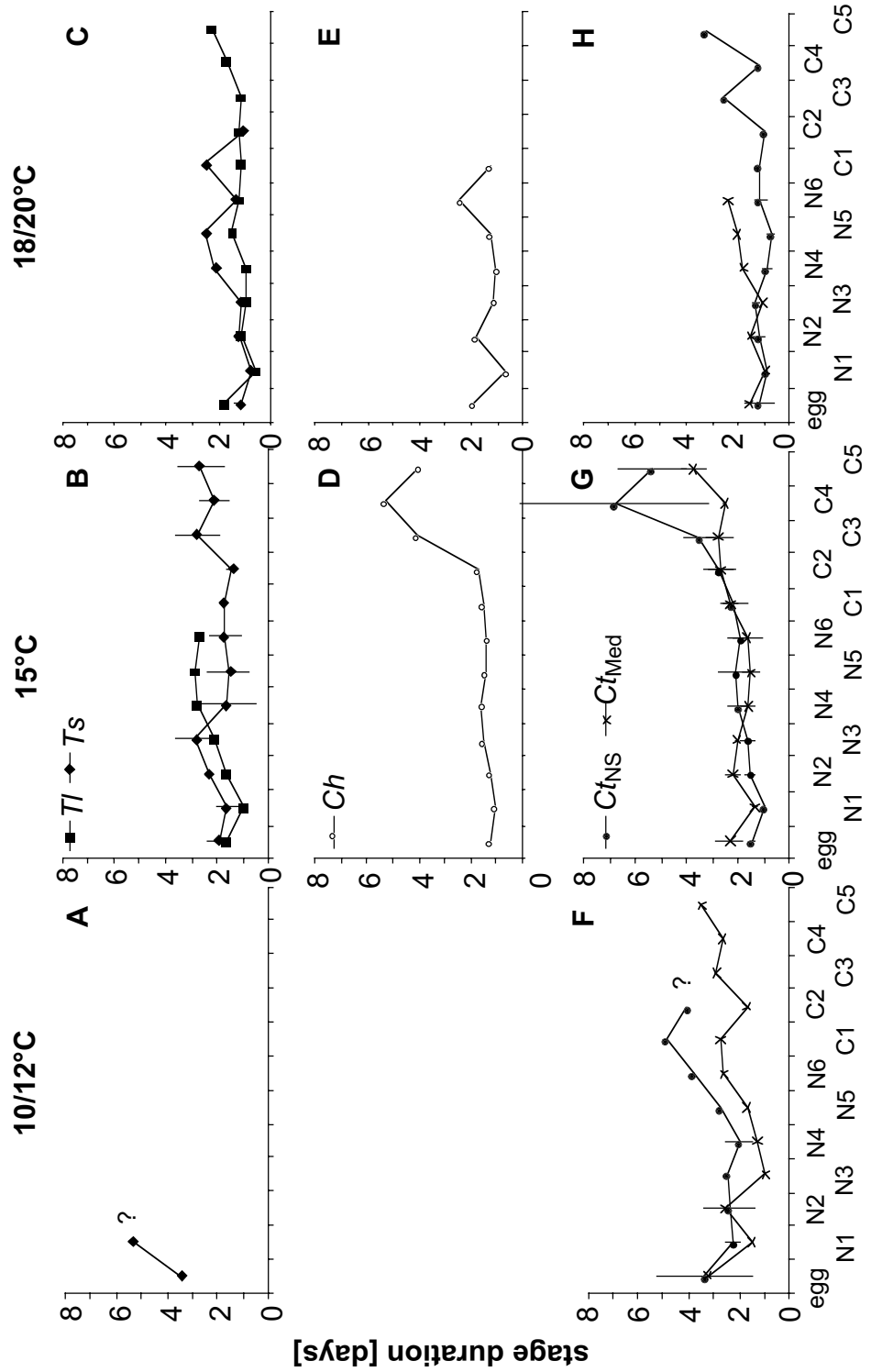


Fig. 3.37: Stage durations [days] of instars from rearing experiments. Comparison of congeners (note that *C. typicus*$_{Med}$ was incubated at 12° and 18°C instead of 10° and 20°C, respectively)

Tab. 3.4. 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
N 1	0.04	0.05	0.12	0.09	0.05	0.11	0.09
N 2	0.07	0.10	0.17	0.14	0.09	0.15	0.14
N 3	0.12	0.17	0.27	0.22	0.13	0.22	0.22
N 4	0.17	0.25	0.30	0.30	0.19	0.28	0.30
N 5	0.23	0.32	0.35	0.36	0.25	0.34	0.36
N 6	0.30	0.37	0.41	0.41	0.31	0.43	0.41
C 1	0.36	0.43	0.51	0.48	0.36	0.52	0.48
C 2	0.43	0.50	0.61	0.56	0.42	0.59	0.56
C 3	0.51	0.56	0.67	0.66	0.48	0.67	0.66
C 4	0.62	0.72	0.78	0.76	0.64	0.74	0.76
C 5	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

3.3.1.6 Seasonal variability of temperature responses

Complementary experiments with *C. typicus*$_{Med}$ (Fig. 3.38) 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. Likewise, the seasonal variability of ETR was not significant (Fig. 3.34E).

In the North Sea, a seasonal comparison of ETR was possible for *T. longicornis* (Fig. 3.34A). In this case, 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 ($p<0.01$).

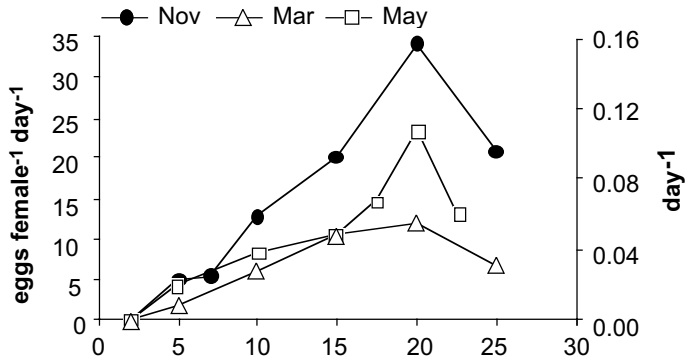


Fig. 3.38: *C. typicus*$_{Med}$. Seasonal variability of the Reproductive thermal response (RTR). Comparison of egg production rates in November, March and May

3.3.2 Comparison of congener pairs and two *C. typicus* populations

3.3.2.1 *T. longicornis* (North Sea) and *T. stylifera* (Mediterranean)

The two *Temora* species showed quite different FTT (Tab. 3.5). *T. stylifera* females stayed alive and maintained reproduction up to 30°C (Figs. 3.29D and 3.31D), whereas *T. longicornis* could not withstand temperatures above 22.5°C (Fig. 3.29A). Optimal survival of *T. stylifera* occurred at 10°C and 15°C, while 2°C and 5°C were lethal. The mortality observed at 20°C (100%) can be considered as suspect (Fig. 3.29D). *T. longicornis* showed high survival between 0 and 22.5°C without any clear optimum (Fig. 3.29A).

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. 3.31A). In contrast, *T. 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. 3.31D).

ETR showed different tolerance limits for *T. longicornis* (0°C to 22.5°C) and *T. stylifera* (10°C to 28°C, Tab. 3.5). The Belehrádek function of *T. stylifera* had a similar curvilinearity as that of *T. longicornis* in March, but was shifted towards higher temperatures (Figs. 3.34A, D). Cold temperatures inhibited development of *T. stylifera* embryos. No nauplii hatched below 10°C and the proportion of viable eggs increased from 10 to 20°C and slightly decreased at 25°C (Fig. 3.35D). 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. 3.35A).

Stage durations of nauplii were slightly shorter in *T. longicornis* than in *T. stylifera* at 15°C and 20°C (Tab. 3.3). Development times of *T. longicornis* decreased from 15 to 20°C, while N IV, N V and C I of *T. stylifera* developed more quickly at 15 than at 20°C (Figs. 3.37A-C). At 10°C no development was observed beyond N I in *T. stylifera* (Fig. 3.37A). Relative development times of both congeners were equiproportional (Tab. 3.4). Mortality rates of *T. longicornis* were 0.15 and 0.17 d^{-1} for nauplii at 15 and 20°C, respectively, and 0.1 d^{-1} for copepodites at 20°C. The very high death rates in nauplii of *T. stylifera* at 20°C (0.34 d^{-1}) prior to collapse of the culture were considered as artefact. At 15°C, nauplii mortality was 0.092 d^{-1} and negative mortality, also an artefact due to sampling technique, was observed in copepodites (Tab. 3.3).

Tab. 3.5. Synthesis of results from incubations in a temperature gradient from 0 to 35°C. Female thermal tolerance (FTT), reproductive thermal response (RTR) and embryonic thermal response (ETR)

	FTT		RTR		ETR	
Species	lethal	optimum	range	optimum	range	optimum
C. typicus$_{NS}$	30°C	5-10°C	2-25°C	20°C	5-25°C	25°C
C. hamatus	25°C	5°C	2-25°C	12.5°C	2-25°C	22.5°C
C. typicus$_{Med}$	2°C/30°C	10-15°C	5-25°C	20°C	5-28°C	25°C
T. longicornis	25°C	2-22.5°C	0-22.5°C	20°C	0-22.5°C	22.5°C
T. stylifera	2°C/30°C	10-15°C	8-30°C	15°C	10-28°C	28°C

3.3.2.2 *C. typicus* and *C. hamatus* in the North Sea

FTT differed between both congeners (Tab. 3.5). *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°C to 25°C), but optima were different. *C. hamatus* produced most eggs at 12.5°C (12.1 eggs female^{-1} day^{-1}) with high standard deviations at 15°C and 20°C (Fig. 3.31B). Therefore the values at 12.5°, 15° and 20°C could not be distinguished statistically (ANOVA p>0.1). *C. typicus* (Fig. 3.31C) had highest egg production rates at 20°C (54 eggs female^{-1} day^{-1}).

Egg development times between congeners were nearly the same between 10°C 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 (Figs. 3.34B, C). Hatching success was more variable in *C. hamatus* (Figs. 3.35B).

Development showed similar patterns in both species with short stage durations in nauplii and slowest development in late copepodites (Fig. 3.37D-H). Nauplii of *C. hamatus* developed more rapidly (9.4 d) than nauplii of *C. typicus* (13.2 d) at 15°C from egg to CI, respectively (Tab. 3.3). 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* (Figs. 3.37D, E). Equiproportionality was observed in both congeners at 15°C (Tab. 3.4). Mortality rates of nauplii and copepodites were the same in *C. hamatus*, while copepodites of *C. typicus* suffered much higher

mortality than nauplii. Mortality increased notably from 15°C to 20°C both in *C. hamatus* and *C. typicus* nauplii (Tab. 3.3).

3.3.2.3 *C. typicus* in the North Sea and the Mediterranean Sea

FTT differed between the two *C. typicus* populations in the North Sea and the Mediterranean (Tab. 3.5). 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 (Figs. 3.29C, E).

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 (Figs. 3.31C, E). 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, egg production was similar in both populations with a slightly higher maximum of *C. typicus*$_{Med}$ (Figs. 3.31C, E).

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 (Figs. 3.34C, E).

Instars of *C. typicus*$_{Med}$ tended to develop more rapidly than those of *C. typicus*$_{NS}$ at 12°C and 15°C (Fig. 3.37F-H, Tab. 3.3), except at 18°C when the culture broke down (Fig. 3.37H). At 15°C and at 12°C, the generation time of *C. typicus*$_{Med}$ was shorter than that of *C. typicus*$_{NS}$ at 15°C (Tab. 4.5). 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 (Tab. 3.4). Mortality rates of nauplii$_{NS}$ were lowest at 15°C with 0.014 d^{-1}, increasing both at 10 and 18°C to 0.086 d^{-1} and 0.088 d^{-1}, respectively (Tab. 3.3). The opposite occurred for copepodites$_{NS}$, which had higher mortality rates at 15°C (0.116 d^{-1}) than at 20°C (0.012 d^{-1}). Mortality rates of nauplii$_{Med}$ and copepodites$_{Med}$ were very similar and decreased constantly with increasing temperature from 0.1 d^{-1} at 12°C to 0.001 d^{-1} at 18°C (Tab. 3.3).

4 DISCUSSION

4.1 Field observations

4.1.1 Seasonal cycles

The annual abundance patterns of *Temora longicornis* and *Centropages hamatus* confirm the current view of the seasonal cycles of these species. They contribute to a large proportion of total zooplankton biomass in the Dutch and German Wadden Sea (Tab. 4.1). Their congeners, *T. stylifera* and *C. typicus*, represent a homologous pair in the Mediterranean Sea (Tab. 4.1), where they dominate the zooplankton community alternately (GAUDY 1962, RAZOULS 1974), while *C. typicus* is an introduced species in the German Bight (FRANSZ *et al.* 1989).

Tab. 4.1: Significance of *Temora* and *Centropages* species in relation to total numbers of copepods (data from the literature)

	species	significance			definition	Reference
North Sea	*T. longicornis*	12%			of all copepods	Rae & Rees 1947
	T. longicornis	30-50%			of all copepods	Wiborg 1955
	Tl, Pe, Ac, Ch	85%			of zooplankton biomass	Hickel 1975
	C. typicus	not mentioned				
	T. longicornis	≈30%			of the cumulated numbers of *Tl, Ac, Pe, Ch**	Fransz 1975
	C. hamatus	≈15%				
	C. typicus	sporadic				
		May	Jul	Sep		Fransz *et al.* 1984
	T. longicornis	64.3%	9.6%	11.5%	of the cumulated numbers of *Tl, Ac, Pe, Ch, Ct* and *Ca**	
	C. hamatus	8.7%	9.6%	0.6%		
	C. typicus	0.0%	0.0%	28.1%		
	Tl, Ch	abundant				Martens 1980
	C. typicus	not mentioned				
Mediterranean	*T. stylifera*	5-25%			of total copepod numbers	Seguin 1981, Ianora et al. 1989, Ianora & Buttino 1990
	C. typicus	10-50%				
	T. stylifera	abundant all year round, particularly in late summer				Gaudy 1962
	C. typicus	abundant all year round, particularly in spring and early summer				
	T. stylifera	abundant in autumn			both species represent primary elements of production	Razouls 1974
	C. typicus	abundant in winter and spring				

* *Tl=T. longicornis, Pe=Pseudocalanus elongatus, Ac=Acartia clausi, Ch=C. hamatus, Ct= C. typicus, Ca=Calanus* spp.

In the North Atlantic, *T. longicornis* is reported to yield 3 to 5 generations per year (Tab. 4.4). At Helgoland Roads, *T. longicornis* was present throughout the year like in the waters off Roscoff (LE RUYET-PERSON *et al.* 1975). These authors suggested 5 successive generations of *T. longicornis* in that region, derived from abundance and body size patterns: the 1st generation appeared in March and lasted until early May, the 2nd generation was recorded from May to June. The 3rd generation was characterized by a decrease in body size and lower numbers of adults in July and August. After a period of intense recruitment, the 4th generation was recorded from the end of August to mid October. The last generation persisted until February, when new large females developed. The abundance data available from Helgoland Roads and the frequency distributions of prosome length seem more or less to confirm this cycle for *T. longicornis* (cf. Figs. 3.4B and 3.25).

The two *Centropages* congeners showed a summer/winter succession at Helgoland Island. Female *C. hamatus* first showed up in March or April and were present until the end of October. Then they were absent from the water column for approximately 6 months from November to April, although in the Kattegat (KIØRBŒ & NIELSEN 1994) and in the English Channel (LE RUYET-PERSON *et al.* 1975) the species was recorded year round. A standing stock seems to persist in specific areas of the North Sea during winter (RAE & REES 1947). MCLAREN (1978) found 8 generations of *C. hamatus* in Loch Striven (Scotland), while MARTENS (1980) stated that *C. hamatus* had longer generation times than *T. longicornis* in the German Wadden Sea. LE RUYET-PERSON *et al.* (1975) registered 5 generations for *C. hamatus* off Roscoff, similar to those of *T. longicornis*: the 1st generation grew up from March to April, characterized by the largest females. The 2nd generation came up in May and June, the 3rd generation in June and July and the 4th developed from mid August to the beginning of September. The 5th generation finally remained present with few specimens until February. At Helgoland Roads, no hibernating specimens of *C. hamatus* were found in the water column and probably were replaced by resting eggs, which developed to adults during February/March, when first females were recorded in the samples (cf. Figs. 3.9B, 3.26).

The large interannual variability in timing of the first appearance of adult *C. typicus* at Helgoland Island, indicates that the occurrence of this species in the German Bight is dependent on advection of Atlantic water into the North Sea every

year (FRANSZ *et al.* 1991, HAY *et al.* 1991). LE RUYET-PERSON *et al.* (1975) deduced a perennial distribution of *C. typicus* in the waters off Roscoff, but noted its numerical inferiority there compared to *C. hamatus*. They proposed 5 generations with major peaks in June, July and August. Abundance and length frequency data from Helgoland Roads were scarce and thus the number of generations could not be estimated properly (cf. Figs. 3.14B, 3.27). *C. typicus* probably colonized the German Bight as an immigrant from the warmer waters south of the British Isles and became most abundant in late summer and autumn towards the end of the reproductive period.

In the north-western Mediterranean *T. stylifera* and *C. typicus* dominate the zooplankton in autumn and spring, respectively. *C. typicus* accounts for 10-50%, *T. stylifera* for 5-25% of total copepod numbers, respectively (SEGUIN, 1981; IANORA *et al.* 1989, IANORA & BUTTINO 1990). Both species are present year round, but they show different seasonal distribution patterns: *C. typicus* generally peaked in April, preceding *T. stylifera*, which was most abundant from September to November (GILAT *et al.* 1965, NIVAL & NIVAL, pers. comm.). The scarcity of *T. stylifera* in spring was attributed to competition for resources with *C. typicus* and a higher sensitivity to turbulence during the mixing phase of the water column (BERNARD 1970). Furthermore, the spring temperatures of around 14°C mark the northern limit of the distribution area of this species. In this warmer environment, 5 to 7 generations per year were assumed for both species (GAUDY 1962 and 1970, RAZOULS 1972, RAZOULS 1974), which– according to LE RUYET-PERSON *et al.* (1975) – were difficult to distinguish and slightly varied between locations. These authors suggested the following sequence for *T. stylifera*: the 1st generation coming up in February and March, the 2nd in April and May, the 3rd in June and July, the 4th in August, the 5th in September, the 6th in October and finally the 7th in November. Although I missed the summer generations in August and September due to interruption of sampling in the Bay of Villefranche, the prosome length frequency distributions, together with the abundance data, approve a similar population development there (cf. Figs. 3.18B, 3.28).

Le Ruyet-Person *et al.* (1975) assumed a similar succession of generations for *C. typicus*, but in contrast to *T. stylifera*, the first generations developing in March and April were the most successful, reaching maximal individual numbers.

Then, 4 to 6 generations followed until the end of November, depending on the area studied (GAUDY 1962, RAZOULS 1972, LE RUYET-PERSON *et al.* 1975). These patterns agree with the population development attained from the abundance and length frequency data in Villefranche during this study (cf. Figs. 3.22B, 3.28), excluding the summer generations in August and September, which are missing due to lacking data.

4.1.2 Reproductive strategies

In the North Sea, the general patterns of the annual reproductive cycles of *T. longicornis* and *C. hamatus* were similar, with a main peak in egg production rate in May, a second smaller and variable peak in late summer and much lower rates during the other months. This similarity is the more surprising, as these species differ considerably in their life history and reproductive strategies in the North Sea. The most striking differences between species concerned the presence of females and the duration of the spawning period (HALSBAND & HIRCHE 2001).

T. longicornis bred continuously throughout the year, although egg production rates and the proportion of spawning females were low in winter. Two explanations could be found for the low spawning activity in winter: (1) At low temperature, spawning intervals increase to more than 24h, so that a great proportion of females did not spawn during the experiments (RUNGE 1984, HIRCHE 1990). (2) Spawning activity was low in spring, probably because the first generation consisted of a high percentage of young, immature females. In summer, the population had reached a steady state, i.e. a constant proportion of mature and immature females in the subsequent summer generations, and more than 80% of the females were spawning. In autumn, the increasing percentage of senescent females diminished spawning activity in the field. *T. longicornis* has been reported to produce resting eggs in addition to subitaneous eggs (LINDLEY 1986, 1990) which might contribute to a rapid increase in abundance in early spring as observed by LE RUYET-PERSON *et al.* (1975). Reproduction peaked in April, while egg production rates were moderate in summer and further declined during autumn. A similar cycle was reported from the Kattegat by KIØRBŒ & NIELSEN (1994). The proportions of clutches laid during day and night suggest that *T. longicornis* exhibited a diurnal spawning cycle, with peak spawning during night, as in a Swedish fjord off Kosterfjorden (TISELIUS *et al.* 1987, TISELIUS 1988).

Tab.4.2: Reproductive parameters of boreal and warm-temperate *Temora* and *Centropages* populations and comparison with data from the literature

		Max EPR	Max. CEPR	Max. ind. EPR	Max. SEPR [d^{-1}]	Max. mean clutch size	Max. ind. clutch size	Prosome length [µm]	Mean female carbon [µg]	Mean egg diameter [µm]	Mean egg carbon [µg]	Season of observation	Location	Reference
Boreal populations	*T. longicornis*	62.4	65.1	122	0.42	45.5	73	726-1360	8.0-24.4	85.3-95.6	0.05-0.07	whole year	German Bight (NS)	present study
		48.0										Aug-Sep	Kattegat (NS)	Kiørboe & Nielsen 1994
		21.0										Mar-May	Plymouth (NS)	Bautista *et al.* 1994
		12.3		40.0	0.05							August	Skagerrak (NS)	Peterson *et al.* 1991
		25.0										Apr-Jul	Oosterschelde Estuary (NS)	van Rijswijk *et al.* 1989
		10.9										Sep-May	Skagerrak	Tiselius 1988
		5.9			0.03							August	Kosterfjorden (NS)	Tiselius *et al.* 1987
		6.5			0.03							September	Buchan area (NS)	Kiørboe & Johansen 1986
	C. hamatus	95.0	95.0	153	0.46	63.3	75	750-1570	3.1-20.4	73.5-80.9	0.02-0.06	whole year	German Bight (NS)	present study
		70.0										Aug-Sep	Kattegat (NS)	Kiørboe & Nielsen 1994
		80.0						920-1050				May-Jun	Skagerrak	Tiselius *et al.* 1991
		27.9										Sep-May	Skagerrak	Tiselius 1988
		15.7			0.08							August	Kosterfjorden (NS)	Tiselius *et al.* 1987
						63		922-1012		78-86		Jun-Oct	White Sea	Pertzova 1974
	C. typicus	101.3	121.6	245	0.41	101.3	245	900-1434	9.7-15.1	69.8-76.5	0.02-0.04	whole year	German Bight (NS)	present study
		90.0										Aug-Sep	Kattegat (NS)	Kiørboe & Nielsen 1994
		116.0		120	0.32							August	Skagerrak (NS)	Peterson *et al.* 1991
		36.5			0.09							August	Kosterfjorden (NS)	Tiselius *et al.* 1987
		24.7			0.06							September	Buchan area (NS)	Kiørboe & Johansen 1986
		41.7		10				1345					Channel (NS)	Le Ruyet-Person *et al.* 1975
		180.0		230.0								spring	New York Bight (A)	Dagg 1978
		76.0			0.06							autumn	New York Bight (A)	Smith & Lane 1987
		8.0		29								July	New York Bight (A)	Smith & Lane 1985
Warm-temperate populations	*T. stylifera*	33.3	65.0	92	0.21	48.0	64	747-1167	12.0	77.7	0.034	whole year	Ligurian Sea (M)	present study
		12.5						977-1011	11.6	73.8		June	Catalan Sea (M)	Saiz *et al.* 1999
		50.0										whole year	Gulf of Naples (M)	Ianora *et al.* 1995
		105.0										whole year	Gulf of Naples (M)	Ianora & Poulet 1993
							45					whole year	Gulf of Naples (M)	Ianora *et al.* 1989
				140						80.5	0.059	laboratory	Ligurian Sea (M)	Abou Debs & Nival 1983
			37.0				184						Gulf of Lion (M)	S. Razouls 1982
		63.0		79								autumn	Gulf of Lion (M)	S. Razouls 1975
		25.0		69				1003					Gulf of Lion (M)	Le Ruyet-Person *et al.* 1975
	C. typicus	33.5	40.3	83	0.21	30.5	72	850-1277	5.5-7.8	74.3	0.030	whole year	Ligurian Sea (M)	present study
		36.0						917-988	5.0	73.5		June	Catalan Sea (M)	Saiz *et al.* 1999
			102.0	157								whole year	Gulf of Naples (M)	Ianora *et al.* 1992
		≈100.0										whole year	Gulf of Naples (M)	Ianora & Buttino 1990
				163								whole year	Gulf of Naples (M)	Ianora & Scotto di Carlo 1988
			49.0				122						Gulf of Lion (M)	Razouls 1982
		75.0		106								spring	Gulf of Lion (M)	Razouls 1975
		40.0		97				1028					Gulf of Lion (M)/	Le Ruyet-Person *et al.* 1975

C. hamatus most likely overwintered as resting eggs in the sediments of the southern North Sea (LINDLEY 1986, 1990) during its absence from the water column in winter. *C. hamatus* was previously reported to produce true diapause eggs (Pertzova 1974, MARCUS 1989, CHEN & MARCUS 1997), which follow a genetic protocol and require a defined refractory phase before hatching can take place (GRICE & MARCUS 1981). Like in *T. longicornis*, the reproductive maximum was observed in early May, shortly after the first adult females emerged. In early summer, reproduction rates declined before a second smaller peak in August and September. A diurnal spawning rhythm as reported for *C. hamatus* in the waters of Kosterfjorden (TISELIUS *et al.* 1987) could not be confirmed at Helgoland Roads, since the difference between times of day was significant only in summer, when females produced more clutches during the day, but not in spring.

Some aspects of interannual variation of reproductive patterns were rather similar in *T. longicornis* and *C. hamatus* and therefore should be attributed to external factors: (1) the differences in female body weights, which were considerably higher in 1995 than in 1999 in both species, partly were reflected in egg production rates, but not in prosome length (Figs. 3.4 C, D, E and 3.9C, D, E), eventually due to different food quality (BONNET & CARLOTTI in press). (2) In July 1996 and August 2000, unusual low spawning activity was observed both in *T. longicornis* and *C. hamatus* (Figs. 3.4H and 3.9H). This might be explained by inadequate diet, increased costs for escape behaviour in the presence of predators or reduced food availability due to competition with other zooplankton. (3) Seasonal variability of hatching success also showed some agreement in *T. longicornis* and *C. hamatus*: Minimal proportions of viable embryos were recorded in April 1996 and in autumn 1995, 1998 and 1999, respectively. The decrease of egg viability in spring 1996 followed a large diatom bloom, leading to the assumption that embryonic development might have been inhibited by chemical compounds of diatoms (see chapter 4.1.4). The decrease of hatching success in autumn, in contrast, seems more likely to indicate the start of the production of resting eggs. These require a shift in temperature and therefore would not hatch under ambient temperature conditions in the laboratory (CHEN & MARCUS 1997).

C. typicus was an exception. Reproduction was maximal later in the year, mainly in September and October in 1995 similar to the species behaviour in the

Kattegat (KIØRBŒ & NIELSEN 1994). However, in 1999 high reproduction was observed already from June on and showed the high interannual variability in spawning activity. For *C. typicus* resting eggs were reported by LINDLEY (1986), but have not been observed by other authors (e.g. SMITH & LANE 1987). Indeed, they seem to play no or a minor role for *C. typicus*. Eggs found along the British Coast (LINDLEY 1986, 1990) should rather be quiescent eggs, persisting a certain time of unfavourable conditions. Therefore, it is not yet clear if *C. typicus* maintains a population that persists in the North Sea with or without overwintering stages. The fact that the biological cycle of *C. typicus* is clearly different from the two other species supports the hypothesis that it is not indigenous in the German Bight, but might have grown in warmer Atlantic waters, e.g. in the English Channel (LE RUYET-PERSON *et al.* 1975, KRAUSE *et al.* 1995).

The comparison of the three North Sea species shows obvious parallels in the strategies of *T. longicornis* and *C. hamatus*, while *C. typicus* was different. These differences reflect the distribution patterns of these species with respect to topographic regions. *T. longicornis* and *C. hamatus* are neritic-coastal species, whereas *C. typicus*, although also common on shelves, tends to a more oceanic extension (Tab. 1.1). Resting eggs are a suitable means as overwintering stages for species living on the shelves, where conditions (e.g. temperature) might become extreme due to the shallow water. Nauplii can emerge from the sediments after phases of hostile environmental conditions. In contrast, such a strategy makes no sense for oceanic species, since the conditions keep more stable and eggs that do not hatch immediately would be lost in the deep sea.

While high reproductive activity is restricted to spring and summer in copepods of boreal regions, *T. stylifera* and *C. typicus* breed continuously in the Gulf of Marseille (GAUDY 1971), the Gulf of Lion (RAZOULS 1975), the Gulf of Naples (IANORA & BUTTINO 1990, IANORA *et al.* 1992) and the Ligurian Sea (HALSBAND-LENK *et al.* 2001). The reproduction cycles of both species were very similar and had maxima in autumn and early summer. Both also showed a diurnal spawning cycle, favouring egg laying at night, except in winter when spawning activity was highest and spawning intervals short. The maximal egg production rates of *T. stylifera* were comparable with those of its congener in the North Sea, while *C. typicus* was smaller and laid less eggs than at Helgoland Roads.

There was a remarkable interannual variability of egg production and clutch size in *T. stylifera*, which might be attributed to differences in body size or to a nutritional effect. Egg production rates and clutch sizes in September and October 1999 exceeded the values from 1998 (Fig. 3.18C, E, F). Since no length measurements were available for that period, this aspect remains speculative.

The peak in body size and reproduction of *T. stylifera* was followed by the breakdown of the population at the end of the year (Fig. 3.18B, C). There is no evident explanation for this, but if larger individuals were a preferred food for size-selective predators, high mortality of large reproducing females could be the reason for the extreme decrease of late stages at that time. Another explanation would be intraspecific competition for resources leading to a decrease in individual numbers. For *C. typicus* no such relationship was found.

The mismatch between the peak in SEPR and EPR observed in *C. typicus* in May 1999 is probably due to the low number of animals incubated for carbon measurements, which had high egg production rates and thus probably overestimated SEPR values.

4.1.3 Control of egg production

4.1.3.1 Regional variability

When comparing the limited data on regional variability of the reproductive activity of the genus *Centropages* during winter, a strong latitudinal gradient became apparent. In warmer waters, such as the Mediterranean, the main spawning season is winter, while at Helgoland Roads none of the species spawned in winter. In the Kattegat, at least during the study of KIØRBŒ & NIELSEN (1994), *C. hamatus* spawned continuously year round. Water temperatures were approximately 10°C warmer in the Mediterranean and 5°C in the Kattegat than at Helgoland Island. These observations strongly suggest that temperature was the controlling factor for reproductive activity, and strong interannual variability in the duration of the reproductive period should be expected in the North Sea. In fact, this was observed for all species considered in this study.

Overwintering strategies were different between species at Helgoland Roads, but the timing of peak egg production in May was very similar in *T. longicornis* and

C. hamatus, whereas the late arriving *C. typicus* had its main peak in summer. Egg production rates recorded here were comparable to those found in other field studies, but the timing of the egg production maximum was often quite different. Thus, in their annual study in the Kattegat, KIØRBØ & NIELSEN (1994) observed several synchronous maxima of all species investigated, the first one in March, when *T. longicornis* produced 50 eggs female^{-1} d^{-1}. This is very similar to Long Island Sound where 50 eggs female^{-1} d^{-1} were recorded by PETERSON & BELLANTONI (1987). At Helgoland *T. longicornis* laid only between 11 and 20 eggs female^{-1} d^{-1} in March. The maximum rate there (62 eggs female^{-1} d^{-1}), however, is similar to maxima in the other studies (Tab. 4.2). In August, fewer eggs (average 6.3 eggs female^{-1} d^{-1}) were produced in the Skagerrak (PETERSON *et al.* 1991) than at Helgoland (16 eggs female^{-1} d^{-1}). BAUTISTA *et al.* (1994) recorded only 20 eggs female^{-1} d^{-1} in spring off the southwest coast of England.

Egg production rates of *C. hamatus* (maximum 95 eggs female^{-1} d^{-1}) were higher at Helgoland than those seen in other parts of the North Sea (reviewed in TISELIUS *et al.* 1991). KIØRBØ & NIELSEN (1994) observed 70 eggs female^{-1} d^{-1} in the Kattegat.

C. typicus in our study produced at most 101 eggs female^{-1} d^{-1} in June. Similarly, PETERSON *et al.* (1991) registered 50-120 eggs female^{-1} d^{-1} (average 91.3 eggs female^{-1} d^{-1}) in the Skagerrak in August, and KIØRBØ & NIELSEN (1994) measured >90 eggs female^{-1} d^{-1} in the Kattegat. In the Middle Atlantic Bight, 76 eggs female^{-1} day^{-1} were reported by SMITH & LANE (1987) and even 230 eggs female^{-1} day^{-1} for the same area in spring (DAGG 1978). Lower rates were observed by TISELIUS *et al.* (1987) with 37 eggs female^{-1}day^{-1} for *C. typicus* from Kosterfjorden in August, matching our observations in the same month. LE RUYET-PERSON *et al.* (1975) compared the English Channel and the Gulf of Lion and found that egg production of *C. typicus* was the same in both regions with 42 and 40 eggs female^{-1}day^{-1}, respectively. KIØRBØ & JOHANSEN (1986) observed a maximum of 25 eggs female^{-1} d^{-1} in the North Sea in September.

Maximal egg production rates of *T. stylifera* and *C. typicus* in the Mediterranean also were variable, depending on region and season (Tab. 4.2). In the Bay of Villefranche maximal egg production rates of 33.5 and 33.3 eggs female^{-1} day^{-1} were found for *T. stylifera* and *C. typicus*, respectively. In the

Catalan Sea maximal egg production rates of *C. typicus* (36 eggs female^{-1}day^{-1}) in June are 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 *T. stylifera* produced between 37 and 63 eggs female^{-1}day^{-1}, the egg production rate of *C. typicus* ranged from 49 to 79 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 *T. stylifera* and *C. typicus*, respectively (IANORA & BUTTINO 1990, IANORA & POULET 1993). Since prosome length of the two species was up to 100-200 µm smaller than that of their counterparts in the North Sea, (Tab. 4.2) their reproductive potential was reduced, mirrored by comparably lower rates in the warmer temperature regime.

4.1.1.2 Temperature and body size

In general, for small calanoids the timing of the spawning maximum is coincident with phytoplankton blooms in spring and autumn (LANDRY 1978, PETERSON & BELLANTONI 1987, NIELSEN 1991, KIØRBŒ & NIELSEN 1994). Of the regions studied so far, Helgoland seems to be the only exception, although the spring bloom there takes place at more or less the same time as in the other regions. What is the reason for this obvious decoupling?

Laboratory studies have clearly shown that egg production in calanoid copepods is mainly controlled by temperature, food and body size (e.g. RUNGE 1984, SMITH & LANE 1985, KIMOTO *et al.* 1986, FRYD *et al.* 1991, BAN 1994, HIRCHE *et al.* 1997). However, in mid latitudes the strong annual variability of temperature makes it often difficult to discern the effects of these factors independently. Thus, LANDRY (1978) showed that the expected increase in fecundity of *Acartia clausi* due to the increasing temperature during the summer was overridden by the large decrease in female size. It has been known for long that body size in crustaceans is a major factor determining potential egg mass (JENSEN 1958, MCLAREN 1965, DAGG 1978). Annual cycles in body length are well documented for temperate calanoid copepods (e.g. CONOVER 1956, DEEVEY 1960, GAUDY 1972, EVANS 1977, LANDRY 1978) and have been negatively correlated with temperature and positively with phytoplankton abundance (DEEVEY 1960). At Helgoland Roads, prosome length followed the predicted pattern with temperature, i.e. the smallest

size at the highest temperatures. The lag between temperature and body size is explained by the fact that temperature during development rather than temperature at collection determined size. Consequently, as at Helgoland Roads during the spring bloom females were still small, because they grew up in the previous summer, their egg production rates were lower than those of the larger females found one or two months later. A positive correlation of egg production and body size has been shown in many calanoid copepod species including *Calanus finmarchicus* (RUNGE 1985, HIRCHE 1996), *Eurytemora affinis* (HIRCHE 1992) and *Acartia clausi* (LANDRY 1978). In *Pseudocalanus* spp. the total volume of eggs in a sac is predictable from female size alone and appears to be unaffected by food supply (CORKETT & MCLAREN 1969).

In Villefranche, no significant relationship between reproduction and temperature was detected in the statistics. Prosome length varied on an annual basis with big females in late autumn and small females in summer, but without any significant correlation to temperature. In 1999, *C. typicus* females were smallest already in April, probably due to strong food limitation during the salp bloom in that year.

Hence, the temperature-body size relationship appeared to be less important in the Mediterranean. DEEVEY (1960) stated that the temperature-size relationship decreases with latitude, since the extent of the annual temperature range becomes narrower towards the equator.

If *T. stylifera* and *C. typicus* performed a diurnal migration cycle as in other regions of the Mediterranean Sea, descending to the deep chlorophyll maximum during daytime and coming up to the surface at night (PAGANO *et al.* 1993, SAIZ *et al.* 1999), they encountered a wide range of temperatures during summer stratification. Thus, interactions between temperature and reproduction are expected to be complex. On the other hand, the copepods might prefer a specific temperature layer. Gaudy (1962) observed that *T. stylifera* inhabited the surface at 15-17°C, but descended in deeper waters when the conditions became unfavourable in winter. Likewise, *C. typicus* obviously fled the surface after temporal cooling events in that study. This indicates that copepods might be able to stay in the most appropriate temperature layer in stratified waters and thus avoid large temperature variations. This would explain the comparatively low

annual variability of prosome lengths. However, egg production of *C. typicus* was significantly related to body size, which in turn depends either on temperature and/or food (RUNGE 1984, MULLIN & BROOKS 1970).

4.1.1.3 Food

The weak correlation of reproduction with food parameters at Helgoland Roads, and the good agreement between fecundity and prosome length suggest that body size was the main controlling factor there, while food was apparently not limiting during the growth season. Even at times between phytoplankton blooms particulate organic material should be largely available as food resource, since the blooms provide large amounts of detritus in the North Sea (HICKEL 1975, ALTHUIS *et al.* 1994). The significant correlations between egg production rates of *T. longicornis* and *C. hamatus* (Tab. 3.2) indicate equally sufficient feeding conditions for these species. Similar correlations were obtained in the Kattegat with five species of calanoid copepods (KIØRBŒ & NIELSEN 1994). However, significant egg production was related to high concentrations of diatoms and other large phytoplankters there, while between blooms egg production was food limited, similar to Long Island Sound (PETERSON 1985, PETERSON & KIMMERER 1994).

Oligotrophy seemed to govern the life cycles in the Bay of Villefranche, rather than temperature variation. Phytoplankton concentrations were up to 25 times lower there than at Helgoland Roads. Thus, food limitation was very strong in the Mediterranean, while it was more or less negligible in the North Sea. However, chlorophyll concentration in Villefranche was a poor indicator for food availability on the annual time scale as in other studies (e.g. IANORA & SCOTTO DI CARLO 1988) and was not related to reproduction of *T. stylifera* or *C. typicus* (Tab. 3.2). Likewise, IANORA & SCOTTO DI CARLO (1988) found no correlation between reproduction and chlorophyll either. Laboratory experiments showed that food selection and prey switching enable copepods to a complex behavioural response in order to cope with strong food limitation (POULET & MARSOT 1980, KIØRBŒ *et al.* 1996). Furthermore, copepods often prefer microzooplankton as food source relative to diatoms; it seems to be a more efficient food for reproduction than phytoplankton. Thus, egg production and growth were significantly enhanced in the laboratory when copepods grazed on ciliates rather than algae (STOECKER & EGLOFF 1987, WIADNYANA & RASSOULZADEGAN 1989, KLEPPEL *et al.* 1991,

FESSENDEN & COWLES 1994). In the field WIADNYANA (1992) found copepod biomass to be related to microzooplankton biomass in the Ligurian Sea and concluded that microzooplankton was of seasonally varying importance as copepod food. In the Bay of Villefranche, *T. stylifera* and *C. typicus* 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, pers. comm.).

4.1.4 Reproduction and population development

Reproduction is an important factor in population dynamics. However, in both regions seasonal distribution did not reflect egg production rates, indicating that mortality rates might be of greater importance for population development than birth rates (PETERSON & KIMMERER 1994, OHMAN & HIRCHE 2001). In the North Sea, reproductive maxima of *T. longicornis* and *C. hamatus* largely agreed and were followed by abundance peaks, but their life cycles were different. This discrepancy was even more obvious in the Mediterranean Sea, where abundance peaks occurred at different times of the year, despite parallel seasonal reproduction patterns of *T. stylifera* and *C. typicus*. The development of the *Centropages* population in spring followed the reproduction peak in autumn, whereas the population of *T. stylifera* nearly broke down completely after the egg production peak. Instead, recruitment seemed to profit from reproduction in summer. How could this mismatch be explained?

Species may differ in (1) physiology, (2) strategies against predation pressure and/or (3) feeding behaviour: (1) Specific temperature adaptations of hatching and development might enhance survival either at high or low temperature. For instance, the variations in length of the tegumental spines of *C. typicus* eggs, which were longer in autumn than in spring, could be considered as a temperature adaptation (GAUDY 1971, VALENTIN 1972). 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 *T. stylifera* eggs might be lost to the sediment. (2) Predation pressure on reproducing females and immature stages might be crucial for differences in population development *in situ* (LANDRY 1978, KIMMERER & MCKINNON 1989, IANORA & 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 & JONSSON 1990, HWANG 1991, FIELDS & YEN 1997). (3) Specific feeding behaviour may influence reproductive success through food quality. The recently discovered "diatom-copepod-paradox" may control recruitment of young stages during diatom blooms. Several authors have shown that either fecundity or hatching success or both can be inhibited by diatoms in various copepod species, including all species considered here (BAN *et al.* 1997 and references therein). Although sometimes supporting copepod growth, evidence has accumulated that diatoms block embryogenesis by inhibitory compounds, which were recently identified as aldehydes that arrest embryonic development in copepod and sea urchin bioassays and have antiproliferative and apoptotic effects, probably as a defence mechanism against copepod grazing (MIRALTO *et al.* 1999).

Another regulatory mechanism of population growth could be cannibalism of females on their offspring at times when other food items are scarce, recently reported by Ohman & Hirche (2001) for *Calanus finmarchicus*.

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 clear the water column efficiently from phytoplankton (ANDERSEN 1985, BRACONNOT *et al.* 1988). Hence, egg production rates of *C. typicus* dropped down dramatically. *T. stylifera* was affected much stronger and disappeared completely from the samples after having ceased reproduction. *Centropages* obviously was more resistant towards this competition and could better maintain its population during the salp bloom than *T. stylifera*, which was completely displaced from the area.

4.2 Temperature impact on reproduction and development of populations from different environments and seasons

4.2.1 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. General 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 (HALSBAND-LENK *et al.* 2002).

4.2.1.1 Thermal tolerance limits

The thermal ranges were rather similar in all parameters considered (Tab. 3.5). However, in some cases a 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 induced death occurred in all species, except *T. stylifera*, at 30°C or below (Figs. 4.1, 4.2), 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 *Acartia clausi, Temora stylifera* and *Centropages 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 induced 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. However, the lower lethal limits were apparently more variable between species than the upper thermal limits, according to recent findings in insects (GASTON & CHOWN 1999, ADDO-BEDIAKO *et al.* 2000)

4.2.1.2 Optimum curves

Survival and reproduction rate are optimum functions of temperature under saturating food conditions, increasing up to the optimum an decreasing beyond (CORKETT & ZILLIOUX 1975, UYE 1981, KIMOTO *et al.* 1986). All species investigated followed this pattern (Tab. 4.5), with differences in tolerance limits and optimal temperatures (Tab. 3.5). In all cases the optima of reproduction were at higher temperatures than the optima of female survival (Figs. 4.1, 4.2). The *Temora* congeners clearly differed in their optima and tolerance limits of reproduction. *T. longicornis* showed increasing egg production rates between 0 and 20°C, matching the values reported by CORKETT & ZILLIOUX (1975, Tab. 4.5). *T. stylifera*, in contrast, showed highest reproductive activity at 15°C with declining rates at higher and lower temperatures according to ABOU-DEBS & NIVAL (1983) (Tab. 4.5). 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 (Tab. 4.5).

4.2.1.3 BELEHRÁDEK curves

As embryos are sheltered in egg shells, their development can take place independently of food and experimental handling (LANDRY 1975). Therefore, eggs were good objects to study temperature effects. BELEHRÁDEK's function $D = a (T-\alpha)^b$ has been widely used in the literature to describe the temperature response of development. In this study, embryonic development followed BELEHRÁDEK functions in all species studied (Tab. 4.3). 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. ABOU-DEBS & NIVAL (1983) presented to equations for *T. stylifera* embryos from spring and autumn. My curve from November matches their values at temperatures >15°C, but does not confirm the very high "biological zero" they suggest for the development of offspring of warm-acclimated parents. 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 matches best with my equation from May (Tab. 4.3).

Embryonic development time has been primarily attributed to egg size both on a seasonal and latitudinal scale (CORKETT 1972, LONSDALE & LEVINTON 1985),

with larger eggs from larger females having lower metabolic rates than smaller eggs due to lower oxygen diffusion rates. During this study, egg-size was almost constant throughout the study period in all species (cf. chapters 3.2.1 and 3.2.2). 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 subitaneous eggs to diapause eggs in fall (GRICE & MARCUS 1981).

Tab. 4.3: Belehrádek functions of embryonic development of *Temora* and *Centropages* populations at different temperatures

	Species	Equation	Reference
Atlantic/North Sea	***T. longicornis***		
	Jul-Sep	$D= 2469.5(T+18.2)^{-2.05}$	this study
	Mar	$D= 1121.7(T+8.1)^{-2.05}$	
	Jun	$D= 1474.9(T+14.7)^{-2.05}$	
		$D= 1346.0(T+10.4)^{-2.05}$	Corkett & McLaren 1970
	C. hamatus		
	Jul-Sep	$D= 1148.9(T+6.9)^{-2.05}$	this study
	C. typicus	$D= 1535.3(T+11.6)^{-2.05}$	this study
	Jul-Sep	$D= 1068(T+9.37)^{-2.05}$	McLaren et al. 1989
Mediterranean	*T. stylifera*		
	Nov	$D= 791.0(T+1.8)^{-2.05}$	this study
	autumn	$D= 3.5(T-12.0)^{-0.50}$	Abou-Debs & Nival 1983
	spring	$D= 45.4(T+0.5)^{-1.14}$	Abou-Debs & Nival 1983
	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

4.2.1.4 Equiproportional development

The thermal response of post-embryonic development followed the patterns scheduled by LANDRY (1983): the first non-feeding stage (N I) developed quickly, while the first feeding stage (N II) was prolonged. Thereafter, development in some experiments approximated isochronal development (e.g. *C. hamatus* at 15°C and *T. longicornis* at 20°). The late copepodites C IV (*C. typicus*$_{NS}$ and *C. hamatus*) or C V (*T. longicornis, T. stylifera, C. typicus*$_{Med}$) 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 & 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*$_{Med}$ (Tab. 3.4). Relative development times did not match in *C. typicus* populations from different locations, but those of the congeners *T. longicornis* and *T. stylifera* and of *C. typicus*$_{NS}$ and *C. hamatus* were very close (Tab. 3.4).

Literature and our results (Tab. 4.5) showed shortest generation time at 20°C for all species investigated (KLEIN BRETELER & SCHOGT 1994, KLEIN BRETELER & GONZALES 1986). LE RUYET-PERSON *et al.* (1975) presented two equations for temperature-dependent generation times of *T. stylifera* (log G = -0.048 T[°C] +2.466) and *C. typicus* (log G=-0.052 T[°C]+2.5312) estimated from field observations off Banyuls (France). The equation derived from generation times of *C. typicus*$_{NS}$ in my cultures reared at 15 and 20°C was log G = -0.0593 T + 2.4011 and gave generation times that were almost half that of LE RUYET-PERSON *et al.* (1975) (Tab. 4.4), since they were obtained with excess food.

Tab. 4.4: Generation times estimated from log-transformed extrapolations derived from my cultures (*C. typicus*$_{NS}$), and from field estimates of *C. typicus* and *T. stylifera* off Banyuls (LE RUYET-PERSON 1975)

T [°C]	*C. typicus*$_{NS}$	*C. typicus*$_{Banyuls}$	*T.stylifera*$_{Banyuls}$
5	127.2 d	-	-
10	64.3 d	102.6 d	96.8 d
15	32.5 d	56.4 d	55.7 d
20	16.4 d	31.0 d	32.1 d
25	8.3 d	17.1 d	18.5 d

Tab. 4.5: EPR [eggs fem.$^{-1}$ day^{-1}] and development times of *Temora longicornis, Centropages hamatus, T. stylifera*, and *C. typicus*. (NS=North Sea, A=Atlantic, M=Mediterranean)

Species		T [°C]	Food	EPR	egg-C1[d]	C1-adul[d]	Generation time [d]	Definition	Reference
Temora longicornis	NS	0	D.t.	8.5				egg-adult	this study
	NS	2	I.g./H.e.	5.3				egg-adult	this study
	A	≈2-8	*in situ*				62.0	egg-adult	Peterson & Kimmerer 1994
	A	4.1	I.g.	4.7					Corkett & Zillioux 1975
	NS	5	O.m., R.sp., I.g.		30.1	31.1	61.2	egg-adult	Klein-Breteler & Gonzales 1986
	NS	5	I.g./H.e.	3.9				egg-adult	this study
		8.5	*in situ*				39	egg-adult	McLaren 1978
	A	≈8-15	*in situ*				≈30	egg-adult	Peterson & Kimmerer 1995
		9.5	I.g.	7.6					Corkett & Zilioux 1975
	NS	10	I.g./H.e.	6.5				egg-adult	this study
	NS	10	O.m., R.sp., I.g.		13.7	16.4	30.0	egg-adult	Klein-Breteler & Gonzales 1986
		10-13	*in situ*				35	egg-adult	McLaren 1978
	NS	12.5	T.r.		13.1		28.2	egg-adult	Harris & Paffenhöfer 1976
	NS	15	O.m., R.sp., I.g.		9.7	10.2	19.9	egg-adult	Klein-Breteler et al. 1994
	NS	15	I.g./H.e.	8.8	14.7			egg-adult	this study
	NS	15	I.g., R.b.				20.6		Klein Breteler 1980
	NS	15	O.m., R.sp., I.g.		8.8	11.7	20.5	egg-adult	Klein-Breteler & Gonzales 1986
		15.4	I.g.	17.3					Corkett & Zillioux 1975
	NS	15-20					21		Martens 1980
	NS	10-20	*in situ*				46-105		Fransz et al. 1984
	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 1975
	NS	20	O.m., R.sp., I.g.		7.8	8.9	16.6	egg-adult	Klein-Breteler & Gonzales 1986
	NS	22.5	I.g./H.e.	7.5				egg-adult	this study
Centropages hamatus	NS	2	I.g./H.e.	4.6				egg-adult	this study
	NS	5	I.g./H.e.	3.3				egg-adult	this study
	NS	10	I.g./H.e.	7.6				egg-adult	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				egg-adult	this study
	NS	15	I.g., R.b.				19.7		Klein Breteler 1980
	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 N2-C1	8.8	16.1	NII-adult	Fryd et al. 1991
	NS	15-20	*in situ*				95-135		Fransz et al. 1984
	NS	≈20					45-52		Martens 1980
	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 1975
	NS	25	I.g./H.e.	7.6				egg-adult	this study
Temora stylifera	M	8	I.g./H.e.	5.3				egg-adult	this study
	M	10	I.g./H.e.	15.3				egg-adult	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 & 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 & Nival 1991
	M	25	I.g./H.e.	13.4				egg-adult	this study
	M	30	I.g./H.e.	5.8				egg-adult	this study
Centropages typicus	NS	2	I.g./H.e.	2.9				egg-adult	this study
	NS	5	I.g./H.e.	10.3				egg-adult	this study
	M	5	I.g./H.e.	5.0				egg-adult	this study
	NS	7.5	I.g./H.e.	15.8				egg-adult	this study
	M	8	I.g./H.e.					egg-adult	this study
	NS	10	I.g./H.e.	28.7	19.9			egg-adult	this study
	A	10	T.w.				34-51	egg-adult	Smith & Lane 1985
	A	10	T.w.		23.0	26.0	49.0	egg-adult	Smith & Lane 1987
	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 N2-C1	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 & 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				egg-adult	this study
	M	20	T.s.				25.0	egg-maturity	Le Ruyet-Person 1975
	NS	22.5	I.g./H.e.	44.3				egg-adult	this study
	NS	25	I.g./H.e.	28.1				egg-adult	this study
	M	25	I.g./H.e.	20.7				egg-adult	this study

I.g.=*Isochrysis galbana*, H.e.=*Hymenomonas elongata*, T.s.=*Tetraselmis suecica*, *D.t.=Dunaliella tertiolecta*, T.w.=*Thalassiosira weissflogii*, T.r.=*Thalassiosira rotula*, R.b.=*Rodomonas baltica*, R.sp.=*Rhodomonas* sp., O.m.=*Oxyrrhis marina*

However, stage duration did not consistently decrease with increasing temperature in the cultures. This might indicate thermal stress of some specific developmental stages at high temperatures in the boreal species *T. longicornis* and *C. hamatus*, but also in both Mediterranean populations. This might be a similar effect as observed by PEDERSEN & TANDE (1992) and TANDE (1988) at the lower temperature range of *C. finmarchicus* from Northern Norway. They noticed that in contrast to adults, earlier stages needed an increase in temperature for successful stage development, while constant low temperature arrested development at C1. In my case, such temperature requirements could be effectual in the opposite direction, insomuch that certain stages were sensitive to temperatures >15°C and stopped development. Those sensitive stages were presumably the earliest copepodite stages, since most of the failed cultures were arrested at C1 or C2 (Fig. 3.37), according to the results of PEDERSEN & TANDE (1992).

4.2.2 Adaptational responses

4.2.2.1 Seasonal variations

Do females grown in spring show a different reproductive temperature response as females grown in autumn? This would imply a shift in the temperature optimum. As *C. typicus*$_{Med}$ could be found in the Bay of Villefranche almost throughout the year, RTR experiments were conducted in autumn 1998 and spring 1999 to detect seasonal variations. These were restricted to the absolute number of eggs produced, reflecting different reproductive potential of females in different seasons, while RTR remained constant (Fig. 3.38). *In situ* egg production was low in spring and, although equally fed in access in the laboratory, less eggs were produced in March and May than in November. The opposite was observed for *T. stylifera* females (ABOU-DEBS & NIVAL 1983), which produced more eggs in March than in October at 3 experimental temperatures. However, also in this case 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 (Fig. 3.34) 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 *Acartia 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 & 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 & 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 & LEVINTON 1985, JÓNASDÓTTIR, 1994).

Due to the high experimental effort, no seasonal comparison of stage development was available in the present study. However, PEDERSEN & TANDE (1992) revealed evidence that maternal acclimation to overwintering temperature could alter the rate-temperature response of females' offspring. Cultures reared from females caught in a warm winter needed a temperature increase during early development to ensure stage progress, while cultures from cold acclimated adults developed normally without a temperature increase. Consequently, seasonal and interannual variability can induce ontogenetic adaptations and modify the physiological responses of species.

4.2.2.2 Regional variations

The Belehrádek curves of cold-acclimated North Sea embryos were displaced by about 5 degrees towards lower temperatures in relation to the curves of their Mediterranean congeners (Fig. 3.34). Post-embryonic stages of *C. typicus* tended to develop more quickly in the Mediterranean than in the North Sea at all

temperatures investigated (Fig. 3.37), suggesting an influence of body size as postulated by Vidal (1980), who stated that smaller individuals have shorter stage durations than larger ones.

4.2.3 Geographic distribution and thermal response

When our results were 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 *T. longicornis* and *C. hamatus* 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, present results). Egg production rate was controlled by body size, which in turn was related to temperature (cf. chapter 4.1.3.2). Analogously, in the Mediterranean *in situ* reproduction peaks of *C. typicus*$_{Med}$ and *T. stylifera* coincided in autumn when females were largest (cf. chapter 4.1.4), 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. 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*$_{NS}$ 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 & SABATINI (1995).

4.2.3.1 *Temora* sp.

The differences of thermal tolerance between these congeners reinforced the classification as a cold-temperate (*T. longicornis*) and a warm-temperate species (*T. stylifera*) and hence explained their geographic distribution. *T. longicornis* tolerated the whole temperature range found in the North Sea as expected from its perennial occurrence there (Fig. 4.1). In summer, individual numbers declined in August when surface waters warmed up to>20°C (cf. Fig. 3.4B) and *T. longicornis* escaped from the surface (FRANSZ *et al.* 1984). 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). The breakdown of the culture at 15°C at stage C 1 must be considered as artefact due to problems related to the culture technique (oxygen supply, pH, parasites, etc.). In fact, KLEIN BRETELER & GONZALES (1986) successfully reared *T. longicornis* at 10 and 5°C in the laboratory (Tab. 4.5).

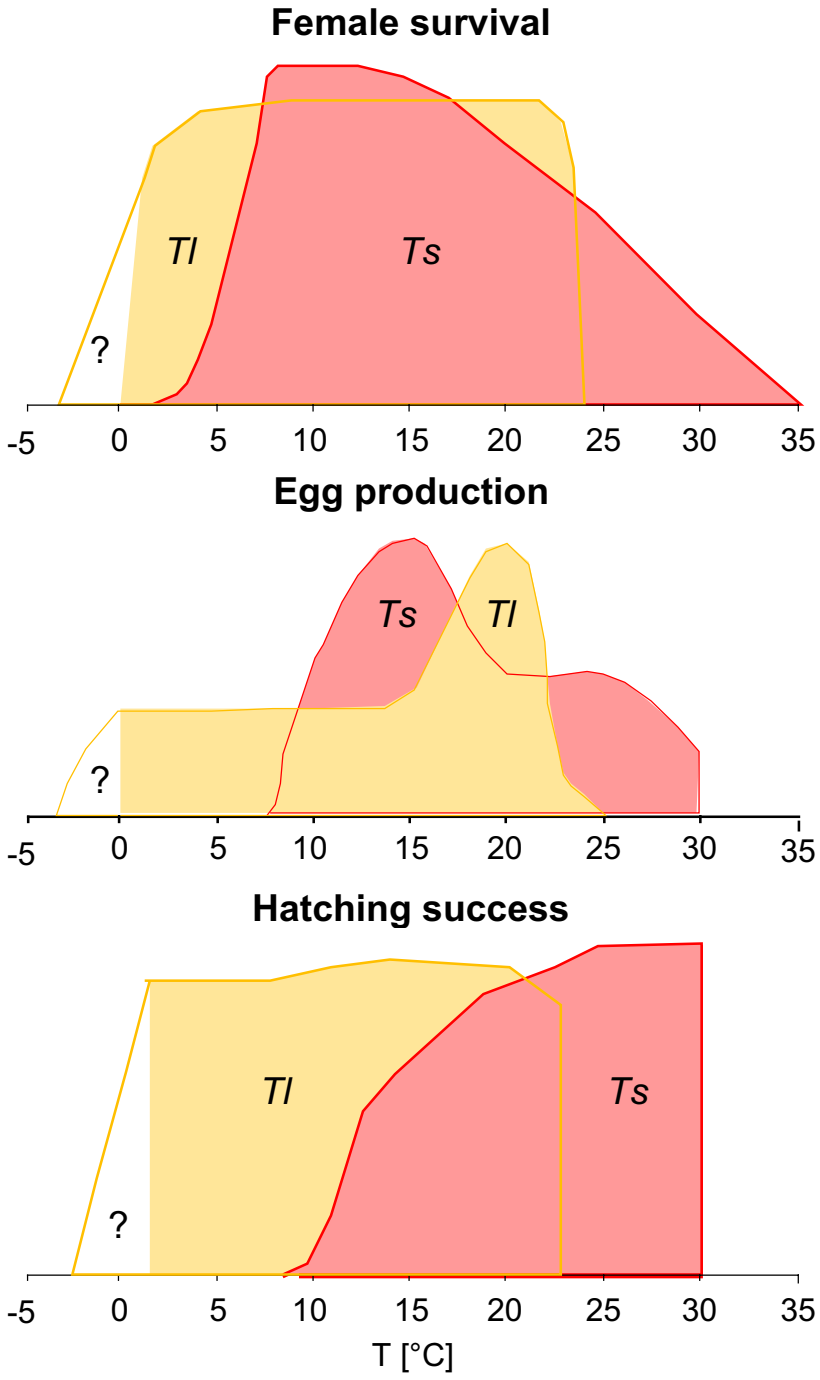


Fig. 4.1: Schematic comparison of temperature responses of female survival, egg production and hatching success of *Temora longicornis* and *T. stylifera*. *Tl*=*T. longicornis*, T*s*=*T. stylifera*

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 (Tab. 3.5) seemed at first sight surprisingly low, since *T. stylifera* is considered as a warm-temperate species (Tab. 1.1). On the other hand, ABOU-DEBS & 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 (see chapter 4.1.2). Similar to FTT and RTR, development of some instars was favoured at 15°C. At 10°C, no development was observed in culture. Assuming that population development takes place in autumn following the reproduction peak, the preference for 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, primarily *C. typicus* (RAZOULS 1974). Consequently, thermal tolerance was not necessarily correlated with the optimum of reproduction and development (Fig. 4.1).

4.2.3.2 *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 (Fig. 4.2). 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 & RANK 2000), needs further investigation.

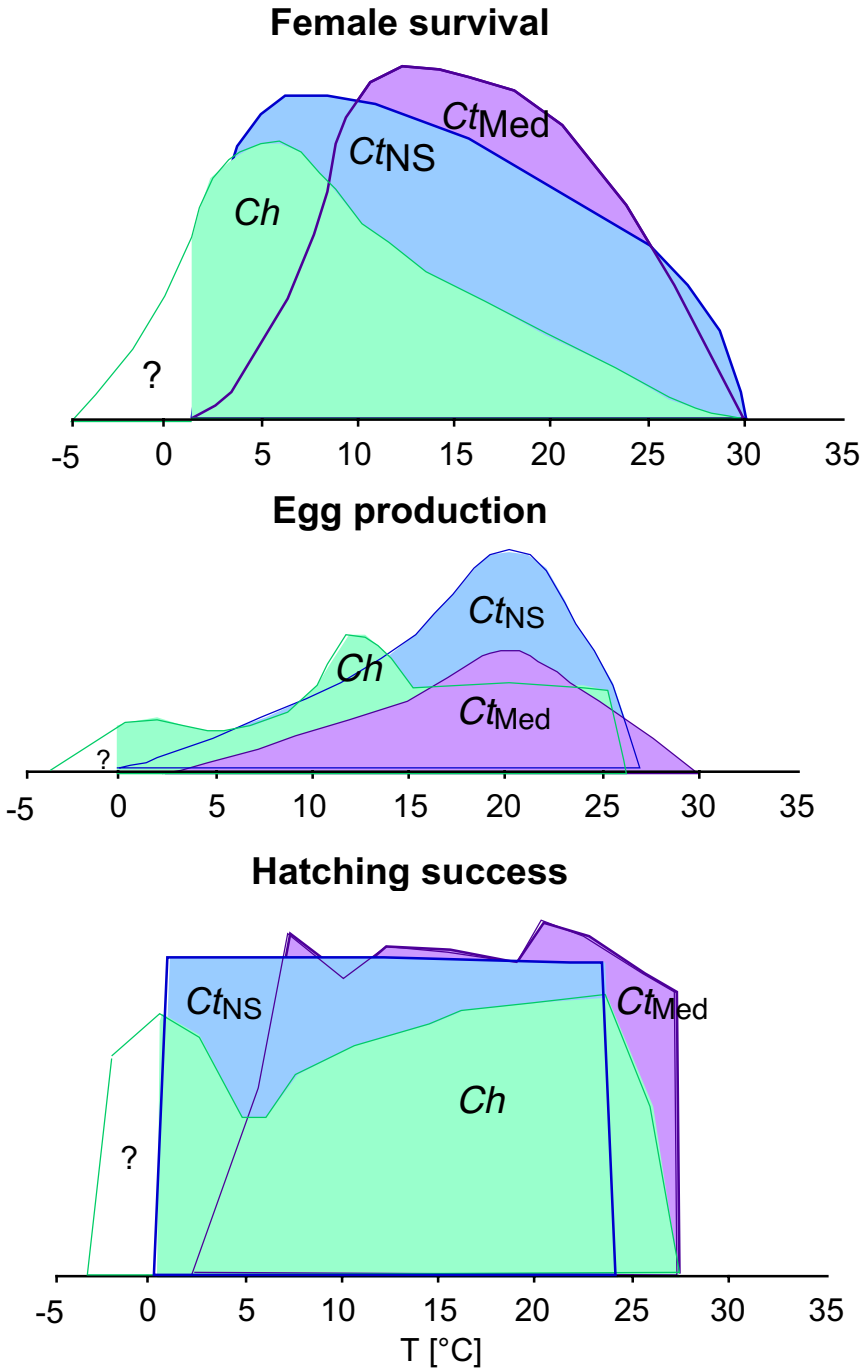


Fig. 4.2: Schematic comparison of temperature responses of female survival, egg production and hatching success of *Centropages hamatus* and *C. typicus*. *Ch*=*C. hamatus*, Ct_{NS}=*C. typicus* in the North Sea, Ct_{Med}=*C. typicus* in the Mediterranean

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). Thus, the latitudinal and seasonal distribution patterns of both congeners reflect clearly the temperature limits of their survival and reproduction as revealed during the 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.

4.3 Conceptual models and estimates of production

The present study contributes a large body of information on the biology of the *Temora* and *Centropages* species investigated. These results are summarized in conceptual models, which present the annual life cycles, including the reproductive and overwintering strategies, that emerged from the interpretation of experiments *in situ* and in the laboratory (Figs. 4.3 to 4.7). The number of generations could be estimated by the help of length measurements in combination with the temperature-development relationship derived from the rearing experiments at different temperatures. The temperature responses of individuals in the laboratory revealed explanations both for the seasonal and geographical succession of species in the field.

The northern species continuously decreased their production after the great peak in spring and evolved a strategy to assure the continuity of the population until the next year: the production of resting eggs in autumn. Pelagic stages either disappeared from the water column (*C. hamatus*) or remained present with low reproductive output (*T. longicornis*) in winter. Such precautions were not necessary in the Mediterranean. There, reproduction could take place year round, if food competitors (e.g. salps) did not disturb the nutritional balance, and *Temora* and *Centropages* alternated seasonally according to their thermal preferences.

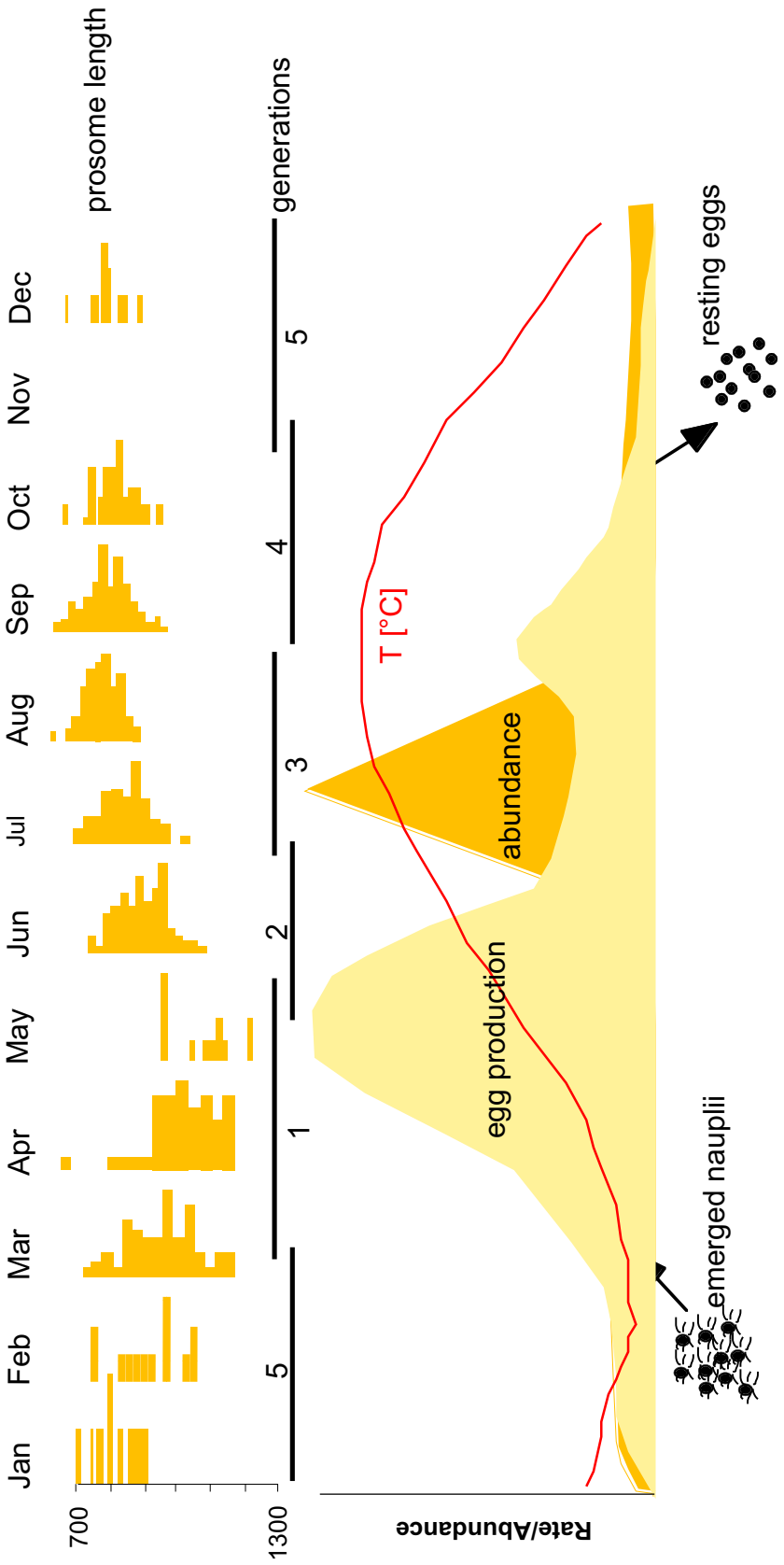


Fig. 4.3: Conceptual model of the life cycle of *T. longicornis* at Helgoland Island

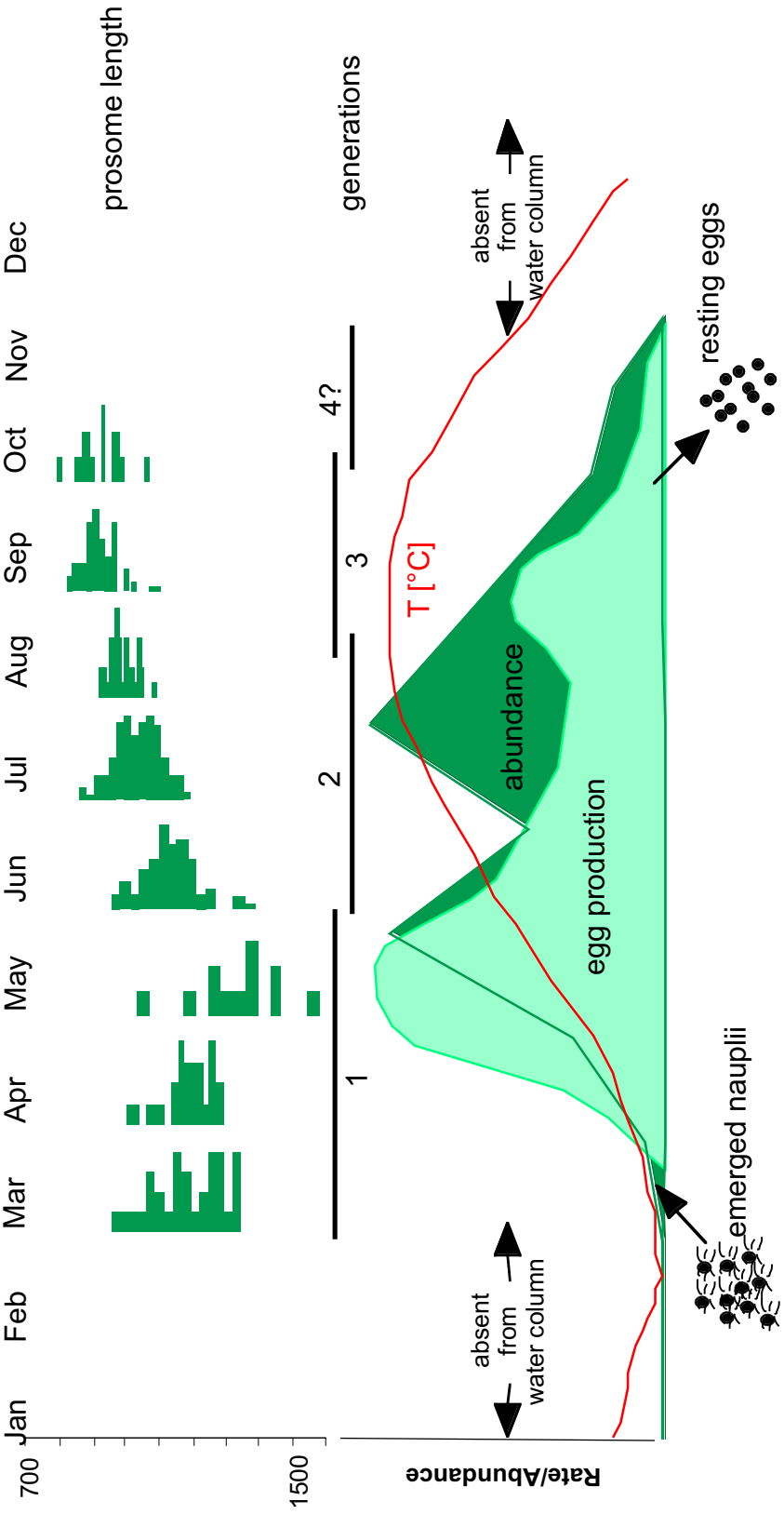


Fig. 4.4: Conceptual model of the life cycle of *C. hamatus* at Helgoland Island

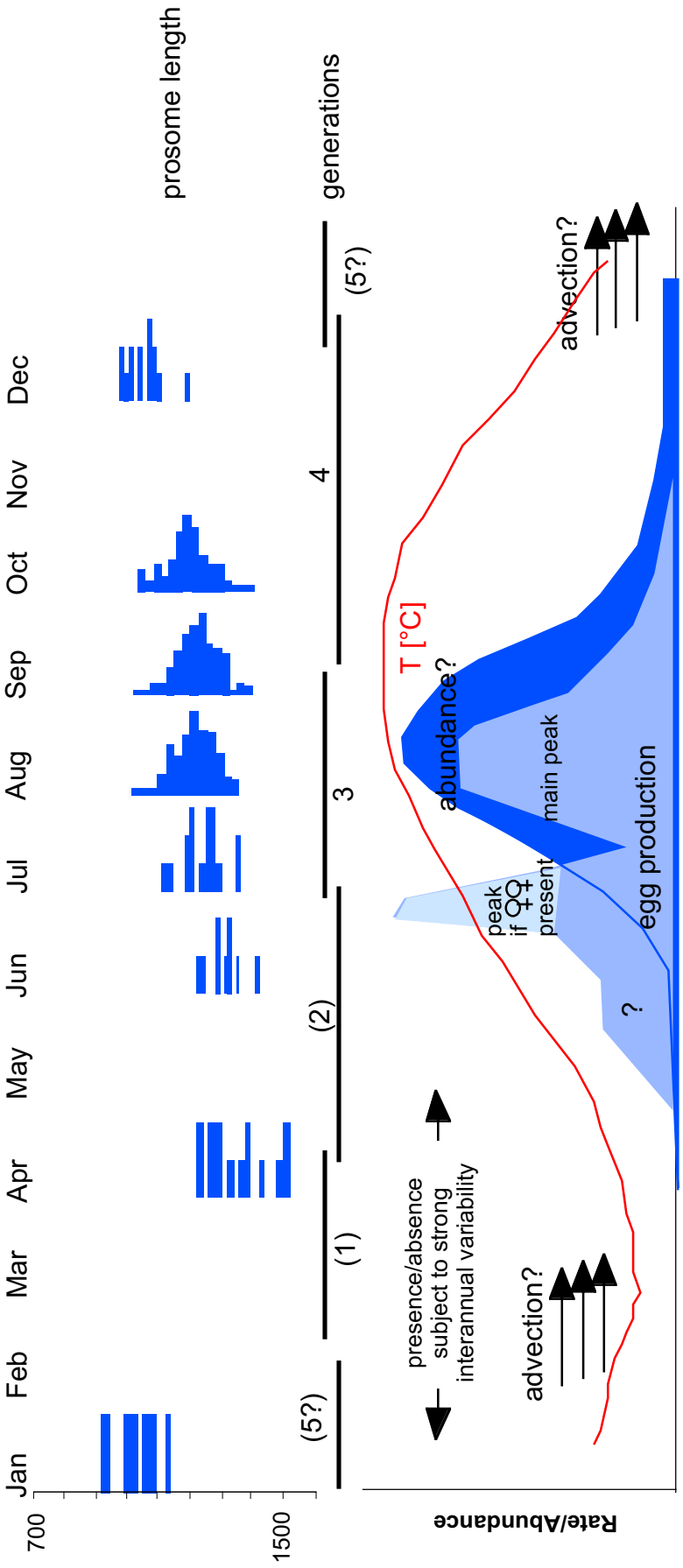


Fig. 4.5: Conceptual model of the life cycle of *C. typicus* at Helgoland Island

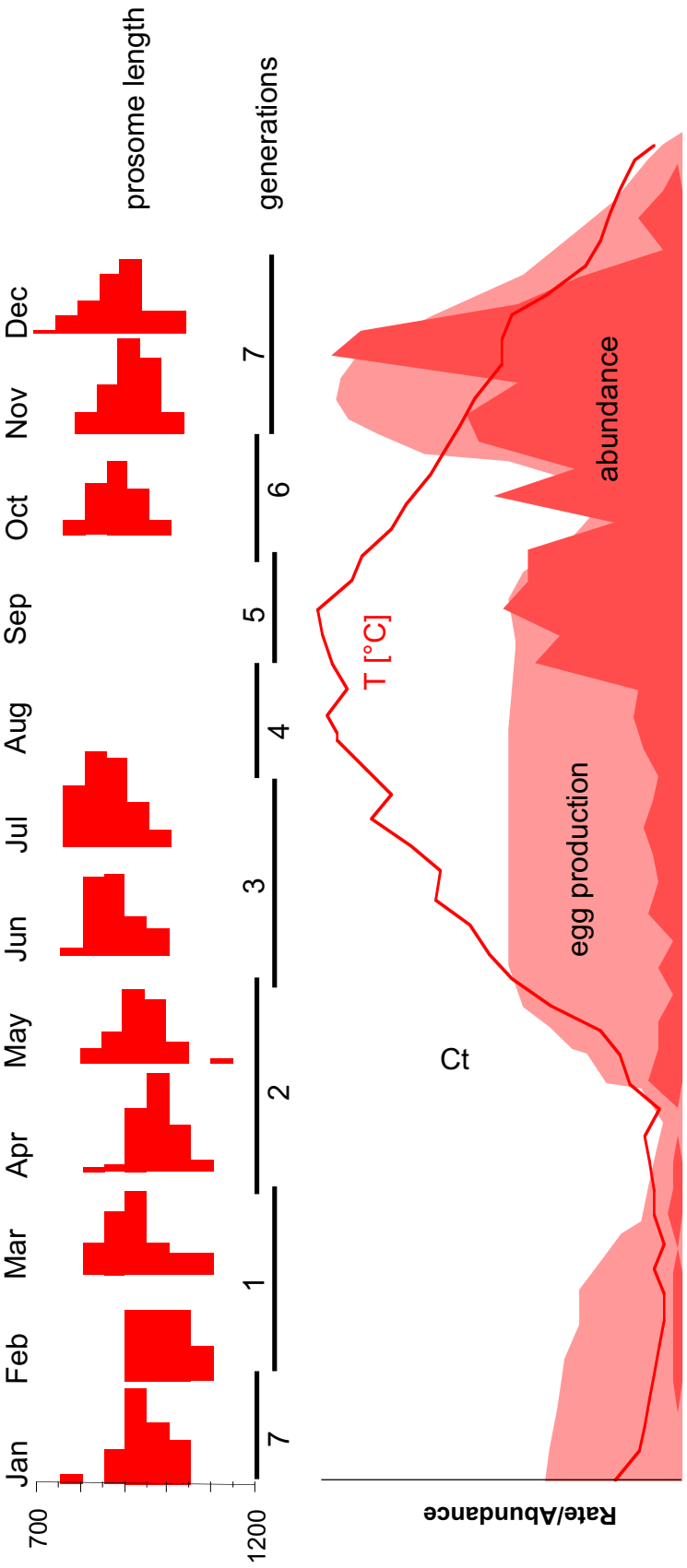


Fig. 4.6: Conceptual model of the life cycle of *T. stylifera* in the Bay of Villefranche

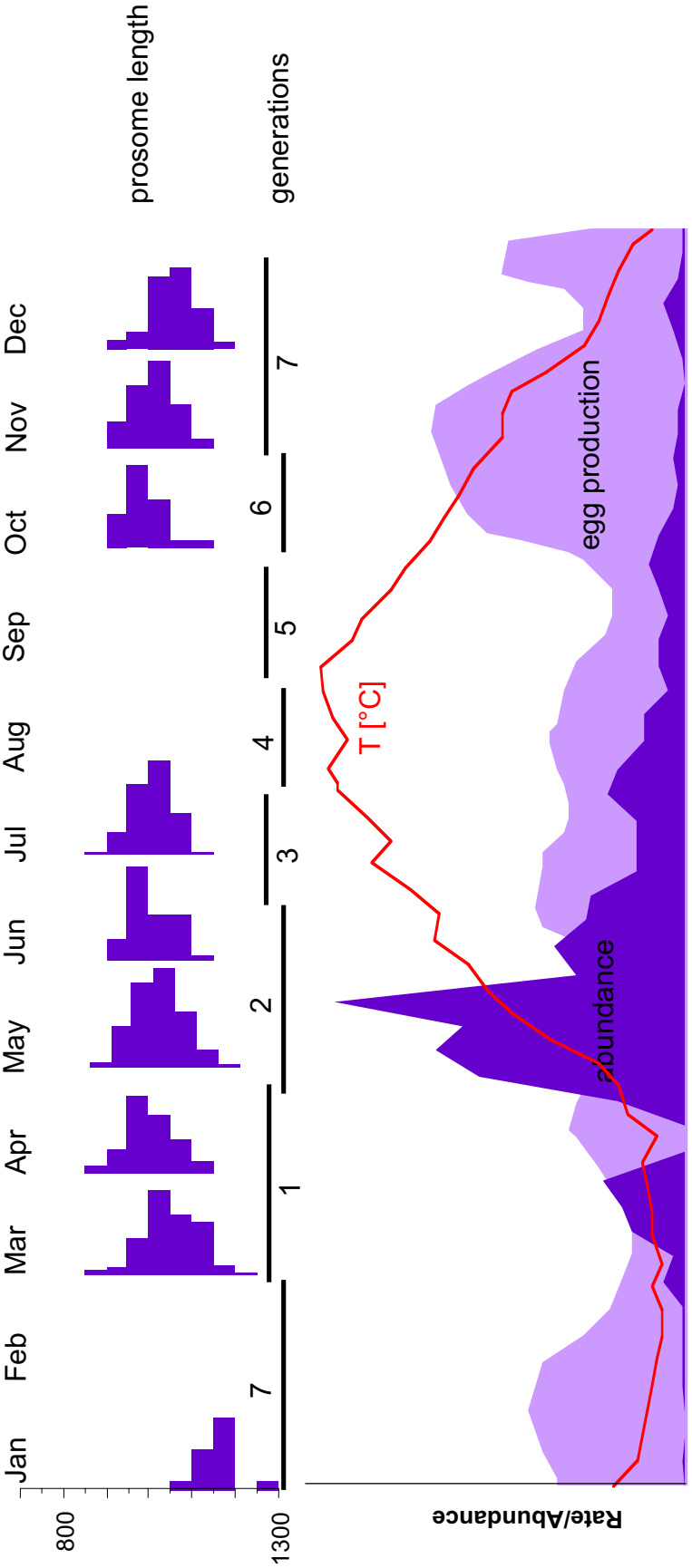


Fig. 4.7: Conceptual model of the life cycle of *C. typicus* in the Bay of Villefranche

The different life cycle strategies of boreal and temperate populations in regard to food limitation, annual temperature gradients and one high reproduction peak opposed to continuous low reproduction, raise the following question: is annual secondary production of these populations similar in the two ecosystems? This question cannot be answered satisfactorily in this study, but it appears possible that the Mediterranean populations compensated their comparably low maximum egg production rates by continuity of reproduction. At least, they yielded at least 2 generations more per year than the boreal ones (Tab. 4.6). Abundance at Helgoland Island was in great favour of *Temora*, while proportions were almost exactly the opposite in the Bay of Villefranche, where *C. typicus* was dominant.

However, the abundance data from the North Sea should be treated with caution, since no complete annual cycle was available.

T. longcornis had a lower carbon content in the North Sea, compensated by a higher weight specific egg production rate in relation to *T. stylifera*. The *Centropages* spp. populations were more difficult to compare, since abundances of both species in the North Sea are expected to be underestimated. Especially in September and October, when *C. hamatus* and *C. typicus* co-occurred and *C. typicus* was most abundant, no individual numbers were available. The northern *C. typicus* had almost twice the carbon content and SEPR of its southern conspecific, while its abundance was very low and the number of generations unknown. *C. hamatus* was in between the values of the two *C. typicus* populations. However, the data provide some hints that secondary production might be fairly comparable between boreal and temperate populations.

Tab. 4.6: Estimates of production of *T. longicornis*, *C. hamatus* and *C. typicus* at Helgoland Island and *T. stylifera* and *C. typicus* in the Bay of Villefranche from mean annual abundance (CIV–adult) [ind. m^{-3} $year^{-1}$], mean annual female carbon [µg C $female^{-1}$] and mean annual SEPR [day^{-1}]

Helgoland Island

species	generations	ind. m^{-3} $year^{-1}$	µg C fem^{-1}	meanSEPR
T. longicornis	3-5	2039.54	9.49	0.127
C. hamatus	3-4	602.32*	9.00	0.150
C. typicus	3-5?	121.49*	13.88	0.136

Bay of Villefranche

species	generations	ind. m^{-3} $year^{-1}$	µg C fem^{-1}	meanSEPR
T. stylifera	5-7	555.22	12.38	0.100
C. typicus	5-7	2399.95	6.61	0.092

*abundance probably underestimated due to lacking data

In the southern North Sea, the delay of maximum secondary production relative to the spring bloom may have strong consequences on the fate of the organic production and on the higher trophic levels. Thus, FRANSZ & GIESKES (1984) observed an unbalance between primary production and copepod grazing in spring and fall in the North Sea, which must lead to a loss of energy potentially available to higher trophic levels. Other workers have noted that a large proportion of the spring bloom in coastal environments does not enter a pelagic food web but rather sediments out of the water column and enters a benthic food web (SMETACEK *et al.* 1978, WALSH 1983). Strong interannual variability in the timing of copepod reproduction due to temperature variability may cause varying degrees of mismatch between the occurrence of fish larvae and their prey, unless temperature affects fish spawning in a similar direction. If indeed, reproduction in the southern North Sea is under control of a single factor, i.e. temperature, predictions of climate induced changes of copepod reproduction would be relatively easy.

In the Mediterranean, conditions are more complex due to the strong oligotrophy and lacking information about primary productivity. Furthermore, stratification of the water column in summer complicates the copepod-temperature interactions, assuming that *T. stylifera* and *C. typicus* are to a certain degree vertically migrating species.

5 CONCLUSIONS AND FUTURE PERSPECTIVES

The *in situ* study revealed inter-site, inter-specific and intra-specific (= interannual) variability of the life cycles of the species investigated, which are summarized in the schemes in chapter 4.3. Life cycle strategies showed on the one hand similarity between locally co-occurring populations, with two homologous pairs in the North Sea (*Temora longicornis* and *Centropages hamatus*) and in the Mediterranean Sea (*T. stylifera* and *C. typicus*). On the other hand, differences between the two regions were related to their different temperature regimes. A discrete reproduction peak, driven by a temperature-dependent annual cycle of body size and almost independent of food, in combination with resting eggs as overwintering strategy, characterized *T. longicornis* and *C. hamatus* in the North Sea. This was in opposition to a continuous reproduction of *T. stylifera* and *C. typicus* in the oligotrophic and warmer Mediterranean. *C. typicus* took an intermediate position between northern and southern species. The species had an irregular life cycle at its northern distribution limit at Helgoland Island and was dependent on favourable environmental conditions there, while it was dominant in the Bay of Villefranche.

Some aspects of the life cycles are not yet clear: The hypothetical sequence of generations and the assumptions on overwintering strategies in the North Sea require validation. Furthermore, the spatial distribution patterns should be studied more intensively in relation to hydrographic features, such as salinity, indicating the origin of watermasses and thus advection of zooplankton species. In the Mediterranean, information on the vertical distribution of species and stages is scarce, but knowledge on the temperature range actually encountered by the animals is essential to relate physiological processes to temperature. The field study reinforced the assumption of a strong temperature dependence of life cycles and distribution patterns, which caused the observed interannual and regional variability.

This assumption was strengthened by the results on different temperature sensitivity of the species investigated in this study. Despite intraspecific variability, the temperature responses were related to the seasonal and geographical distribution of the species investigated, with the most northerly species having the lowest minimal temperatures and vice-versa. Thus, the present results indicate that thermal tolerance of survival, reproduction and development may at least

partly determine horizontal and seasonal distribution patterns of these species. The two *Temora* species and *C. hamatus* showed distinct temperature ranges, whereas *C. typicus* was able to tolerate different temperature conditions and was particularly productive, explaining its wide distribution range from the subarctic to the tropics. Beside temperature, other abiotic factors, such as salinity (GAUDY *et al.* 2000), or biotic factors, e.g. behaviour or ontogeny, could be decisive. Behavioural traits like migration, swimming and escape behaviour may determine mortality patterns (OHMAN 1990, TITELMAN 2001) and thus temporal distribution of species, while different life cycle strategies (e.g. undergoing diapause or not) are responsible for seasonal succession of species.

Although on a global scale generation time at a given temperature was fairly similar for all species (Tab. 4.5) and fell in the range of the temperature function presented by HUNTLEY & LOPEZ (1992, their Fig. 3), the present work demands not to apply the commonly used empirical temperature functions (BELEHRÁDEK 1935, MCLAREN 1978) to different localities or species. Tolerance experiments for less resistant (gametes, spermatophores, oocytes) and most resistant stages (dormant stages, non reproducing adults) are still lacking, but are needed to estimate the complete tolerance range of a species.

An unifactorial approach under constant laboratory conditions is useful to focus on one given environmental aspect. However, organisms respond to the entirety of environmental stimuli, such as temperature, salinity, oxygen, light etc., and therefore only multifactorial analyses can reveal ecological significant results.

Data on other species and regions should complete our understanding on temperature effects on population dynamics in aquatic ecosystems. Especially in regard to the topical discussion on global warming, a long-term temperature increase could have a great impact on zooplankton distribution patterns in specific regions (ROEMMICH & MCGOWAN 1995, CHEN & FOLT 1996). 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 may alter the combination of species. An assessment of the impact of such long-term changes on the zooplankton communities demands more information on how populations respond to critical temperatures, both from an ecological and physiological approach.

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7 ANNEX

7.1 ANOVA analysis on differences between egg diameters in different months

(***=p<0.0001, **=p<0.001, *=p<0.01, ns=not significant)

Temora longicornis

	Sep 95	Oct 95	Nov 95	Dec 95	Jan 96	Feb 96	Mar 96	Apr 96	May 96	Jun 96	Jul 96	Aug 96	Jun 99	Jul 99	Aug 99	Sep 99	Oct 99
Sep 95	–	ns	ns	***	ns	ns	ns	ns	ns	ns	ns	***	ns	ns	ns	ns	ns
Oct 95		–	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Nov 95			–		ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Dec 95				–	***	***	**	***	***	***	ns	ns	***	***	***	***	ns
Jan 96					–	ns	ns	ns	ns	ns	ns	***	ns	ns	ns	ns	ns
Feb 96						–	ns	ns	ns	ns	ns	***	ns	ns	ns	ns	ns
Mar 96							–	***	ns	***	ns	**	ns	ns	ns	ns	ns
Apr 96								–	ns	ns	ns	***	ns	ns	ns	***	ns
May 96									–	ns	ns	***	ns	ns	ns	ns	ns
Jun 96										–	ns	***	ns	ns	ns	***	ns
Jul 96											–	ns	ns	ns	ns	ns	ns
Aug 96												–	***	***	***	***	ns
Jun 99													–		ns	ns	ns
Jul 99														–	ns	ns	ns
Aug 99															–	ns	ns
Sep 99																–	ns
Oct 99																	–

Centropages hamatus

	Oct 95	May 96	Jun 96	Aug 96	Jun 99	Jul 99	Sep 99
Oct 95	–	ns	ns	ns	ns	ns	ns
May 96		–	***	ns	ns	**	***
Jun 96			–	***	***	ns	ns
Aug 96				–	***	***	***
Jun 99					–	ns	ns
Jul 99						–	ns
Sep 99							–

Centropages typicus in the North Sea

	Sep 95	Oct 95	Nov 95	Jun 99	Aug 99	Sep 99
Sep 95	–	ns	ns	ns	***	***
Oct 95		–	ns	ns	***	***
Nov 95			–	ns	***	***
Jun 99				–	***	***
Aug 99					–	***
Sep 99						–

Temora stylifera

	Jan 98	Feb 98	Apr 98	Oct 98	Nov 98	Dec 98
Jan 98	–	ns	***	***	***	ns
Feb 98		–	***	***	***	**
Apr 98			–	ns	ns	**
Oct 98				–	ns	**
Nov 98					–	ns
Dec 98						–

Centropages typicus in the Bay of Villefranche

	Feb 98	Apr 98	May 98	Nov 98	Dec 98	Apr 99	May99
Feb 98	–	ns	ns	ns	ns	***	ns
Apr 98		–	ns	ns	ns	***	ns
May 98			–	ns	ns	***	*
Nov 98				–	ns	***	ns
Dec 98					–	***	ns
Apr 99						–	ns
May99							–

7.2 Regressions of reproductive and environmental parameters in the North Sea and the Mediterranean Sea

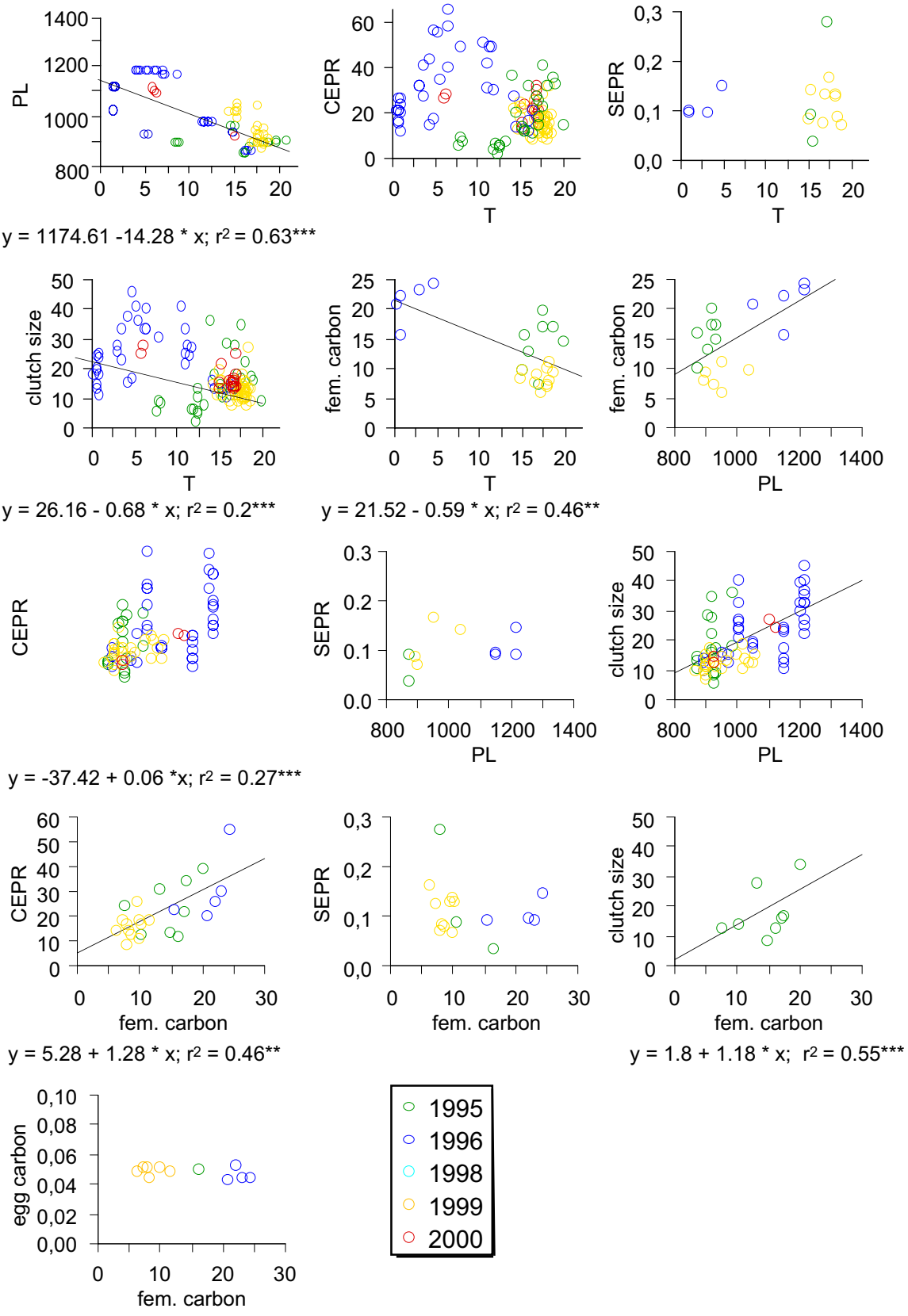


Fig. 7.1: *Temora longicornis*. PL=prosome length [µm], CEPR=corrected egg production rate [eggs female^{-1} day^{-1}], SEPR= weight specific egg production rate [d^{-1}], T=temperature [°C]

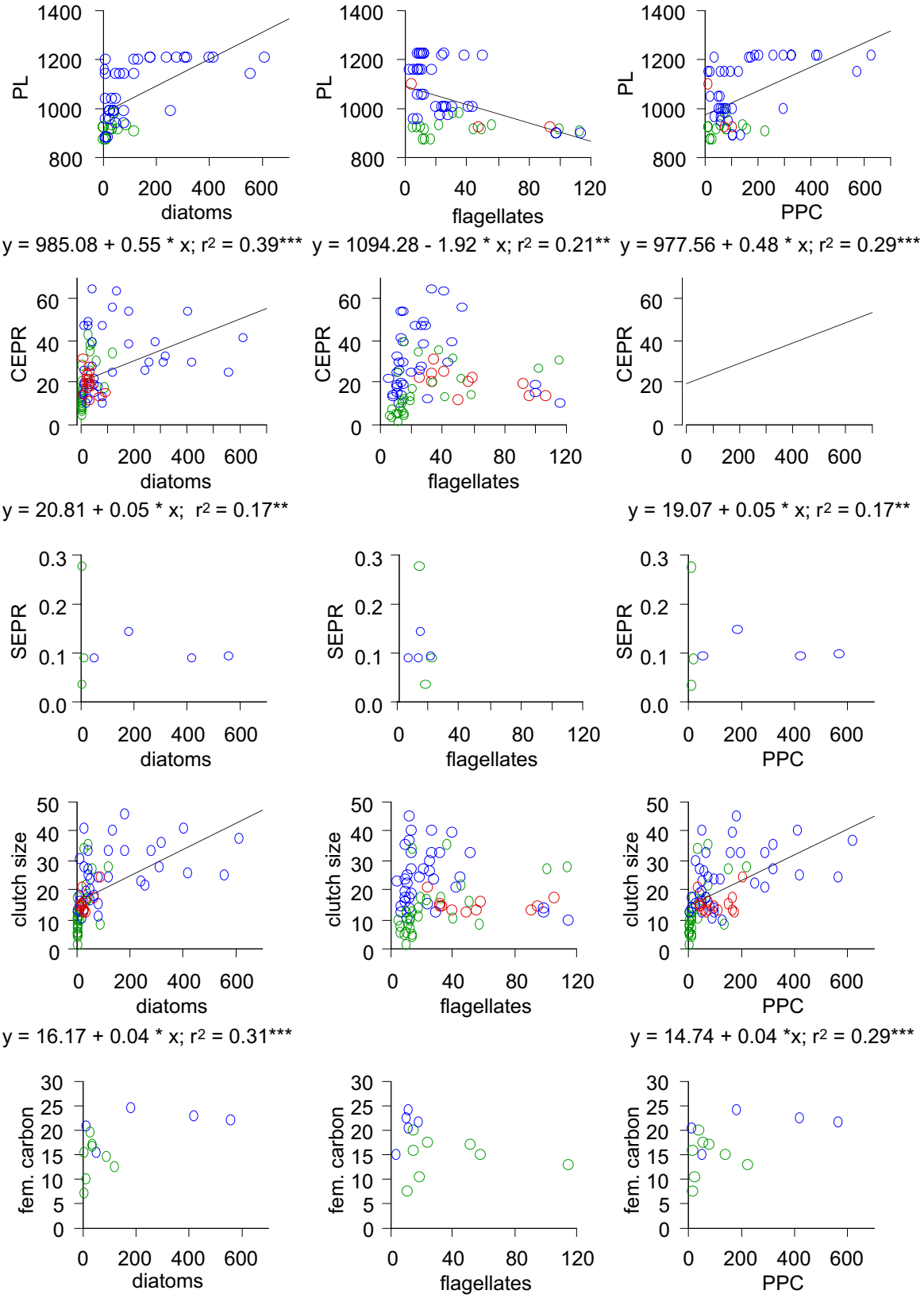


Fig. 7.2: *Temora longicornis*. PL=prosome length [µm], CEPR=corrected egg production rate [eggs female^{-1} day^{-1}], SEPR=weight specific egg production rate [d^{-1}], PPC=particulate phytoplankton carbon (diatoms+flagellates) [µg l^{-1}]

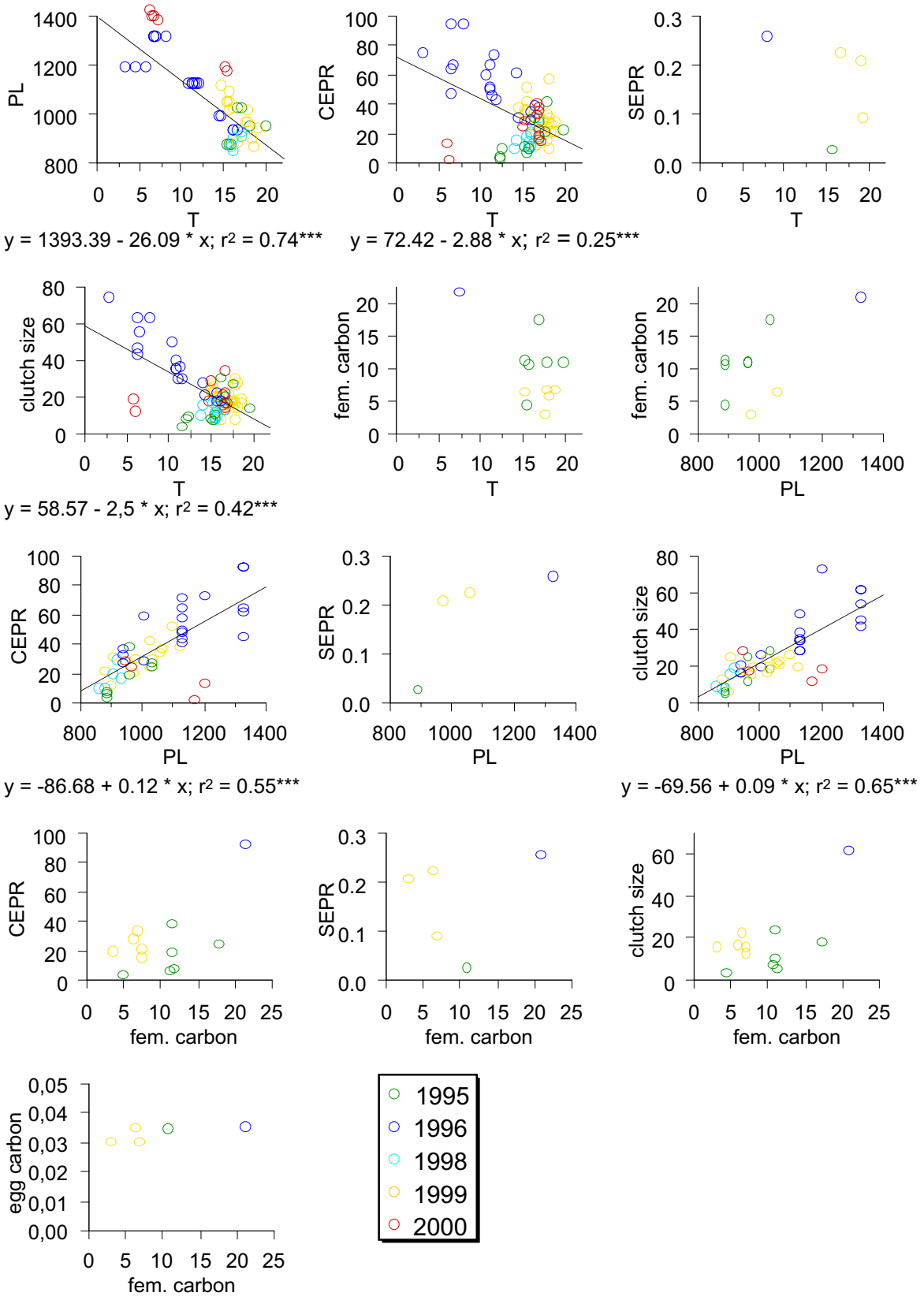


Fig. 7.3: *Centropages hamatus*. PL=prosome length [µm], CEPR=corrected egg production rate [eggs female^{-1} day^{-1}], SEPR= weight specific egg production rate [d^{-1}], T=temperature [°C]

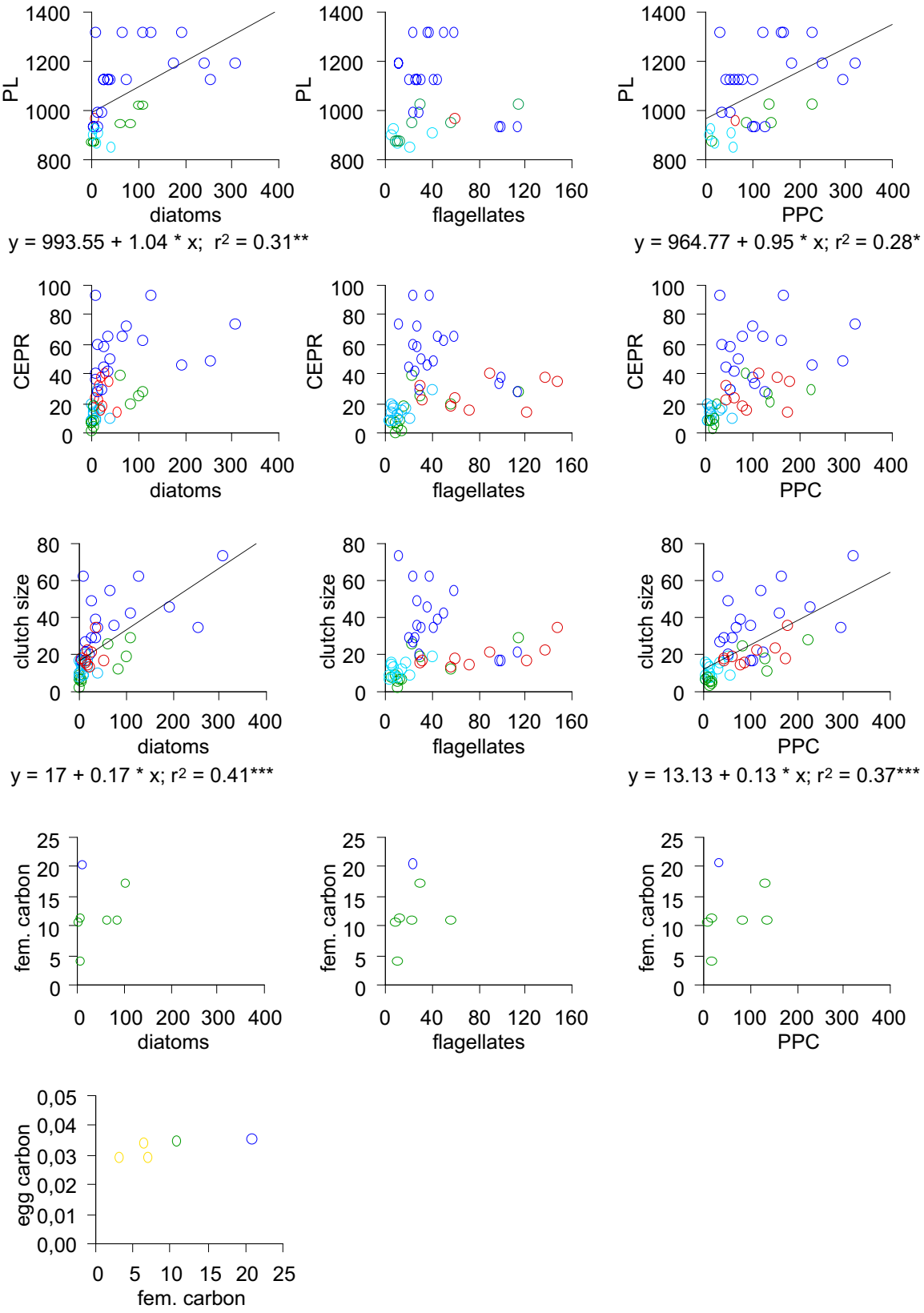


Fig. 7.4: *Centropages hamatus*. PL=prosome length [µm], CEPR=corrected egg production rate [eggs female^{-1} day^{-1}], SEPR=weight specific egg production rate [d^{-1}], PPC=particulate phytoplankton carbon (diatoms+flagellates) [µg l^{-1}]

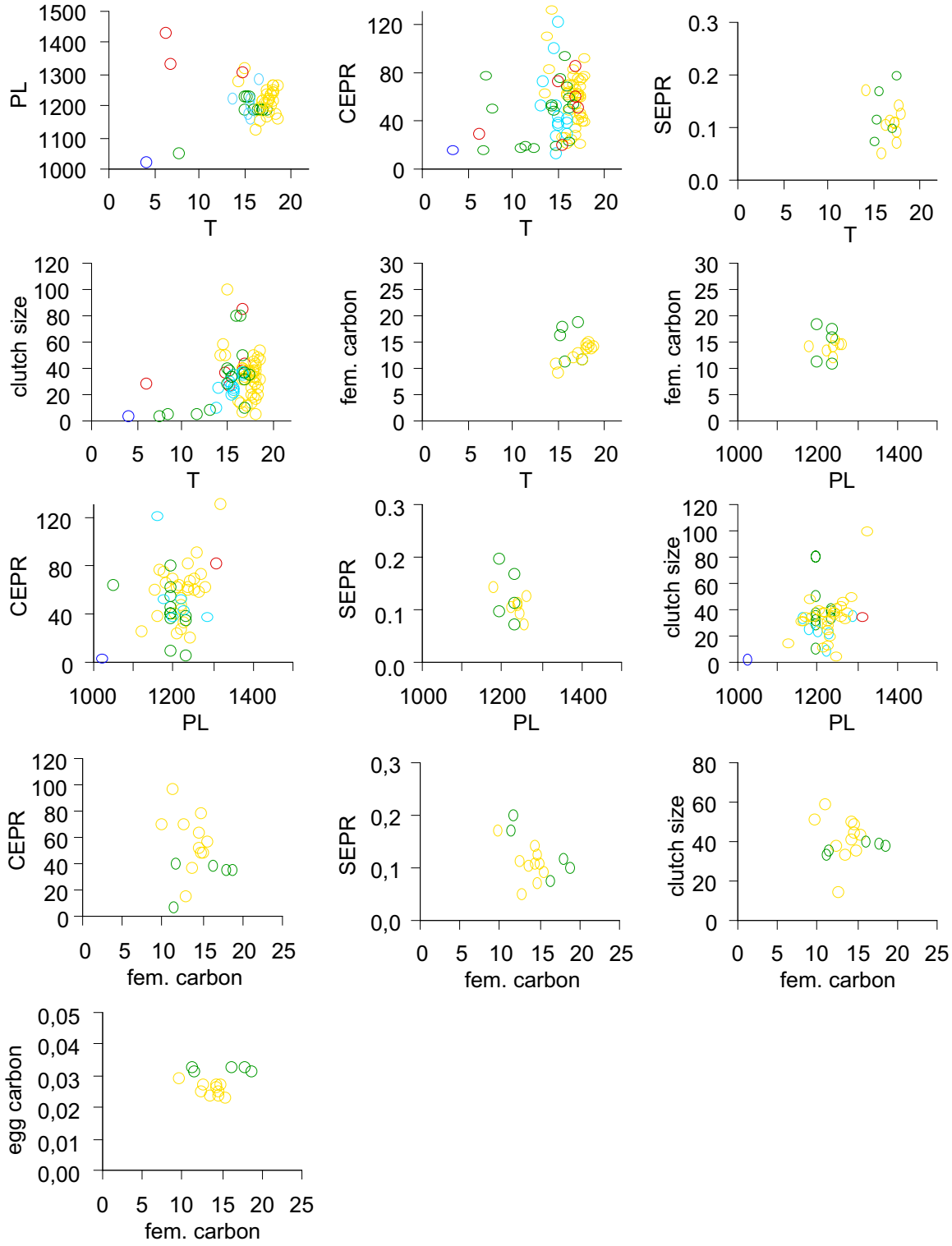


Fig. 7.5: *Centropages typicus*. PL=prosome length [µm], CEPR=corrected egg production rate [eggs female^{-1} day^{-1}], SEPR= weight specific egg production rate [d^{-1}], T=temperature [°C]

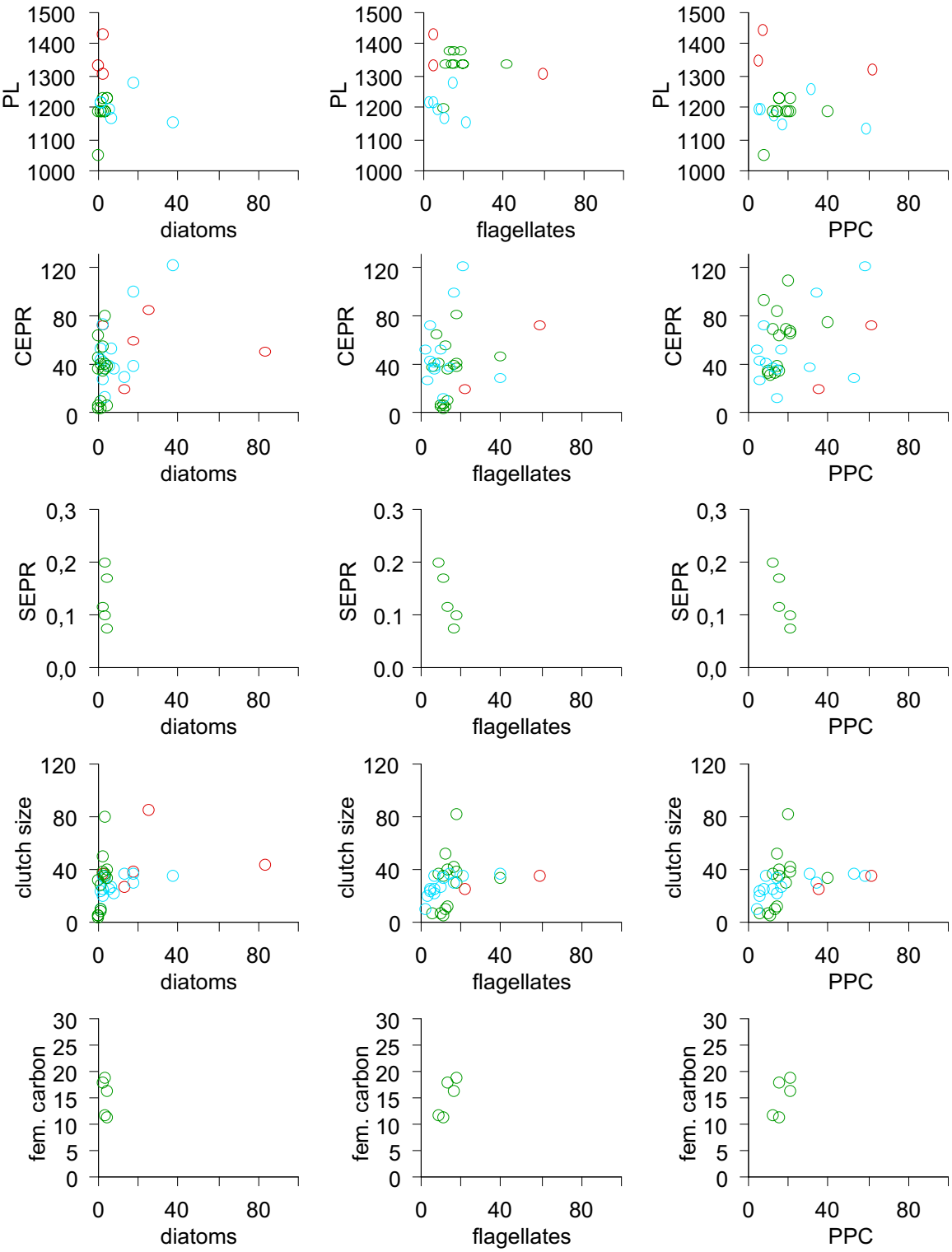


Fig. 7.6: *Centropahes typicus*. PL=prosome length [µm], CEPR=corrected egg production rate [eggs female^{-1} day^{-1}], SEPR=weight specific egg production rate [d^{-1}], PPC=particulate phytoplankton carbon (diatoms+flagellates) [µg l^{-1}]

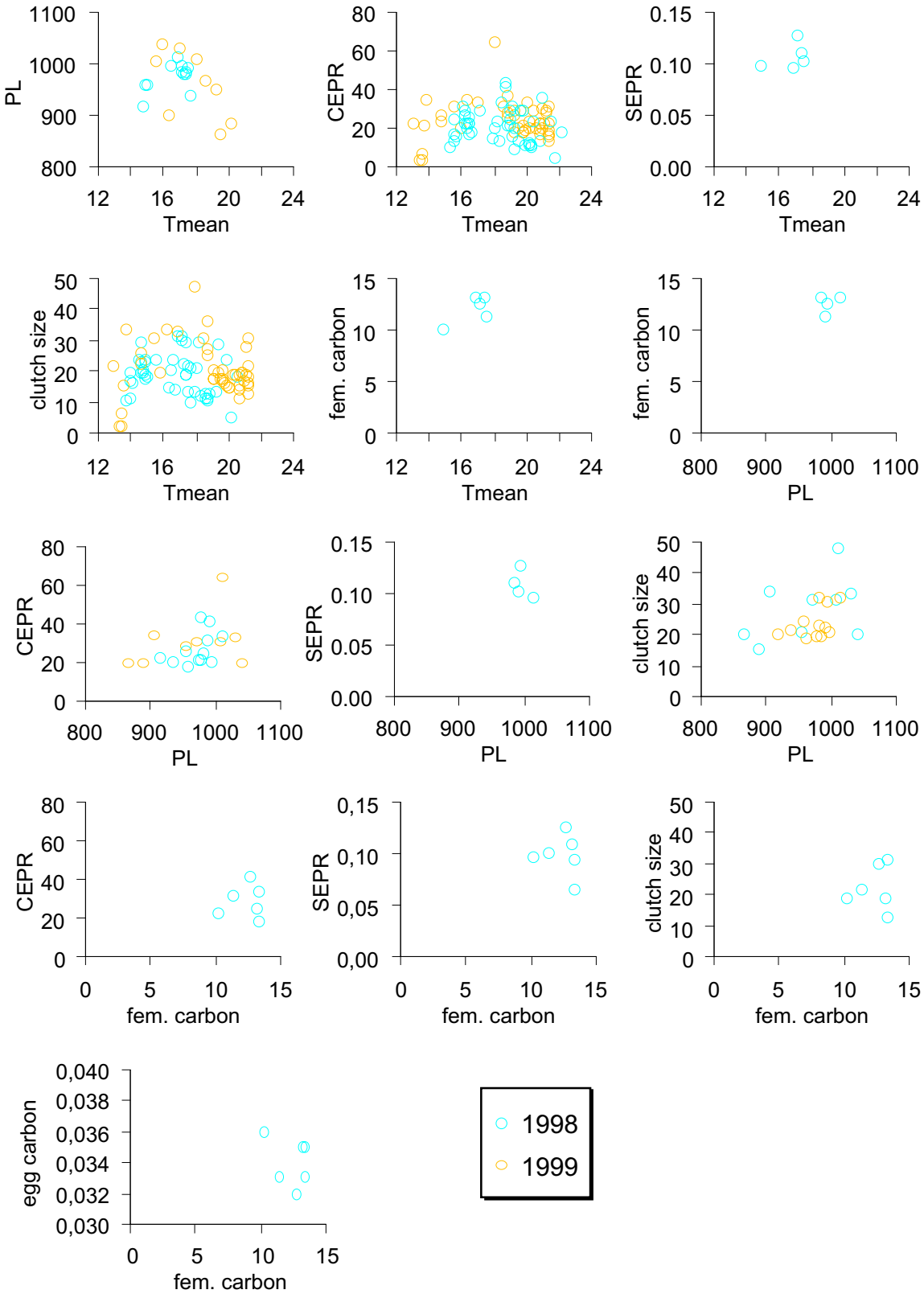


Fig. 7.7: *Temora stylifera*. PL=prosome length [µm], CEPR=corrected egg production rate [eggs female^{-1} day^{-1}], SEPR= weight specific egg production rate [d^{-1}], Tmean=mean temperature of the water column (0-75 m) [°C]

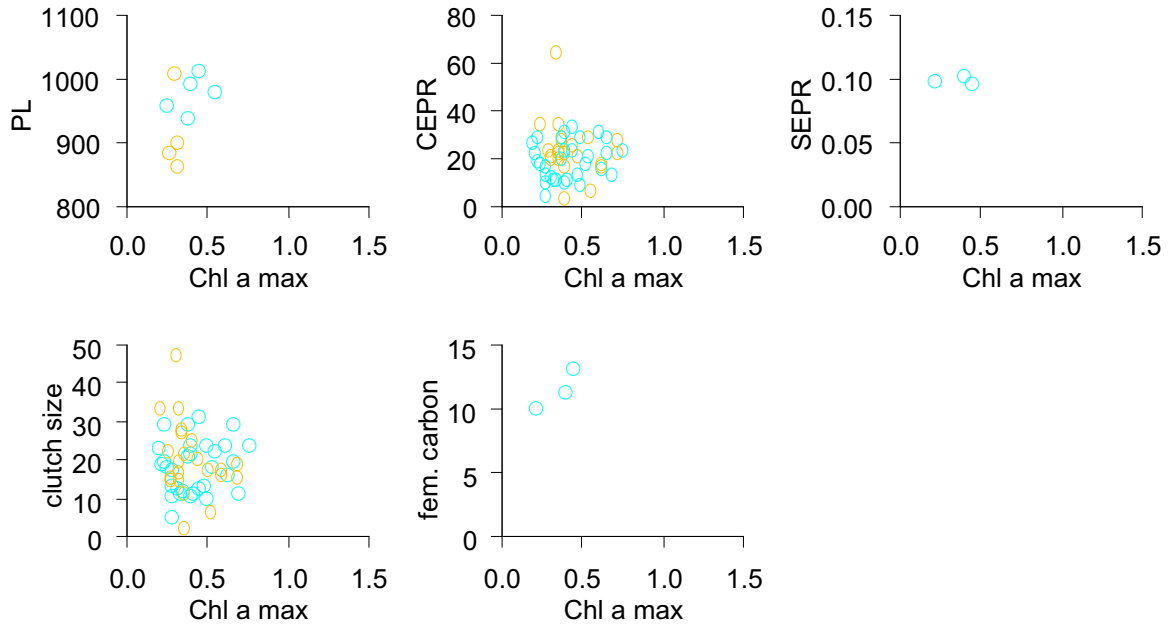


Fig. 7.8: *Temora stylifera*. PL=prosome length [µm], CEPR=corrected egg production rate [eggs female^{-1} day^{-1}], SEPR=weight specific egg production rate [d^{-1}], Chl$_a$ max=Chlorophyll$_a$ maximum of the water column (0-75 m) [µg l^{-1}]

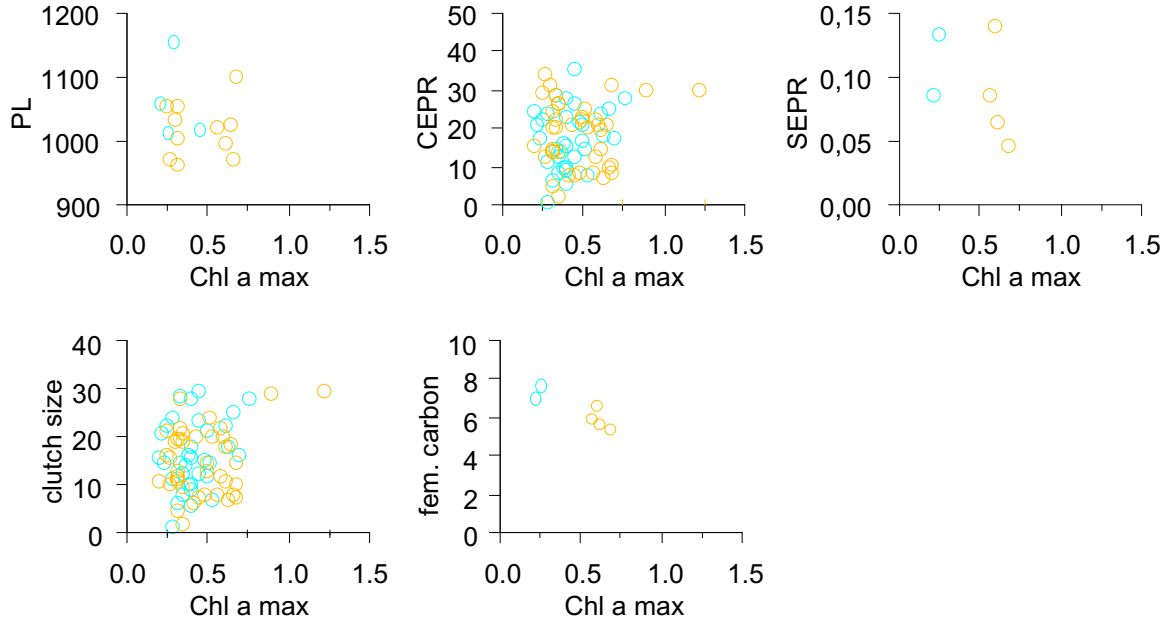


Fig. 7.9: *Centropages typicus*. PL=prosome length [µm], CEPR=corrected egg production rate [eggs female^{-1} day^{-1}], SEPR=weight specific egg production rate [d^{-1}], Chl$_a$ max=Chlorophyll$_a$ maximum of the water column (0-75 m) [µg l^{-1}]

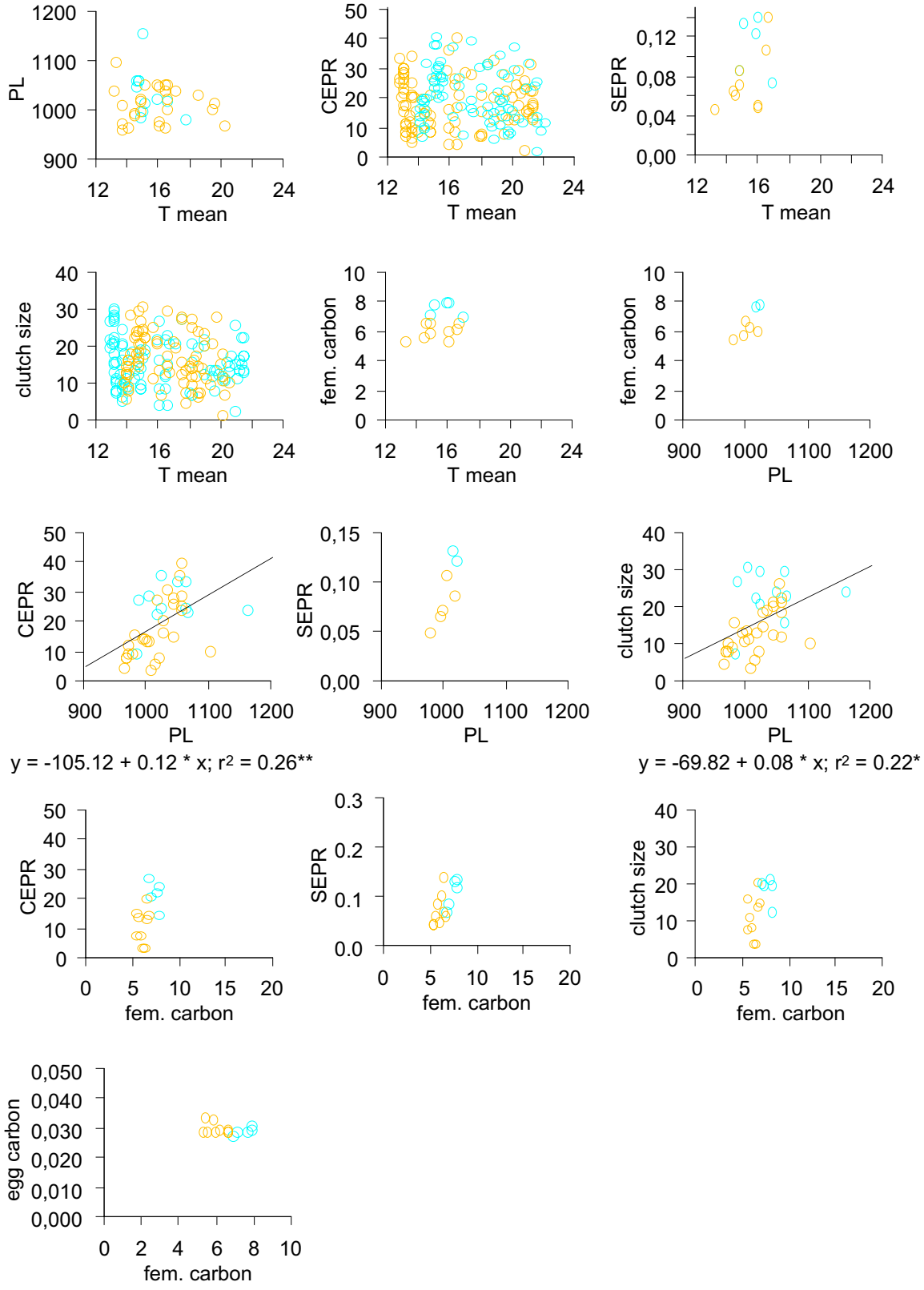


Fig. 7.10: *Centropages typicus*. PL=prosome length [µm], CEPR=corrected egg production rate [eggs female^{-1} day^{-1}], SEPR= weight specific egg production rate [d^{-1}], Tmean=mean temperature of the water column (0-75 m) [°C]

7.3 Rearing experiments. Population development in mesocosms of 5 L volume

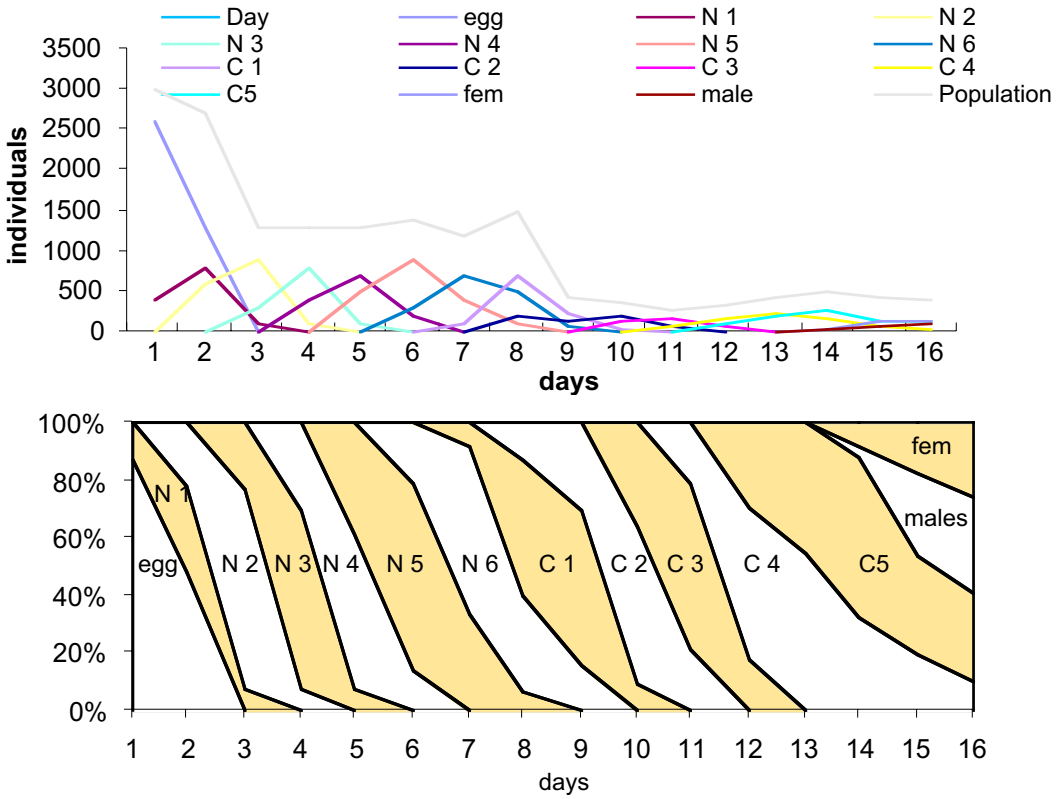


Fig. 7.11: *Temora longicornis* at 20°C

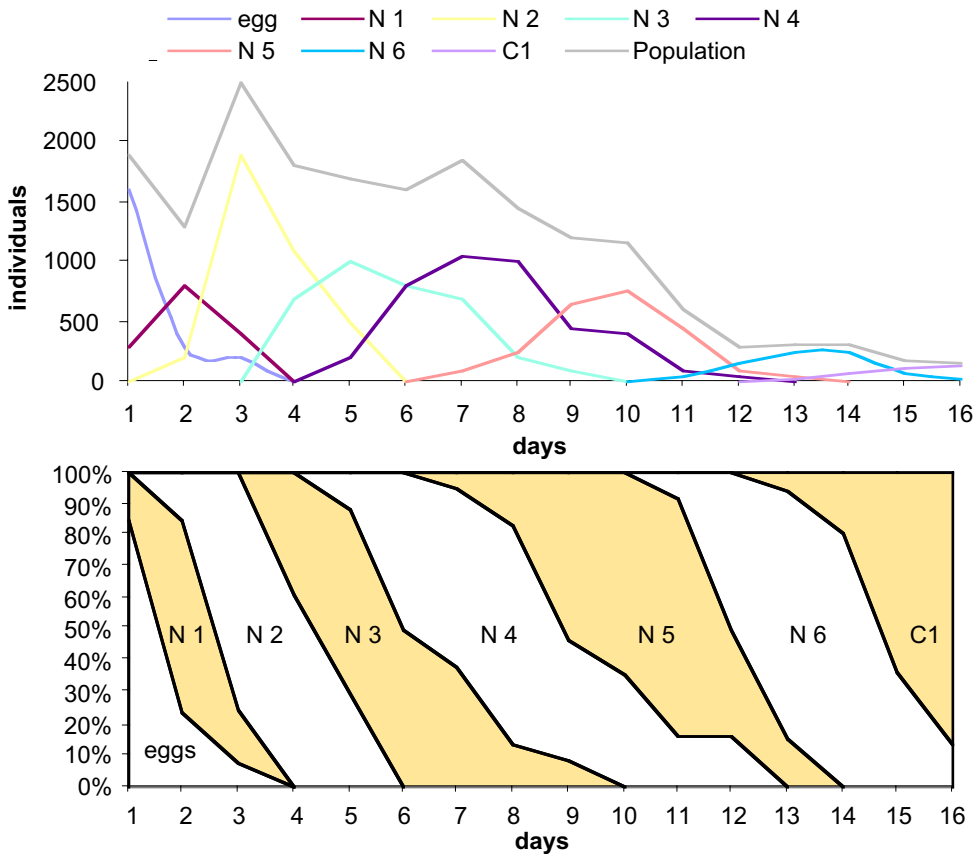


Fig. 7.12: *T. longicornis* at 15°C

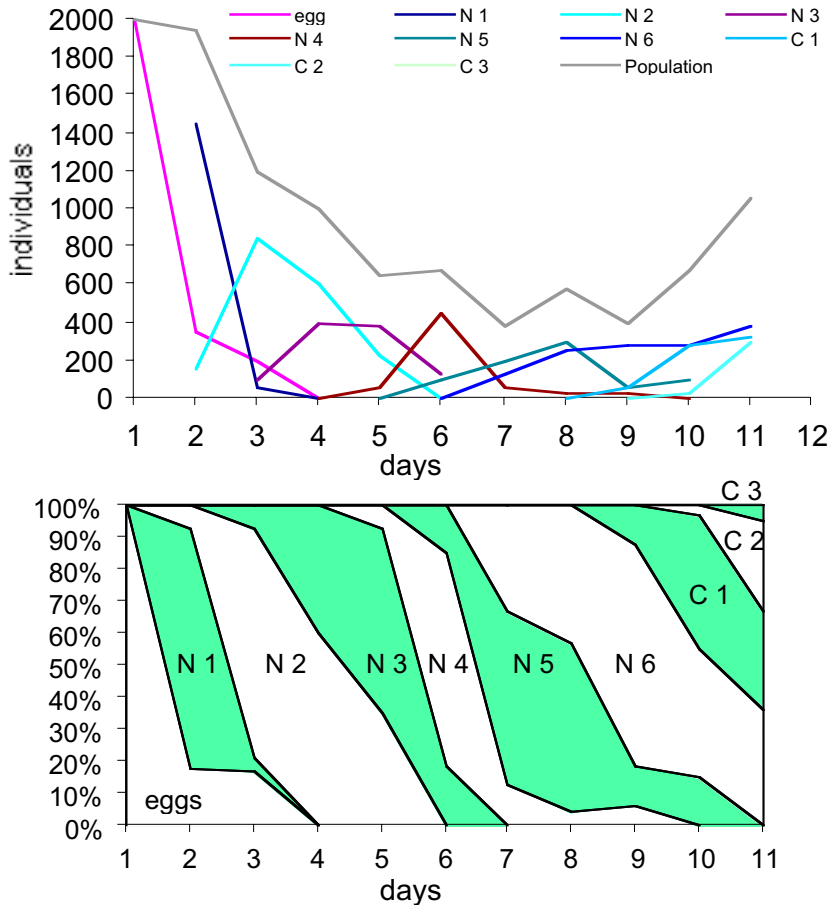


Fig. 7.13: *Centropages hamatus* at 20°C

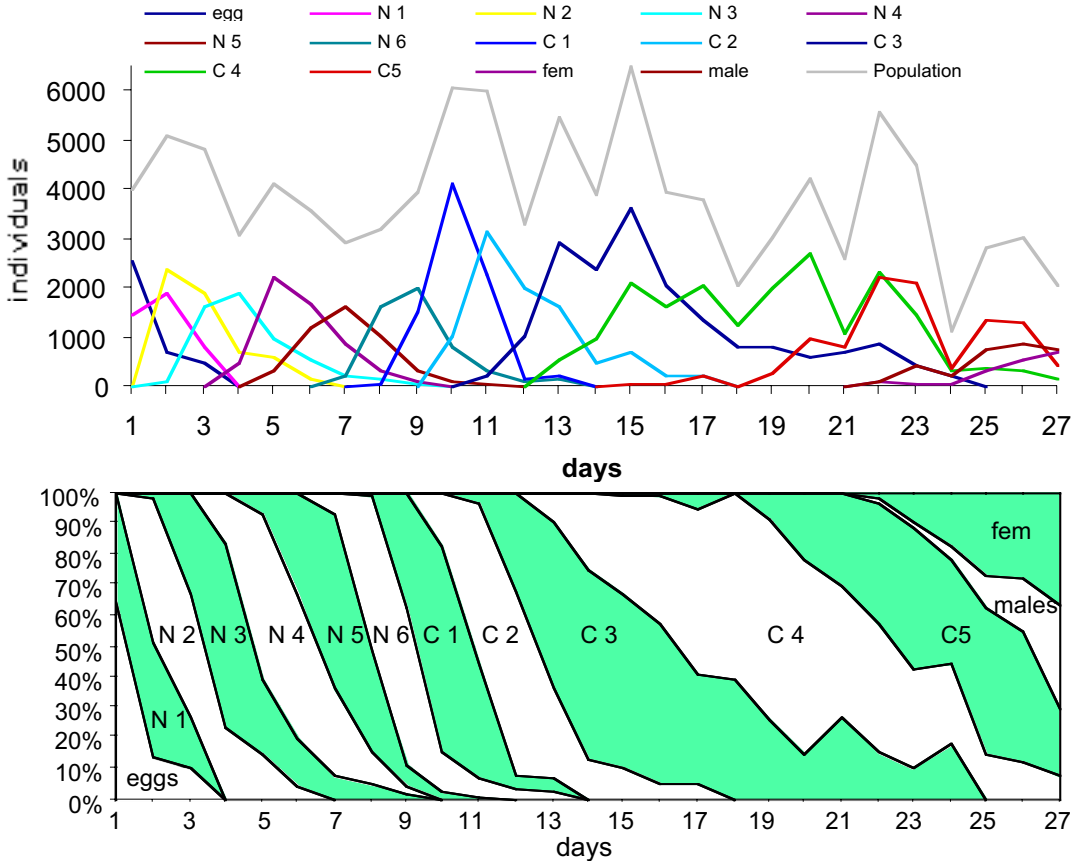
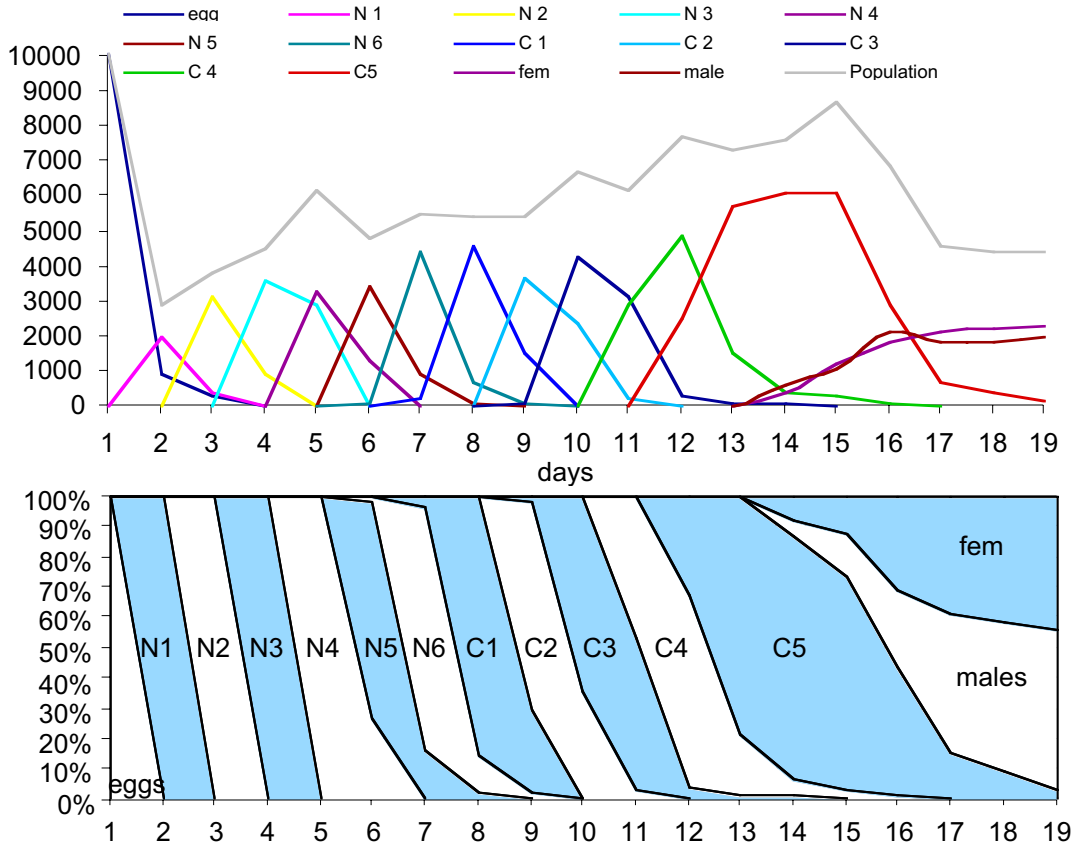


Fig. 7.14: *Centropages hamatus* at 15°C

A



B

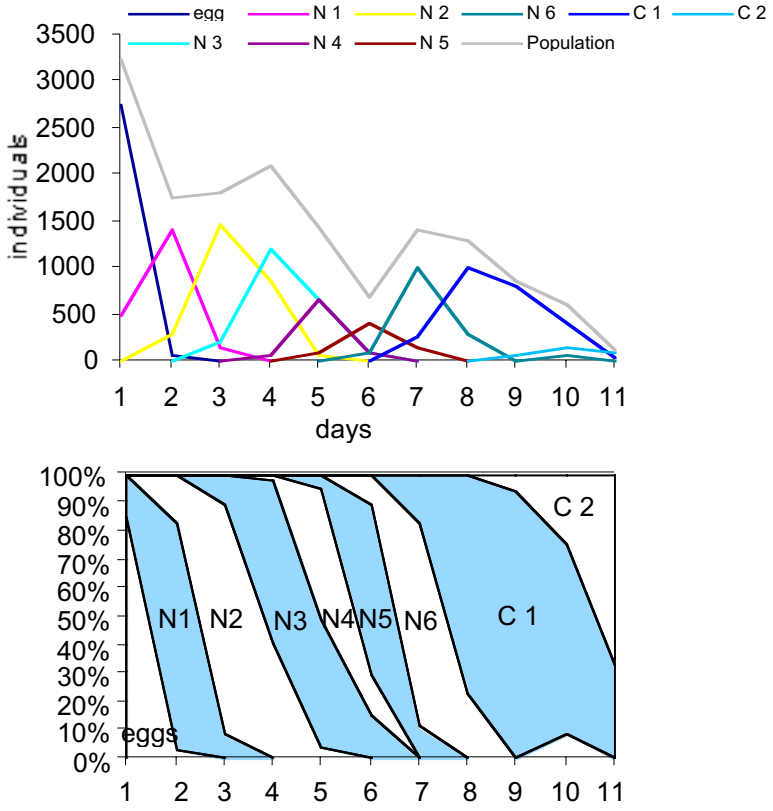


Fig. 7.15: A+B: replicate cultures of *Centropages typicus* (North Sea) at 20°C

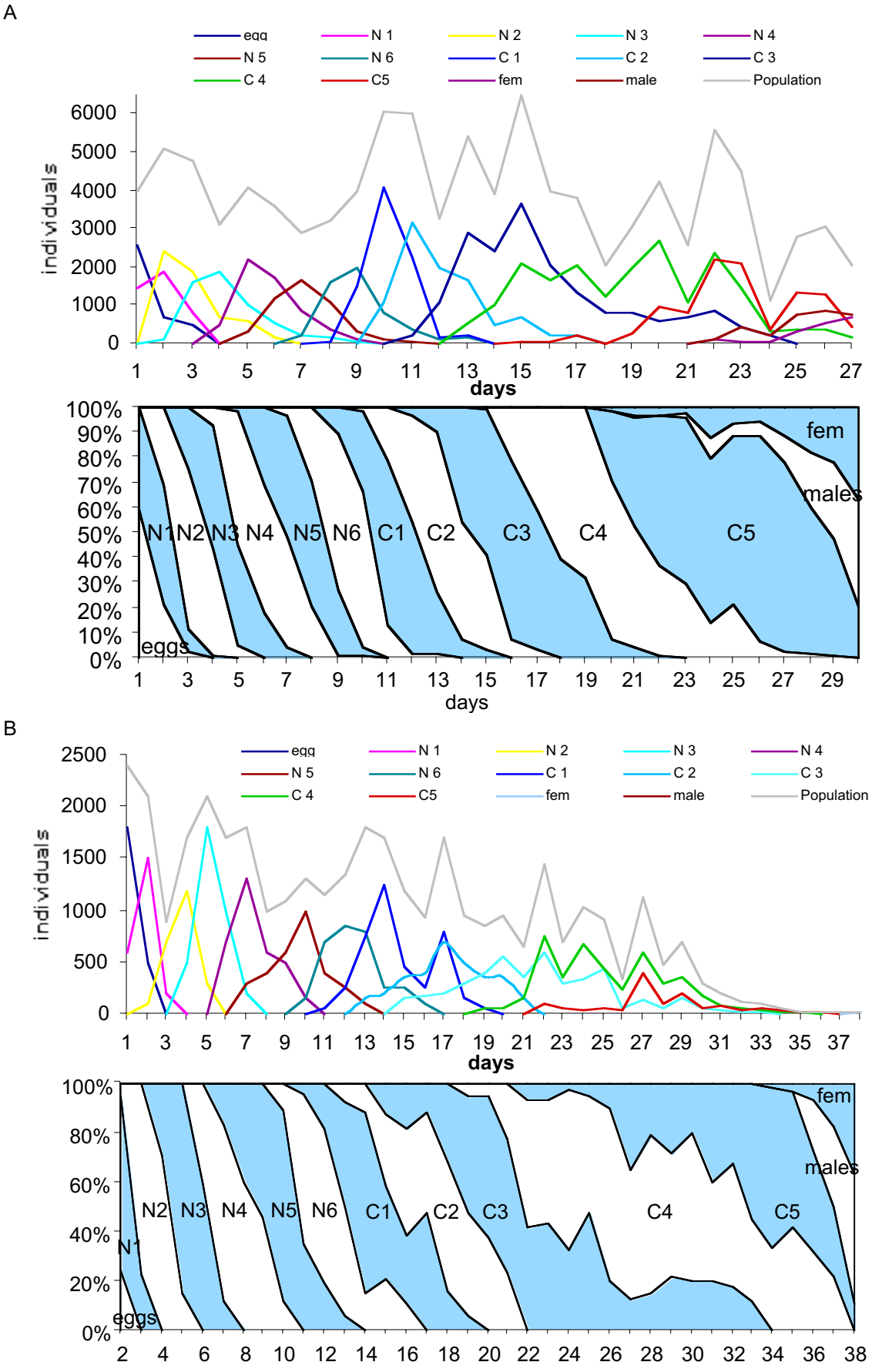
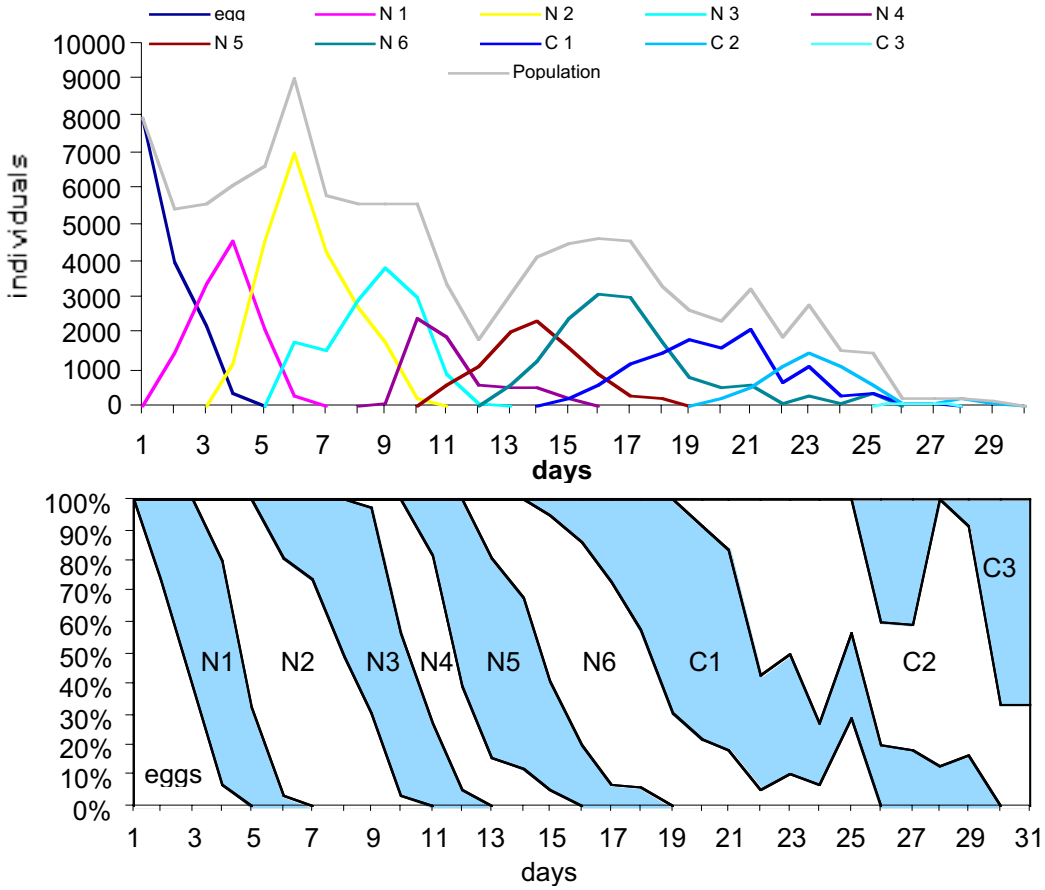


Fig. 7.16: A+B: replicate cultures of *C. typicus* (North Sea) at 15°C

A



B

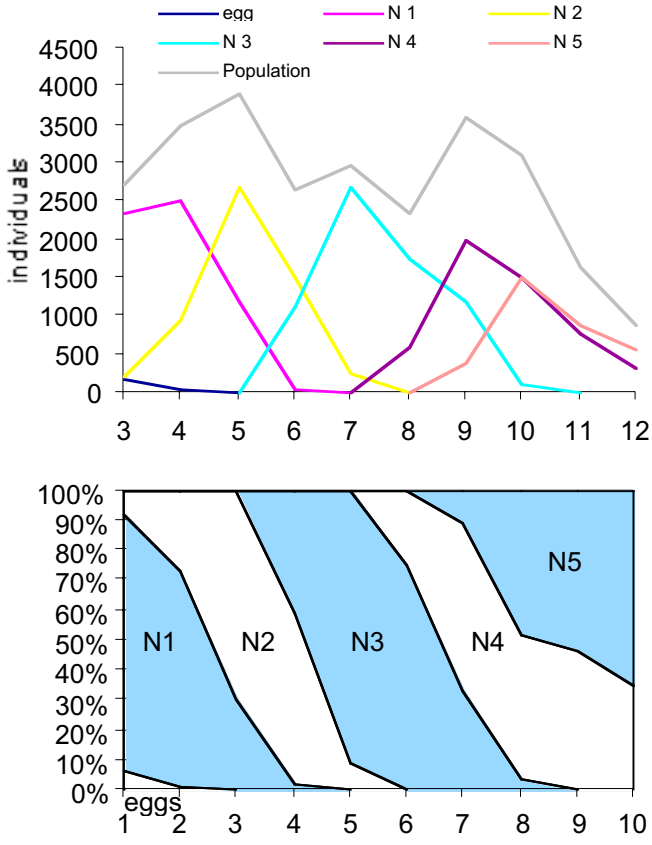
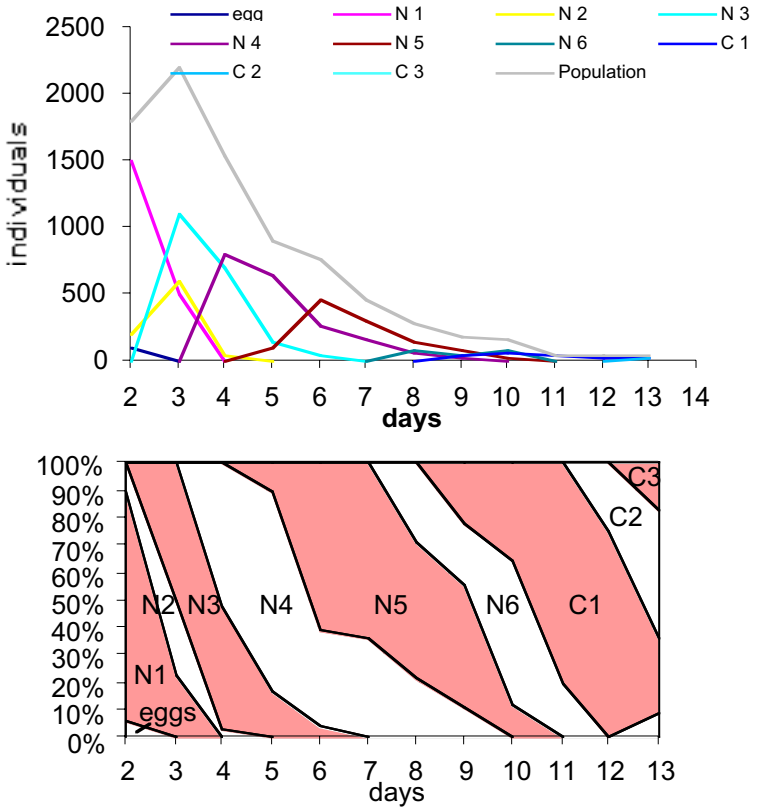


Fig. 7.17: A+B: replicate cultures of *C. typicus* (North Sea) at 10°C

A



B

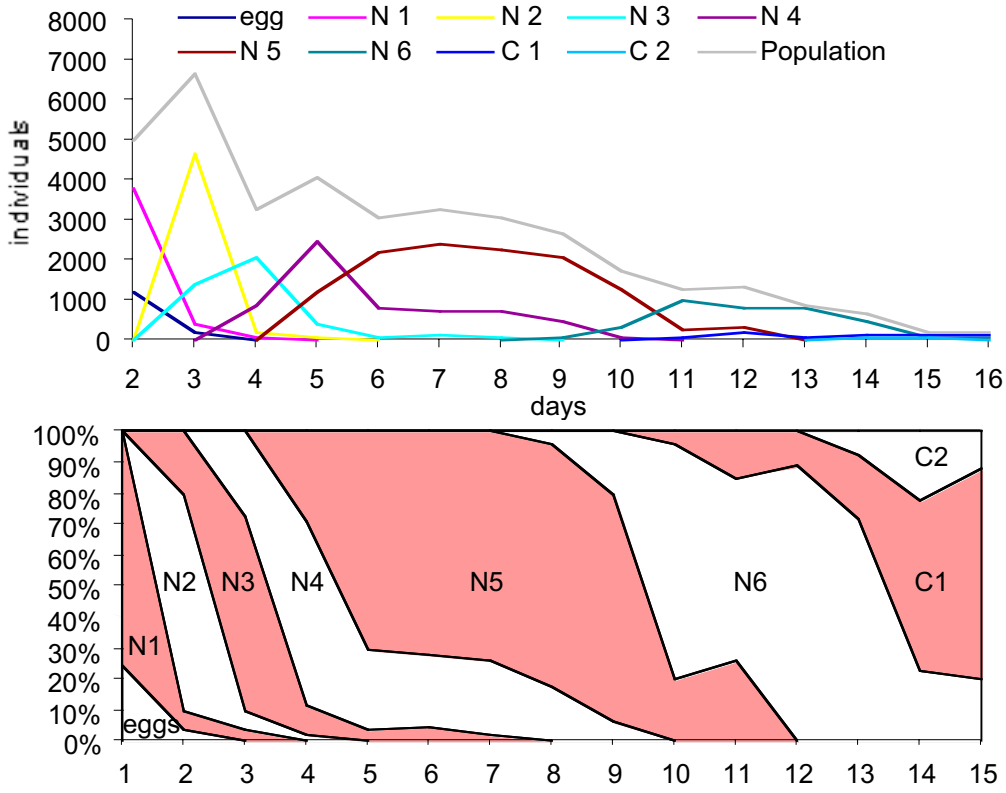
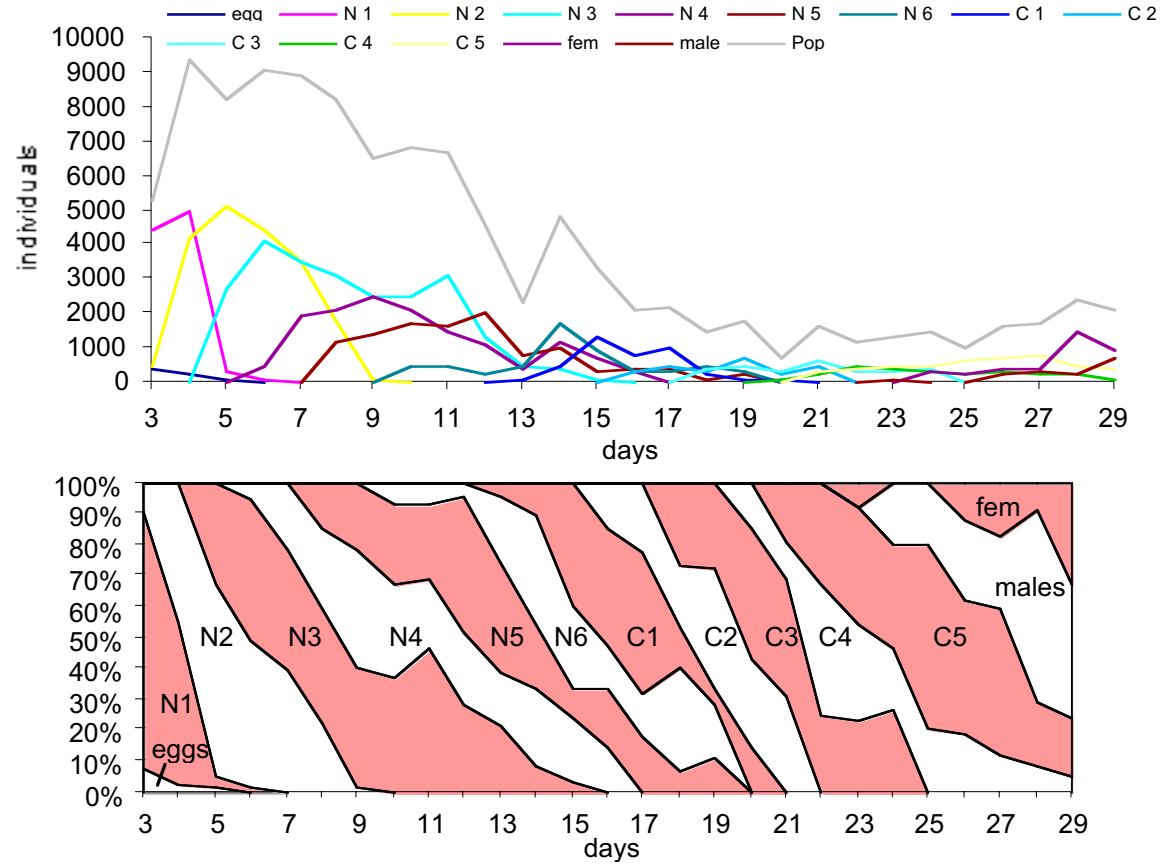
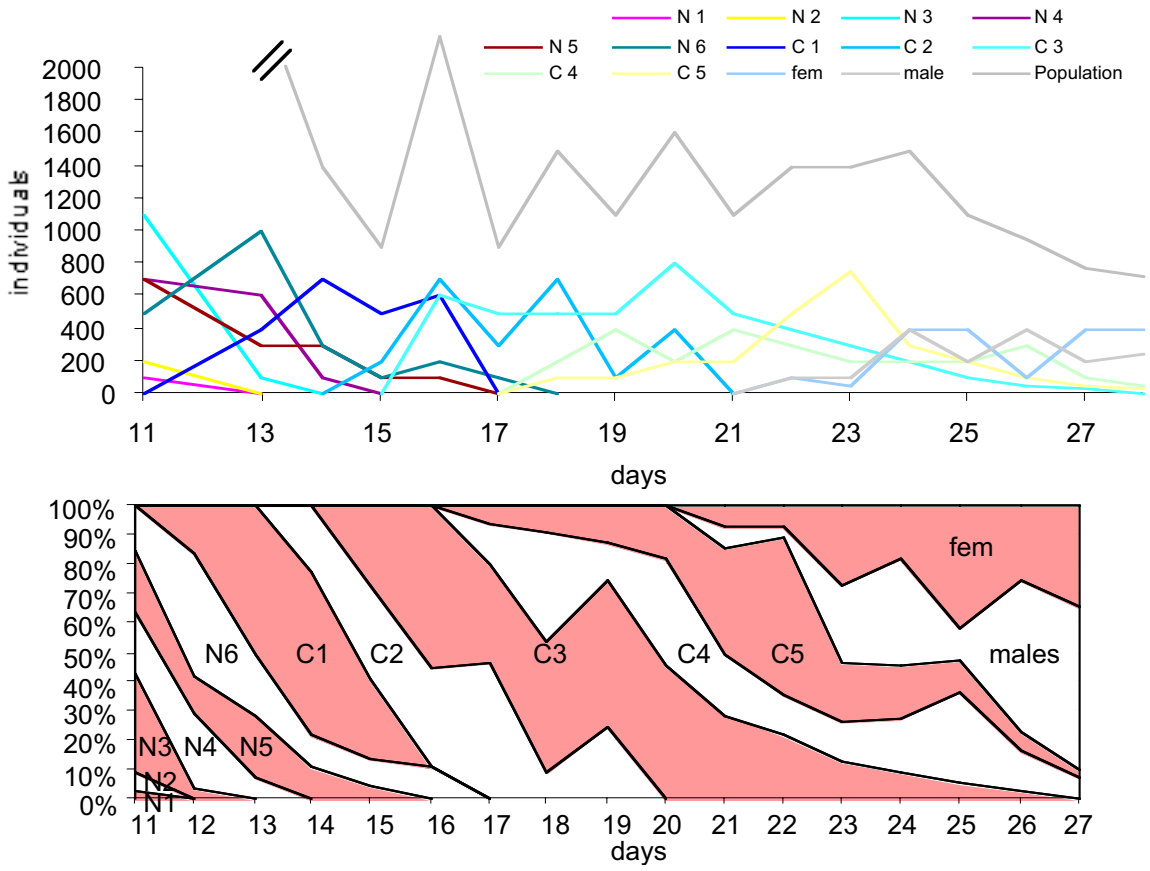


Fig. 7.18: A+B: replicate cultures of *Temora stylifera* at 20°C

A


egg
N 1
N 2
N 3
N 4
N 5
N 6
C 1
C 2
C 3
C 4
C 5
fem
male
Pop
individuals
days
N1
N2
N3
N4
N5
N6
C1
C2
C3
C4
C5
fem
males
eggs

B


N 1
N 2
N 3
N 4
N 5
N 6
C 1
C 2
C 3
C 4
C 5
fem
male
Population
individuals
days
N1
N2
N3
N4
N5
N6
C1
C2
C3
C4
C5
fem
males

C

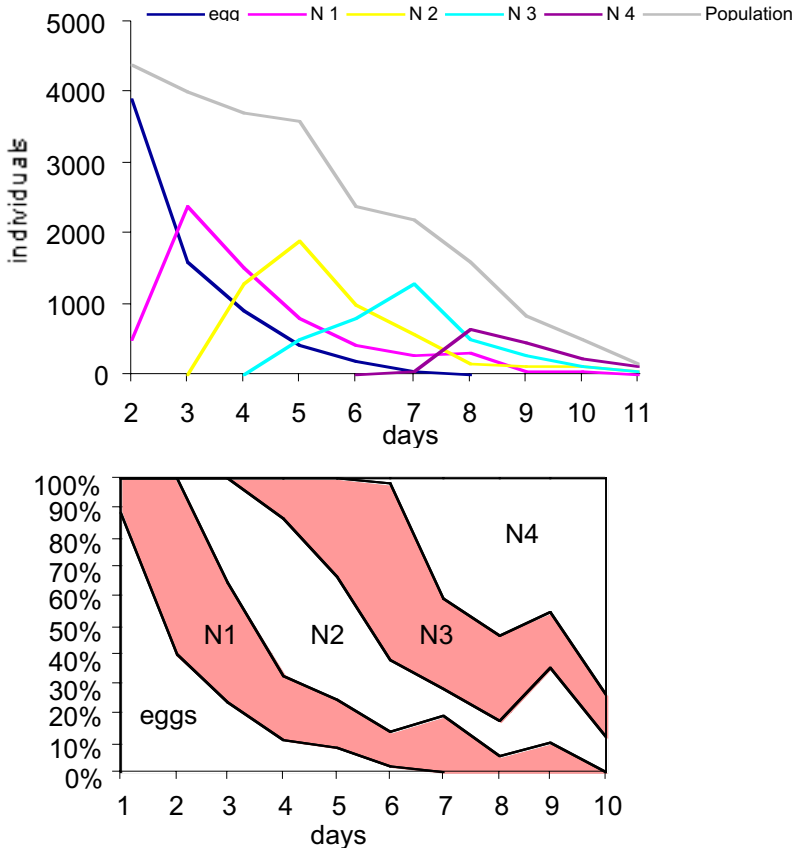


Fig. 7.19: A-C: replicate cultures of *Temora stylifera* at 15°C

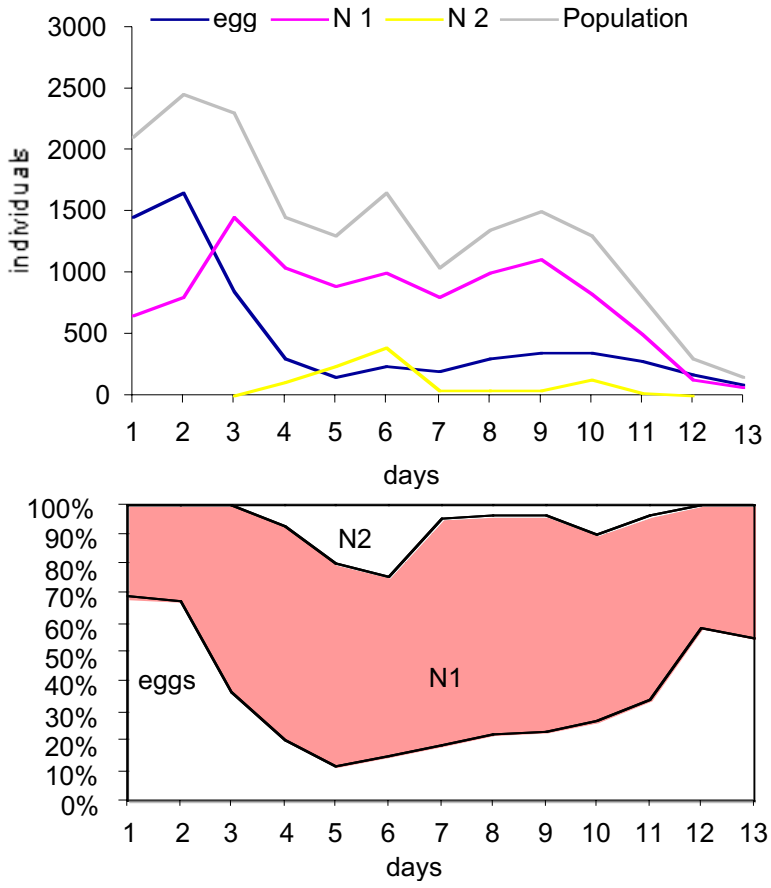


Fig. 7.20: *Temora stylifera* at 10°C

8 PUBLICATIONS

The results presented in this study partly are based on the following publications:

Reprinted with permission from Inter Research:

Halsband, C., Hirche H.-J. (2001) Reproductive cycles of dominant calanoid copepods in the North Sea.
Marine Ecology Progress Series 209, 219-229

Reprinted with permission from Oxford University Press:

Halsband-Lenk, C., Nival, S., Carlotti, F., Hirche, H.-J. (2001) Seasonal cycles of egg production of two planktonic copepods, *Centropages typicus* and *Temora stylifera*, in the north-western Mediterranean Sea.
Journal of Plankton Research 23, 597-609

Reprinted with permission from Elsevier Science:

Halsband-Lenk, C., Hirche, H.-J., Carlotti, F., (2002) Temperature impact on reproduction and development of congener copepod populations.
Journal of Experimental Marine Biology and Ecology 271, 121-153

Hiermit versichere ich, daß ich die vorliegende Arbeit mit dem Thema

Temperature impact on reproduction and development of congener marine copepods – a key to distribution patterns?

selbständig verfaßt und ausschließlich die angegebenen Quellen als Hilfsmittel verwendet habe.

Bremerhaven, den 24.09.01 Claudia Hasbard-Lenz

Datum Unterschrift