Comparative seasonal dynamics of *Centropages typicus* at seven coastal monitoring stations in the North Sea, English Channel and Bay of Biscay

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Abstract

We review current knowledge and understanding of the biology and ecology of *Centropages typicus* in the European shelf-seas (e.g. North Sea, English Channel and Bay of Biscay). Our study is based on observations at seven coastal time-series stations as well as on the Continuous Plankton Recorder dataset. This paper focuses on the influence of the environmental parameters (e.g. temperature and Chl*a*) on the life cycle and distribution of *C. typicus* and provides a comparison with its congeneric species *C. hamatus* and *C. chierchiae* in the study area. Data on abundance, seasonality and egg production have been used to define the temperature and chlorophyll optima for occurrence and reproduction of *Centropages* spp. within this region of the European shelf-seas.
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Keywords: *Centropages*; Seasonal cycle; North Sea; English Channel; Bay of Biscay

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1. Introduction

Centropages typicus (Copepoda Calanoida) has a wide range of distribution in the North Atlantic (see Durbin and Kane, this issue for NW Atlantic) and adjacent shelf seas from 6°S to 66°N (CPR survey team, 2004) as well as in the Mediterranean Sea (Mazzochi et al, this issue). In the North Atlantic, this species is abundant in the North Sea, Celtic Sea, English Channel and Bay of Biscay. The Continuous Plankton Recorder (CPR) survey has monitored long-term changes in the North Atlantic plankton since the middle of the last century (CPR survey team, 2004). This basin-scale survey (see Beaugrand, this issue) confirms that the North Sea, English Channel, Celtic Sea and Bay of Biscay are major centres of distribution for the species in the eastern North Atlantic.

Here, we focus on the potential effects of environmental parameters on the population dynamics of *Centropages* spp. using long-term series located in European shelf seas (North Sea-Helgoland Roads, English Channel-Station L4, Bay of Biscay-Santander and La Coruña) (Fig. 1). Long-term trends in the abundance and seasonality of *Centropages typicus* are studied in relation to temperature and to Chl*a* concentration. In addition, data on reproduction, length of individuals and comparisons with congeneric species are reviewed together with environmental conditions.
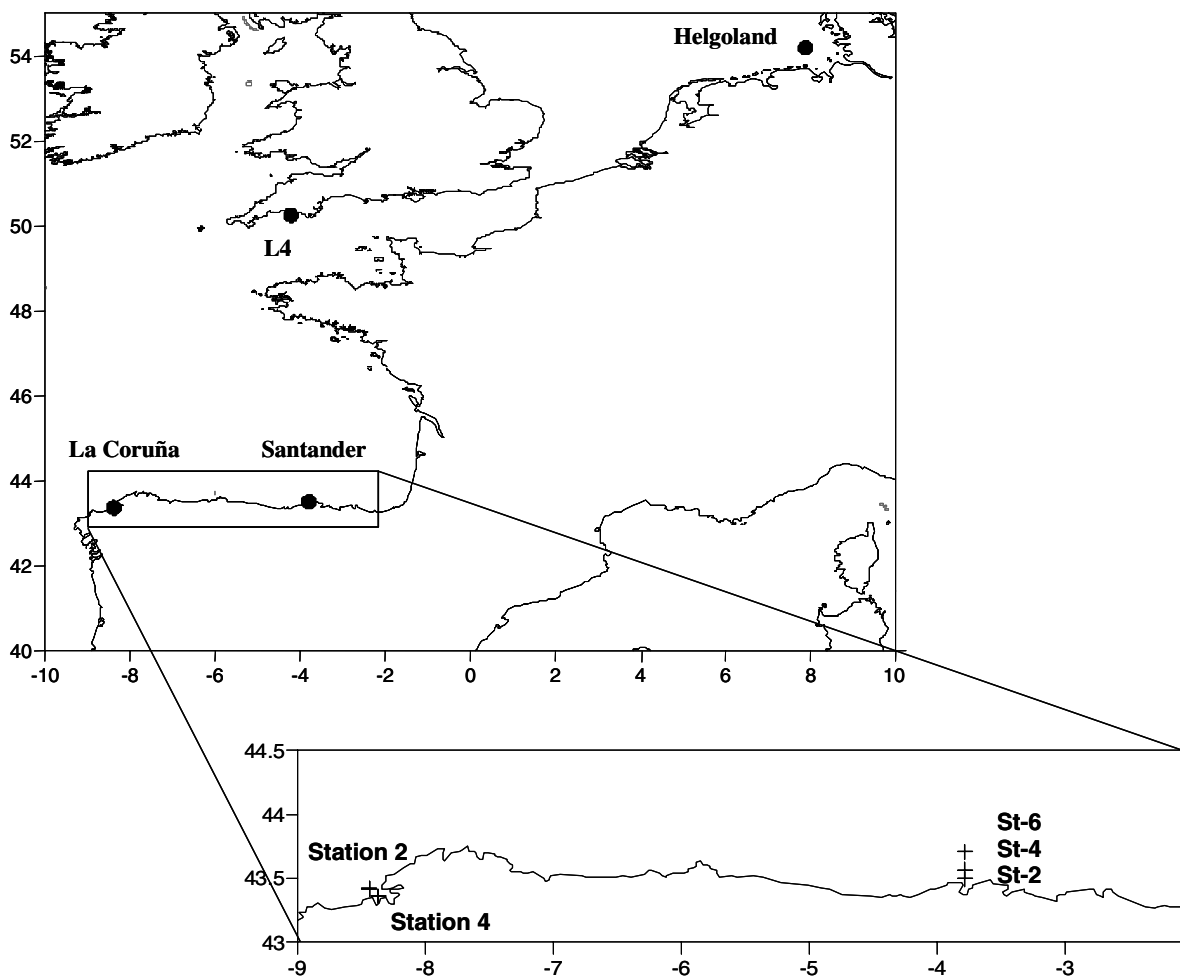

Fig. 1. Map of the long-term monitoring stations with details on the Spanish stations.

2. Time-series stations: North Sea, English Channel and Bay of Biscay

2.1. North Sea, Helgoland Roads (54°11′18″N, 7°54′E)-(1975–2004)

From 1975 until the present, two oblique plankton net samples (150 μm, 500 μm) have been collected in Helgoland Roads in the North Sea three times a week. The sampling station is located in a 1 km wide channel between the main island of Helgoland and a sandy dune, at a water depth of 10 m. Almost 400 taxonomic entities of holoplankton and meroplankton are counted. The time-series was started by the Biologische Anstalt Helgoland and has been continued jointly by the German Centre for Marine Biodiversity, the Federal Maritime and Hydrographic Agency and the Biologische Anstalt Helgoland (Greve et al., 2004). *Centropages typicus* and *C. hamatus* co-occur at Helgoland Roads and females are identified from the 150 μm mesh net to the species level, but other developmental stages are pooled together. The (*C. hamatus*/*C. typicus*) female ratio was applied to the rest of *Centropages* spp. developmental stages (CI-CVI male) to estimate a total *C. typicus* abundance.

2.2. Western English Channel, station L4 (50°15′N, 04°12′W)-(1988–2004)

Station L4 is located 10 nautical miles south-west of Plymouth in the Western English Channel. Weekly zooplankton sampling at this station has been carried out since 1988. Samples are collected by vertical net hauls (WP2 net, 200 μm) from the bottom (∼55 m) to the surface. Samples are counted for major taxonomic groups as well as the dominant copepod species. *Centropages typicus* and *C. hamatus* are routinely discriminated while *C. chierchiae* has only been found for some periods in the time-series. *Centropages cherchiae* and *C. hamatus* are rarely present at L4 and in low numbers (for further details, see http://web.pml.ac.uk/L4/). Females of each species are identified while juveniles (CI-CV) are pooled together and likely represent a good estimate of total *C. typicus* population abundance.

2.3. Southern Bay of Biscay, Santander (43°30′N, 3°47′W; 43°34′N, 3°47′W and 43°42.6′N, 3°47′W)-(1991–2000)

Samples were obtained on a cross-shelf section located off Santander. Hydrographic parameters and plankton communities were sampled monthly over the period from June 1991 to December 2000 at three stations characterizing coastal (St-2), neritic (St-4) and oceanic conditions (St-6) at depths of 25, 110 and 850 m, respectively. Zooplankton were sampled with a 250 μm, 50 cm diameter, Juday-Bogorov net equipped with a General Oceanics Flowmeter and with a depth recorder fixed to the net frame to monitor the maximum depth of the haul. Double oblique tows were made at a speed of 1–1.5 knots down to a depth of 50 m (or to the sea floor if shallower). For calculating total abundance, at least three subsamples were counted (for further details, see http://www.seriestemporales-ieo.net/BDZoo/santander/index.html). Taxonomic analysis was carried out to the species level with two *Centropages* species (*C. typicus* and *C. chierchiae*) routinely discriminated. However, *C. chierchiae* is rare off Santander. Adults of both species are discriminated but juveniles are pooled together and considered to be an approximation of *C. typicus* juvenile abundance.

2.4. South West Bay of Biscay, La Coruña (43°21.8N, 8°22.2 W and 43°25.3N, 8°26.3 W)-(1994–2004)

Two stations have been sampled on a monthly basis since 1992. Station 4 is located in the mouth of La Coruña ria. This is a shallow station (20 m water depth) subject to the freshwater runoff from the river Mero. For Station 4, there is a gap in the *Centropages typicus* time series because samples from 1998 until 2001 have not yet been analysed. Station 2 is located on the continental shelf off La Coruña where the water column is approximately 79 m. Mesozooplankton samples were collected as for the Santander sites but with a 200 μm net (for further details see http://www.seriestemporales-ieo.net/). *Centropages* adults are recognized to the species level with three main species consistently appearing throughout the series, but juveniles are pooled together.

The contributions (in percentage) of each *Centropages* species to the total copepod abundance and their rankings at each long-term monitoring station are presented in Table 1. The highest contribution of a *Centropages* species to the total copepod abundance is observed at station L4 where *C. typicus* contributes 3.58% of the total copepod abundance and is ranked the fifth most abundant copepod species. La Coruña is the only location of the seven long-term monitoring stations where the three *Centropages* species co-occur continuously throughout the time series.

Frequency of sampling is important when determining the period of appearance of a species or defining its maximum abundance. This is especially so when the generation time of the targeted species is close to a month. For this reason, only the Helgoland Roads dataset, where samples are collected three times a week is particularly appropriate for seasonal analysis. The other datasets are, however, very valuable for developing a large scale picture of the spatial and temporal distribution of *Centropages* spp.

In order to compare environmental information between the different sites, we used sea surface temperature (SST) monitored at each station and Chl*a* measurements when available. Off Helgoland, Chl*a* concentration was derived from diatom counts converted to carbon biomass using a 1:30 Chl*a*:C ratio (Wiltshire and Düreselen, 2004).

Off Santander, Chl*a* measurements started in 2002, while *Centropages* data had been collected previously. Therefore, we used the average seasonal cycle as the best proxy for Chl*a* concentration for the previous years.

3. Distribution and seasonal cycle

More than 10 *Centropages* species occur in the Atlantic Ocean, the North Sea and the Mediterranean, including the three species reported in this study: *C. typicus* Krøyer, *C. hamatus* (Lilljeborg) and *C. chierchiae* Giesbrecht (for further details see: http://copepodes.obs-banyuls.fr/).

Centropages typicus has been observed at various latitudes, from the Gulf of Guinea to the Northern North Sea. There are even two reported occurrences off Namibia (Carola, 1994) and South Africa (Senô et al., 1963a,b) that we have not taken into account for the latitudinal range of distribution (for further details see: http://copepodes.obs-banyuls.fr/). *Centropages hamatus* is found between 20°S and 64°N including the North Sea, White Sea and Kara Sea and along the coasts of Norway and Spitsbergen. There are also records of this species off South Africa (Carter, 1978). *Centropages chierchiae* has a little wider range of distribution from 35°S to 53°N, mainly in the Bay of Biscay and the south west coast of Portugal, but it has also been observed in the Celtic Sea, the English Channel and in the South Eastern Atlantic (De Decker, 1984).

At Helgoland Roads, where two *Centropages* species coexist, a seasonal succession is observed between *C. hamatus* and *C. typicus*. *Centropages typicus* prefers the saline and relatively warm waters of Atlantic origin and is usually abundant there in the second half of the year (Fransz et al., 1991; Rae and Rees, 1947). Fig. 2 shows an increase in abundance in April, highest values in July and August and then a slight decrease from September to December with high abundances (>50 ind m^{-3}) from July onward. *Centropages typicus* is advected into the German Bight with the Atlantic water inflow (Fransz et al., 1991; Hay et al., 1991). This advection results in a large interannual variability in timing of the first appearance of *C. typicus* adults at Helgoland (Halsband-Lenk et al., 2004).

Centropages typicus has been considered as a rare or sporadic immigrant in the North Sea or was not mentioned at all in earlier studies (e.g. Rae and Rees, 1947; Wiborg, 1955; Fransz, 1975; Hickel, 1975). It has

Table 1
Contribution (in percentage) and ranking (in parenthesis) of each *Centropages* species to the total copepod abundance at each long-term monitoring station

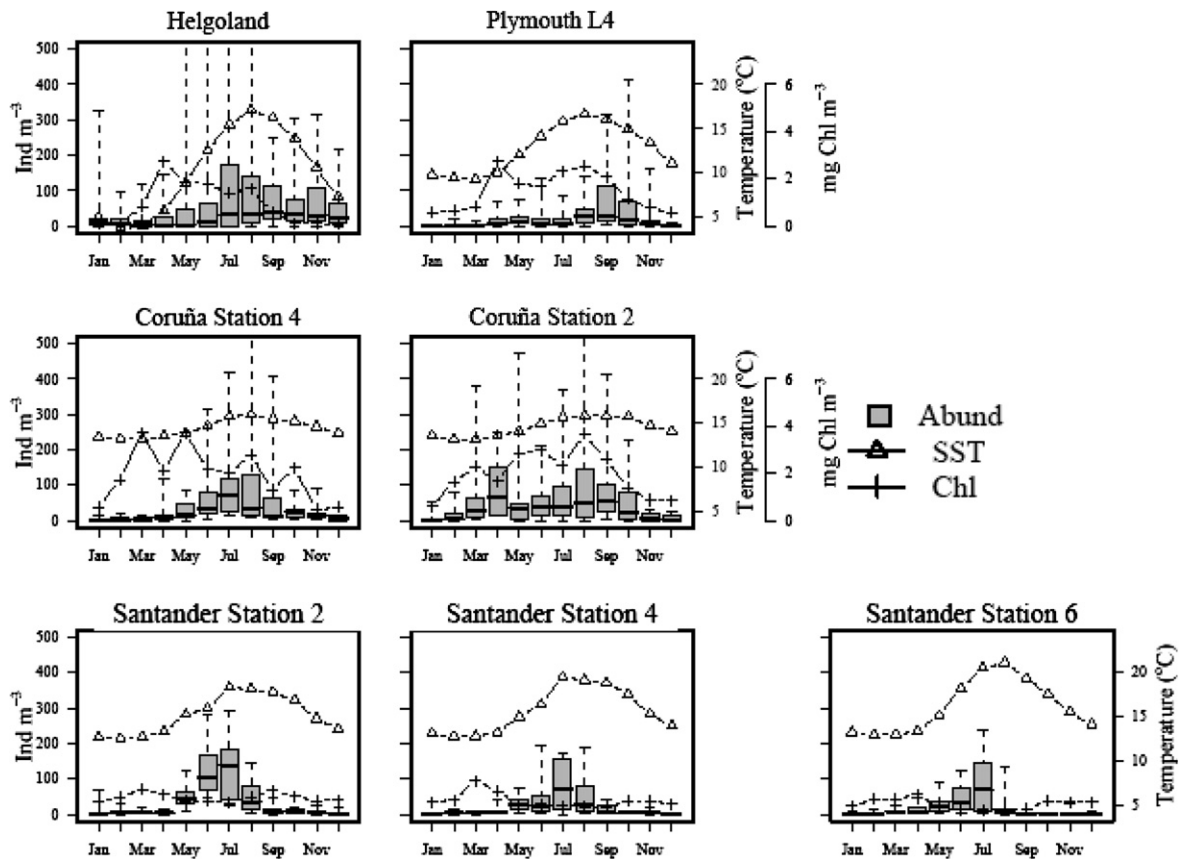|	La Coruña Station 4	La Coruña Station 2	Santander St2	Santander St4	Santander St6	L4	Helgoland
Centropages typicus	1.6% (9)	2.71% (9)	2.70% (6)	2.52% (9)	3.27% (6)	3.58% (5)	0.16% (7)
Centropages chierchiae	0.77% (13)	2.12% (13)	3.20% (7)	1.99% (11)	0.74% (12)	–	–
Centropages hamatus	0.2% (22)	0.02% (48)	–	–	–	–	0.17% (6)

Fig. 2. *Centropages typicus* – Seasonal cycles of *C. typicus* abundance, temperature and chlorophyll *a* throughout the time series (Helgoland Roads, Station L4, Santander and La Coruña). The central box show the data between the "hinges" (the first and third quartile) with the median represented as a line. The whiskers extend to the most extreme data point (maximum and minimum values).

become more regular in the last decade (Halsband-Lenk et al., 2004) with increased abundance at Helgoland Roads, although no population of *C. typicus* is permanent in that vicinity (Hirche, personal communication), indicating that it is always advected into the German Bight as hypothesized by Krause et al. (1995). Whether this increase is exceptional, induced by a singular inflow event (Edwards et al., 1999), or a long-term trend (Lindley and Batten, 2002), remains to be determined.

Maximum abundances of *C. hamatus* are usually found, before the *C. typicus* abundance peak, between May and August (Fig. 3; Halsband-Lenk et al., 2004) *Centropages hamatus* disappears from the water column in winter while *C. typicus* is usually found until January. At Helgoland Roads, no overwintering *C. hamatus* are found in the water column. In the Kattegat (Kiørboe and Nielsen, 1994), *C. hamatus* is recorded year round while it is observed from May to November in the southernwest English Channel (Le Ruyet-Person et al., 1975). A population seems to persist in specific areas of the North Sea during winter (Rae and Rees, 1947). Resting eggs of *C. hamatus* have been identified in the Southern North Sea (Lindley, 1986, 1990), and it is generally assumed that such resting eggs initiate a first generation which hatches and then develops to adulthood during March, when the first females are recorded in the plankton.

Based on abundance and length measurements, Halsband-Lenk et al. (2004) suggest that five generations of *C. typicus* and 3–4 of *C. hamatus* occur during the year at Helgoland Roads. However, it is important to note that abundance and length frequency data from Helgoland Roads were scarce and thus the number of generations could not be estimated properly.

At L4, the seasonal cycle of *C. typicus* shows two peaks of abundance during the year (Fig. 2). The species appears first in April–May in low abundances and then reaches high abundances in August. This is consistent with Digby's (1950) study on the biology of this species at the same station off Plymouth in 1947. Specific dis-
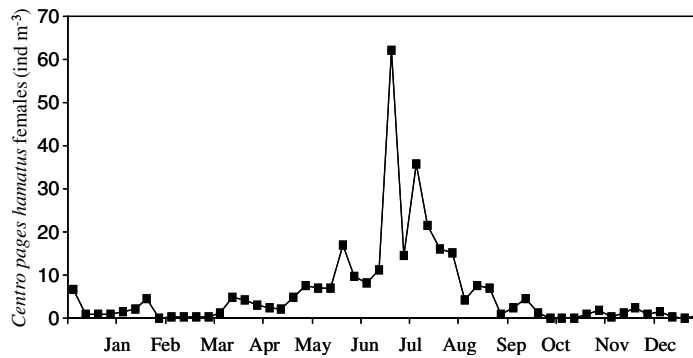
Fig. 3. *Centropages hamatus* seasonal abundance at Helgoland Roads.

tinction between *C. typicus* and *C. hamatus* was not made in Digby's study because of the numerical dominance of *C. typicus* in the samples. Subsequent work at L4 indicates that the inshore species *C. hamatus* is rarely observed at this station (Dave Conway, personal communication). A late summer, early autumn abundance maximum is also observed in the western North Atlantic off the US coast (see Durbin and Kane, this volume).

Le Ruyet-Person et al. (1975) suggest five generations of *C. hamatus* off Roscoff based on the abundance of developmental stages and length measurements. The 1st generation (largest females) grows up from March to April. The 2nd generation is observed in May and June, the 3rd one in June and July and the 4th from mid August to early September. The last generation finally remains present with a few specimens until February.

McLaren (1978) found eight generations of *C. hamatus* in Loch Striven off the west coast of Scotland. His conclusions are based on extensive data on specific stages and size measurements of the population; he considered that only copepodites should be used to trace synchronous cohorts from relative abundance of stages, and that only the long-lived adults correctly indicate new generations from size changes.

The seasonal cycles of *C. chierchiae* are very similar to those of *C. typicus* in the English Channel and Celtic Sea (Lindley and Daykin, 2005). These authors suggest that since the late 1990s, *C. chierchiae* has developed a resident population in the Celtic Sea and the English Channel. Furthermore, it persists in the plankton during low temperature periods, suggesting that it does not produce diapause eggs (Lindley and Daykin, 2005).

Off La Coruña (Fig. 2), the duration of the period of *C. typicus* abundance at the coastal Station 2, from May to October is shorter than at Station 4 in shallow waters, where *C. typicus* is present throughout the whole year. At Station 2, *C. typicus* shows two peaks of maximum abundance in April and August (Fig. 2). This pattern has recurred since 1992, the beginning of the monitoring. Seasonal variations in temperature are not important at this station (between 13 and 16.5 °C), and therefore not likely to be the precursor of abundance increase. The maximum abundance of *C. typicus* at Station 2 is observed in April, just after the March phytoplankton bloom, while the second peak of abundance occurs simultaneously with the maximum of Chl*a* at this station (Fig. 2). The observations at the coastal Station 2 contrast with the seasonal cycle at station 4 in shallow waters. At Station 2, there is only one peak of abundance during the year; *C. typicus* maximum abundance occurs in August and coincides with the highest temperature and a bloom of phytoplankton. For the Santander stations, *C. typicus* abundance shows a single seasonal peak (Fig. 2). Maximum abundance decreases with distance from the coast and occurs in July at Stations 4 and 6, while at the closest station to the coast (Station 2), high abundances develop in June and July.

In the Bay of Biscay and Iberian coastal waters, *C. chierchiae* is found all the year round (Fig. 4). Abundance increases with increasing distance from the coast. Off Santander, maximum abundance occurs in June, while at La Coruña highest abundances are observed in July at Station 4 and August at Station 2. In general, *C. chierchiae* is less abundant than *C. typicus*, but at Santander Station 2, abundances of both congeners can be rather similar in June (around 160 ind m^{-3}). Alvarez Marques (1983) studied the seasonal dynamics of *Centropages typicus* and *C. chierchiae* in the Southern Bay of Biscay and also found higher abundances from spring to autumn. She estimated a total of six generations for *C. typicus* from length frequency distributions, although she suggested that there appears to be continuous reproduction with peaks instead of distinct generations.
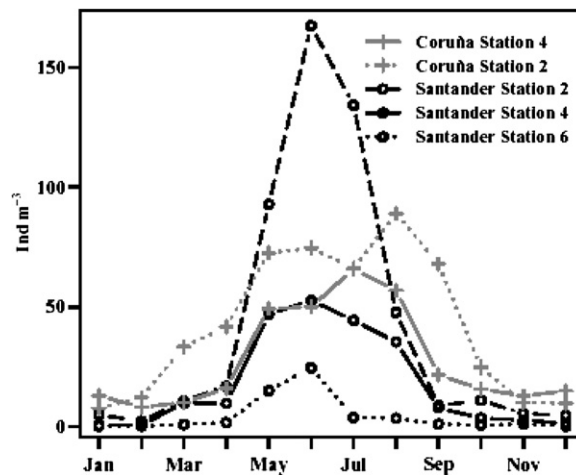
Fig. 4. *Centropages chierchiae* seasonal cycle in the Southern Bay of Biscay.

4. Thermal niches

Fig. 5 presents a synthesis of the abundance of each *Centropages* species at the seven stations in relation to temperature and chlorophyll. *Centropages typicus* is present over a wide range of temperatures, ranging from 1 to 24 °C. Between, 1 and 10 °C, *C. typicus* abundance is low; it increases between 11 and 17–18 °C where it reaches its maximum average abundance and then decreases at temperatures above 18 °C. *C. chierchiae* is absent or only present in very low abundance at temperatures below 13 °C. Its abundance increases for temperatures between 13 °C and 20 °C and then decreases above 20 °C. Maximum average abundances are observed at 18 °C for both *C. typicus* and *C. chierchiae* (Fig. 5). *Centropages hamatus* is mainly abundant at temperatures below 12 °C, with a maximum average abundance at 7–8 °C.

The thermal niche of *Centropages typicus* was estimated from CPR samples collected in the North Atlantic (Boxes B1, B2, B4, C1, C2, C3, C4, D1, D2, D3, D4, E4, F4; $n = 190{,}470$; for details see http://www.sahfos.ac.uk/) (Fig. 6). Sea surface temperature from the HadISST dataset (Hadley Centre, UK Met Office version 1.1) was assigned to each CPR sample based on its latitude, longitude, month and year. For each 1 °C temperature bin, the mean abundance of *Centropages typicus* was calculated. For comparison, the thermal niches for *C. hamatus* and *C. chierchiae* were also calculated (Fig. 6).

The compilation of results from coastal monitoring stations is in good agreement with the CPR data for both *C. typicus* and *C. chierchiae* (Fig. 5). However, the CPR data show that *C. hamatus* has a second peak of maximum abundance around 15 °C which was not detected with data from the monitoring coastal stations. This may be due to the fact that *Centropages* spp. thermal niche was determined from several CPR boxes covering the whole North Sea while our coastal monitoring station in Helgoland Roads is located in the Southern North Sea. As suggested by our results and several other studies (e.g. Grant, 1988; Halsband-Lenk et al., 2004), *C. hamatus* is a cold water species while *C. typicus* shows a wide tolerance for temperature.

Centropages typicus and *C. chierchiae* occur over a wide range of Chl*a* concentrations (0.5–9.5 mg m^{-3}) but mainly below 6 mg m^{-3}, whereas high abundances of *C. hamatus* are observed for Chl*a* concentrations above 6 mg m^{-3} (Fig. 5).

5. Long-term changes of *Centropages typicus*

The seasonal and inter-annual variability of *C. typicus* abundance at the stations off Helgoland, Plymouth, La Coruňa and Santander is illustrated in Fig. 7.

At Helgoland Roads, there is an important interannual variability, both in terms of seasonality and abundance. *Centropages typicus* peaks of abundance were observed between April and August from 1984 to 1990, while in 2000 and 2001 the maximum abundance occurred later in the year, from July to October. Based on the
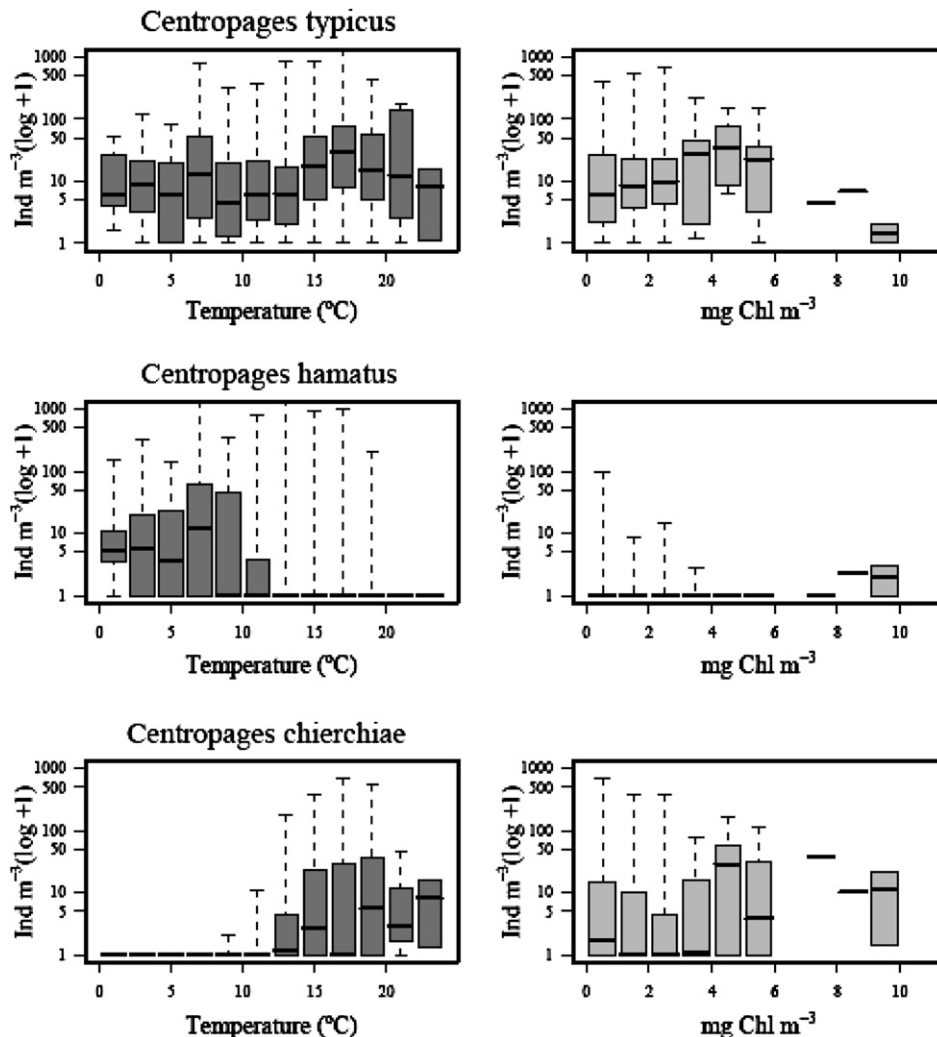
Fig. 5. Abundance of *C. typicus*, *C. hamatus* and *C. chierchiae* related to temperature and chlorophyll for all the time-series stations combined. The central box shows the data between the "hinges" (the first and third quartile) with the median represented as a line. The whiskers extend to the most extreme data point (maximum and minimum values).

CPR data, Fransz et al. (1991) similarly observed that *C. typicus* occurred from July to November, but that this pattern differed in 1975, 1984–1990 and 1993. This variability in the timing of appearance of *C. typicus* is not due to temperature, as the pattern of temperature seasonal cycle is quite constant throughout the Helgoland Roads time series. However, when looking in detail at the phytoplankton seasonal cycle and more specifically at diatom abundance for the targeted periods, changes in timing and intensity of diatom blooms are very important. For example, from 1984 to 1990 and in 1993, the diatom concentration started to increase in March, reached a maximum between April and June and then decreased until September before disappearing totally in winter. For these years, *C. typicus* abundance is very well correlated with the timing of the diatom bloom. In contrast, in 1975 and in 2000–2001, two peaks of diatoms were observed. The first peak occurred between March and June and the second between July and October with low diatom concentrations observed between the two blooms. During these periods, *C. typicus* maximum abundance occurred later in the year, between July and October, simultaneously with the second diatom bloom. We can therefore suggest that together with inflow events of Atlantic water, diatom concentration, and probably species composition, control the timing of appearance of *C. typicus* at Helgoland Roads.
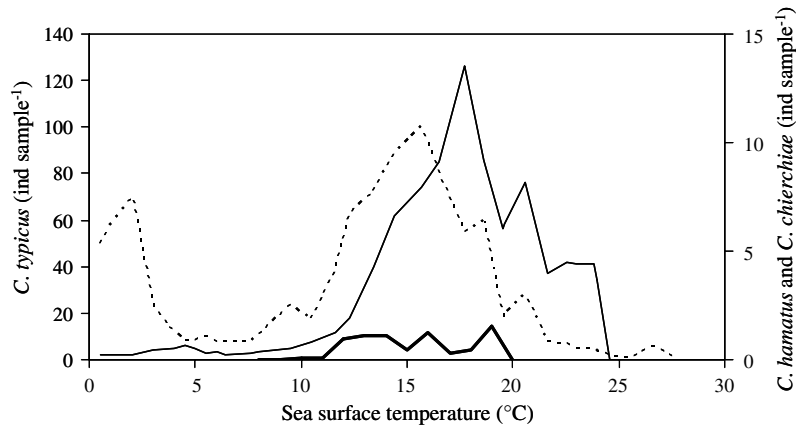
Fig. 6. Mean abundance of *Centropages typicus* (plain line), *C. hamatus* (dotted line) and *C. chierchiae* (bold line) species for CPR samples from the North Sea, English Channel and Bay of Biscay in relation to temperature.
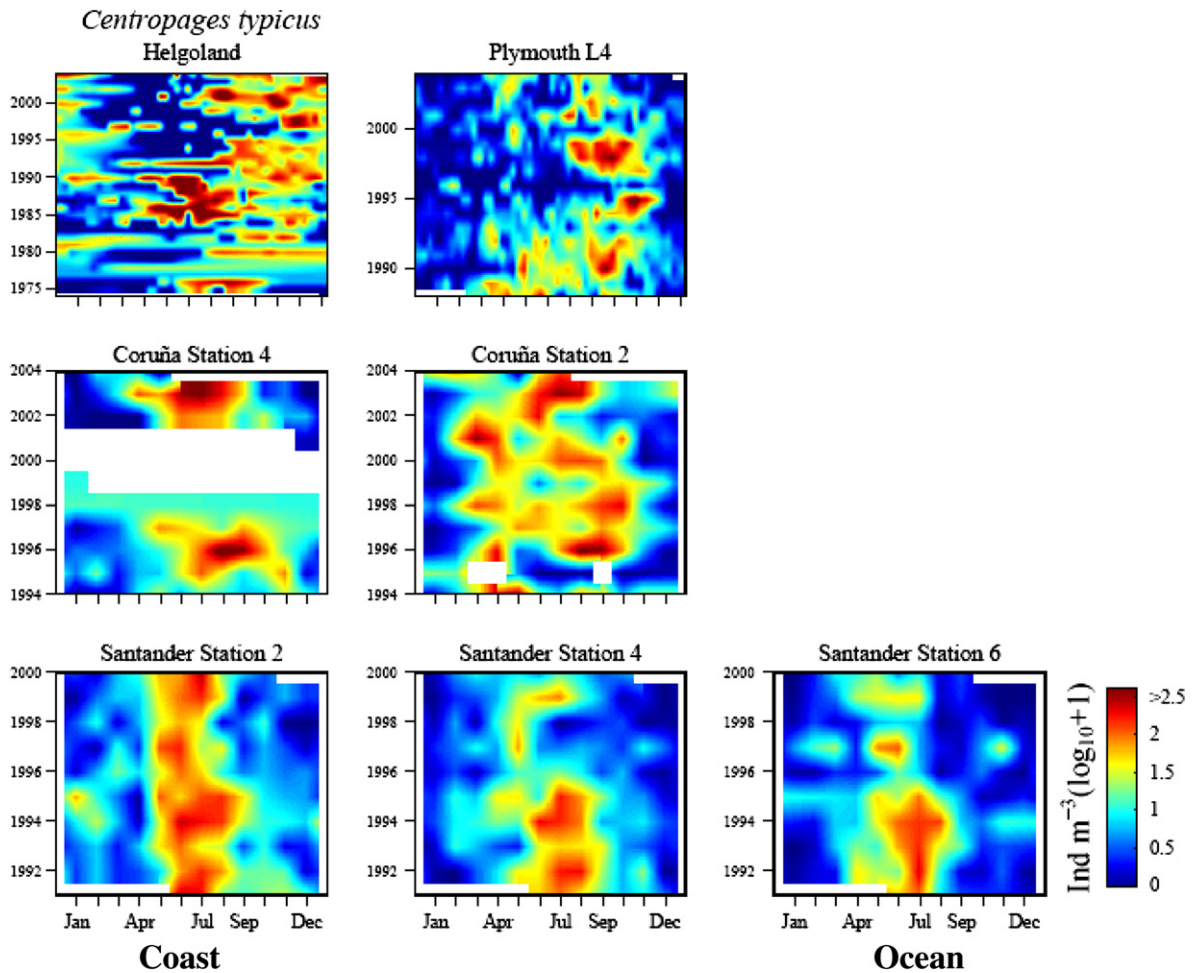

Fig. 7. *Centropages typicus* – long-term series of abundance estimates in the English Channel (Station L4), North Sea (Helgoland Roads), Bay of Biscay (La Coruña and Santander). For Helgoland, the abundance of *C. typicus* was estimated by multiplying the total *Centropages* spp. by species ratio obtained from female (*C. hamatus*/*C.typicus*) counts.

At L4, *C. typicus* abundance was higher during the period 1988 to 1995 with lower abundances from 1996 to 2002. The yearly average abundance was highest in 1995 (annual mean density 53.89 ind m^{-3}) and decreased dramatically in 1996 (annual mean density 3.51 ind m^{-3}). Subsequently abundances have increased gradually though they are still not comparable to those at the beginning of the time-series. These changes in abundance are not correlated with changes in temperature or Chl*a*. These variations may be due to recruitment and predation. Apart from these features there is no clear evidence of a longer-term trend in the L4 time-series. The seasonal pattern is rather heterogeneous and reflects the autumn abundance maximum at this station.

Off La Coruña, there is some indication, at Station 4, of a decrease in summertime abundance in 1998. However, a subsequent break in the time-series data set does not confirm this possible trend. The original (1994–1993) level of abundance has resumed in 2002 with even higher numbers observed in 2003. La Coruña, Station 2 shows two seasonal peaks of abundance with high inter-annual variability. *Centropages typicus* seasonal pattern is very different at the two stations (Figs. 2 and 7), while the temperature seasonal cycles are similar. Therefore, variations intensity of *C. typicus* maximum abundances could be due to timing, which differs between the stations (Fig. 2), and/or composition of the phytoplankton blooms. The Santander offshore Stations 4 and 6 show a striking decrease in summertime abundance after 1995, whereas Station 2 shows a consistent pattern of abundance, peaking in June and July throughout the time series (see Figs. 2 and 7).

Mazzocchi et al. (this volume) in their review of *C. typicus* in the Mediterranean Sea also demonstrated that the seasonal cycle varies interannually, both in abundance and seasonal timing.

6. Reproduction

At Helgoland, *C. typicus* mainly spawns in summer and autumn, before females disappear from the water column in winter (Halsband-Lenk et al., 2004). 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; temperature ranging from 20.5 to 14 °C). Maximal reproduction occurs in late summer and beginning of the autumn as in the Kattegat (Kiørbœ and Nielsen, 1994). *Centropages typicus* thus seems to be an exception from the general pattern of other calanoid species in the same area, which usually achieve maximal reproduction rates earlier, at lower temperatures (Halsband and Hirche, 2001). An inverse temperature–size relationship was observed for *C. typicus*, with individuals in spring being largest and the smallest specimens being observed in late summer (Halsband-Lenk et al., 2004). Not all females examined were reproducing, and the monthly mean percentage of spawning females can vary between 10% and 80%.

At L4, *C. typicus* egg production was monitored during 1992 and 2005 (Fig. 8). A first peak of egg production occurs in April followed by a longer period of production from May to September. Maximum egg production was at the end of May-beginning of June for both years (151 eggs female^{-1} d^{-1}at 15 °C, and 118 eggs female^{-1} d^{-1} at 16.4 °C in 1992 and 2005, respectively). Overall, egg production rates were much higher than those observed in the North Sea. Mean egg production over the productive period (April–September) was around 84.6 eggs female^{-1} d^{-1} when temperature averaged 13.6 °C in 1992 and was 62.5 eggs female^{-1} d^{-1} at a 15.2 °C average in 2005.

An optimal reproductive thermal response of 20 °C has been determined in the laboratory for *C. typicus* both in the North Sea and in the Mediterranean (Halsband-Lenk et al., 2002) (Fig. 9A). In contrast, *C. hamatus* egg production is optimal over a wide range of temperatures above 10 °C (Fig. 9B). While the optimal temperature (20 °C) for *C. typicus* maximal reproductive response is rarely reached in the North Sea or in the English Channel, egg production rates are generally higher (e.g. Peterson et al., 1991; Kiørbœ and Nielsen, 1994; Halsband-Lenk et al., 2004) than in the Mediterranean Sea (e.g. Ianora and Buttino, 1990; Razouls, 1982). Indeed, egg production is also dependent on the food availability and quality in the environment.

Information on secondary production in the Bay of Biscay is scarce (e.g. López-Jamar et al., 1991; Poulet et al., 1996). Ruiz and Motos (2000) suggested that the zooplankton of the region is generally food limited and therefore that growth and egg production are never optimal. Bonnet (2001) found that *C. typicus* egg production in the Bay of Biscay showed a wide range of values in May 2000 and 2001 during the post bloom period. In 2000, very low egg production was observed (1–5 eggs female^{-1} d^{-1}) while in 2001, it increased from 20 to 85 eggs female^{-1} d^{-1}. For both years, egg production was not correlated with Chl*a*, temperature, nor size of the females.
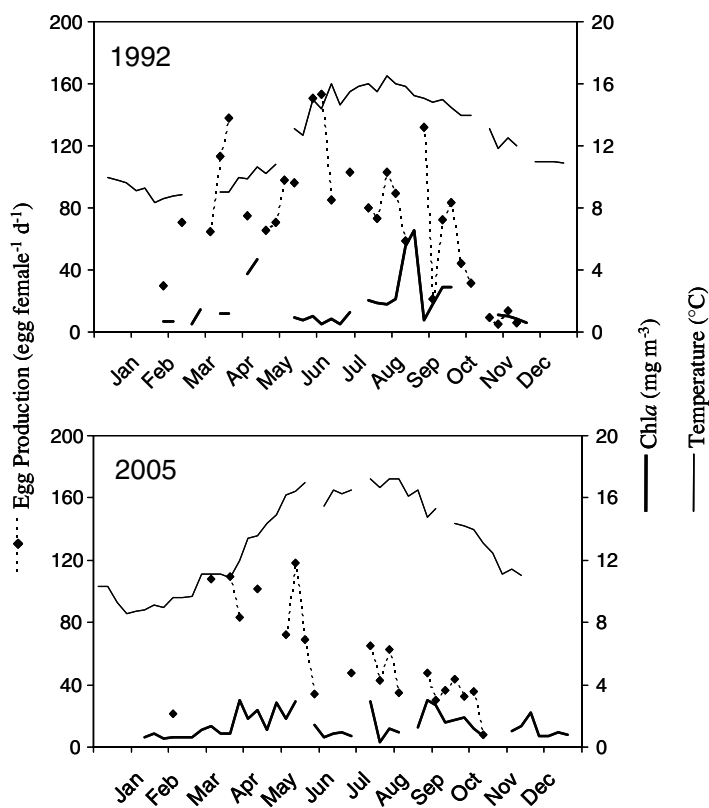
Fig. 8. *Centropages typicus* – egg production, Chl*a* and temperature at Station L4 in 1992 and 2005.
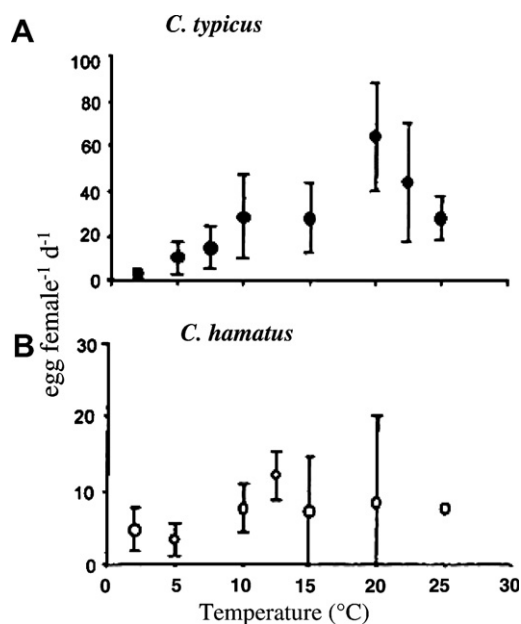

Fig. 9. Optimal reproductive thermal responses for *C. typicus* (A) and *C. hamatus* (B) from Helgoland Roads (from Halsband-Lenk et al., 2002).
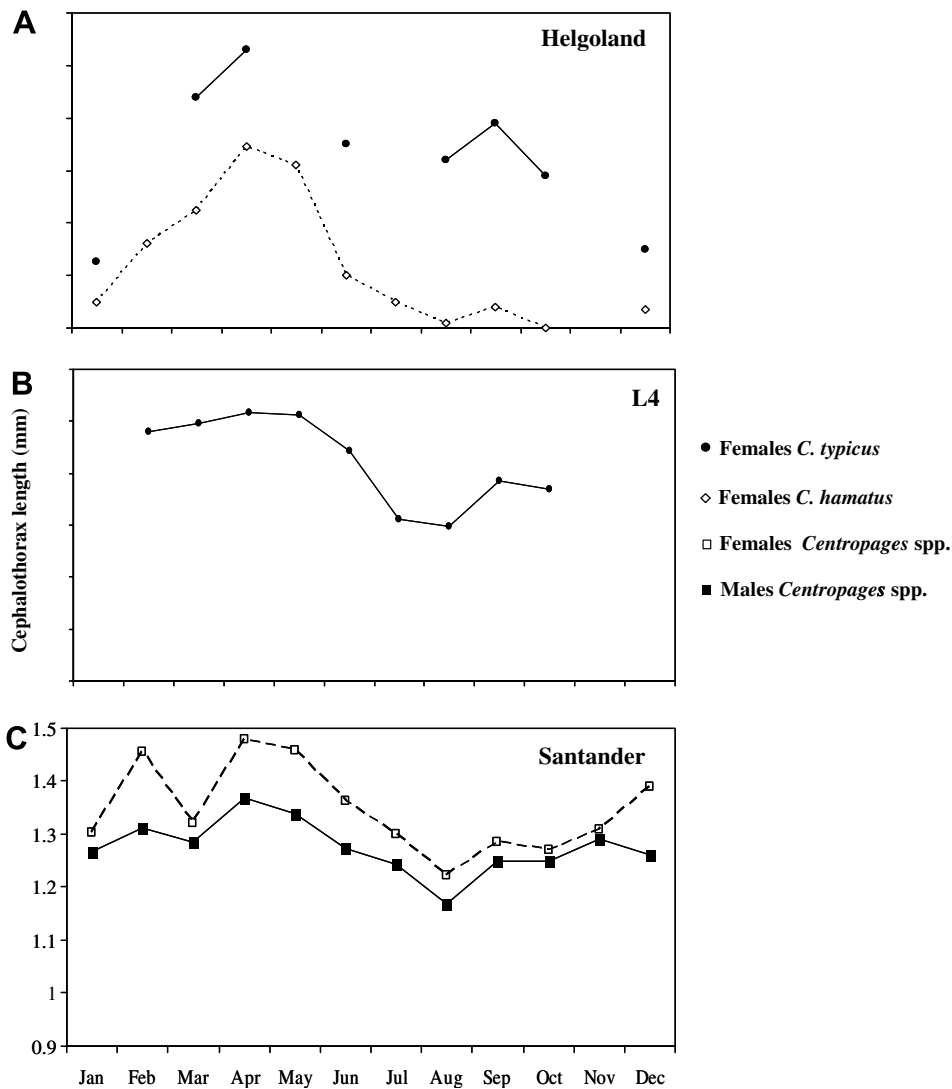
Fig. 10. Cephalothorax length (mm) of *Centropages* at (A) Helgoland Roads (adapted from Halsband-Lenk et al., 2004), (B) Station L4, and (C) Santander.

7. Resting eggs

In the North Sea, *C. typicus* disappeared from the water column in winter, but production of resting eggs or retention areas, are still unclear. Lindley (1986, 1990) reported resting eggs for *C. typicus*, but these have not been observed by other authors (e.g. Marcus, 1989, 1996; Smith and Lane, 1987). He observed a few nauplii emerging from sediment samples from the English Channel and southern North Sea. Such eggs found along the British coast (Lindley, 1986, 1990) may be quiescent rather than true diapause eggs, persisting during unfavourable conditions. However, they seem to play a minor role for *C. typicus*. Later studies in the New York Bight (Smith and Lane, 1987) and around Helgoland (Engel and Hirche, 2004) could not verify the production of resting eggs, and Durbin and Kane, this volume reviewing the western North Atlantic conclude that there is no clear evidence that *C. typicus* produces resting eggs.

In contrast, the congener *C. hamatus* is known to produce true diapause eggs which follow a genetic protocol and require a defined refractory phase before hatching can take place. Resting eggs in *C. hamatus* can be very abundant and they occur throughout the geographic range of the species (Engel, 2005). They have been

reported from the White Sea (Pertzova, 1974), the Gulf of Mexico (Chen and Marcus, 1997; Marcus, 1989), the Baltic Sea (Madhupratap et al., 1996), marine aquaculture enclosures in Norway (Naess, 1996), the Irish Sea (Lindley, 1990) and many areas of the North Sea, including the German Bight (Engel and Hirche, 2004), the southern North Sea and the English Channel (Lindley, 1990). *Centropages hamatus* nauplii equivalent to approximately 300,000 specimens per square metre of seafloor hatched from sediment samples collected in the North Sea (Engel and Hirche, 2004; Lindley, 1990), but maximum densities are probably even higher (Engel and Hirche, 2004).

Around Helgoland, resting eggs of *C. hamatus* were second in abundance among those of all copepod species (Engel and Hirche, 2004). In the German Bight *C. hamatus* adults are absent from the plankton from December to February (Halsband-Lenk et al., 2004) and thus resting eggs have been suggested to ensure the perpetuation of the species during the winter. This assumption is supported by the longevity of these eggs, >1 year (Lindley, 1990; Engel and Hirche, 2004), as well as their high abundance and impact on recruitment (Engel, 2005). Many nauplii hatched in spring, but there is also a large peak of emergence in fall.

Marcus (1996) and Lindley and Daykin (2005) did not observe any production of resting eggs in *Centropages chierchiae*.

The factors triggering the production and hatching of resting eggs of *Centropages* spp. and other small copepod species still remain largely unknown (Castellani and Lucas, 2003; Marcus, 1996), and more studies are required to get a better understanding of this process.

8. Seasonal changes in prosome length

Body size of *C. typicus* was relatively consistent through the seasonal cycle over several years (1995–2000) at Helgoland Roads (Fig. 10). Individual female lengths ranged from 1020 to 1434 μm. Females are largest in early April and smallest in December and January. Prosome length of *C. hamatus* varies from the minimum of 900 μm recorded in October to a maximum of 1300 μm observed in April at the same station. Significant relationships between temperature, clutch size, egg production rate and prosome length were found for *C. hamatus*, but not for *C. typicus* (Halsband and Hirche, 2001).

Prosome length measurements of *C. typicus* females at station L4 range from 1420 μm in April to 1190 μm in August. It is thought that, as in Helgoland, even smaller individuals occur during the winter, but no measurements are available for this period as the individuals are scarce in the field.

At Santander, *C. typicus* and *C. chierchiae* were not differentiated, while males and females were distinguished when measured. As expected, females were always bigger than males. Maximum size (1480 μm) was observed in April and the minimum size in August (1220 μm). However, the size range is narrower than for the northern stations. Although *C. chierchiae* is not very abundant in this area (Table 1), it is much bigger than *C. typicus* (Table 2) and its inclusion may have influenced the values of the upper end of the size measurements.

Body size–egg production relationships have been previously observed in *C. typicus* by Smith and Lane (1985). They found maximum egg production in May and then a reduction in body size until July, corresponding with a decrease in the numbers of eggs produced. Razouls and Guinness (1973) and Le Ruyet-Person et al. (1975) off Roscoff also observed that *C. typicus* cephalothorax length inversely correlated with temperature. Indeed, size is usually directly correlated with development time, and temperature has a major influence on *C. typicus* development time (from 49 to 16 days) at 10 and 20 °C respectively; see Carlotti et al. (this volume).

9. Potential impacts of climate change

Changes in abundance of *C. typicus* and *C. chierchiae* have been shown to be correlated with long-term changes in temperature in the North Sea and the Bay of Biscay, respectively (Lindley and Reid, 2002; Lindley and Daykin, 2005). When investigating the changes in the distribution of *C. chierchiae* in the north-eastern Atlantic and western European shelf waters, Lindley and Daykin (2005) showed that its abundance was positively correlated with the strength of the shelf edge current and negatively with the North Atlantic Oscillation. They suggested that *C. typicus* and *C. chierchiae* might be used as key species for monitoring climate changes in the North Sea and the Bay of Biscay, respectively.

Table 2
Comparison of congeneric species of *Centropages* in the North Sea, English Channel and Celtic Sea, and Bay of Biscay (43–60°N)

	Centropages typicus	*Centropages hamatus*	*Centropages chierchiae*
Latitudinal range	6°S–66°N[a,b]	20°S–64°N [b,c]	35°S–53°N[b,d]
Preferred temperature range of occurrence (°C)	10–24[n]	3–12[n]	13–23[n]
Number of generations per year	5[e]–6[f]	3[g] to 8[h]	5?[g]
Main period of abundance			
North Sea	July–November[g]	March–September	–
English Channel	April–October	May–November[i]	Summer[j]
Bay of Biscay	May–October/throughout the year	January–April[m]	April–August
Female prosome size range (μm)	900–1434[g]	750–1570[g]	1800–1900[i]
Maximum egg production (egg female^{-1} d^{-1})	151	96	–
Resting eggs	Yes and no[j,k,l]	Yes[k,l]	No[k,l]

References.
[a] Marques (1966).
[b] CPR survey team (2004).
[c] Carter (1978).
[d] De Decker (1984).
[e] Digby (1950).
[f] Alvarez Marques (1983).
[g] Fransz et al. (1991).
[h] McLaren (1978).
[i] Le Ruyet-Person et al. (1975).
[j] Lindley (1986).
[k] Lindley and Daykin (2005).
[l] Marcus (1996).
[m] Valdes (1993).
[n] This study.

The differences in thermal tolerance and optimal temperatures for maximum abundance among the congeners of *Centropages* spp. explain their distributions and seasonality in European waters (Halsband-Lenk et al., 2002). With climate warming, we can speculate how their spatial distribution is likely to change and whether, as has been suggested by Perry et al. (2004), there may be global synchronies in population dynamics and abundance. Climate warming will affect copepod species assemblages as Beaugrand et al. (2002) noticed in the North Sea. *Centropages typicus* long-term abundance is positively correlated with temperature in the North Sea (Lindley and Reid, 2002), and it has previously been chosen as an indicator of temperate oceanic waters (Beaugrand et al., 2002; Bonnet and Frid, 2004; Fransz et al., 1991). We think that, because of the differences between *Centropages* congeners, *Centropages* spp. are likely to be good indicators of climate change over a wide range of ecosystems.

10. Conclusions

Centropages typicus is widely distributed in Northern European waters, but surprisingly little information is available on its life cycle from published field data. Our goal was to summarise data on *C. typicus* ecology, describe its seasonal dynamics and compare it to two of its congeneric species.

Centropages typicus occurs preferentially between 10 and 24 °C, while *C. hamatus* is mainly found between 3 and 12 °C and *C. cherchiae* between 13 and 23 °C. *Centropages typicus* and *C. chierchiae* occur over a wide range of Chl*a* concentrations, but mainly below 6 mg Chl*a* m^{-3}, while high abundances of *C. hamatus* are observed at Chl*a* concentrations above 6 mg Chl*a* m^{-3}.

Five generations of *C. typicus* are observed in the North Sea and English Channel, while six generations per year have been recorded in the Bay of Biscay. Three to four generations are suggested for *C. hamatus* in the North Sea and eight have been determined on the west coast of Scotland.

Centropages typicus maximum egg production occurs from late spring to the end of the summer and egg production is optimal at temperatures above 15 °C. In contrast, *C. hamatus* egg production is optimal at temperatures above 10 °C.

Long-term series of vital rate measurements are very scarce. However, they are necessary to complement laboratory work, since processes measured in the field are affected by the complex interactions among several environmental parameters. Field data on egg production, hatching success and egg clutch size for targeted species are needed to get better understanding of their population dynamics both at spatial and temporal scales.

Acknowledgements

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