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Hatching phenology of the brown shrimp *Crangon crangon* in the southern North Sea: inter-annual temperature variations and climate change effects

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Crangon crangon is a key species in the southern North Sea and the most valuable target of coastal fisheries. Recruitment and stock development are highly variable. As recruitment is based on larval production, we determined the timing of larval release in relation to the annual temperature course and the winter water temperature. The annual temperature courses over 50 years (1961–2010) showed a strong inter-annual variation but also a continuous increase in winter water temperatures. The share of ovigerous *C. crangon* females starts to increase in October/November, reaches a maximum in May, and decreases continuously towards September/October. During cold winters (0°C), egg development is strongly retarded and hatching of larvae culminates in a sharp peak in early June. Warm winters (6°C) facilitate embryogenesis and the earliest larvae hatch in January and February. The temperature sums from November to April correlated significantly with the lowest winter water temperatures. Consequently, the lowest winter water temperatures provide a good indication for the appearance of *C. crangon* larvae and an estimate for the match or mismatch with the spring bloom and the production of microzooplankton, the preferred food of *C. crangon* larvae.

Keywords: crustacea, embryogenesis, global warming, hatching, larvae, mismatch.

Introduction

The epibenthic brown shrimp, *Crangon crangon*, inhabits the coastal areas of the northeast Atlantic from the Mediterranean to the White Sea, the British islands, and Iceland (Holthuis, 1980; Gunnarsson *et al.*, 2007; Luttikhuizen *et al.*, 2008). It appears at highest abundances in the shallow coastal areas of the North Sea, and particularly off the Wadden Sea, where densities of up to 82 juveniles m⁻² were reported (Boddeke *et al.*, 1986).

The lifespan of *C. crangon* may reach 3 years. After hatching, the larvae pass through five to seven stages and reach the juvenile stage after 30–35 days (at 12°C, Criales and Anger, 1986). At a size of 10–20 mm, the juveniles settle in the tidal flats of the Wadden Sea, leave the nursery grounds in late summer, and reach maturity at the end of the year (Kuipers and Dapper, 1984). The population is dominated by the first year class. *Crangon crangon* are r-strategists (Martínez-Alarcón *et al.*, 2019). Ovigerous females may carry up 3 000–5 000 eggs (Boddeke, 1982).

Due to its abundance and life style, *C. crangon* is a key species in the North Sea ecosystem, strongly influencing the benthic as well as the pelagic realm. It exploits various food sources, and is the major prey of many other crustaceans, fishes, and seabirds. Moreover, *C. crangon* is the most valuable target of coastal fisheries in the North Sea with annual landings exceeding 30000 tons and yielding more than 100 million euros (BLE, 2019; ICES, 2022).

Over the last decades, the North Sea has been subjected to continuously increasing water temperatures of almost 0.03°C per year (Wiltshire and Manly, 2004). The warming trend

resulted in a regime shift in the 1980s (Beaugrand, 2004) with a change to more oceanic conditions and changes in the pelagic and benthic species composition around Helgoland (e.g. Nehring, 1998; Franke and Gutow, 2004; Pehlke and Bartsch, 2008).

So far, *C. crangon* seems not to be negatively affected by the warming of the North Sea. The adults show extraordinary physiological properties, such as high tolerance against changes of water temperature and salinity. They are opportunistic feeders, and are extremely fertile with multiple spawning during the extended reproductive period (Ehrenbaum, 1890; Havinga, 1938; Plagmann, 1939; Reiser *et al.*, 2014; Hünerlage *et al.*, 2019). However, the early life stages are more vulnerable to environmental changes than the adults. As ectotherms, metabolic rates and other physiological processes are determined by ambient water temperature. Accordingly, the time of maturation of eggs and larvae also depends on the water temperature. As embryogenesis is strongly retarded at low temperatures, the water temperatures in winter and spring primarily determine the development time of eggs and, thus, the phenology of hatching. The colder the winter, the later in the year the larvae hatch and settle in the Wadden Sea areas (Wear, 1974). The peak of hatching can appear at quite different months (Siegel *et al.*, 2005).

Freshly hatched *Crangon* larvae possess no substantial energy reserves (Paschke *et al.*, 2004). Thus, immediate feeding is essential for survival. The larvae preferentially feed on microzooplankton, which emerge in sequence with the spring phytoplankton bloom (Criales and Anger, 1986). In contrast to the embryogenesis of *C. crangon*, the spring phytoplankton

bloom is presumably triggered by the photoperiod. The onset of the bloom in the North Sea, and, hence, the food supply of *Crangon* larvae, is considerably stable and less dependent on climate variation (Wiltshire *et al.*, 2008, 2015). This case raises the question to what extent changes in the winter water temperature may lead to a mismatch of *Crangon* hatching and the appearance of food, which is crucial for the survival and development of the larvae.

This study aimed to simulate the temperature-dependent embryogenesis of *C. crangon*, to reveal the inter-annual variation of peak larval production, and to assess climate-induced implications with regard to hatching phenology. Therefore, we analysed the water temperature in the southern North Sea over five decades from 1961 to 2010 and identified both the range of inter-annual variation and the long-term trend. Based on these results, we simulated the course of embryogenesis for annual cycles with average, extreme low, and extreme high temperatures. Moreover, we recalculated the appearance of larvae for every year of the period investigated. This study contributes to a more precise prediction of inter-annual variation of larval production and, ultimately, an estimation of *C. crangon* recruitment at present and in future warming scenarios.

Material and methods

Data processing of *in-situ* seawater temperatures

Time-series data of surface seawater temperature were provided by the Federal Maritime and Hydrographic Agency (Bundesanstalt für Seeschifffahrt und Hydrographie, Hamburg, Germany). The temperatures were measured every working day during routine plankton sampling at Helgoland Roads (North Sea, 54°11.30N 7°54.00E). The present investigation uses data from 1961 to 2010. Missing data due to weekends, holidays, bad weather, or technical failures were extrapolated to obtain a continuous data set on a daily basis.

Helgoland Roads as well as the majority of the German Bight are shallow (<30 m) and do not develop a distinct and continuous water stratification due to strong tidal and residual currents and winds (Becker *et al.*, 1992; R. Saborowski, pers. obs.). Therefore, the water temperature measured at the surface represents the mixed water temperature at this location. In order to avoid overestimation of exceptional values, annual minimum and maximum temperatures were identified by calculating moving averages across 7 days within the coldest and warmest periods. The resulting lowest or highest average value were defined as annual minimum and maximum, respectively.

The coldest day, the days with temperatures below 4°C, and the number of days below 4°C were extracted from the data set and used for regression analysis. Temperature sums (ΣT) were calculated on a daily basis (°C d) for the winter period (1 November–30 April) and for entire annual cycles (1 November–31 October).

Simulated annual seawater temperature cycles

Sinusoidal temperature cycles were calculated for scenarios of changing winter water temperatures and constant summer water temperatures (0–18, 3–18, and 6–18°C) as well as synchronous increase of both winter and summer temperatures (2–20, 4–22, and 6–24°C). The sine function was phase-shifted by 140 days to schedule the annual minimum
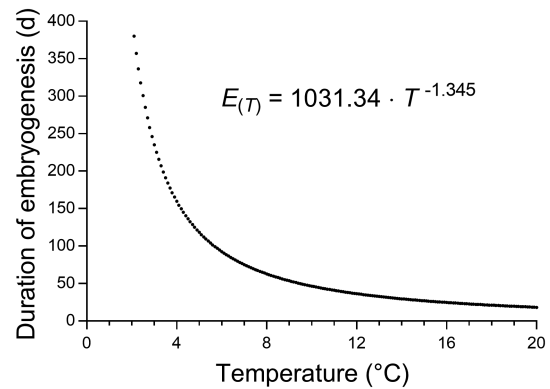

Figure 1. Relationship between seawater temperature (*T*) and the duration of embryogenesis ($E_{(T)}$) in days (d) of *C. crangon* following the negative exponential equation.

temperature on 18 February and the maximum on 19 August.

$$T_{(d)} = [1 + \sin\left((d - 140) \cdot \left(\frac{2\pi}{365}\right)\right)] \cdot \left(\frac{S}{2}\right) + o,$$

with $T_{(d)}$ = temperature of a specific day in °C, d = day of the year (1–365), S = span between lowest and highest temperatures (e.g. 0–18°C), and o = offset of temperature from zero in °C.

Appearance and frequency of ovigerous females

Data on the seasonal appearance and frequency of ovigerous females were extracted from Siegel *et al.* (2008). These data are based on long-term observations in the German Bight from 1958 to 1992.

Temperature and embryogenesis

Few controlled laboratory experiments on the duration of embryogenesis of *C. crangon* at different temperatures have been reported (e.g. Havinga, 1938; Tiews, 1970; Meixner, 1969; Wear, 1974). We used a combined function introduced by Redant (1978) and applied by Temming and Damm (2002), in which the duration of embryogenesis follows a negative exponential function: At 18°C, which is about the average maximum temperature in summer, embryogenesis will be accomplished within 21 days; at 8°C, it will last for 63 days, and below 4°C, embryogenesis will exceed 160 days (Figure 1).

Simulation of embryogenesis and appearance of larvae

We calculated the development time of eggs, which were hypothetically spawned at regular intervals of ~1 week throughout the reproductive cycle. The start dates were set on days 1, 8, 15, and 23 of each month. The progress of development was calculated for every successive day with regard to the development function of *C. crangon* eggs and the respective temperature calculated from the model sine functions or the *in-situ* temperatures. Egg development was completed and larvae hatched when the sum of the daily fractions reached the value of 1:

$$f_{(i)} = \sum_{i=1}^{i=N} \left(\frac{1}{D}\right)_i$$

with D = duration of embryogenesis in days, N = $\max_{(i)}$, and $\max_{(i)}$ calculated from the first i-value corresponding to $f_{(i)} \geq 1$.

To calculate the relative abundance of larvae at the hatching day, the frequency of ovigerous females at the respective spawning day of the eggs was ascribed to the hatch day. The hatches were combined on a weekly basis according to the scaling of the spawning intervals. The frequency distribution was smoothed by a moving average over 3 weeks. A second spawning event was simulated in the same way, assuming that the new clutch of eggs was laid shortly after the larvae of the previous eggs had hatched.

The seasonal cycle of embryogenesis was simulated for different temperature scenarios. Simulation 1 investigated the sole increase of minimum winter seawater temperatures but constant maximum summer temperature (0–18, 3–18, and 6–18°C; Figure 2a). Simulation 2 addressed the simultaneous increase of both winter and summer temperatures (2–20, 4–22, and 6–24°C; Figure 2b). For comparison to actual past conditions, simulations were additionally calculated for the annual temperature cycle of 1962/1963 with an exceptionally cold winter (minimum water temperature of −1.2°C), 1985/1986 with average temperatures, and 2007/2008 with an exceptionally warm winter (minimum water temperature of +5.9°C) (Figure 2c).

The appearance of stage I larvae was calculated for every year between 1961 and 2010 on the basis of the real *in-situ* seawater temperatures at Helgoland Roads. The results were presented as heat maps with 4 intervals per month and 48 intervals per year. The interval with the highest value within each year was set at 100% and all other values were calculated in relation to this annual maximum.

Results

In-situ seawater temperatures

The minimum winter water temperatures at Helgoland Roads ranged from −1.2°C (1963) to 5.9°C (2007) and the maximum summer water temperature from 15.9°C (1962) to 19.6°C (1995). Both the minimum winter temperatures (Figure 3a) and the maximum summer temperatures (data not shown) increased significantly during the analysed period from 1961 to 2010.

The temperature sums of the winter period (November–April) ranged from 646°C·d in 1962/1963 to 1541°C·d in 2006/2007. The temperature sums increased significantly from 1960/1961 to 2009/2010 (Figure 3b). The temperature sums were closely correlated with the lowest annual water temperature (Figure 3c, $r^2 = 0.88$, $n = 50$). The temperature sums of the winter period (November–April) as well as the temperature sums of the entire annual cycle (November–October) increased significantly during the period investigated.

The variability of the winter water minimum between subsequent years accounted on average for 1.46 ± 1.04°C and showed a maximum change of −3.8°C between 1995 and 1996 (Figure 4a). This corresponded with a decrease of degree days from 1267 to 848°C·d (−33%, Figure 3b).

The lowest winter temperature appeared earliest on 20 December in the season 1973/1974 and latest on 25 March in 1968/1969 (Figure 4b). On average, the lowest winter temperatures appeared on 21/22 February ± 20 days (1 February–14 March). The appearance of the lowest temperature did not change significantly during the studied period ($y = -0.2055 x + 458.8$, $r^2 = 0.022$, $p = 0.307$).
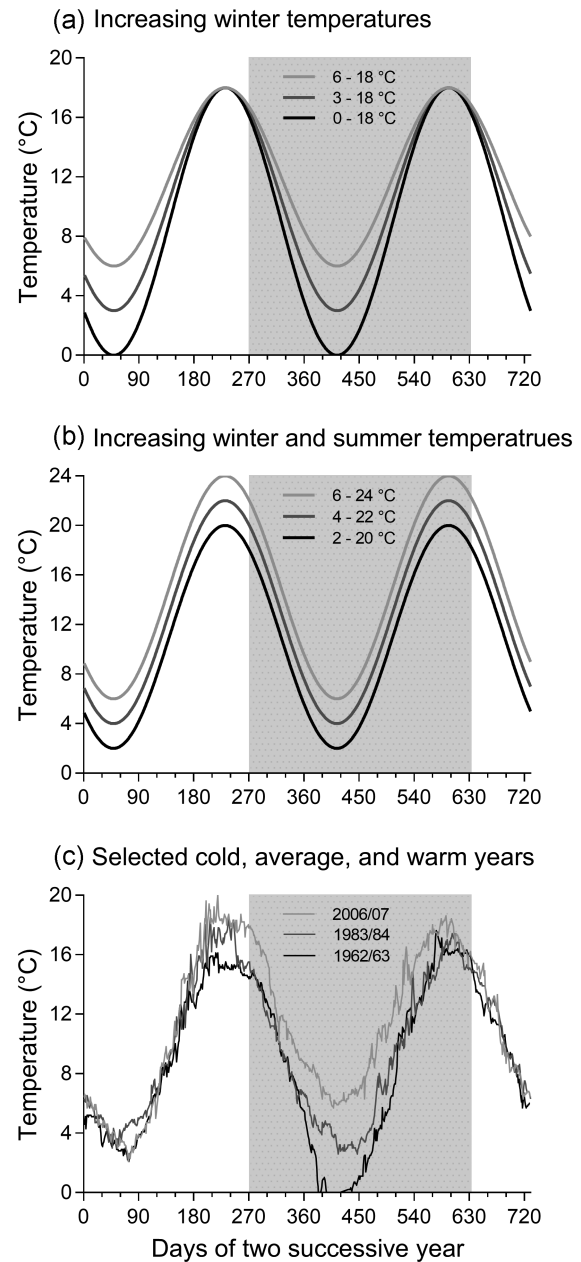

Figure 2. Seasonal cycle of seawater temperature at Helgoland Roads assuming two different scenarios: (a) increase of minimum winter seawater temperatures (0, 3, and 6°C) but constant maximum summer temperature (18°C); and (b) simultaneous increase of both winter and summer temperatures (2–20, 4–22, and 6–24°C). Furthermore, (c) shows actual temperature cycles of the past: an exceptionally cold winter in 1962/1963, a winter with average temperatures in 1985/1986, and an exceptionally warm winter in 2007/2008.

The number of days below 4°C ranged between 0 in several years and 112 days in 1963 and decreased significantly over the period investigated ($y = -0.9037x + 1837$, $r^2 = 0.122$, $p = 0.013$; Figure 4c).

Appearance and frequency of ovigerous females

According to the data provided by Siegel *et al.* (2008), the share of ovigerous females (compared to all females in the catch) increased from 44% in January to 66% in May (Figure 5). Thereafter, the share decreased continuously
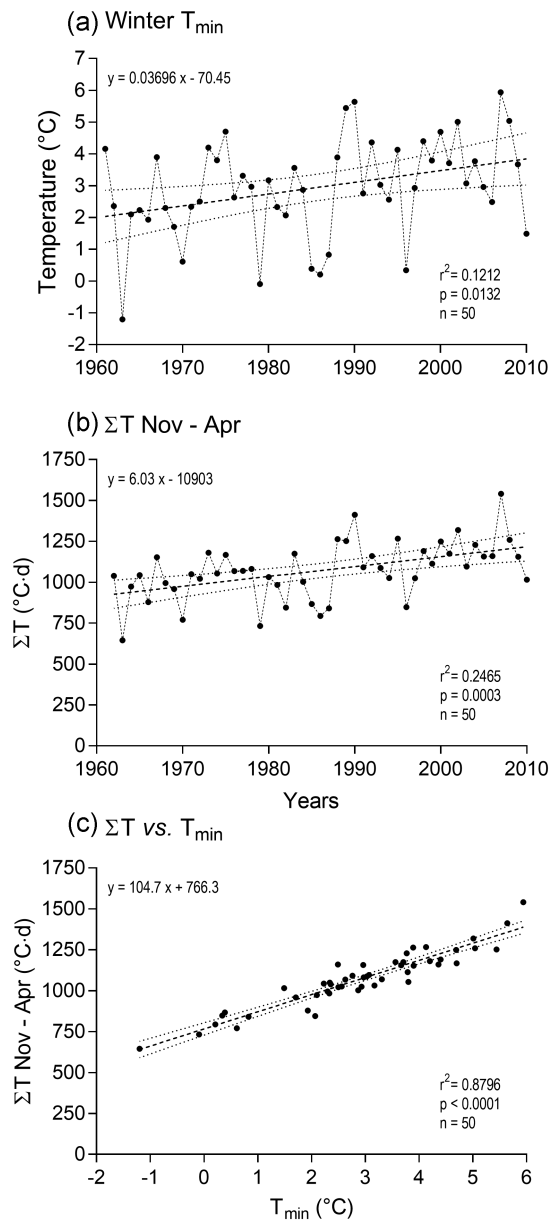
Figure 3. *In-situ* seawater temperatures at Helgoland Roads from 1961 to 2010 depicted as (a) minimum winter temperature (T_{min}), (b) temperature sums (ΣT) of the winter period (from November to April), and (c) correlation of temperature sums and minimum winter temperature.

Figure 4. Winter seawater temperature at Helgoland Roads with emphasis on (a) annual change of minimum winter temperature between consecutive years (ΔT_{min}), (b) days of the year with temperatures <4°C (black dots showing the coldest day of the year), and (c) annual number of days with temperatures <4°C from 1961 to 2010.

towards 11% in September and 9% in October. The course of appearance was phase-shifted for 3 months compared to the civil calendar. It started in October and followed significantly a polynomial function:

$$y = -0.136\,x^3 + 0.89\,x^2 + 9.98\,x - 1.464$$
$$\left(r^2 = 0.992, n = 12,\ \text{Figure 5}\right).$$

Simulation of embryogenesis and appearance of larvae

The course and duration of *C. crangon* embryogenesis during an annual cycle and at different temperature scenarios are shown in detail in Figure 6a–i. Since ovigerous females are present all over the year, although with a minimum in October and a maximum in May, we implemented spawning events
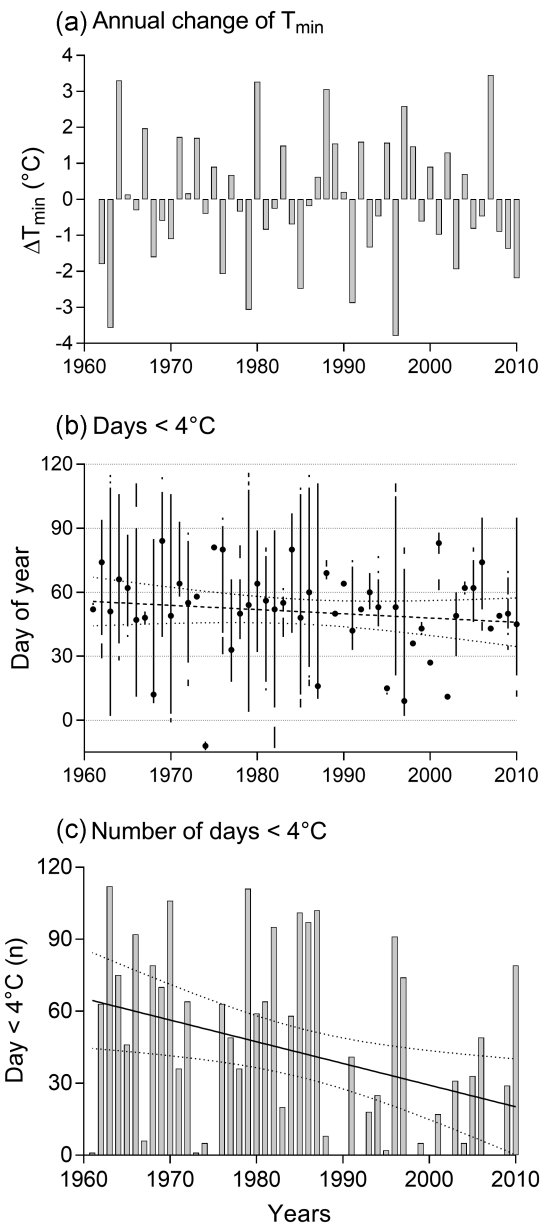
on a weekly basis. Eggs spawned in October can accomplish their development at the relatively warm autumn water temperatures within a few weeks (Figure 6a) bearing early larvae already in November and early December. Eggs spawned in November pass a rapid development, which completely ceases as temperatures approach the lowest winter values of 0°C. The development is first accelerated with rising water temperatures in late March and April. Eggs spawned later (December–March) start with a period of stagnation before rising spring temperature facilitates their development. As a result, larval hatching will accumulate to a maximum at the end of May and early June (Figure 6a).

Warmer winter temperatures will progressively disperse the larval hatching maximum. At lowest winter temperature
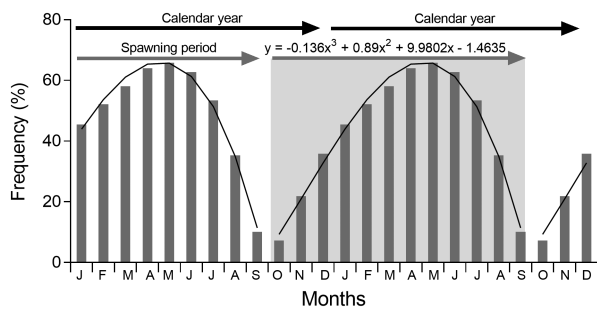
Figure 5. Appearance and frequency of ovigerous females following the polynomial function $y = -0.136x^3 + 0.89x^2 + 9.9802x - 1.4635$ ($r^2 = 0.992$, $n = 12$). Bars represent the monthly percentage share of ovigerous *C. crangon* females. Arrows show the phase-shifted between the calendar year [January (J)–December (D); black] and the spawning period of *C. crangon* [October (O)–September (S); grey]. The grey-shaded area highlights one reproductive cycle of *C. crangon*. The data are based on long-term observations from 1958 to 1992 (Siegel *et al.*, 2008).

of 3°C, a higher share of larvae will hatch in autumn and winter (Figure 6b). The development over the winter is still strongly reduced but not completely ceased. A higher number of larvae hatch in March, but the majority of larvae will appear in May.

High winter water temperatures of 6°C allow for a reduced but continuously ongoing embryogenesis (Figure 6c). The concentration effect, which is present at lower temperatures, is almost abolished. Larvae may hatch all over the winter.

The scenarios with concomitantly increasing winter and summer temperatures show a similar pattern of dispersing embryogenesis and hatching (Figure 6d–f). Low winter temperatures (Figure 6d) slow down embryogenesis, which leads to a concentration of hatches in May and June. Higher temperatures entail a progressive dispersal of hatched larvae. Warmer summer temperatures, which are accompanied by warmer autumn temperatures, accelerate the embryogenesis of the early spawned eggs in October–December (Figure 6e and f). However, the effect of increasing summer temperatures on

embryogenesis is less distinct than the effect of increasing winter temperatures.

Embryogenesis of selected years with low, medium, and high winter temperatures is presented in Figure 6g–i. According to the model, distinct dispersion is evident between the coldest year (1962/1963, Figure 6g) and the warmest year (2007/2008, Figure 6i).

Since the share of ovigerous females is quite low in October, the total number of larvae originating from these females and appearing in late autumn and early winter is negligible. In cold winters with temperatures close to 0°C, *C. crangon* embryogenesis is strongly retarded. At 0°C, the development totally ceases. At 2°C, it will last more than 1 year, and at constant 4°C, it will last more than 5 months (Figure 1). Therefore, no or only very few *Crangon* larvae can be expected in cold winters and the subsequent cold spring months. Moreover, the stagnation of development of eggs spawned over the winter and the increasing share of ovigerous females during the winter leads to a strong concentration effect and a narrow hatching peak of ~3 weeks in June (Figure 7a). A second hatch can be expected in a narrow timeframe in July. At winter temperatures below 3°C, only a small share of larvae (< 8%) will hatch before the phytoplankton spring bloom (Figure 8).

In years with more moderate temperature courses (3–18°C), the share of winter larvae increases slightly, but the total number still remains negligible. The peak spawning period appears ~3 weeks earlier and covers a wider range from mid-May, to mid-June. The weeks thereafter still show an elevated hatching activity, though slightly decreasing towards August (Figure 7b). The peak of a second hatch would start in late June and proceed towards July. The period between the peak of the first and the second hatches shortens. The share of larvae that hatch before the assumed phytoplankton spring bloom increases to about 10% (at $T_{min} = 4$°C) (Figure 8).

Warm winters (6–18°C) increase the amount of winter larvae and extend their appearance almost over the entire winter and spring. But still, their number is negligible compared to the main hatching peak in late spring. The hatching maximum is dated for mid-May, but the peak appears wide with a high production of larvae from April to August (Figure 7c). A second
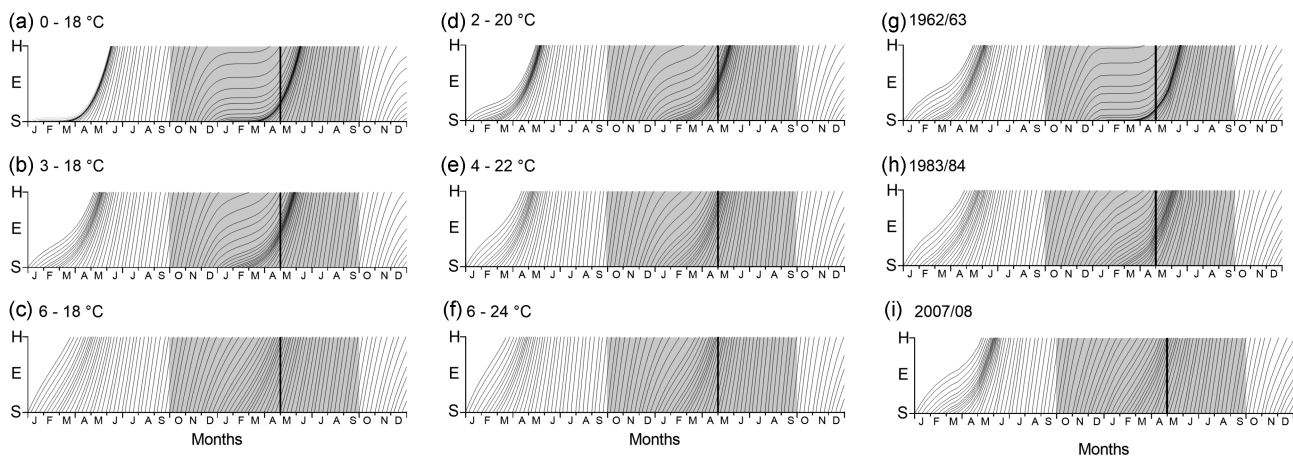

Figure 6. Seasonal cycle of *C. crangon* embryogenesis and peak larvae appearance simulated by assuming spawning at a weekly basis and different temperature scenarios: [(a)–(c)] increase of minimum winter seawater temperatures but constant maximum summer temperature (see Figure 2a); and [(d)–(f)] simultaneous increase of both winter and summer temperatures (see Figure 2b). Furthermore, [(g)–(i)] show the results from the calculations for real temperature cycles of the past: an exceptionally cold winter in 1962/1963, a winter with average temperatures in 1985/1986, and an exceptionally warm winter in 2007/2008 (see also Figure 2c). Capital letters indicate important steps during embryogenesis: S = spawning of eggs, E = embryogenesis, H = hatching of larvae. The grey shaded area highlights one reproductive cycle of *C. crangon* from October to September.
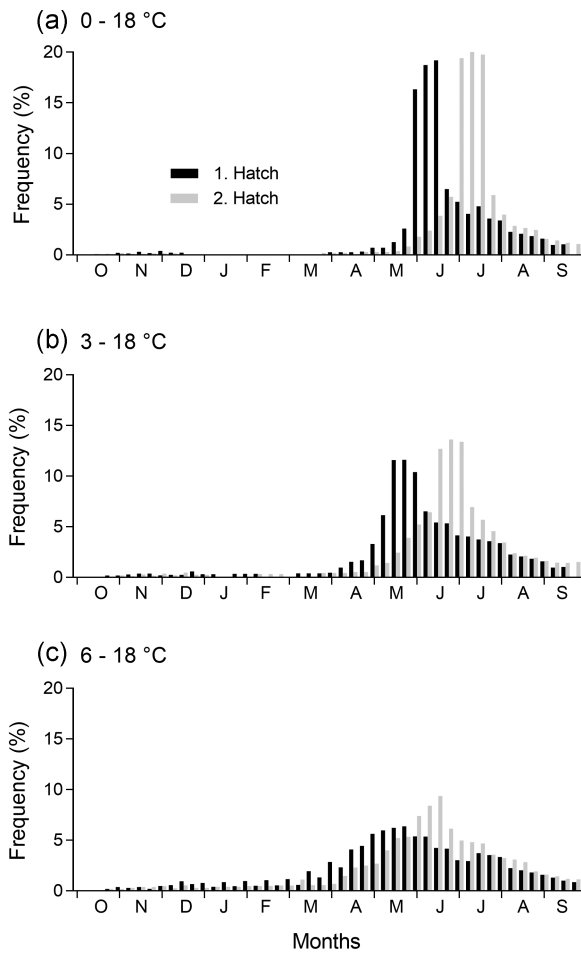
Figure 7. Calculated frequency of *C. crangon* stage I larvae derived from the first hatch (1. hatch, black) and the second hatch (2. hatch, grey) assuming an increase of minimum winter seawater temperatures [(a) 0°C, (b) 3°C, and (c) 6°C] but constant maximum summer temperature [(a)–(c) = 18°C].
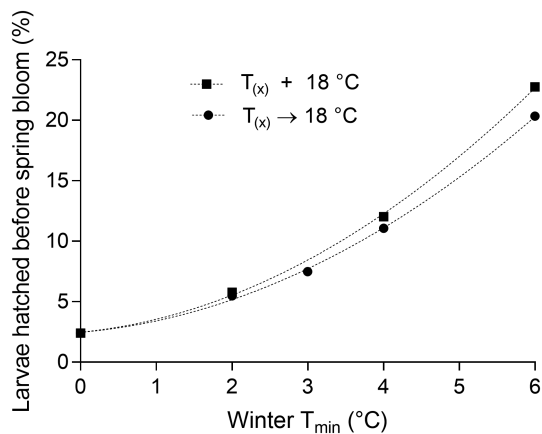

Figure 8. *Crangon crangon* larvae from the first spawn hatching before the spring phytoplankton bloom (between end of March and early May) in relation to minimum winter seawater temperature (T_{min} in°C). Squares show the share of spawners at increasing winter and summer temperatures, e.g. 4 + 18 = 22°C. Circles show the share of spawners at increasing winter temperatures but constant summer temperatures of 18°C.
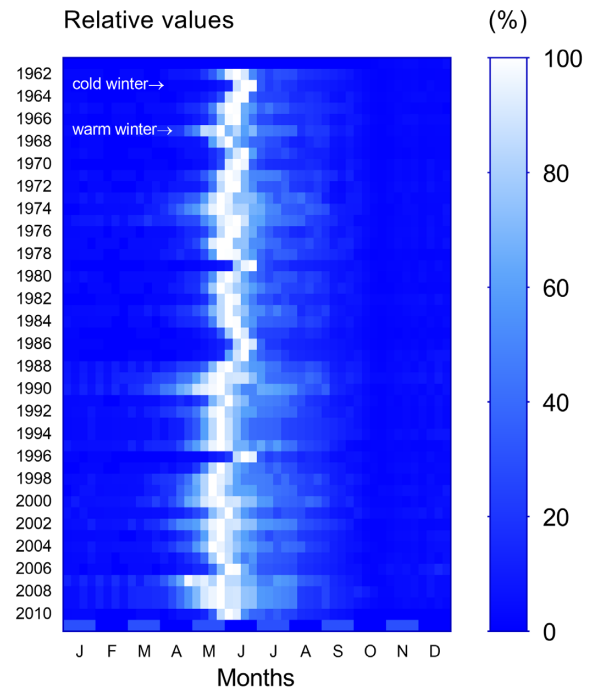

Figure 9. Heat map showing the relative values (%) of *C. crangon* larvae hatching from the first spawn. The appearance of larvae was calculated and displayed from 1961 to 2010. One cold winter and one warm winter are indicated for example.

hatch of the early spawners may already start in April. Larvae of the first and second hatches appear simultaneously. The peaks of the first and second hatch merge. The share of larvae hatching before the spring bloom reaches ∼20% (Figure 8).

The winter water temperatures varied strongly during the investigated period. The computed appearance of the first hatch of larvae of each year is presented as a heat map (Figure 9). Cold winters (as indicated in Figure 9) lead to a short and focused peak of hatching late in the year (May–July). Extremely warm winters entail early production of larvae. The peak of hatching is stretched and flattened, reaching from March to September. The maximum of the larvae production appears in May.

The peak of larvae appears ∼3 weeks earlier in the years in response to rising winter water temperatures (Figure 10a). However, a substantial share of the hatch appears earlier in the year. In cold winters, 10% of the eggs hatch by the end of May. At high winter temperatures (5–6°C), this share has already hatched by the end of January and early February. Concomitantly with the extension of the hatching period, the peak of larvae appearance flattened (Figure 10b).

Discussion

Crangon crangon larvae have been reported during almost the entire year in the German Bight and the estuaries of the larger rivers (Kühl and Mann, 1963, 1969; Elss, 1973). Although the peak of spawning clearly appears in spring and early summer, it shows distinct inter-annual variations in timing and shape. Based on temperature data, the occurrence of ovigerous females, and the duration of embryogenesis, we provide an approach to predict the appearance of *C. crangon*
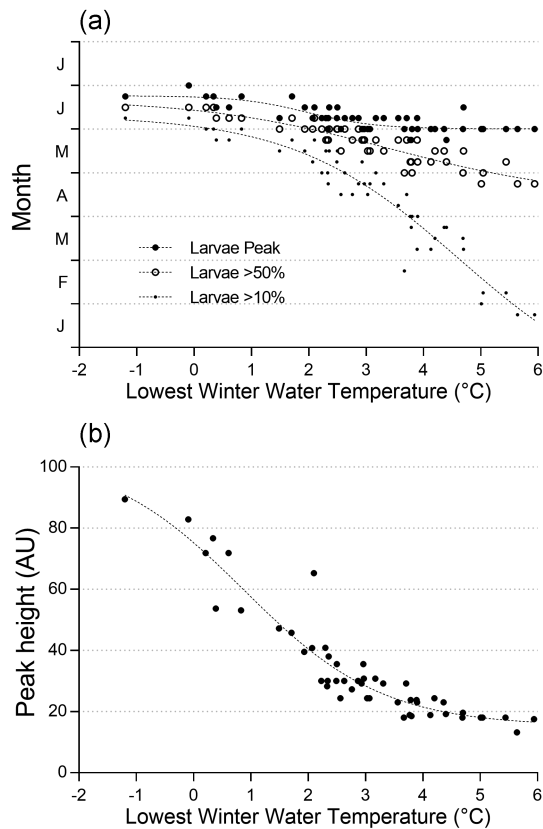
Figure 10. Relation of lowest winter seawater temperatures (1961–2010) and monthly *C. crangon* larval appearance as a result from the hatch of the first spawn (between the end of January and beginning of July). (a) Peak of larvae hatch is indicated by big black dots, time when 50% of larvae have hatched by empty circles, and time when 10% of larvae have hatched is shown by small dots. (b) The height of the peak (AU = arbitrary units) in relation to lowest winter seawater temperature is given.

larvae in the German Bight and validated our predictions with documented observations.

Spawning period, embryogenesis, and water temperature

There has been an intensive debate about the sequence and duration of spawning of *C. crangon* in the North Sea. Early researchers suggested two spawning seasons, one related to the winter and the other to the summer (Ehrenbaum, 1890; Boddeke, 1982). Only recently, Siegel *et al.* (2008) combined three different data sources from 1958 to 2005 to study the degree of inter-annual variation in the maturation of *C. crangon*. These data sets were (1) the spring and autumn survey data of the international "Demersal Young Fish Survey, DYFS", which dates back to 1974, (2) the national "Winter Shrimp Survey" in January, and (3) a series of by-catch samples from the commercial shrimp fishery, which covered the period 1958–1994. The analysis of the occurrence of ovigerous females suggested one continuous spawning period starting from October and lasting until September of the upcoming year. All egg development stages were present during the seasonal cycle, indicating that spawning happens continuously. During this period, *C. crangon* may spawn several times, but the peak spawning activity in the coastal areas of the southeast North Sea is centred around May. The gap in ovigerous females in September/October is believed to be due to endocrine

regulation of vitellogenesis (Klęk-Kawińska and Bomirski, 1975). Siegel *et al.* (2008) concluded that the "basic seasonal life cycle of the brown shrimp population in the German Bight is well synchronized and fairly constant over time. The cycle seems to continue relatively unchanged without major time displacement". Therefore, we used the data of Siegel *et al.* (2008) as a basis for our calculations on the seasonal appearance of ovigerous females and stage I larvae.

The relationship between the duration of embryogenesis and temperature was investigated by Havinga (1938), Tiews (1970), Meixner (1969), and Wear (1974). Redant (1978) combined the data with his own results and set up a combined equation, which we also adopted for our calculations. The development of the *C. crangon* eggs strongly depends on the water temperature. A lower threshold temperature for larval development was not defined, but below ∼4°C, embryogenesis is so much retarded that it would take more than 5 months until hatching. Generally, hatching would appear later in the year after cold winters than after warm winters. However, from 1961 to 2010, the lowest winter water temperature at Helgoland Roads increased significantly by 1.85°C and the highest summer water temperature by 1.63°C. These values are in the same range, though slightly higher, as reported previously for average annual temperatures by Wiltshire and Manly (2004). More strikingly, the winter temperature sums (ΣT_d) covering November–April increased by about one-third from 1961 to 2010. Concomitantly, numbers of cold winter days (<4°C) decreased significantly. The coldest days appeared 10 days earlier at the end of the studied period than at the beginning, but this shift was not statistically significant.

Beside the continuous warming trend, the inter-annual variation was high, accounting for up to 3.8°C in the minimum winter water temperatures of subsequent years. The high inter-annual variability significantly alters the duration of embryogenesis and, consequently, the time of hatching. The temperature course and, thus, the temperature sums over winter determine the development and the hatching of the larvae. Nevertheless, the close correlations between temperature sums and the lowest winter temperature allow using the latter as a good proxy for embryogenesis and hatching.

Time of hatching

The general warming trend in the German Bight entails earlier hatching of larvae. In the early 1960s, the lowest winter temperature was on average 2°C and the appearance of a defined larval peak occurred by the end of May/early June. At the end of the investigated period, the lowest winter temperature increased towards 3.8°C and the peak of larvae is predicted to appear ∼1 week earlier. In contrast to the appearance of the peak, the onset of hatching starts significantly earlier and is shifted from early May towards early March. Consequently, the appearance of larvae changes from a sharp peak in late spring towards an early starting and broad distribution pattern over several weeks.

A similar change in the larval phenology with increasing water temperatures was observed for the boreal shrimp *Pandalus borealis*. Richards (2012) reported an earlier start of hatching and a delay in the completion of hatching, which, taken together, prolonged the hatching period. A longer hatching period might be beneficial because it could increase the window of opportunity for larvae to encounter good survival conditions (Richards, 2012). However, Richards *et al.* (2012,

2016) also found that colder temperatures during the subsequent pelagic larval stage were associated with higher recruitment, which is not consistent with putative benefits of warmer temperatures on hatch period duration.

The continuous warming trend in the North Sea is superimposed by inter-annual variations of the lowest winter water temperatures, which can account for up to 3.8°C between subsequent years. Accordingly, the appearance of *C. crangon* larvae varies strongly between years but can be predicted on the basis of the progress of embryogenesis and the *in-situ* water temperatures. The investigated period included six exceptional cold winters (1963, 1979, 1985–1987, and 1996) and eight exceptional warm winters (1961, 1967, 1973–1975, 1989, 1990, and 2007). Our calculations predict late appearance of larvae with a distinct and short peak for the cold winters and an early appearance of larvae over a long period for the warm winters. These predictions are in accordance with various documented field observations.

In the frame of an extended investigation on the fluctuation of the shrimp stock off the German North Sea coast, Plett (1965) studied the appearance of *C. crangon* larvae along several transects in estuaries and off the coast. After the exceptionally severe winter 1962/1963, Plett (1965) found no *C. crangon* larvae in April 1963 and ascribed the lack of larvae to the still low water temperature of 4°C. However, high numbers of larvae appeared in summer around Helgoland with a maximum in August (Plett, 1965). Our calculations also show no larvae in April 1963, but the onset of hatching in middle of May followed by a huge amount of almost simultaneously released larvae. Plankton samples taken 1 year later, in April 1964, at water temperatures of 4.0–5.5°C contained shrimp larvae, which is also in accordance with our model (Plett, 1965). Elss (1973) collected *C. crangon* larvae in April 1967 when the water temperatures were 6.6–7.0°C. Likewise, the late appearance of *C. crangon* larvae around Helgoland in 1985 was related to the cold winter of 1984/1985 and the resulting low temperatures in spring 1985 (Koslowski, 1985). Wehrtmann (1989) reported the first appearance of stage I larvae around Helgoland in the second week of May 1985 when the water temperature reached 7.8°C after the cold winter 1984/1985. Thereafter, larvae were present throughout the entire sampling period, which lasted from January 1985 to January 1986, although very few were collected in December 1985 and January 1986. Larvae were very common from June to September 1985 with peak abundance (~7 larvae m^{-3}) in August. The plankton samples contained all larval stages as well as juveniles. Elss (1973) found few larvae in the winters of 1969/1970 and 1970/1971 but highest densities in July/August 1969 and discussed their variable appearance between years. After the relatively mild winter of 1982/1983, Gerdes (1985) collected *C. crangon* larvae already hatched in March 1983 at an average temperature of 4.5°C. Our model predicts the onset of hatching after very mild winters (>5°C) at the end of January and beginning of February. Since the frequency of warm winter continuously increases, *C. crangon* larvae will appear earlier in upcoming years.

Second hatch of larvae

Crangon crangon are multiple spawners. Under favorable conditions in terms of nutrition and temperature, oogenesis continues while females still carry eggs (Meyer, 1935). When the larvae have hatched, females spawn again 1–2 days after the

upcoming molting. Two to five spawns between April and August were observed in the laboratory (Meixner, 1969). In the field, at least two spawns are suggested (Meyer, 1935; Lloyd and Yonge, 1947).

Kühl and Mann (1963) indicated June as the month of the second maximum of larva appearance in the Elbe estuary. Oh and Hartnoll (2004) as well reported the second maximum of larval appearance in the Irish Sea by June. Other authors observed the second larval maximum in the North Sea over a much longer period, e.g. from March to September (Boddeke, 1982), from April to August (Kuipers and Dapper, 1984), and from April to July (Neudecker and Damm, 1992). Henderson and Holmes (1987) report a period from March to July for the appearance of larvae in the Bristol Channel.

Our calculations predict the most distinct peak of larvae originating from the second hatch in years following cold winters. The slow development of the first clutch of eggs leads to an accumulation of hatches in the first half of June. Assuming favourable nutritional conditions in early summer, the majority of females would subsequently release the second clutch of eggs, which develop almost synchronously to release the second cohort of larvae in July/August. A third cohort may follow but presumably less distinct as the previous ones. Wehrtmann (1989) reported no stage I larvae between 2 and 23 August, but they occurred regularly until October 1985. The last stage I larvae were sampled in early December at a temperature of 6.4°C.

After moderate winters, a stronger conglomeration of cohorts will appear. A small share of females will release the first larvae during winter and spring, being prepared to breed the second clutch of eggs. Larvae of the second clutch of the early breeders will already be hatched by the time when the majority of females release the larvae of the first clutch of eggs. At warm winters (6°C), a wide mingling of putative cohorts will appear throughout the reproductive season.

The successive and unsynchronized reproductive behaviour and continuous almost year-round fertility hampers distinction of *C. crangon* cohorts. Accordingly, several authors reported the simultaneous presence of various larval stages. Elss (1973) investigated explicitly the appearance and distribution of *C. crangon* larvae during winter off the German coast. Although few, the larvae represented all stages, mostly early ones (I–IV) but also some late ones (V and VI).

Feeding habits and nutritional requirements of larvae

Very limited information exists about the food spectrum, the feeding preferences, and the nutritional requirements of *Crangon* larvae. Freshly hatched larvae are planktivorous. They possess no substantial yolk reserves. Their internal energy reserves allow survival for ~3–4 days without feeding before mortality severely increases (Paschke *et al.*, 2004). In the laboratory, *Crangon* larvae developed and grew best when they were fed with a mix of *Artemia* nauplii and rotifers (*Brachionus plicatilis*), apparently showing preference for the rotifer by early stages and for the *Artemia* nauplii by older stages (Criales and Anger, 1986). Sole phytoplankton diet was less suitable. Accordingly, the larvae can be considered omnivorous with a strong tendency towards carnivory, preferentially utilizing microzooplankton.

Microzooplankton, representing the size fraction between 20 and 200 μm of heterotrophic plankton, responds quickly

to the spring phytoplankton bloom and establishes high biomasses closely following the chlorophyll-a development (Löder *et al.*, 2012). Accordingly, optimum nutritional conditions for *C. crangon* larvae can be expected 1–2 weeks after the onset of the spring phytoplankton bloom.

Marine pelagic communities are sensitive to climate change (Edwards and Richardson, 2004). The warming of the central North Sea between 1958 and 2002 entailed shifts in the chronological appearance of functional groups in both direction, towards earliness as well as delay. This, in turn, causes mismatches of established trophic networks and seasonal successions. The appearance of diatom peaks in spring and autumn, however, remained relatively static (Edwards and Richardson, 2004). Although single diatom species showed great variability in phenology, collectively, the timing of the spring bloom did not shift largely. Presumably, it is triggered by the photoperiod rather than temperature. A considerable constancy for the onset of the spring phytoplankton bloom was also observed at Helgoland Roads (Wiltshire *et al.*, 2008, 2015). The onset of the bloom starts at week 12 to week 18 of the year, which covers end of March to the early May. We projected for the following considerations the onset of the spring bloom to mid-April and the subsequent production of microzooplankton to the beginning of May.

During cold winters, the development of the *C. crangon* eggs would be strongly reduced and almost cease. The vast majority of larvae would spawn in late May and June and, thus, well beyond the onset of the phytoplankton spring bloom and a presumably well-established zooplankton population. Only 2.5% of the larvae of the first hatch would appear in winter and before the onset of the spring bloom. This share would increase to 5.5–7.5% in intermediate winters of minimum 2–3°C. Still, most of the larvae would meet the spring bloom. The mismatch becomes more distinct at 4°C (11%) and, particularly, at 6°C (20%). At the scenario of the highest winter temperature, a low but continuous release of larvae would happen throughout the winter and early spring with a marked increase at the end of March. Adversely, it appears that the spring bloom tends to start slightly later after warmer winters (Wiltshire *et al.*, 2008), probably due to grazing effects mainly by herbivorous copepods but also by the already hatched *Crangon* larvae and other meroplankton species. This effect would further stretch the shift between the share of spawned larvae and the start of the spring bloom.

The probability for survival of early *C. crangon* larvae in the field is low. Elss (1973) observed in the larvae samples of the winters of 1968–1979 almost exclusively early stages but only very few late stages. After the mild winter of 1989/1990, larvae occurred throughout the winter months with a peak of newly hatched stages in February 1990 (Wehrtmann, 1989). These early larvae apparently did not develop into late stages and juveniles because late stages were lacking in the plankton samples until June 1990. Kattner *et al.* (1994) suggested malnutrition of larvae, because the early stages sampled in 1990 showed deficiencies of unsaturated fatty acids and a lack of triacylglycerols, which are important energy stores of crustaceans.

Conclusion

The combined implementation of the seasonal reproductive cycle, the experimental developmental data, and the natural water temperatures allowed for a reliable computation of the timing of hatching of *C. crangon* larvae. It was verified that the lowest winter water temperature is a good proxy for the estimation of the timing of the seasonal appearance of larvae. Although the North Sea experiences continuous warming, the peak release of larvae has been determined by the strong interannual variation of winter temperatures rather than the overall temperature increase over the last decades. We predict that warm winters will lead to a mismatch of larval appearance with spring food sources and, thus, higher mortality due to malnutrition. Our approach may help to improve estimates on the reproduction success and annual stock development of *C. crangon* in the North Sea.

Data Availability Statement

The data underlying this article will be shared on reasonable request to the corresponding author.

Conflict of interest

The authors declare no conflict of interest.

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