

Reproduction and recruitment of the brown shrimp *Crangon crangon* in the inner German Bight (North Sea): An interannual study and critical reappraisal

Kim Hünlerlage¹  | Volker Siegel¹ | Reinhard Saborowski² 

¹Johann Heinrich von Thünen-Institute, Institute of Sea Fisheries, Bremerhaven, Germany

²Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven, Germany

Correspondence

Kim Hünlerlage, Johann Heinrich von Thünen-Institute, Institute of Sea Fisheries, Herzogstraße 31, 27572 Bremerhaven, Germany.
Email: kim.huenerlage@thuenen.de

Abstract

The brown shrimp, *Crangon crangon*, is the most important target of the coastal crustacean fisheries in the German Bight. In order to evaluate the relation between the abundance of ovigerous females and larvae in spring and the recruitment success in autumn, we first analysed the seasonal appearance of ovigerous females and larvae from weekly samples throughout 2012. The spawning season in the German Bight extends over several months comprising multiple unsynchronized spawning events. The minimum shares of ovigerous females appeared in early autumn, and the highest shares in late winter bearing mostly early egg stages. We defined the putative start of the reproductive cycle for November when the frequency of ovigerous females started to increase. There was no distinct separation between winter and summer eggs, but a continuous transition between large eggs spawned in winter (the early spawning season) and batches of smaller eggs in spring and summer. Larval densities peaked in April/May. Consequently, regular annual larval surveys from 2013 to 2016 were scheduled for April/May and extended to six transects covering the inner German Bight. Ovigerous females were most abundant in shallow waters above the 20-m isobaths, which also explained regional differences in abundance between the regions off North Frisia and East Frisia. No relation was obvious between the number of larvae in spring and recruited stock in autumn. Due to the short lifespan of *C. crangon*, the combination of various abiotic factors and predator presence seems to be the principal parameters controlling stock size.

KEYWORDS

eggs, larvae, life history traits, predators, recruitment, stock development, temperature

1 | INTRODUCTION

The brown shrimp (*Crangon crangon*, Linnaeus 1758) is a small (up to 80 mm) but ecologically and economically important epibenthic decapod crustacean in the North Sea. First evidence for small-scale fisheries on *C. crangon* dates back to the 17th century (Lotze,

2007). Until the early 19th century, it did not exceed subsidiary relevance but advanced rapidly when sailing boats and, later, engine-driven boats were deployed for sea-going trawling. Today, the brown shrimp is the most important target of coastal crustacean fisheries in the southern North Sea, keeping 500 vessels in operation and providing income for about 1,000 fishermen. In

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2019 The Authors. *Fisheries Oceanography* Published by John Wiley & Sons Ltd

2014, the overall *Crangon* landings in the North Sea approached 40,000 tons yielding a total value of more than 120 million € with a German share of 16,000 tons and a value of 44 million € (STECF, 2016).

Crangon crangon successfully copes with the particular environmental conditions of the southern North Sea, such as strong changes in temperature, salinity and food availability due to the extraordinary ecophysiological adaptations (Campos & van der Veer, 2008; Reiser, Herrmann, Neudecker, & Temming, 2014; Reiser, Herrmann, & Temming, 2014; Saborowski, Schatte, & Gimenez, 2012). Stock estimates of brown shrimp yielded variable and occasionally extremely high numbers of up to 82 specimens per m², including juveniles (Boddeke, 1986). Major predators are cod (*Gadus morhua*) and whiting (*Merlangius merlangus*) (Berghahn, 1996). Although fishing mortality on commercial-sized *C. crangon* (>50 mm) is suggested to have exceeded natural mortality, the stock shows no signs of overfishing (Hufnagl, Temming, Siegel, Tulp, & Bolle, 2010). Furthermore, the short lifespan in concert with high fertility enables this species to recover quickly from detrimental events (Berghahn, 1996; Siegel, Damm, & Neudecker, 2008).

The interannual variation in *C. crangon* densities is high, and stock sizes are hard to predict (Siegel, Gröger, Neudecker, Damm, & Jansen, 2005; Spaargaren, 2000; Tulp et al., 2016). Early investigations on the reproductive cycle of *C. crangon* in the North Sea suggested two main breeding seasons, one in winter and one in summer, within a 9 months lasting cycle (Boddeke, 1982; Ehrenbaum, 1890; Havinga, 1929, 1930; Lloyd & Yonge, 1947; Meredith, 1952). Recent studies, however, revealed a coherent breeding period with a core-spawning season between January and late June. Minimum numbers (<10%) of ovigerous females within the annual cycle were present between August and early December (Siegel et al., 2008). Fast growth, the extended reproductive period and the

lack of accurate age determination methods (Campos, Bio, Freitas, Moreira, & van der Veer, 2013) render cohort analysis and, thus, age-based assessments of *C. crangon* stocks almost impossible. Consequently, fisheries targeting brown shrimp have been difficult to manage and to regulate.

The production of larvae in spring is supposed to be the dominant resource forming the exploitable stock in the autumn shrimp fishery (Hufnagl & Temming, 2011). Therefore, the aim of the present study was to investigate the interannual relationships between the reproductive efforts of *C. crangon* in the inner German Bight (North Sea) during successive reproductive seasons. Over a 5-year period, we determined first the seasonal appearance of larvae and, in the subsequent years, the abundances of ovigerous females and larvae in spring and compared these data with the densities of exploitable shrimps in autumn. We addressed the questions whether recruitment depends on the same year's spring abundance of ovigerous females and larvae, and whether the *C. crangon* spawning stock size in autumn determines the number offspring in the following season? Data on winter water temperature and predator occurrence were included to discuss factors affecting the reproductive performance of *C. crangon* and to scrutinize established views on the reproductive biology and life cycle traits of *C. crangon* in the German Bight.

2 | MATERIALS AND METHODS

Samples of brown shrimp, *Crangon crangon*, were collected within three coordinated sampling campaigns from 2012 to 2016 as detailed below. The study area in the inner German Bight covered the regions East Frisia (EF), Weser Estuary (WE) and North Frisia (NF) (Figure 1, Table S1). Laboratory analyses were carried out at the Thünen Institute for Sea Fisheries in Hamburg.

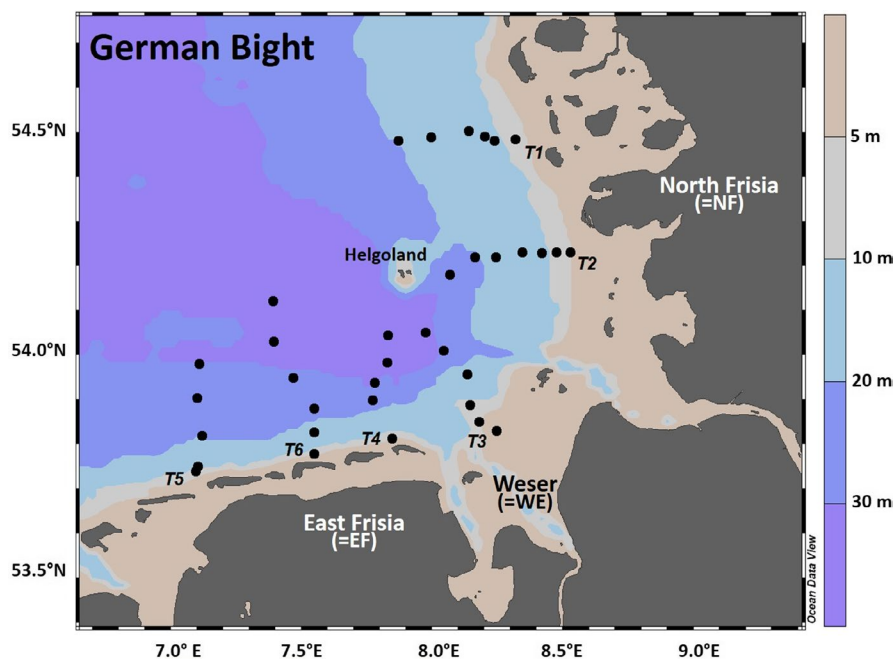


FIGURE 1 Transects and stations in the inner German Bight sampled during the *Crangon crangon* surveys in spring 2013–2016. Geographic coordinates and depths at stations are listed the Table S1 [Colour figure can be viewed at wileyonlinelibrary.com]

2.1 | Weekly sampling of *Crangon crangon* eggs and ovigerous females

Brown shrimp samples were obtained from commercial cutters from the inner German Bight (2012 and 2014). No samples were taken in December due to bad weather. Before the first sieving on board, the fishermen took random samples of one kg shrimps from each catch. The samples were frozen at -20°C . In the laboratory, the samples were analysed for the proportion of ovigerous females, egg size and egg developmental stage.

The egg size was measured in filtered seawater under a stereo microscope with a micrometre eyepiece (60-fold magnification). Due to the spheroidal shape of the eggs, the smaller diameter (D_1) and the larger diameter (D_2) were recorded. The volumes (V) of the eggs were calculated accordingly:

$$V = (\pi \cdot D_1^2 \cdot D_2) / 6$$

The development stage of eggs was recorded following Meredith (1952), but the number of stages was condensed to stages A–D without considering sub-stages: A: newly laid and spherical, B: early segmentation of the embryo, C: eye and outline of carapace become visible and D: prelarval stage with long abdomen separated from the cephalothorax. Data from weekly samples were pooled on a monthly basis and used to describe the seasonal reproductive pattern of *C. crangon*.

2.2 | Spring sampling of *Crangon crangon* larvae and ovigerous females

Sampling of *C. crangon* larvae and ovigerous females started in 2013 with two transects off North Frisia (T1 and T2), one transect off the Weser Estuary (T3), and two transects off East Frisia (T4 and T5). In 2015, transect T6 was added to the region EF (Figure 1). Spring sampling was always done during late April/early May with RV Uthörn. The depths at the stations ranged from 5 to 38 m (Table S1).

Larvae of *C. crangon* were collected with an Indian Ocean Standard net (IOS ring trawl, 1.13 m diameter, 1 m² mouth opening, 400 μm mesh size). At each station, the net was lowered to the bottom with 0.5 m/s and retrieved vertically with 0.3 m/s. The plankton samples were preserved with borax-buffered formalin (4%, pH 7.8). In the laboratory, *C. crangon* larvae were sorted quantitatively under a stereo microscope and the numbers were normalized for 1 m² sea surface and 1 m³ water volume, respectively. Larval stages were classified as zoea 1 to zoea 6 (Z1–Z6) after Gurney (1982).

Adult *C. crangon* were captured by beam trawling (3 m width, 20 mm mesh size in the cod end). At each station, hauls were carried out for 15 min at a speed of 3.5–4 knots. *Crangon* subsamples (250–300 g) were randomly taken from each catch and stored at -20°C until analyses. Length (from the tip of the scaphocerites to the end of the uropods), sex and share of ovigerous females were determined in the laboratory. Abundances were normalized for 1,000 m².

2.3 | Autumn sampling of *Crangon crangon*

The autumn samples of adult *Crangon crangon* were obtained from the Demersal Young Fish Survey (DYFS). Since 1974, the DYFS is carried out annually from September to the first week in October with chartered commercial vessels and, since 2012, with RV Clupea (for the original survey design see Boddeke et al., 1972). Shrimp samples were collected and processed as described above (2.2). Data on the overall shrimp abundance were used for estimating the interannual variation of the autumn stock, hence as a proxy for recruitment.

2.4 | Data analysis

The data sets showed high variation, which hampered multifactorial data analysis. Therefore, data sets were combined, whenever reasonable. Data sets were first tested for normal distribution and equality of variances. If appropriate, parametric methods (Student's *t* test and one-way ANOVA) were applied. Otherwise, data sets were compared with non-parametric rank-sum tests (Mann–Whitney test and Kruskal–Wallis test). The applied statistical methods are always indicated along with the relevant statistical parameters in the Results section. The significance level was set at $p < .05$. All data are presented as means \pm standard deviation (SD) or standard error of the mean (SEM).

Correlations were assessed using Pearson's correlation coefficient with two-tailed *p* value. Frequency distributions of data sets were analysed with contingency tables and chi-square tests.

Data on the abundance of shrimp predators in autumn (i.e. whiting, cod, portunid crabs) were extracted from the DYFS data sets (Thünen Institute of Sea Fisheries). Winter water temperature at Helgoland roads was extrapolated from SST plots provided by the Bundesamt für Seeschifffahrt und Hydrografie, Hamburg; https://www.bsh.de/DE/DATEN/Meeresumweltmessnetz/Historische_Daten/Historische_Daten_node.html.

All statistical analyses were performed with the GRAPHPAD PRISM 5 software (GraphPad Software, Inc.). The graphs and figures were designed with GRAPHPAD PRISM 5 and OCEAN DATA VIEW (Schlitzer, R., <https://odv.awi.de>, 2018).

3 | RESULTS

3.1 | Frequency and distribution of ovigerous females

The lengths of the ovigerous females investigated within this study ranged between 43.5 and 85.5 mm. The ratios of egg-bearing females followed a distinct seasonal pattern (Figure 2). The highest share appeared in March (70%) and continuously decreased towards almost zero in October. In November, the share increased again towards 40%. No samples were collected in December due to bad weather. This annual pattern closely matches with the average

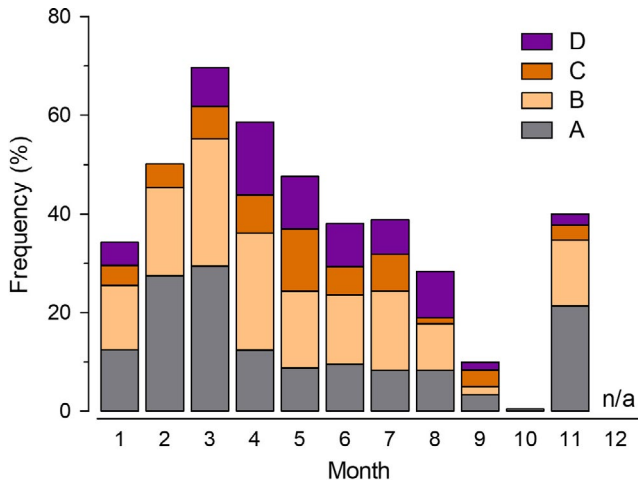


FIGURE 2 Monthly share (%) of *Crangon crangon* ovigerous females in relation to all females in the sample and relative frequency of egg stages A–D [Colour figure can be viewed at wileyonlinelibrary.com]

seasonal cycle based on data from 1958 to 1992 (Siegel et al., 2008) (Pearson's correlation, $r^2 = .678$, $p = .0018$, $n = 11$).

During the repeated spring samplings in late April from 2013 to 2016, the densities of ovigerous females varied strongly between years and stations (Figure 3, Table 1, Table S2). The highest abundances of egg-carrying females in the entire study area were noted in 2013 and 2015 (Table 1). In 2016, the overall densities reached 63%, and in 2014, only 23% of the maximum observed in 2013. However, due to high variation, the differences between years were not statistically significant (Kruskal–Wallis test, $p = .0596$).

Despite high variation, differences between transects were statistically significant (Kruskal–Wallis test, $p = .0001$). Highest densities of egg-bearing females appeared along transects T1 and T2 off the North Friesian coast with average values of 45.8 and 68.0 animals per 1,000 m² (Table 1). These transects also showed relatively uniform densities of egg-carrying females (e.g. T1 in 2013, T1 and T2 in 2015). The transects off the East Friesian coast and the Weser estuary showed higher variability between stations. The transects off the North Friesian coast (T1 and T2) showed over the entire sampling period (2013–2016) on average 57.4 animals per 1,000 m². These values were significantly higher than those of ovigerous females off East Frisia (T4–T6; Mann–Whitney test, $p < .001$).

The highest densities of egg-bearing females appeared at the coastal stations (up to 278 animals per 1,000 m²) and decreased strongly with distance from the coast where several stations showed no ovigerous females (Figure 3, Table 1, Table S2). The densities of egg-bearing females were significantly higher in shallow waters of less than about 20 m depth (Kruskal–Wallis test, $p < .0001$). Maximum densities appeared at approx. the 10 m depth line (up to 320 specimens per 1,000 m²). Beyond the 20-m isobath, densities of egg-bearing females did not exceed 47 animals per 1,000 m² (Figure 4). Lowest abundances of egg-carrying females were present at the outermost and, thus, deepest stations.

3.2 | Developmental stage and size of *Crangon crangon* eggs

In every month, except February and October, all four egg development stages A–D (newly spawned to close to hatch) were present but in changing ratios ($\chi^2 = 177.4$, $df = 27$, $p < .001$). Stages A and B dominated in every month (Figure 2). The shares of stages C and D increased from March to May and remained at a high level until September, while the total abundance of egg-carrying females decreased concurrently, reaching the minimum in October.

The eggs of *C. crangon* increase in size during their development and change shape from spherical to spheroidal. The volumes of stage A eggs ranged between 0.007 and 0.104 mm³ (average 0.0419 ± 0.0128 mm³; Figure 5). The volumes of stage B eggs ranged between 0.020 and 0.197 mm³ (average 0.0683 ± 0.0302 mm³). Stage C eggs showed volumes from 0.0299 to 0.2769 mm³ (average 0.1022 ± 0.0394 mm³) and stage D eggs from 0.0252 to 0.4100 mm³ (average 0.1273 ± 0.0531 mm³). The differences between volumes of egg stages were highly significant (Kruskal–Wallis test, $p < .0001$).

The volumes of newly spawned eggs (stage A) varied significantly during the annual cycle (Figure 6, Kruskal–Wallis test, $p < .0001$). The largest eggs (0.058 ± 0.012 mm³) were laid in November (week 44 and 47) and the smallest (0.031 ± 0.010 and 0.029 ± 0.004 mm³) in May and July (weeks 19 and 28, respectively). The transition between large eggs in late autumn and small eggs in summer appeared continuously and broadly following a sine function. Eggs smaller than the annual mean (0.042 mm³) dominated approximately from mid of March to September. Eggs larger than the annual mean were frequent from October to mid of March.

3.3 | Distribution and abundance of *Crangon crangon* larvae

Crangon larvae were present in April/May 2013–2016 across the entire sampling area in the inner German Bight (Figure 7). The densities, however, varied considerably between years and stations. The overall average was 103 larvae m⁻² (7 larvae m⁻³), and the maximum was 1,244 larvae m⁻² (207 larvae m⁻³) at station 30 in 2015 (Tables S3 and S4).

Lowest densities appeared in 2013 (Table 2). On average, <38 larvae m⁻² (2.3 m⁻³) were counted across all transects. Only few stations of transect T4 showed slightly higher larvae concentrations (Figure 7). The highest mean larvae density per m² across all transects appeared in 2014 and 2015 (Table 2). The differences between years were statistically significant (Kruskal–Wallis test, $p = .0019$).

Within the area investigated, highest average concentrations of brown shrimp larvae were found across transects T1, T4 and T6 (Figure 7, Table 2, Tables S3 and S4). T2 showed the lowest average density of 53 larvae m⁻² (4 larvae m⁻³). Due to high variation, the densities were not statistically significant between transects (Kruskal–Wallis test, $p = .1550$). Comparison between the regions

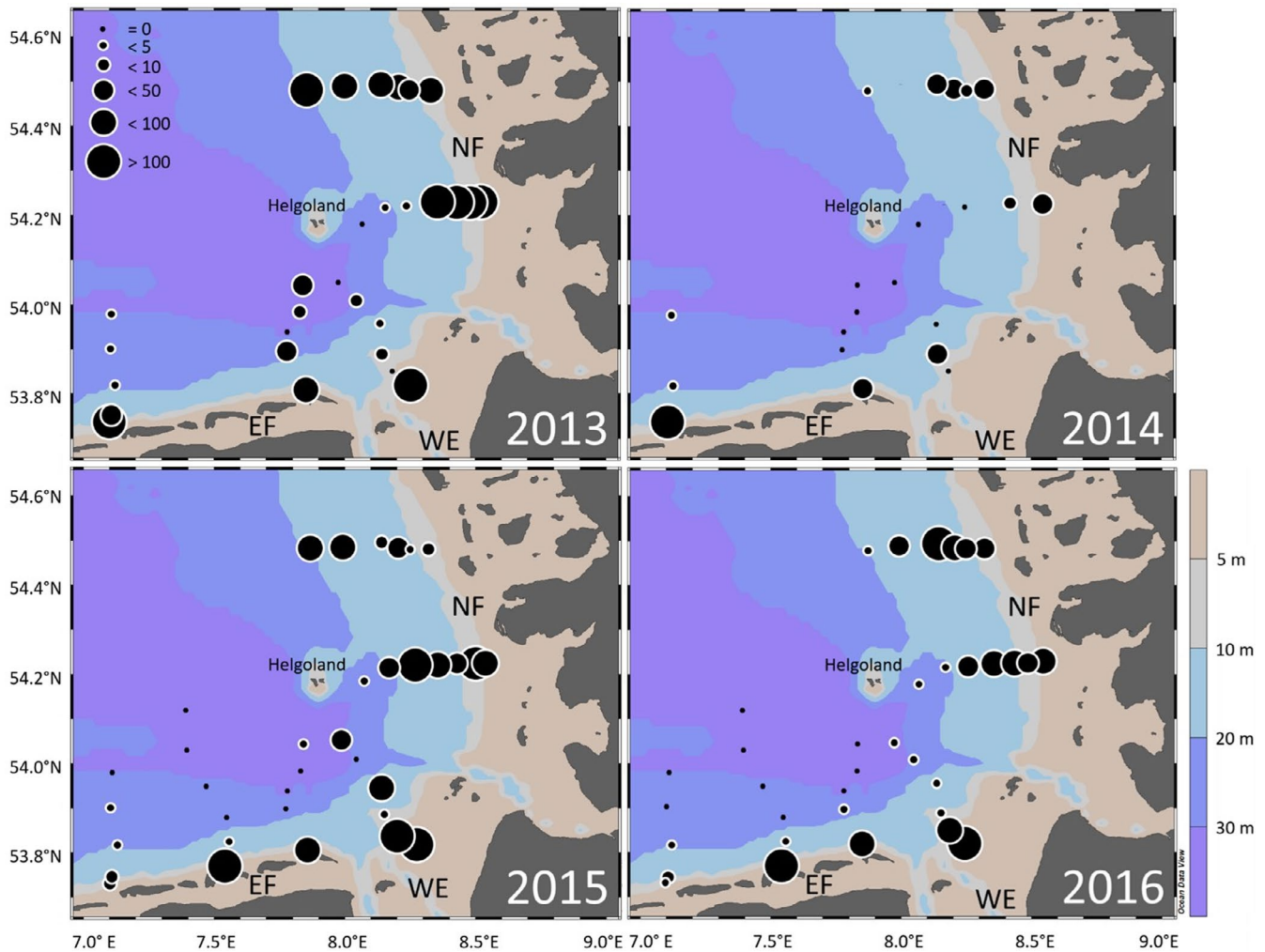


FIGURE 3 Distribution and density ($n \text{ } 1,000 \text{ m}^{-2}$) of *Crangon crangon* ovigerous females in the inner German Bight in spring 2013–2016. Details are listed in the Table S2 [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Mean density ($n \text{ } 1,000 \text{ m}^{-2}$) of *Crangon crangon* ovigerous females sampled at different transects (sorted from W to E) during the spring surveys in 2013–2016 (Mean \pm SEM; $n = 3\text{--}7$)

Year	Transect						$\bar{\varnothing}_{\text{Area}}$
	EF T5	EF T6	EF T4	WE T3	NF T2	NF T1	
2013	59.2 \pm 54.7	–	22.9 \pm 9.8	53.3 \pm 49.6	103.6 \pm 38.7	70.4 \pm 9.0	64.8 \pm 16.5
2014	57.7 \pm 55.9	–	8.2 \pm 8.2	2.7 \pm 2.7	6.7 \pm 5.1	10.9 \pm 2.5	14.6 \pm 8.1
2015	4.5 \pm 1.7	39.0 \pm 38.8	18.2 \pm 18.2	64.7 \pm 26.7	97.0 \pm 41.9	36.8 \pm 15.2	46.7 \pm 12.5
2016	2.8 \pm 1.6	14.9 \pm 14.8	13.0 \pm 12.9	37.4 \pm 22.9	38.5 \pm 12.6	59.5 \pm 22.5	29.1 \pm 7.1
$\bar{\varnothing}_{\text{Trans}}$	28.1 \pm 17.4	27.0 \pm 20.1	15.6 \pm 6.0	42.9 \pm 16.2	68.0 \pm 17.3	45.8 \pm 8.4	40.3 \pm 6.1

Note: $\bar{\varnothing}_{\text{Area}}$ = mean across the whole investigation area per year ($n = 21\text{--}35$). $\bar{\varnothing}_{\text{Trans}}$ = mean density across the whole investigation period per transect ($n = 12\text{--}25$). EF = region East Frisia, WE = region Weser, NF = region North Frisia.

off North Frisia (T1 and T2) and East Frisia (T4, 5, and 6), however, revealed a significantly lower density of larvae in the north than in the southwest (Mann–Whitney test, $p = .0341$).

The densities of larvae were fairly uniform across transects. Transects T3, T4 and T5 showed on average slightly increasing densities from the coast towards offshore (Figure 7). T4 and T5 off East

Frisia showed consistently high densities of larvae from shallow towards deeper waters. Average densities over depth strata ranged between 64.5 larvae per m^2 (10–<15 m) and 164.9 larvae per m^2 (30–<35 m). The Kruskal–Wallis test yielded a significant difference between depth strata ($p = .0162$) but Dunn's multiple comparison test could not identify differences between groups.

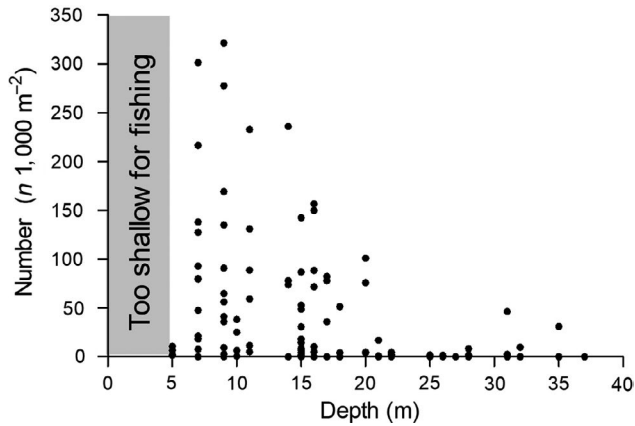


FIGURE 4 Distribution of ovigerous *Crangon crangon* across depth strata during spring 2013–2016

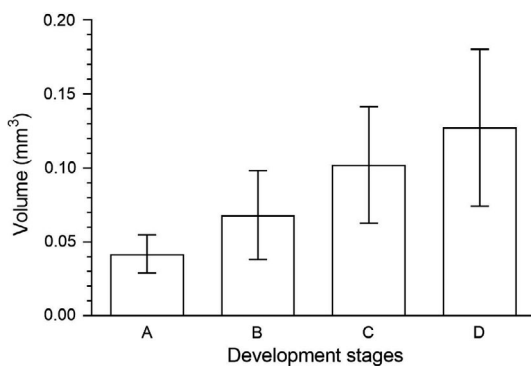


FIGURE 5 Volumes of egg stages A–D of *Crangon crangon*. Values are given as mean \pm SD ($n = 920$ – 1189). Kruskal–Wallis test, $p < .0001$

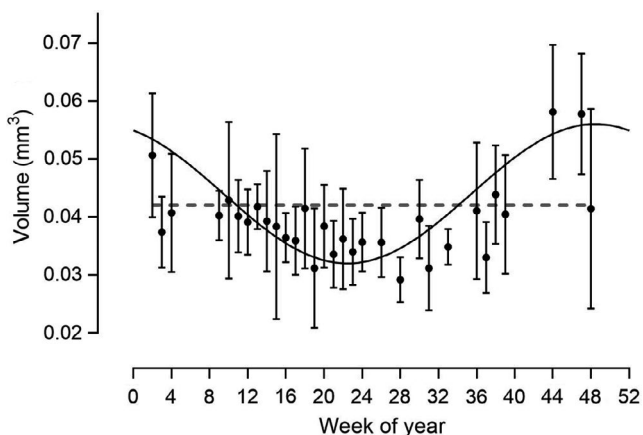


FIGURE 6 Intra-annual variation of *Crangon crangon* egg volume (stage A). Values are shown as mean \pm SD ($n = 10$ – 150). Kruskal–Wallis test, $p < .0001$. The dashed line indicates the annual mean volume of stage A eggs (0.042 mm^3). The annual course of egg volume is indicated by the sine curve

All larval stages (Z1–Z6) were present during the spring sampling (Figure 8). However, Z1 stages represented the major fraction and dominated particularly in 2014. In 2013, the distribution of larval stages was quite similar across all transects ($\chi^2 = 33.92$, $df = 16$,

$p = .0056$). From 2014 onward, higher shares of older larvae (Z2–Z6) appeared along transects T5, T6 and T4 (East Frisia and Weser). In 2014, the westernmost transect (T5) showed the highest share of older larvae ($>65\%$) and the other transects (T1–T4) only 15%–38% ($\chi^2 = 801.7$, $df = 20$, $p < .0001$). In 2015, older larvae dominated in transects T5 and T6 ($\chi^2 = 1,321$, $df = 25$, $p < .0001$) and in 2016 in transects T5, T6 and T4 ($\chi^2 = 608.8$, $df = 25$, $p < .0001$). Transects off North Frisia (T2 and T1) were dominated by Z1 larvae.

Larvae of all stages appeared in waters across the entire depth range (Figure 9). Zoa 1 stages were quite evenly distributed from the coast (5 m depth) towards the 35 m depth line. More than 60% of Z1 larvae were captured between the 15- and 30-m isobaths. Only 23% of the Z1 larvae appeared in shallower zones. Beyond the 30 m depth line, abundances of all larval stages declined distinctly. Z2 stages were more frequent in shallower waters <15 m (32%) than Z1 stages. The share of later stages (Z3–Z6) progressively increased in the shallow zones of <15 m ($\chi^2 = 2,162$, $df = 30$, $p < .0001$).

3.4 | Stock size development

The densities of brown shrimp in autumn as determined during the annual Demersal Young Fish Surveys (DYFS) varied between years (Figure 10). They decreased from 1904 individuals per 1,000 m^2 in 2013 to 1,476 individuals per 1,000 m^2 in 2015. 2016 was an exceptional poor year yielding only 211 individuals per 1,000 m^2 .

Our study showed no correlation between the densities of the adult *C. crangon* stock in autumn and the densities of larvae in spring ($r = -.07$, $p = .93$) and a moderate correlation to the densities of ovigerous females in spring ($r = .48$, $p = .51$; Table 3). The autumn brown shrimp stock showed a significant negative correlation to the same years abundance of whiting ($r = -.91$, $p = .03$; Table 3; for data on predator abundances see Table S5). Furthermore, densities of *C. crangon* larvae during spring showed a strong positive correlation to the abundance of ovigerous females of the respective following year ($r = .94$, $p = .22$).

The densities of *C. crangon* ovigerous females in spring indicated a strong negative correlation to the presence of predators of the previous year (all predators: $r = -.93$, $p = .06$; cod: $r = -.58$, $p = .42$; whiting: $r = -.73$, $p = .22$; crabs: $r = -.94$, $r = .07$). In contrast, the stock size of spring ovigerous females correlated positively to the same years predator densities during autumn ($r = .89$, $p = .11$).

The densities of both *C. crangon* ovigerous females during spring as well as of the *Crangon* stock during autumn correlated negatively with winter water temperatures (ovigerous females: $r = -.88$, $p = .12$; autumn stock: $r = -.63$, $p = .36$). In contrast, densities of *C. crangon* larvae correlated positively with winter water temperatures ($r = .72$, $p = .28$; Table 3).

4 | DISCUSSION

The reproductive effort of brown shrimp, *Crangon crangon*, is high. Females of, for example, 50 mm produce more than 3,000 eggs and the largest of them (>70 mm) even more than 10,000 (Havinga,

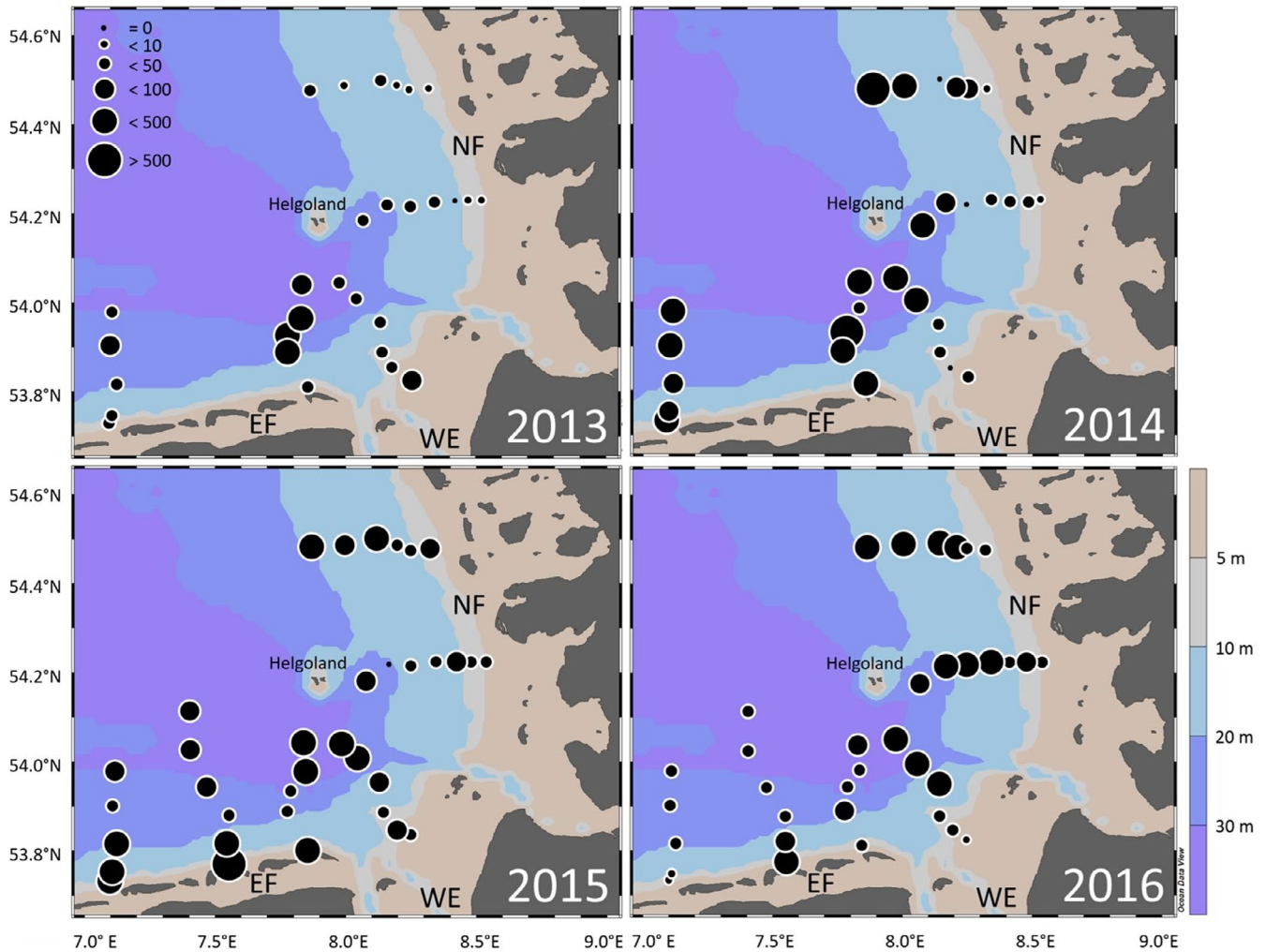


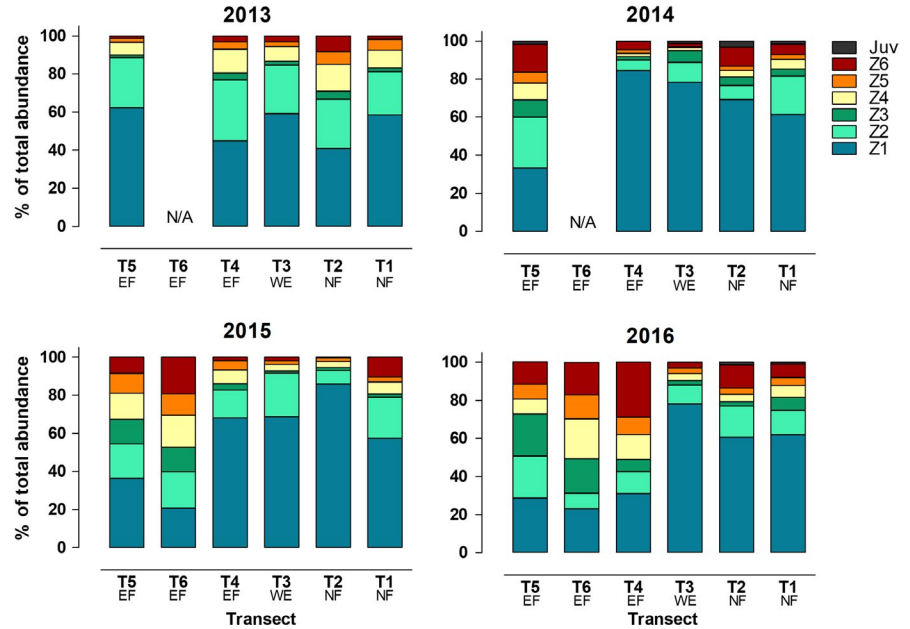
FIGURE 7 Distribution and density ($n\ m^{-2}$) of *Crangon crangon* larvae in the inner German Bight in spring 2013–2016. Details are listed in the Tables S3 and S4 [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Mean density ($n\ m^{-2}$) of *Crangon crangon* larvae sampled at different transects (sorted from W to E) during the spring surveys 2013–2016 ($n = 5-7$). Numbers in brackets display larvae density in $n\ m^{-3}$

Year	Transect						\emptyset_{Area}
	EF T5	EF T6	EF T4	WE T3	NF T2	NF T1	
2013	29.6 ± 8.3 (2.5 ± 0.9)	–	104.0 ± 24.5 (4.3 ± 1.0)	40.8 ± 7.1 (3.6 ± 1.2)	17.1 ± 7.1 (1.1 ± 0.4)	8.8 ± 1.9 (0.7 ± 0.1)	37.4 ± 7.6 (2.3 ± 0.4)
2014	136.2 ± 27.6 (10.0 ± 3.7)	–	312.0 ± 196.7 (12.8 ± 6.8)	66.2 ± 32.6 (3.5 ± 1.1)	54.3 ± 20.9 (3.9 ± 0.9)	213.0 ± 109.7 (14.2 ± 6.4)	148.1 ± 42.4 (8.5 ± 2.0)
2015	141.4 ± 41.7 (8.9 ± 3.6)	285.3 ± 194.1 (38.2 ± 33.9)	215.6 ± 80.1 (10.9 ± 5.4)	137.2 ± 62.6 (6.0 ± 1.6)	30.1 ± 8.7 (2.5 ± 0.8)	82.3 ± 27.0 (6.5 ± 1.5)	143.6 ± 37.7 (12.0 ± 5.8)
2016	15.4 ± 6.7 (0.8 ± 0.3)	55.5 ± 28.1 (3.9 ± 2.7)	43.8 ± 11.6 (2.1 ± 0.6)	98.7 ± 43.3 (4.3 ± 1.4)	112.0 ± 29.3 (8.3 ± 1.9)	119.8 ± 32.0 (8.2 ± 1.9)	77.8 ± 13.0 (4.9 ± 0.8)
\emptyset_{Trans}	80.7 ± 17.8 (5.5 ± 1.5)	170.4 ± 99.7 (21.0 ± 17.0)	168.9 ± 54.5 (7.5 ± 2.2)	85.7 ± 20.8 (4.4 ± 0.7)	53.4 ± 11.3 (4.0 ± 0.8)	106.0 ± 31.4 (7.4 ± 1.9)	

Note: \emptyset = mean across the whole investigation area per year ($n = 29-35$). \emptyset_{Trans} = mean density across the whole investigation period per transect ($n = 12-28$). EF = region East Frisia. WE = region Weser. NF = region North Frisia.

FIGURE 8 Frequency (%) of *Crangon crangon* zoea larval stages Z1–Z6 sampled at different transects (sorted from W to E) during spring 2013–2016. EF = East Frisia, WE = Weser Estuary, NF = North Frisia. Juv = juveniles/post-larvae. N/A = no data available [Colour figure can be viewed at wileyonlinelibrary.com]



1930). Following a typical phase III survivorship curve, only a very small share reach maturity (Hufnagl & Temming, 2011). Moreover, high mortality, particularly in early larval stages due to potential food limitation and/or high predation pressure, is compensated by repeated spawning and a long spawning season.

4.1 | Frequency and distribution of ovigerous females

The annual pattern of ovigerous females in our study deviated from that of Havinga (1930), who reported a gap of occurrence of egg-bearing females in February (see Figure S1). This previous observation served as an argument for the existence of separate summer and winter spawning events (Havinga, 1930). Similarly, the early researchers like Ehrenbaum (1890) and Meyer-Waarden (1935) reported two spawning seasons, one in spring/early summer and the other in winter. This observation could not be confirmed in the present study. In contrast, we observed a strong increase in the ratio of egg-bearing females from November to a maximum in February and

March, following by a successive decline towards October (Figure 2). Moreover, the present observations confirm previous findings based on a long-term study from 1958 to 1992 by Siegel et al. (2008) which also support the presence of one continuous spawning season starting in November rather than two separate spawning periods.

As the spawning season in the German Bight extends over several months, it potentially covers multiple spawning events. There have been controversial discussions on the number of spawning events, the duration of the spawning season and the synchronization of spawning events. In the German Bight, *C. crangon* females may spawn two to three times during the season (Ehrenbaum, 1890; Havinga, 1930; Meyer-Waarden, 1935; Tiewes, 1954). In an aquarium

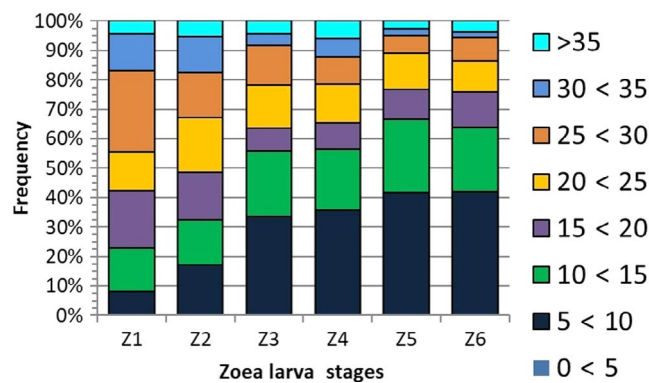


FIGURE 9 Frequency (%) of *Crangon crangon* zoea stage (Z1–Z6) across depth strata during spring 2013–2016 [Colour figure can be viewed at wileyonlinelibrary.com]

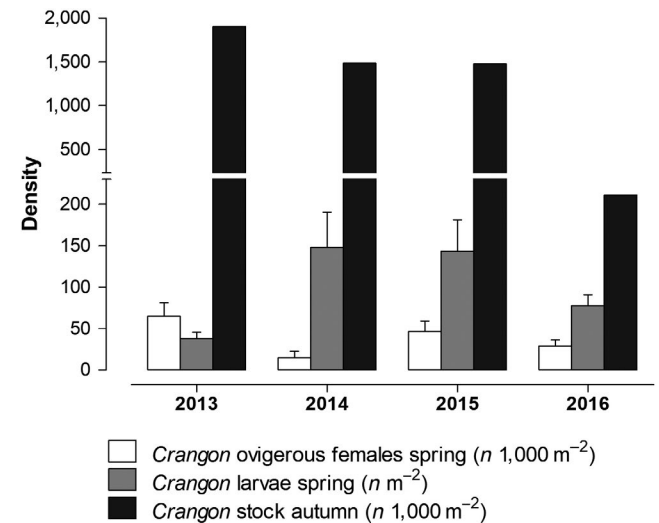


FIGURE 10 Mean density of *Crangon crangon* ovigerous females (n 1,000 m^{-2} ; white = spawning stock size) and *C. crangon* larvae sampled in spring (n m^{-2} ; grey = larval offspring) and adult *C. crangon* sampled in autumn (n 1,000 m^{-2} ; black = recruits of the year/prospective parent generation for the following year). Values are shown as mean \pm SEM

TABLE 3 Correlation coefficients (*r*) from Pearson's correlation. *Indicates significant correlation; n/a = not applicable

	Spring <i>Crangon</i> Larvae	Autumn <i>Crangon</i> stock	Spring ovigerous <i>Crangon</i> females following year	Spring <i>Crangon</i> Larvae following year	All predators (cod/whiting/portunid crabs)	All predators year before (cod/whiting/portunid crabs)	Winter water temperature
Spring ovigerous <i>Crangon</i> females	-0.71	0.48	n/a	n/a	0.89 (0.76/-0.19/0.85)	-0.93 (-0.73/-0.58/-0.94)	-0.88
Spring <i>Crangon</i> Larvae	n/a	-0.07	0.94	n/a	-0.47 (-0.75/-0.30/-0.43)	0.63 (0.60/0.36/0.63)	0.72
Autumn <i>Crangon</i> stock	n/a	n/a	-0.45	0.45	0.67 (0.53/-0.91*/0.73)	n/a	-0.63

experiment at 14°C water temperature, Meixner (1966) reported even up to five spawnings within 5 months. Due to the almost year-round presence of ovigerous females bearing all egg development stages, the spawning events seem not to be synchronized. Moreover, larger females spawn earlier than smaller ones (Henking, 1927; Tiews, 1954) which additionally obstruct a clear cohort pattern.

Ovigerous females were most abundant in shallow waters, preferably above the 20-m isobath. This pattern reflects the general depth distribution of *C. crangon* as reported by Siegel et al. (2005) and is in accordance with Tiews (1954) who reported that mating and spawning along the German coast take place on shallow (<20 m) muddy and sandy grounds. Accordingly, the preference of shallow waters explains the different abundances of ovigerous *Crangon* females between the East Frisian and the North Frisian transects. The North Frisian coast slopes down gently and continuously towards the central German Bight and provides a large shallow area which is preferred by *C. crangon*. The East Frisian coast, in contrast, is steeper and, thus, provides a smaller preferential area than the North Frisian coast. Therefore, the *C. crangon* densities at the outermost stations of the East Frisian transects are much lower than those at the North Frisian transects.

4.2 | Developmental stage and size of *Crangon* *crangon* eggs

The volumes of freshly spawned eggs (stage A) varied between seasons. Larger eggs were present during late fall and winter and smaller eggs during early summer to fall, whereas the overall share of egg-bearing females in early fall was negligible. These were previously denoted as 'winter eggs' and 'summer eggs' (Boddeke, 1982; Havinga, 1930). However, the seasonal pattern of egg size observed in our study does not match with the strict distinction of Havinga (1930) and Boddeke (1982) (see Figure S2). It rather confirms the observation of Urzúa, Paschke, Gebauer, and Anger (2012) who found no distinct separation between winter and summer eggs but suggested a continuous transition from larger to smaller eggs. Moreover, we observed the largest eggs to appear at the beginning of the spawning period, which we schedule to start in November.

The larger eggs reflect an enhanced maternal energy investment to the embryo but do not increase the overall energy demand of the female. The biochemical gross composition does not differ

qualitatively but quantitatively between larger and smaller eggs but females produce significantly less large eggs in winter than small eggs in summer (Urzúa & Anger, 2013). The larger eggs contain more nutrients and enable the early hatching larvae to better cope with poor nutritive conditions in early spring and, particularly, if larvae hatch before the onset of the phytoplankton spring bloom (Urzúa & Anger, 2013). Paschke, Gebauer, Buchholz, and Anger (2004) showed significantly higher starvation resistance of larvae hatched from larger eggs compared with those from the smaller eggs. Such maternal or carry-over effect is not unique for *C. crangon* but was also described in other crustacean species, such as the copepods *Calanus helgolandicus* and *C. finmarchicus*, which are exposed to distinct seasonal cycles of production and food availability (Jónasdóttir, Trung, & Hansen, 2005; Pond, Harris, Head, & Harbour, 1996).

All developmental stages of eggs appeared simultaneous over the reproductive season. This was also observed by Havinga (1930) and reflects the widely unsynchronized and continuous reproductive activity of *C. crangon*. Maturity and first spawning were reported to appear earliest in January (Henderson & Holmes, 1987; Kuipers & Dapper, 1984). Highest frequency of late egg developmental stages (shortly before hatching) occur in April/May and, thus, maximum numbers of larvae appear in the upcoming months (Boddeke, 1982).

4.3 | Distribution and abundance of *Crangon* *crangon* larvae

In our study, ovigerous *Crangon* females were frequent along the coast at depths of 20 m and less. Therefore, this area may be considered the preferred hatching region. Plett (1965) reported highest larvae occurrence between the 10- and the 20-m isobaths along the East Frisian coast. In the area between the North Frisian coast off Büsum and the island of Helgoland, the area of high larvae densities extended further seaward almost reaching Helgoland. The average larvae densities in our study ranged between 38 and 178 specimen per m², whereas maximum numbers in 2014 and 2015 often exceeded 200 larvae per m² and reaching 1,244 per m² in East Frisia. For the year 1963, Plett (1965) reported densities of 100–450 larvae per m² off East Frisia and 800–2,500 larvae per m² off the Elbe estuary. In 1964, larvae densities were distinctly different showing lower values of about 300 larvae per m² off the Elbe estuary, indicating strong variability between years.

Freshly hatched larvae can drift with the currents along the coast to shallower and warmer waters where they continue their development over six larval stages, finally reaching the epibenthic juvenile stage. However, the spatial distribution of larvae in the study area and their frequency distribution within depth zones indicate that larvae appear throughout the inner German Bight. Freshly hatched Z1 larvae even prefer a region further offshore along the 25–30 m depth lines. *C. crangon* Z1 larvae and later stages appeared regularly in spring and summer distant from the coast. Wehrtmann (1989) found highest densities of *Crangon* larvae in late June and August 1985 at Helgoland Roads reaching 6–7 individuals per cubic metre. *Crangon crangon* Z1 stages appeared first in May and peaked in June, quite late in the season, probably because of the cold winter 1984/85 (Wehrtmann, 1989). These numbers correspond well with our data, which generally ranged between 1 and 14 larvae per cubic metre close to Helgoland. Only at one occasion, we found an exceptional high number of 38 larvae per cubic metre (Table 2). With the progress of development, the larvae shift towards the coasts and the majority of the Z5 and Z6 stages appear in waters shallower than 15 m. Although the preferred settlement grounds of the majority of juveniles are the shallow sandy Wadden areas (Kühl & Mann, 1963), our results indicate that major hatching does not only take place close to the coastline but also in more distant and, thus, deeper areas of the German Bight.

The duration of the development of eggs and larvae depends on water temperature. The colder the winter, the later in the year the larvae hatch and the later the post-larvae reach the Wadden areas to settle (Wear, 1974). Accordingly, follow-up spawnings will delay as well. Larval maximum may appear very variably between years. Kühl and Mann (1963) indicated June as the month of the second larval maximum in the Elbe estuary. This was also reported by Oh and Hartnoll (2004) for the Irish Sea. Other authors dated the second larval appearance in the North Sea over a much wider period, for example March to September (Boddeke, 1982), April to August (Kuipers & Dapper, 1984) and April to July (Neudecker & Damm, 1992). Henderson and Holmes (1987) report the main larval appearance in the Bristol Channel between March and July, which concurs with our data from 2012 showing a rapid decline in larval occurrence from August onwards. Because of the multiple and continuous spawning during a long period of the year (with a reproductive minimum in September/October), identification of distinct cohorts or year classes appears unreliable.

Our results provide some indication that larval development may appear earlier in the season in the southwestern transects than in the northern parts. Although the survey of 2013 showed a quite similar distribution of larval stages between transects, the picture changed in the upcoming years 2014–2016. The southwestern stations showed a higher diversity of larval stages than the northern ones where Z1 stages dominated, suggesting that off East Frisia the majority of Z1 stages already grew into older stages. Indeed, due to the prevailing currents, average seawater winter temperatures are more than 1°C higher at the east Frisian coast than at the north

Frisian coast (Becker, Frey, & Wegner, 1986), thus accelerating larval development.

These results also indicate that a long-distance transport of larvae with the major currents along the coast from southwest to northeast appears unlikely. If this was the case, the more developed larval stages should appear in North Frisian waters furthest away from their putative spawning habitat in the southwest. In the North Frisian waters, however, we mostly found the earliest stages Z1, which indicates that these larvae are of local origin and hatched at least in close vicinity. The strong mesoscale variability of the German Bight hydrography is fairly well documented (Becker, Dick, & Dippner, 1992) and is probably responsible for the local and temporal variability in larval dispersion.

4.4 | Stock size development

Prediction of the upcoming *C. crangon* stock size for management purpose has been difficult since (Campos et al., 2010; Schulte et al., 2018; Temming & Damm, 2002). Nevertheless, Driver (1976) could demonstrate a correlation between a year's shrimps landings and the previous year's landings off Lancashire (Irish Sea) by multiple regression analysis including weather data. Campos et al. (2010) identified predator abundance as major factor correlated with shrimp abundance in autumn and found a positive relationship between spring and autumn abundance and annual commercial landings. Siegel et al. (2005) confirmed the complex interplay of various factors finally determining the stock size of shrimps in autumn. On a large spatial scale, shrimp abundance in autumn was positively correlated with low winter water temperature, high autumn river runoff and the low winter NAO index, which triggers the wind-driven circulation. In the same analysis, predators (fish) also played an important role in those years when they were exceptionally abundant.

In our study, a large stock of ovigerous females in 2013 was accompanied by a low number of larvae, whereas a low stock in 2014 yielded high numbers of larvae. In 2016, the frequency of ovigerous females was approximately as high as in 2015 but the number of larvae was distinctly lower in 2016 than in 2015. Though data are few, a negative correlation between numbers of ovigerous females and numbers of larvae was evident over the years of investigation. These results may be explained by the sampling strategy. Ovigerous females and larvae were sampled at the same time during the fixed survey periods in spring around the expected maximum of larvae occurrence. If the ovigerous females still carried their first clutch of eggs, then they could not have contributed to the larvae stock. This means that the earlier the sampling happened ahead of the spawning peak (which can vary between years; see '4.3 Distribution and abundance of *Crangon crangon* larvae'), the lower the relative ratio between larvae and ovigerous females will be, but will increase towards peak hatching. Our data from 2013 and 2016 may indicate such early sampling.

Furthermore, our study showed no correlation between the density of larvae in spring and the density of the adult stock in autumn. Average or relatively low numbers of larvae seem to allow for

a relatively high stock recruitment in the following autumn like in 2013. In 2016, larval density was low and, likewise, yielded an extremely low stock size. 2016, however, was exceptional due to high predation pressure by jellyfish in spring and by whiting in late summer (own data, Table S3). Accordingly, prediction from spring larvae density to recruitment success in autumn appears still uncertain and needs further investigation.

4.5 | Regulation and control of *Crangon* population

Factors determining stock size of *C. crangon* act during the entire life cycle, and overall mortality of *C. crangon* is very high. Only about 1% or less of the juveniles from the so-called 'winter egg cohort' reach a size of 50 mm in autumn (Hufnagl & Temming, 2011). Mortality may peak during critical phases of the life cycle like the larval stages and the transitions from the pelagic to the benthic mode of life. Therefore, we complement our study by considerations on the major factors regulating and controlling the population development of *C. crangon* in the North Sea.

4.5.1 | Winter water temperature

Onset and peak of larvae hatching vary between years and between regions (Tiews, 1970). This variation is related to water temperature. Below, approx. 4°C embryogenesis and oogenesis as well as larval development is arrested (Paschke, 1998; Wear, 1974). Cold winters will delay larval development, and peak spawning will appear late, in May or even June (Siegel et al., 2005). Late hatching larvae, however, may not reach commercial size until autumn (Kuipers & Dapper, 1984). High winter water temperatures, in contrast, accelerate the development of embryos and may trigger early hatching, occasionally already starting in January or February or even in December as observed by Kühl and Mann (1963) and in the present study. Accordingly, peak hatching may also appear earlier in the year. The earliest larvae, although hatched from energy-rich early eggs may miss the onset of the spring plankton bloom and, thus, may starve or even die.

4.5.2 | Food availability

Up to 75% of the *C. crangon* population showed signs of starvation in winter between November and April (Hufnagl, Temming, Dänhardt, & Perger, 2010). The authors, however, concluded that food limitation predominantly impairs growth performance rather than mortality. In the Bristol Channel, winter mortality of *C. crangon* varied with population size but resulted in a quite stable adult population in the upcoming spring (Henderson, Seaby, & Somes, 2006).

While larval development and hatching depend on temperature, larval survival relies on sufficient food supply (Criales & Anger, 1986; Paschke et al., 2004). Decapod larvae are opportunistic carnivorous. The main food source for *C. crangon* larvae is (micro-) zooplankton and larger phytoplankton (Criales, 1985; Criales & Anger, 1986). The concentration of phytoplankton (chlorophyll a) may serve as a

measure for the productivity of a system. The start and intensity of the bloom is mainly based on light (sun hours), temperature and nutrient availability (Siegel et al., 2005; Wiltshire et al., 2015). With regard to the latter, Siegel et al. (2005) found a significant positive correlation between Elbe river runoff in autumn and the shrimp stock density during autumn of the following year. The authors related an increased river runoff to an increased nutrient input into the system. This would trigger a higher plankton production in spring and, hence, support growth and survival of the *C. crangon* offspring.

In the German Bight, the diatom spring bloom starts between end of March (week 12) and end of April (week 18) (Wiltshire et al., 2015) and small zooplankton grazers follow with a time lag of about 2 weeks (Greve, Reiners, Nast, & Hoffmann, 2004). With one exception, the seasonal pattern of primary production is in accordance with the conditions during our study period. Satellite images from 2012 to 2015 show highest chlorophyll a concentration in March and April (Figure S3). In contrast, 2016 display lowest chlorophyll a concentrations throughout the whole spring season (March to May). During that time, larvae density was intermediate and larval development was advanced compared with the other sampling years. 2016 was preceded by a warm winter. Larvae hatching may therefore have occurred early that year and may have resulted in the above-mentioned mismatch scenario, suppressing larval survival. Additionally, this mismatch may have coincided with the high predation pressure in 2016, which would explain the exceptional low *C. crangon* abundance in autumn 2016.

4.5.3 | Predation

Tiews (1965) estimated that in earlier years, the loss of the shrimp stock by predation was much higher than the landings by fisheries. A negative correlation between predator abundance and landing in the subsequent year indicates predation as controlling factor of size, density and size composition of the *C. crangon* population. Campos et al. (2010) found that predator abundance, particularly fishes and unspecified decapods, was the main factor correlated to *C. crangon* abundance, explaining up to 55% of variance in spring and up to 85% in autumn. The authors, however, did not consider pelagic predators like jellyfish and their impact on the larvae population.

During the larval survey in April 2016, the share of ovigerous females was high and the total density of females was average. However, the number of larvae was rather low. Medusae and ctenophores were already frequent in April/May in our plankton nets (Siegel, V., unpublished data) and may have caused a severe grazing impact on pelagic *Crangon* larvae. The prey of scyphomedusae in the Southern North Sea ranges from small mm-sized copepods to almost 1-cm-long fish larvae (Barz & Hirche, 2007). The size of *Crangon* larvae (ca. 2–5 mm; Criales, 1985) matches exactly the prey size spectrum of scyphomedusae. Hence, although the predation of *C. crangon* larvae by jellyfish has not been quantified, it can be assumed that in 2016, a significant share of the pelagic *C. crangon* larvae was captured by jellyfish.

Different to the pelagic larvae, the major predators of juvenile (and adult) epibenthic *C. crangon* are juvenile fish. Boddeke (1978) reported on high predation pressure by juvenile 1-year-old cod mainly in the period from October to April (see also Jansen, 2002). Small fish like the sand goby (*Pomatoschistus minutus*) feed as well on small juvenile *C. crangon* (Hamerlynck & Cattrijsse, 1994; Salgado, Nogueira Cabral, & Costa, 2004). Many other fish species feed on juvenile and adult *C. crangon*, mostly whiting (*Merlangius merlangus*) and cod (*Gadus morhua*) but also armed bullhead (*Agonus catapraectus*), short spined sea scorpion (*Myoxocephalus scorpius*), rockling (*Ciliata mustela*) or gunnel (*Pholis gunnellus*) (Kühl, 1961; Tiews, 1965). In certain years, mass occurrences of juvenile gadoid fishes (whiting and cod) caused severe extinctions of the shrimp populations and entailed collapses of shrimp fisheries (Berghahn, 1996). Summer and autumn 2016 also showed high abundances of whiting. The low numbers of *C. crangon* recruits in September indicate high predation pressure. Thus, 2016 was a year where both pelagic larvae and epibenthic juveniles and adults were strongly diminished. However, the shrimp population can recover rapidly already in the following year as could be demonstrated for the extremely low stock size in 1990 and its recovery within 1–2 years (Siegel et al., 2008).

Additionally, swimming crabs of the genus *Liocarcinus* are serious benthic predators of juvenile *C. crangon* which have just switched from a pelagic larval to a benthic juvenile phase. About 50% of the foregut content of *Liocarcinus holsatus* consisted of juvenile *C. crangon* (Choy, 1986). Predation by the green shore crab *Carcinus maenas* and cannibalism was reported by Pihl and Rosenberg (1984) and Pihl (1985). The extent of predation by other decapods is widely unknown but may represent a critical factor in the different phase of the life cycle of *C. crangon*.

4.5.4 | Fisheries

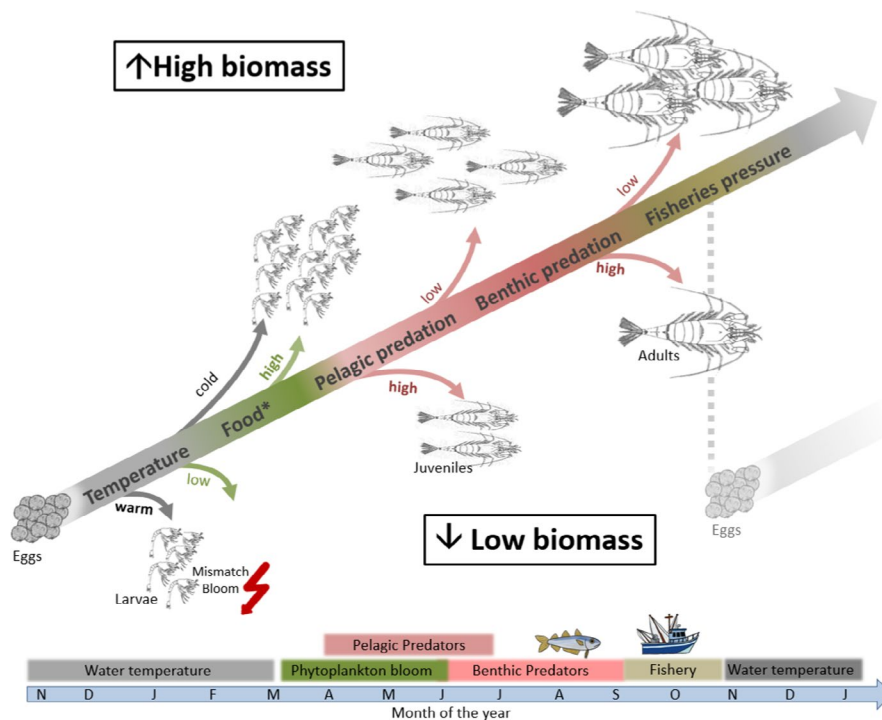
The total annual landings of *C. crangon* in the North Sea exceeded 30,000 tons in 1997 and increased thereafter towards 37,000 tons in 2015. Landings are about 40% higher than in the 1980s and 1990s. However, due to diverse processes after catch (such as two sieving and selection steps on board vessel: one before and another after boiling), the true fishing mortality is much higher than the landing values. Neudecker, Damm, and Kühnhold (2006) estimated the loss by discard to about the same amount as the landings. Accordingly, about 70,000 tons of *C. crangon* would be removed from the North Sea stock every year.

Considering the decline of key predators of *C. crangon* in the North Sea during the last decades, Temming and Hufnagl (2015) demonstrated that at the end of the 1990s fishing mortality on animals larger than 50 mm began to dominate over mortality by predation. However, despite the recent increase in landings, both Neudecker et al. (2006) and Temming and Hufnagl (2015) found no signs of overfishing. Siegel et al. (2005) also concluded that the shrimp fishery had only a minor effect on stock size. In a long-term study (1973–2003), the authors found fishery data only explaining <5% of the variance in *Crangon* stock variability. The variability was rather explained by other physical and biological variables, especially temperature and predator presence.

5 | SUMMARY

Ovigerous females, larvae and the stock of *Crangon crangon* showed high interannual variability. We found no correlation between the abundance of ovigerous females and larvae in spring

FIGURE 11 From egg to commercial size in one year. Conceptual presentation of how different factors may influence the life cycle of *Crangon crangon*. Drawings of *C. crangon* eggs, larvae and adults were obtained from Ehrenbaum (1890), Meredith (1952) and Gurney (1982). *Food availability is positively correlated to autumn river runoff (Siegel et al, 2008) [Colour figure can be viewed at wileyonlinelibrary.com]



and the *Crangon* stock in autumn. Neither did we see a relation between the stock size in autumn and the number of offspring in the following year. However, a close and significant inverse relation was evident between the abundance of predators and the stock in autumn. The life history traits of *Crangon crangon* are subject to the seasonal interplay of multiple abiotic and biotic factors (Figure 11) like the winter water temperature, the seasonal cycles of primary and secondary production, the impact of predators and fisheries. Prediction of stock size development is hampered by the gap of knowledge of mortality within each of the ontogenetic stages. Apparent critical phases like the transition from the pelagic to the benthic life style and the early benthic juvenile stages need more detailed investigation. Prospectively, monitoring of juvenile is required to fill the present gap of knowledge in population development between larvae and adults. Additionally, a more intensive monitoring of predators, including jellyfish and portunid crabs, will provide better estimates on the mortality of pelagic larvae and early benthic juveniles.

ACKNOWLEDGEMENTS

We are grateful to Captain Thomas Semrau from the cutter 'Glückauf' (Tönning) for weekly shrimp sampling and the captain and crew of RV Uthörn for their great support during the annual larval survey. We greatly acknowledge the technical assistance at sea and in the laboratory of Karin Krüger and Thomas Kehlert. Thanks are also due to Susanne Schöling and Gitta Hemken for technical assistance in the laboratory.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest regarding the publication of this article.

AUTHOR CONTRIBUTIONS

VS and RS designed the study, supervised the data collection and drafted the initial version of the manuscript. KH, RS and VS analysed the results and produced the figures. The statistical analyses were conducted by KH and RS. KH and RS drafted and edited the final manuscript, critically revised the paper and provided comments on revisions.

DATA AVAILABILITY STATEMENT

The data that support this study are available from the authors upon reasonable request.

ORCID

Kim Hünerlage  <https://orcid.org/0000-0002-1997-4556>

Reinhard Saborowski  <https://orcid.org/0000-0003-0289-6501>

REFERENCES

- Barz, K., & Hirche, H.-J. (2007). Abundance, distribution and prey composition of scyphomedusae in the southern North Sea. *Marine Biology*, 151, 1021–1033. <https://doi.org/10.1007/s00227-006-0545-4>
- Becker, G. A., Dick, S., & Dippner, J. W. (1992). Hydrography of the German bight. *Marine Ecology Progress Series*, 91, 9–18. <https://doi.org/10.3354/meps091009>
- Becker, G. A., Frey, H., & Wegner, G. (1986). *Atlas der Temperatur an der Oberfläche der Nordsee. Wöchentliche und monatliche Mittelwerte für den Zeitraum 1971 bis 1980* (p. 127). Deutsche Hydrografische Zeitschrift, Ergänzungsheft Reihe B, Nr. 17.
- Berghahn, R. (1996). Episodic mass invasions of juvenile Gadoids into the Wadden Sea and their consequences for the population dynamics of Brown shrimp (*Crangon crangon*). *Marine Ecology*, 17, 251–260. <https://doi.org/10.1111/j.1439-0485.1996.tb00506.x>
- Boddeke, R. (1978). *Changes in the stock of brown shrimp (Crangon crangon L.) in the coastal area of the Netherlands. Rapports et Procès-verbaux des Réunion. Conseil International pour l'Exploration de la Mer*, 172, 239–249.
- Boddeke, R. (1982). The occurrence of winter and summer eggs in the brown shrimp (*Crangon crangon*) and the pattern of recruitment. *Netherlands Journal of Sea Research*, 16, 151–162. [https://doi.org/10.1016/0077-7579\(82\)90026-6](https://doi.org/10.1016/0077-7579(82)90026-6)
- Boddeke, R. (1986). Food availability and predator presence in a coastal nursery area of the brown shrimp (*Crangon crangon*). *Ophelia*, 26, 77–90. <https://doi.org/10.1080/00785326.1986.10421980>
- Boddeke, R., Clerck, R. D., Daan, N., Müller, A., Postuma, K. H., Veen, J. F., & Zijlstra, J. J. (1972). Young fish and brown shrimp surveys in the North Sea. *Annales Biologiques*, 27, 183–187.
- Campos, J., Bio, A., Cardoso, J. F. M. C., Dapper, R., Witte, J. I. J., & van der Veer, H. W. (2010). Fluctuations of brown shrimp *Crangon crangon* abundance in the western Dutch Wadden Sea. *Marine Ecology Progress Series*, 405, 203–219. <https://doi.org/10.3354/meps08493>
- Campos, J., Bio, A., Freitas, V., Moreira, C., & van der Veer, H. W. (2013). Age estimation of brown shrimp *Crangon crangon* (L.): Comparison of two approaches applied to populations at the biogeographic edges. *Aquatic Biology*, 19, 167–184. <https://doi.org/10.3354/ab00524>
- Campos, J., & van der Veer, H. (2008). Autecology of *Crangon crangon* (L.) with an emphasis on latitudinal trends. *Oceanography and Marine Biology: an Annual Review*, 46, 65–104. <https://doi.org/10.1201/9781420065756.ch3>
- Choy, S. C. (1986). Natural diet and feeding habits of the crabs *Liocarcinus puber* and *L. holsatus* (Decapoda, Brachyura, Portunidae). *Marine Ecology Progress Series*, 31, 87–99. <https://doi.org/10.3354/meps031087>
- Criales, M. M. (1985). *Untersuchungen zur Larvalentwicklung von Crangon crangon L. und Crangon allmanni Kinhan (Decapoda, Natania, Caridea)* (p. 179). Dissertation, Mathematisch-Naturwissenschaftliche Fakultät, Universität Kiel, Germany.
- Criales, M. M., & Anger, K. (1986). Experimental studies on the larval development of the shrimps *Crangon crangon* and *C. allmanni*. *Helgoländer Meeresuntersuchungen*, 40, 241–265. <https://doi.org/10.1007/BF01983735>
- Driver, P. A. (1976). Prediction of fluctuations in the landings of brown shrimp (*Crangon crangon*) in the Lancashire and Western Sea Fisheries District. *Estuarine and Coastal Marine Science*, 4, 567–573. [https://doi.org/10.1016/0302-3524\(76\)90031-1](https://doi.org/10.1016/0302-3524(76)90031-1)
- Ehrenbaum, E. (1890) *Zur Naturgeschichte von Crangon vulgaris Fabr., Studien über Bau, Entwicklung, Lebensweise und Fangverhältnisse des Nordsee-Granat* (p. 124). Sonderbeilage zu den Mitteilungen der Sektion für Küsten- und Hochseefischerei 1890.
- Greve, W., Reiners, F., Nast, J., & Hoffmann, S. (2004). Helgoland Roads meso- and macrozooplankton time-series 1974 to 2004: Lessons from 30 years of single spot. High frequency sampling at the only

- off-shore island of the North Sea. *Helgoland Marine Research*, 58, 274–288. <https://doi.org/10.1007/s10152-004-0191-5>
- Gurney, A. R. (1982). The larval development of *Crangon crangon* (Fabr. 1795) (Crustacea: Decapoda). *Bulletin of the British Museum (Natural History)*, 42, 247–262.
- Hamerlynck, O., & Cattrijsse, A. (1994). The food of *Pomatoschistus minutus* (Pisces, Gobiidae) in Belgian coastal waters and a comparison with the food of its potential competitor *P. lozanoi*. *Journal of Fish Biology*, 44, 753–771. <https://doi.org/10.1111/j.1095-8649.1994.tb01253.x>
- Havinga, B. (1929). Krebse und Weichtiere: Granat; Krebse. In A. Willer (Eds.), *Handbuch der Seefischerei Nordeuropas, Band III, Systematik und Biologie anderer wirtschaftlich wichtiger Meerestiere Nordeuropas, Heft, Vol. 2* (pp. 53–62). Stuttgart, Germany: E.Schweizerbart'sche Verlagsbuchhandlung (Erwin Nägele).
- Havinga, B. (1930). *Der Granat (Crangon vulgaris Fabr.) in den holländischen Gewässern*. *Journal Du Conseil-Conseil Permanent International Pour L'exploration De La Mer*, 5, 57–87.
- Henderson, P. A., & Holmes, R. H. A. (1987). On the population biology of the common shrimp *Crangon crangon* (L.) (Crustacea: Caridea) in the Severn Estuary and Bristol Channel. *Journal of the Marine Biological Association of the United Kingdom*, 67, 825–847. <https://doi.org/10.1017/S0025315400057076>
- Henderson, P. A., Seaby, R. M., & Somes, J. R. (2006). A 25-year study of climatic and density-dependent population regulation of common shrimp *Crangon crangon* (Crustacea: Caridea) in the Bristol Channel. *Journal of the Marine Biological Association of the United Kingdom*, 86, 287–298. <https://doi.org/10.1017/S0025315406013142>
- Henking, H. (1927). Der Fang der Nordseegarnelen (*Crangon vulgaris* L.) in der Ostsee. *Mitteilungen Des Deutschen Seefischerei-Vereins*, 43, 2–14.
- Hufnagl, M., & Temming, A. (2011). Growth in the brown shrimp *Crangon crangon*. II Meta-analysis and modelling. *Marine Ecology Progress Series*, 435, 155–172. <https://doi.org/10.3354/meps09224>
- Hufnagl, M., Temming, A., Dänhardt, A., & Perger, R. (2010). Is *Crangon crangon* (L. 1758, Decapoda, Caridea) food limited in the Wadden Sea? *Journal of Sea Research*, 64, 386–400. <https://doi.org/10.1016/j.seares.2010.06.001>
- Hufnagl, M., Temming, A., Siegel, V., Tulp, I., & Bolle, L. (2010). Estimating total mortality and asymptotic length of *Crangon crangon* between 1955 and 2006. *ICES Journal of Marine Science*, 67, 875–884. <https://doi.org/10.1093/icesjms/fsq003>
- Jansen, S. (2002). *Das Räuber-Beutesystem juveniler Gadiden, Grundeln und Garnelen im Wattenmeer nördlich von Sylt* (p. 155). Dissertation, University of Hamburg, Germany.
- Jónasdóttir, S. H., Trung, N. H., & Hansen, F. (2005). Egg production and hatching success of the Calanoid copepods *Calanus helgolandicus* and *Calanus finmarchicus* in the North Sea from March to September 2001. *Journal of Plankton Research*, 27, 1239–1259. <https://doi.org/10.1093/plankt/fbi091>
- Kühl, H. (1961). Nahrungsuntersuchungen an einigen Fischen im Elbe-Mündungsgebiet. *Berichte Der Deutschen Wissenschaftlichen Kommission Für Meeresforschung*, 16(2), 90–104.
- Kühl, H., & Mann, H. (1963). Das Vorkommen der Garnelenlarven (*Crangon crangon* L.) in der Elbmündung. *Archiv Für Fischereiwissenschaften*, 14, 1–7.
- Kuipers, B. R., & Dapper, R. (1984). Nursery function of Wadden Sea tidal flats for the brown shrimp *Crangon crangon*. *Marine Ecology Progress Series*, 17, 171–181. <https://doi.org/10.3354/meps017171>
- Lloyd, A. J., & Yonge, C. M. (1947). The Biology of *Crangon vulgaris* L in the Bristol Channel and Severn Estuary. *Journal of the Marine Biological Association of the United Kingdom*, 26, 626–661.
- Lotze, H. K. (2007). Rise and fall of fishing and marine resource use in the Wadden Sea, southern North Sea. *Fisheries Research*, 87, 208–218. <https://doi.org/10.1016/j.fishres.2006.12.009>
- Meixner, R. (1966). *The effects of food supply on moulting, growth and spawning of the shrimp Crangon crangon* (L.) (p. 7). ICES C.M.1966/M:5, Shellfish committee.
- Meredith, S. S. (1952). A study of *Crangon vulgaris* in the Liverpool Bay area. *Proceedings and Transactions of the Liverpool Biological Society*, 58, 75–110.
- Meyer-Waarden, P. F. (1935). Wachstum und Altersuntersuchungen an der Nordseekrabbe (Granat) *Crangon vulgaris* Fabr. *Zoologischer Anzeiger*, 111, 145–152.
- Neudecker, T., & Damm, U. (1992). Seasonality of egg-bearing shrimp (*Crangon crangon* L.) in coastal waters of the German Bight (p. 10). ICES C.M.1992/K:28, Shellfish committee.
- Neudecker, T., Damm, U., & Kühnhold, W. (2006). *Fang, Anlandungen, Discard und Bestand der Nordseegarnele (Crangon crangon L.)*. Informationen Für Die Fischwirtschaft, 53, 82–85.
- Oh, C.-W., & Hartnoll, R. G. (2004). Reproductive biology of the common shrimp *Crangon crangon* (Decapoda: Crangonidae) in the central Irish Sea. *Marine Biology*, 144(2), 303–316. <https://doi.org/10.1007/s00227-003-1205-6>
- Paschke, K. (1998). *Untersuchungen zum Energiestoffwechsel während der Embryonalentwicklung der Nordseegarnele Crangon crangon (Linnaeus 1758) (Decapoda: Caridea)* (p. 93). Dissertation, Universität Hamburg, Germany.
- Paschke, K. A., Gebauer, P., Buchholz, F., & Anger, K. (2004). Seasonal variation in starvation resistance of early larval North Sea shrimp *Crangon crangon* (Decapoda: Crangonidae). *Marine Ecology Progress Series*, 22, 169–179. <https://doi.org/10.3354/meps279183>
- Pihl, L. (1985). Food selection and consumption of mobile epibenthic fauna in shallow marine areas. *Marine Ecology Progress Series*, 22, 169–179. <https://doi.org/10.3354/meps022169>
- Pihl, L., & Rosenberg, R. (1984). Food selection and consumption of the shrimp *Crangon crangon* in some shallow marine areas in western Sweden. *Marine Ecology Progress Series*, 15, 159–168. <https://doi.org/10.3354/meps015159>
- Plett, A. (1965). Über das Vorkommen von Garnelenlarven (*Crangon crangon* L.) vor der Deutschen Küste in den Jahren 1963 und 1964. *Archiv Für Fischereiwissenschaft*, 16, 54–67.
- Pond, D. W., Harris, R. P., Head, R. N., & Harbour, D. (1996). Environmental and nutritional factors determining seasonal variability in the fecundity and egg viability of *Calanus helgolandicus* in coastal waters off Plymouth, UK. *Marine Ecology Progress Series*, 143, 45–63. <https://doi.org/10.3354/meps143045>
- Reiser, S., Herrmann, J.-P., Neudecker, T., & Temming, A. (2014). Lower thermal capacity limits of the common brown shrimp (*Crangon crangon*, L.). *Marine Biology*, 161, 447–458. <https://doi.org/10.1007/s00227-013-2350-1>
- Reiser, S., Herrmann, J.-P., & Temming, A. (2014). Thermal preference of the common brown shrimp (*Crangon crangon*, L.) determined by the acute and gravitational method. *Journal of Experimental Marine Biology and Ecology*, 461, 250–256. <https://doi.org/10.1016/j.jembe.2014.08.018>
- Saborowski, R., Schatte, J., & Gimenez, L. (2012). Catalytic properties an polymorphism of serine endopeptidases from the midgut gland of the brown shrimp *Crangon crangon* (Decapoda, Caridea). *Marine Biology*, 159, 1107–1118. <https://doi.org/10.1007/s00227-012-1890-0>
- Salgado, J. P., Nogueira Cabral, H., & Costa, M. J. (2004). Feeding ecology of the gobies *Pomatoschistus minutus* (Pallas, 1770) and *Pomatoschistus microps* (Krøyer, 1883) in the upper Tagus estuary, Portugal. *Scientia Marina*, 68(3), 425–434.
- Schulte, K. F., Dänhardt, A., Hufnagl, M., Siegel, V., Wosniok, W., & Temming, A. (2018). Not easy to catch: Multiple co-variables influence catch rates of brown shrimp (*Crangon crangon* L.), potentially affecting inferences drawn from catch and landings data. *ICES Journal of Marine Science*, 75, 1318–1328. <https://doi.org/10.1093/icesjms/fsx203>

- Siegel, V., Damm, U., & Neudecker, T. (2008). Sex-ratio, seasonality and long-term variation in maturation and spawning of the brown shrimp *Crangon crangon* (L.) in the German Bight (North Sea). *Helgoland Marine Research*, 62, 339–349. <https://doi.org/10.1007/s10152-008-0121-z>
- Siegel, V., Gröger, J., Neudecker, T., Damm, U., & Jansen, S. (2005). Long-term variation in the abundance of the brown shrimp *Crangon crangon* (L.) population of the German Bight and possible causes for its interannual variability. *Fisheries Oceanography*, 14, 1–16. <https://doi.org/10.1111/j.1365-2419.2004.00301.x>
- Spaargaren, D. H. (2000). Seasonal and annual variations in the catches of *Crangon crangon*, (L., 1758) (Decapoda, Natantia) near the coast of Texel, The Netherlands. *Crustaceana*, 73(5), 547–563. <https://doi.org/10.1163/156854000504651>
- STECF (2016). *Scientific technical and economic committee for fisheries-the 2016 annual economic report on the eu fishing fleet (STECF 16-11)* (p. 472). Luxembourg: Publications Office of the European Union.
- Temming, A., & Damm, U. (2002). Life cycle of *Crangon crangon* in the North Sea: A simulation of the timing of recruitment as a function of the seasonal temperature signal. *Fisheries Oceanography*, 11, 45–58. <https://doi.org/10.1046/j.1365-2419.2002.00184.x>
- Temming, A., & Hufnagl, M. (2015). Decreasing predation levels and increasing landings challenge the paradigm of non-management of North Sea shrimp (*Crangon crangon*). *ICES Journal of Marine Science*, 72, 804–823. <https://doi.org/10.1093/icesjms/fsu194>
- Tiews, K. (1954). *Die biologischen Grundlagen der Büsser Garnelenfischerei*. Berichte Der Deutschen Wissenschaftlichen Kommission Für Meeresforschung, 13, 235–269.
- Tiews, K. (1965). Lichtung des Nordseegarnelenbestandes (*Crangon crangon* L.) durch Wegfrass. *Archiv Für Fischereiwissenschaft*, 16, 169–181.
- Tiews, K. (1970). *Synopsis of biological data on the common shrimp Crangon crangon (Linnaeus, 1758)*. FAO Fisheries Report, 57, 1167–1224.
- Tulp, I., Chen, C., Haslob, H., Schulte, K., Siegel, V., Steenbergen, J., ... Hufnagl, M. (2016). Annual brown shrimp (*Crangon crangon*) biomass production in Northwestern Europe contrasted to annual landings. *ICES Journal of Marine Science*, 73, 2539–2551. <https://doi.org/10.1093/icesjms/fsw141>
- Urzúa, Á., & Anger, K. (2013). Seasonal variations in larval biomass and biochemical composition of brown shrimp, *Crangon crangon* (Decapoda, Caridea), at hatching. *Helgoland Marine Research*, 67, 267–277. <https://doi.org/10.1007/s10152-012-0321-4>
- Urzúa, Á., Paschke, K., Gebauer, P., & Anger, K. (2012). Seasonal and interannual variations in size, biomass and chemical composition of the eggs of North Sea shrimp, *Crangon crangon* (Decapoda: Caridea). *Marine Biology*, 159, 583–599. <https://doi.org/10.1007/s00227-011-1837-x>
- Wear, R. G. (1974). Incubation in British decapod Crustacea, and the effect of temperature on the rate and success of embryonic development. *Journal of the Marine Biological Association of the United Kingdom*, 54, 745–762. <https://doi.org/10.1017/S0025315400022918>
- Wehrtmann, I. S. (1989). Seasonal occurrence and abundance of caridean shrimp larvae at Helgoland, German bight. *Helgoländer Meeresuntersuchungen*, 43, 87–112. <https://doi.org/10.1007/BF02365553>
- Wiltshire, K. H., Boersma, M., Carstens, K., Kraberg, A. C., Peters, S., & Scharfe, M. (2015). Control of phytoplankton in a shelf sea: Determination of the main drivers based on the Helgoland Roads time series. *Journal of Sea Research*, 105, 43–52. <https://doi.org/10.1016/j.seares.2015.06.022>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Hünerlage K, Siegel V, Saborowski R. Reproduction and recruitment of the brown shrimp *Crangon crangon* in the inner German Bight (North Sea): An interannual study and critical reappraisal. *Fish Oceanogr*. 2019;28:708–722. <https://doi.org/10.1111/fog.12453>