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ORIGINAL PAPER

Advancing presence and changes in body size of brown shrimp *Crangon crangon* on intertidal flats in the western Dutch Wadden Sea, 1984–2018

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Abstract

Upon settlement after a pelagic larval phase, brown shrimp *Crangon crangon* depend on intertidal flats. During low as well as high tide the young brown shrimp play roles as predators of meiofauna and as prey for fish and birds. Unlike the biology of the commercially important adults, knowledge on these juveniles remains sketchy. Here we provide an analysis of 35 years (1984–2018) of brown shrimp monitoring in May–June on intertidal flats in the westernmost Dutch Wadden Sea. Intertidal shrimp densities were sampled bi-weekly at three stations during low tide, using sampling corers. We show that over this 35-year period the appearance of shrimp on mudflats advanced by 12 days (– 0.34 days yr^{-1}). Simultaneously, densities on 7 May increased by more than 2.4 times, from 28 shrimp m^{-2} in 1984 to 69 shrimp m^{-2} in 2018. Across years, mean shrimp length decreased from 12.6 to 10.7 mm, but length in early May did not change. The advancement in settlement and the increasing shrimp densities correlated with increases in the seawater temperatures in April more than during earlier times of the year. We propose four interpretations of these changes: (1) shrimp settle on the mudflat when they reach a certain 'threshold' length, (2) settlement of shrimp is controlled by a critical period of 'threshold' temperature sensitivity, (3) timing of shrimp settlement is a response to food availability on mudflats or (4) a direct response to inferred predation pressure. The different interpretations will lead to different scenarios of change in a warming world.

Keywords Seasonal timing · Life cycle · Intertidal food web · Benthos · Wadden Sea · Long-term monitoring · *Crangon crangon*

Introduction

Intertidal flat systems often support high benthic primary production (Christianen et al. 2017) and a high number of primary and secondary consumers (Mathot et al. 2019). An abundance of bivalves, polychaete worms and crustaceans attracts birds and fish to these flats (Piersma et al. 1993). The international Wadden Sea, the most extensive intertidal system in the world, is visited on a yearly basis by hundreds of thousand shorebirds, who aggregate here to refuel during long-distance migrations between northern breeding areas and more southernly wintering areas (van de Kam et al. 2004; Rakhimberdiev et al. 2018). Among the intertidal benthic invertebrates, brown shrimp *Crangon crangon* are important prey for e.g. Eurasian spoonbills *Platalea leucorodia* (Jouta et al. 2018), sanderling *Calidris alba* (Penning et al. unpubl. data) and dunlin *Calidris alpina* (Nehls and Tiedemann 1993). When submerged, shrimp are prey for offshore pelagic fish like whiting *Merlangius merlangus* and cod *Gadus morhua* and in the Wadden Sea for demersal species like plaice *Pleuronectes platessa* and gobies Gobiidae (Tiews 1970; del Norte Campos and Temming 1994).

The Wadden Sea supports a high biomass of brown shrimp which are of ecological and commercial importance (Campos

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and van der Veer 2008; Tulp et al. 2016). Shrimp play a central role in the food web, acting both as key prey and key predators (Pihl and Rosenberg 1984; Oh et al. 1999). The main food of large shrimp (> 20 mm) consists of juvenile plaice (van der Veer and Bergman 1987; Gibson et al. 1995) and several of the small benthic macrofaunal species (Pihl and Rosenberg 1984; Jensen and Jensen 1985; van der Veer et al. 1998); on this basis top–down control of bivalve recruitment by shrimp has been proposed (van der Veer et al. 1998; Philippart et al. 2003; Beukema and Dekker 2005, 2014; Andresen and van der Meer 2010; van der Heide et al. 2014). On the mudflats, shrimp smaller than 20 mm mainly eat meiofaunal organisms such as copepods and ostracods (Pihl and Rosenberg 1984; Boddeke et al. 1985; Jensen and Jensen 1985). Cannibalism of larger on smaller size classes is not uncommon (Marchand 1981; Pihl and Rosenberg 1984), but the impact on juvenile survival and mortality rates remains unknown (Campos and van der Veer 2008).

The life-cycle of shrimp can be sketched as consisting of three stages (Fig. 1) in which (1) the larvae are planktonic, (2) post-larvae settle on the intertidal flats, and (3) adults live demersally in the subtidal zone (Lloyd and Yonge 1947). Females carry the eggs until they hatch, after which the larvae join the zooplankton (Smaldon 1979). The planktonic larvae go through different stages before they reach a length of 4.7 mm and settle on intertidal soft sediments supported by North Sea currents and selective tidal stream transport (Tiews 1970; Daewel et al. 2011); by now they are called 'post-larvae' living in 'nursery areas' (Tiews 1970; Beukema 1992; Campos and van der Veer 2008). Records of shrimp < 20 mm in the subtidal are scarce, but appropriate sampling to catch those small-sized shrimp has not been carried out (Janssen and Kuipers 1980; Boddeke et al. 1985; Beukema 1992). Therefore, it remains surprisingly unclear if post-larvae make use of the subtidal zone at all.

In autumn, adults make a seasonal migration to deeper waters, returning in spring with the incoming tides to coastal areas such as the Wadden Sea (Broekema 1941; van der Baan 1975; Boddeke 1976; Spaargaren 2000). In addition to *seasonal* migrations, adult shrimp show *tidal* migrations: they move to the mudflats with the incoming tide and move to deeper waters again with the outgoing tide (Hartsuyker 1966; Al-Adhub and Naylor 1975). These movements may be triggered by changes in hydrostatic pressure which are sensed by adult shrimp (Tielmann et al. 2015). No such movements are known for the settling post-larvae and juveniles, which appear to remain on the intertidal flats during both low and high tide (Janssen and Kuipers 1980). Large juveniles have been reported to gradually leave the intertidal zone when they reach lengths of 20–25 mm, moving to the subtidal parts of the Wadden Sea and to the nearshore parts of the North Sea (van der Baan 1975; Kuipers and Dapper 1981, 1984; Beukema 1992). However, in an experimental setting, shrimp 15–20 mm showed selective ebb tide activity, indicating that juvenile departure from intertidal mudflats may even start a bit earlier than at lengths of 20–25 mm (Hufnagl et al. 2014).

Male shrimp become sexually mature at smaller lengths (22–43 mm) than females (30–55 mm) (Lloyd and Yonge 1947; ICES 2015). Spawning can take place in as long a period as 46 of the 52 weeks of the year, with egg-bearing females being observed year-round (Tiews 1970; Boddeke 1982; Hünerlage et al. 2019). Nevertheless, there are peaks of egg-bearing females in winter and early summer (Boddeke and Becker 1979; Boddeke 1982; Kuipers and Dapper 1984; Siegel et al. 2008; Hünerlage et al. 2019). Egg-bearing females are most abundant in shallow offshore waters up to 20 m deep (Hünerlage et al. 2019). The average egg size gradually changes during the spawning season (Hünerlage et al. 2019), with winter eggs being larger than summer eggs (Boddeke 1982). The peak of post-larvae and juvenile shrimp on mudflats in spring mainly originates from winter

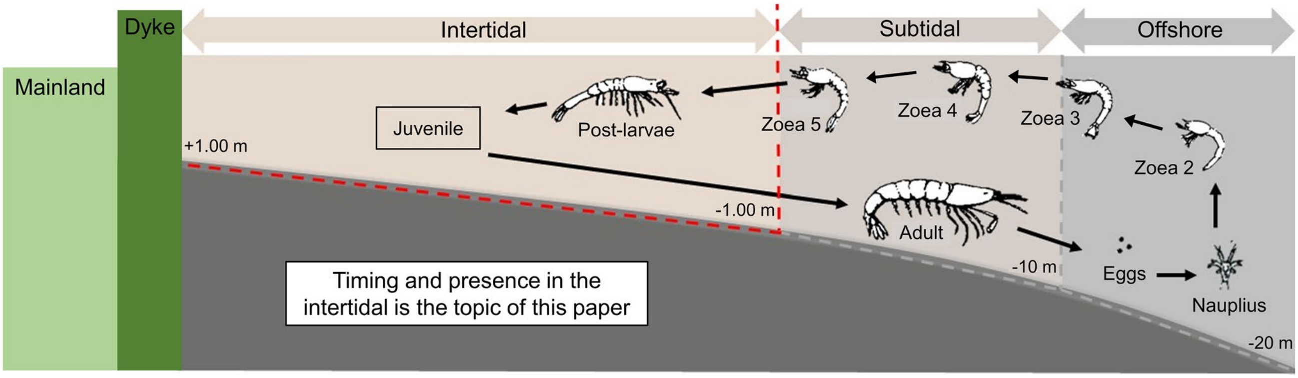


Fig. 1 Illustration of the known and described life-cycle of shrimp (based on Tiews 1970, Janssen and Kuipers 1980, Kuipers and Dapper 1984 and Campos 2009). Adult females carry eggs until they hatch. The hatched eggs go through different larval stages as plankton (up to zoea 5) before they settle on intertidal mudflats as post-larvae. Here they continue to develop as juveniles. Before shrimp become adult, they leave the intertidal and move to deeper waters of the subtidal and offshore

spawning (Temming and Damm 2002). Nevertheless, Temming et al. (2017) argue that later in spring and early summer, shrimp from summer eggs also contribute.

The extent to which the intertidal flats of the Wadden Sea act as nurseries for brown shrimp has been suggested to be affected by winter seawater temperatures (Beukema 1992), sediment type (Beukema and Dekker 2005), surface water nutrient loads (Boddeke and Hagel 1991; Boddeke 1996; Philippart et al. 2007), with obvious direct and indirect effects of fisheries (cf. Tulp et al. 2020). Shrimp may be affected in different ways: cold winters would delay the settlement of post-larvae (Beukema 1992), shrimp densities may be higher in coarse sediments than fine sediments (Beukema and Dekker 2005), eutrophication may correlate with an increase in secondary production (Philippart et al. 2007) boosting shrimp recruitment or growth as a result (Boddeke and Hagel 1991; Boddeke 1996). The trawling for shrimp disturbs the seafloor and make it less habitable for juvenile shrimp (Tulp et al. 2020).

Between 1983 and 2012, juvenile shrimp densities in spring on the mudflats increased (Beukema and Dekker 2014). At the same time, long-term trends in the timing of shrimp settlement on mudflats remain unknown. The timing of settlement may be influenced by water temperature, as higher temperatures speed up the development of shrimp from eggs to adults (Criales and Anger 1986). With the mean water temperature of the Dutch Wadden Sea have increased over the past decades (van Aken 2008), this could have advanced the timing of shrimp settlement on intertidal flats. To update the situation and re-assess some previous correlations with environmental factors, we here provide an analysis of 35 years (1984–2018) of monitoring in May–June of post-larvae and juvenile shrimp on the intertidal flats in the westernmost Dutch Wadden Sea (Balgzand). We aimed to study shrimp in terms of: (1) timing of appearance on the intertidal flats, (2) abundance, and (3) body size. A lack of clear predictions and precise enough relevant environmental data made it impossible to simultaneously assess correlations with factors such as sediment characteristics, nutrient loadings of the seawater and sediment and fishery pressures. Thus, rather than go out on a ‘fishing expedition’ to survey correlates with all possible environmental covariates, we made the choice to focus on the most obvious previously established relationship, i.e. to examine correlations with seawater temperatures over different time periods preceding the occurrence of post-larval settling shrimp in May–June.

Methods

Study area

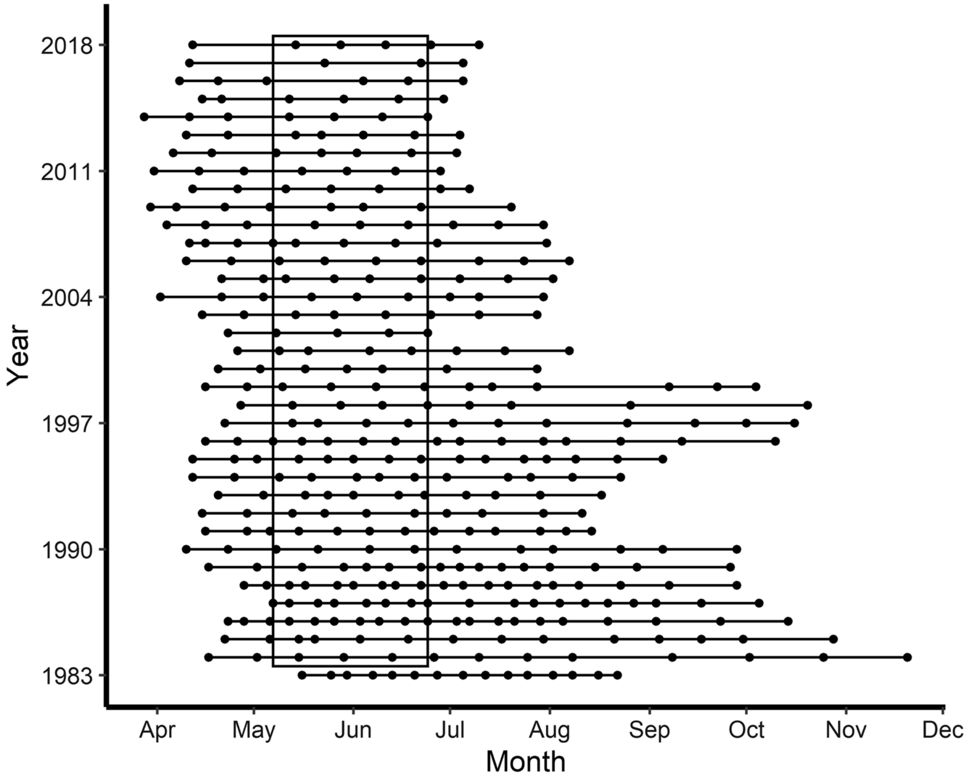
The Balgzand area is a tidal flat system of 50 km^2 in the western part of the Dutch Wadden Sea, at ~ 53ºN and 5ºE. The area is characterized by a semi-diurnal tide with an amplitude of 1.5–2.5 m, depending on the exact location, lunar phase and wind conditions (Dapper and van der Veer 1981). Height of intertidal mud- and sandflats ranges from ~ 70 cm above to ~ 80 cm below mean tide level (MTL). The majority of the area is located under MTL. Details of physical parameters of Balgzand can be found in Beukema and Cadée (1997).

Shrimp densities were measured at three sampling stations in the southwestern part of Balgzand (Beukema 1992; Beukema and Dekker 2005). For practical reasons, these stations were chosen to be close to each other but at different heights (from ~ 0.1 m above to ~ 0.4 m below MTL) and with different sediment characteristics (silt content ranging from 2 to 10%). The stations were located along a transect roughly perpendicular to the coast, at distances of 0.1–1 km from the shore and 0.3–1 km from a major tidal channel. The coordinates of the 3 stations are (1): 52º55′02″N, 4º48′40″E, (2): 52º55′18″N, 4º48′51″E and (3): 52º55′26″N, 4º49′02″E.

Sampling

From 1983 to 2018 each spring, from April to at least late June, samples were collected weekly or bi-weekly during low tide (Fig. 2). The method, using a sampling corer, was used to include shrimps < 10–15 mm in the samples, which were lost in historic samples due to the 5 mm mesh size that was commonly used (Beukema 1992). For this study, three stations were visited, at each of these stations 4 samples consisting of 10 pooled cores of 0.009 m^2 each were taken to a depth of ca. 5 cm and sieved over a 1 mm mesh (Beukema 1992). Up to and including 2009 material was taken back alive to the laboratory. From 2010 onwards all samples were preserved directly after sampling in the field with 4% formaldehyde and in the laboratory stained with rose bengal. After sorting the samples in the laboratory each individual shrimp was measured to the nearest mm from the tip of the scaphocerite to the end of the telson (Beukema 1992). For calculations, the data on shrimp were pooled per sampling event, resulting in a total area of 1.08 m^2 sampled per sampling day. The first year (1983) was excluded from further analyses as the sampling period did not match well with those in subsequent years (see Fig. 2). For the analyses, the time window of 7 May–24 June was selected as the only one covered in all years from 1984 to 2018. Seawater temperatures were measured at the NIOZ jetty (53°00′06″N, 4°47′21″E) at − 1.5 m (relative to Amsterdam Ordnance Datum, NAP). The jetty is located at the tidal inlet nearest to the sampling stations 9 km away from the center of the three sampling stations (see van Aken 2008). The water that passes the jetty is therefore representative for the water temperature that the larvae experience. Monthly averages were calculated and the yearly cumulative sum of the seawater

Fig. 2 Sampling period per year from 1983–2018. Rectangle marks time window that was used in the analyses: 7 May–24 June 1984–2018



temperatures from November until May. The cumulative sum of seawater temperatures was calculated with the water temperatures measured at 0800 h every day. Missing values were replaced by the mean of the measured temperatures before and after the gaps.

Shrimp length

To examine seasonal changes in mean shrimp length, the mean shrimp length per week was calculated (Fig. S1). After inspecting year-by-year patterns for consistency and change, we split the full period (1984–2018) into four decennia: 1984–1989, 1990–1999, 2000–2009, 2010–2018. All measured lengths were plotted per time period per half month period. To find out if long-term changes in the average shrimp length happened, the mean shrimp lengths on 7 May, 31 May and 24 June were calculated using linear interpolation between datapoints. The minimal shrimp length per sampling was calculated to see if changes in the length at settlement could be detected. The settlement of new shrimp on the mudflat may occur in waves that are related to the lunar cycle or large amplitude flood tides, as is the case in other Decapoda (Mense et al. 1995; Christy and Morgan 1998). First, we calculated the median shrimp length per sampling. Then, we scrutinized the correlations between median shrimp length per sampling and moon phase or tidal height to see if such a mechanism could exist in shrimp too. The moon phase one day preceding each sampling date was extracted with software (see Statistics). Tidal heights in Den Helder (52°57′52″N, 4°44′42″E) were collected by Rijkswaterstaat (http://www.rijkswaterstaat.nl). The water height of the highest high tide of the day preceding each sampling day in Den Helder was selected to calculate correlations between shrimp length and tidal height.

Densities and cumulative densities per time period

The sum of shrimp per sampling day was divided by the sampling area (1.08 m^2) to obtain the density of shrimp per square meter (Fig. S2). In years without a sampling occasion on 7 May or 24 June, the density on these dates was obtained by linear interpolation between the adjacent data points. To show the timing of shrimps arriving on the sampled mudflats, we computed the ‘standardized cumulative shrimp density’: the shrimp density of the current week plus the density of the previous week (except for the first sample). The timing and number of observations per year are given in Fig. 2. Between year comparisons were made using three computed variables: (1) the date when 50% of the annual cumulative shrimp density is reached, (2) the cumulative shrimp density on 31 May, halfway the sampling period, and (3) the shrimp density on 7 May, the starting date of sampling periods. The values were obtained by linearly interpolating between datapoints. A Pearson’s product-moment correlation test determined the correlation between the date when 50% of the standardized annual cumulative shrimp density was reached and the standardized cumulative shrimp density on 31 May.

Statistics

All calculations and analyses were carried out using R (R Development Core Team 2020, R version 3.6.3). The distribution of the data was tested for normality with the Shapiro Wilk test with no significant results. Temporal differences in shrimp density, timing and length were analyzed with linear models from the lm function in base R with year as an explanatory variable. To check if the change in preservation and staining improved the detection of small shrimp, a segmented regression analysis was carried out using the R package "segmented" (Muggeo 2008). With this analysis sudden changes in the slope of a trend, in this case a change in the mean length from 2010 onwards, could be detected. The results of the segmented regression were compared with linear regression of the same data. The best model explained most variation.

The existence of settlement waves was studied in relation to the moon phase. The moon phase one day before each sampling date was extracted using the package "lunar" (Lazaridis 2014). Differences in the median shrimp length between moon phases were analyzed in an analysis of variance (ANOVA). The association between the median shrimp length and the height of the tide was analyzed by linear regression.

To find out during which time of the year the water temperature has the strongest association with the shrimp density on 7 May and the 50% date, several linear regression analyses were carried out. The same was done to assess during which time of year the water temperature best explained the mean shrimp length on either 7 May, 31 May or 24 June. For each year, the mean water temperature of the separate months January, February, March and April were calculated to be used as explanatory variables. Second, the mean of the months January, February and March was calculated per year to represent the mean water temperature in winter, as in Beukema (1992). Lastly, the cumulative sum of the sea water temperature was calculated per year for the time period of November until May. The time of year (month, winter or cumulative sum) of which temperature showed the strongest correlation with shrimp density on 7 May and 50% density date was then further analyzed based on the amount of variation explained. The relative importance of water temperature and year in explaining (1) the date at which 50% of the shrimp density was reached and (2) the shrimp density on 7 May, was analyzed with linear models. Time and temperature were tested separately and together, including and excluding a two-way interaction. The best model was selected on the basis of Akaike's Information Criterion (AIC; Burnham and Anderson 2002).

Finally, shrimp density may not be independent of year as density in one year may be influenced by shrimp density in the preceding year. Therefore, an autocorrelation function was plotted, based on the standardized residuals from the linear model that describes shrimp density. Visual inspection of this plot did not show indications for autocorrelation. Still, we checked for temporal autocorrelation by adding two types of autocorrelation structures from the gls function to the final model. The autocorrelation structures we used were: Compound Symmetry Correlation Structure (CompSymm) and First Order Autoregressive Structure AR-1 (Zuur et al. 2007).

Results

Length

From 1984 to 2018 a total of 141 sampling occasions took place (Fig. 2). Over all the years, the estimated mean length on 7 May, the start of the study season, was 9.69 ± 0.091 mm and the shrimp length on the last day of the study season 24 June was 12.93 ± 0.083 mm (Fig. 3a). Based on visual inspection of the histograms in Fig. 3c, in May smaller shrimp occurred more than in June. However, throughout the years, median lengths as small as 5 mm occurred only on 1% of the sampling days. Across the 35 year study period, mean shrimp length in this time window decreased significantly from 12.6 mm to 10.7 mm (linear regression: $r^2 = 0.22$, $F_{1,33} = 9.49$, $p = 0.004$) (Fig. 3b). Visual inspection of the boxplots in Fig. 3d did not suggest that such decreases in length occurred during specific years. Indeed, the mean lengths on either 7 May, 31 May or 24 June did not change over the years (linear regression: April $F_{1,33} = 2.02$, $p = 0.16$, May $F_{1,33} = 1.03$, $p = 0.32$, June $F_{1,33} = 3.33$, $p = 0.07$). Segmented regression did not estimate a break point in the shrimp length after the year 2010 and the model explained less variation than the simple linear regression (segmented regression: $r^2 = 0.19$, linear regression: $r^2 = 0.22$). Therefore, there is no indication that the results have been biased by the change in preservation and staining of samples from 2010 onwards.

Lengths on the dates when 50% of cumulative density was reached did not change over time either (linear regression: $F_{1,33} = 1.70$, $p = 0.20$). Furthermore, mean shrimp length on 7 May was not significantly correlated with the January temperature, nor the April water temperature but it was with water temperatures in winter, February and March (Table S3). The minimal shrimp length did not change over the season (linear regression: $F_{1,141} = 0.0003$, $p = 0.99$) and the median length per sampling was not correlated with a specific moon phase (ANOVA: $F_{1,7} = 0.75$, $p = 0.63$) or

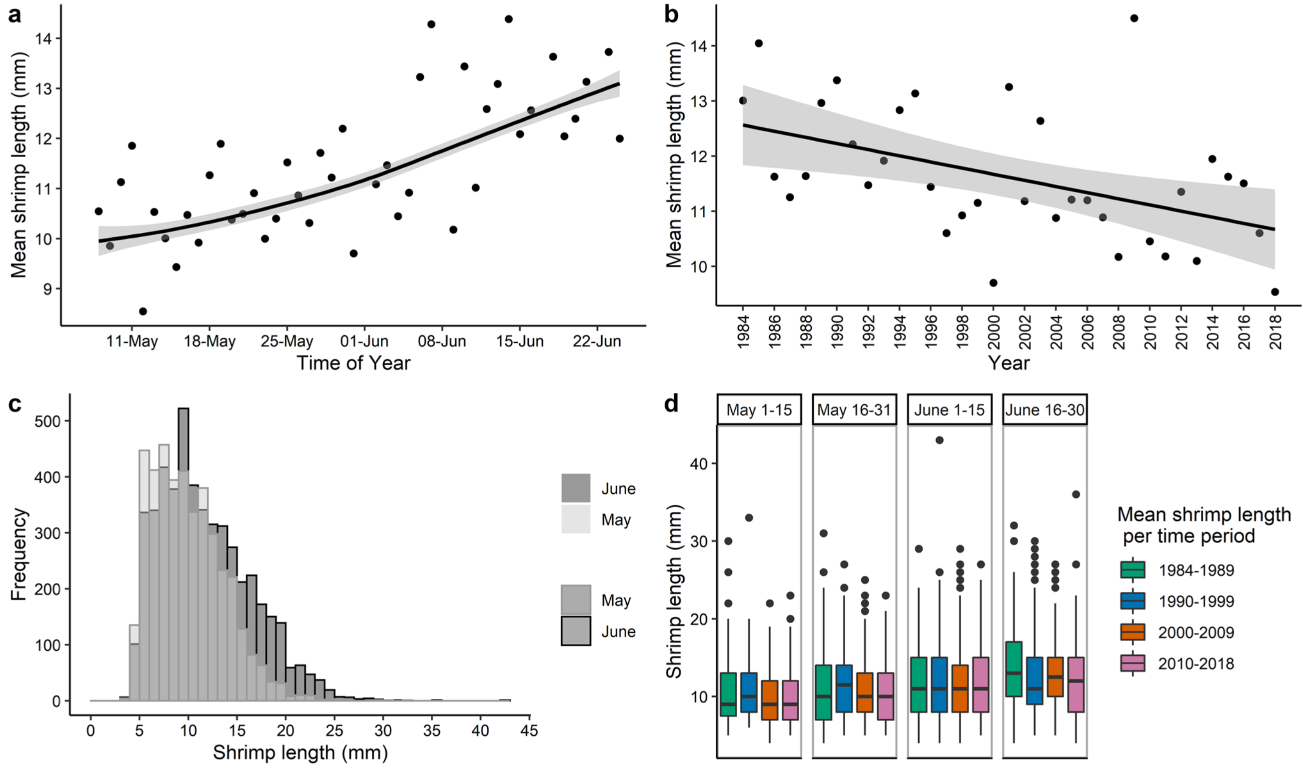


Fig. 3 The shrimp length over time: seasonal and annual changes **a** mean shrimp length during the sampling season, general additive model (GAM) was used as a smoother. **b** The mean shrimp length per year, linear regression line plotted ($r^2 = 0.22$, $F_{1,33} = 9.49$, $p = 0.004$). **c** The length-frequency distribution from 1984 to 2018 in May (light grey, grey border) and June (dark grey, black border). **d** boxplots of the shrimp lengths per half month from 1984 to 2018. The titles give the time period that was selected for each graph

the height of the preceding high tide (linear regression: $F_{1,141} = 0.02$, $p = 0.89$). The same analyses were carried out per month separately to see if the effect would be present in a specific time period but none of these tests results were significant either.

Density

Changes in shrimp density over time were analyzed using the standardized shrimp density and the density on 7 May (Fig. 4a). The date when 50% of the standardized annual cumulative shrimp density was reached was strongly correlated with the standardized cumulative shrimp density on 31 May (Pearson's product-moment correlation coefficient $r = 0.93$, $n = 35$, $p < 0.001$). Therefore, we only analyzed the date when 50% of the cumulative shrimp density was reached and dropped the cumulative shrimp density on 31 May from further analyses. Mean shrimp density (calculated per year) remained stable over time (linear regression: $F_{1,33} = 2.89$, $p = 0.10$). The date when 50% of the yearly cumulative shrimp density was reached advanced significantly in the past 35 years at a slope of 0.34 days per year (Fig. 4b). In total, the 50% cumulative shrimp density advanced with 12 days in the 35 years study period. Between 1984 and 2018 the shrimp density on 7 May increased significantly by more than 2.4 times, from 28 to 69 m^{-2} (Fig. 4c).

Seawater temperatures

The correlations between seawater temperature and the 50% density date and shrimp density on 7 May were strongest with temperatures in April (Table S3). April seawater temperature increased significantly in the course of the 35-year study period (Fig. 5a; linear regression: r^2: 0.35, $F_{1,33} = 17.58$, $p < 0.001$). The date when the cumulative shrimp density reached 50% advanced by 3.4 days for every 1 °C higher mean April seawater temperature ($r^2 = 0.24$, $F_{1,33} = 10.55$, $p = 0.003$, Fig. 5b). In line with this, shrimp density on 7 May was significantly higher with high April seawater temperature ($r^2 = 0.44$, $F_{1,33} = 26.06$, $p < 0.001$, Fig. 5c). Shrimp density increased with 14.7 m^{-2} per 1 °C higher mean April seawater temperature.

Based on the lowest AIC values, April water temperatures best explained the timing of arrival of shrimp on the mudflats (Table 1). For both response variables that were tested (timing of 50% of yearly cumulative density and shrimp density on 7 May), year did not contribute significantly to

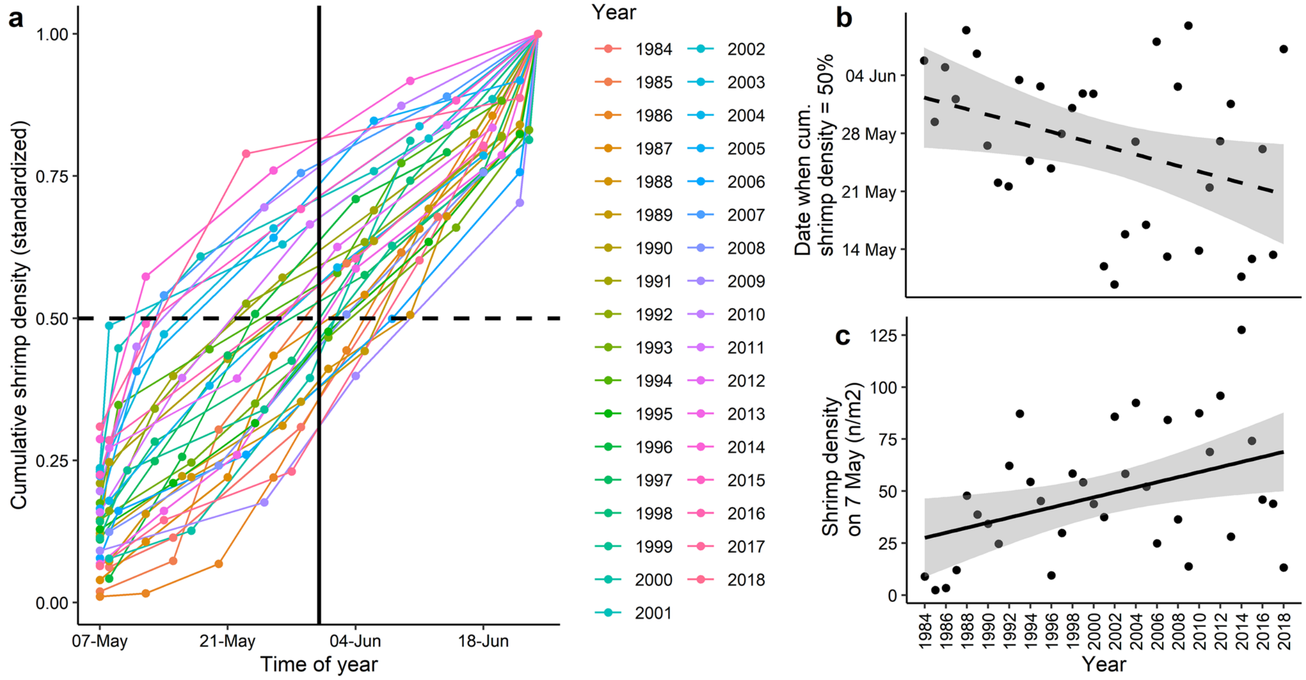


Fig. 4 **a** The standardized cumulative shrimp density runs (0–1) and is plotted against time of year. Each year is plotted separately in a different color. The solid line marks the middle of the sampling period on 31 May. The dashed line marks the moment in time when 50% of the yearly shrimp density has been reached. **b** The time of year when 50% of the cumulative shrimp density has been reached through time (years). Linear regression line plotted ($r^2=0.14$ $F_{1,33}=5.22$, $p=0.029$). **c** Shrimp density on 7 May, the start of the sampling season with the linear regression line plotted ($r^2=0.17$, $F_{1,33}=6.72$, $p=0.014$). Shaded area in b and c mark the 95% confidence interval (CI)

the explanation of variation. Models including an autocorrelation structure did not have a lower AIC value (model without autocorrelation structure AIC: 327.6, models with autocorrelation structure AIC: 329.6).

Discussion

We show that in the 35 years from 1984 to 2018 the settlement of juvenile post-larval brown shrimp on the intertidal flats of the Dutch Wadden Sea advanced by 12 days. Additionally, densities at the start of the study season more than doubled, with an estimated overall average shrimp density on 7 May of 69 m^{-2}. The mean length of shrimp at the start of the season did not change, nor was it correlated with water temperatures in April. Instead, mean shrimp length on 7 May was correlated strongest with the mean water temperature of the winter months. In summary, in warm springs we find higher shrimp densities earlier in the sampling season and at that time they are not of a larger size compared to colder springs.

The correlation between the advanced appearance of shrimp and sea water temperature was higher for the temperatures in April than for the temperatures in the whole previous winter season, and indeed became better as the time approached the time of appearance of shrimp, with the highest correlations for the April seawater temperatures. This is consistent with various known biological processes such as egg development and larval growth, both of which speed up with higher water temperatures (Wear 1974; Criales and Anger 1986; Paschke et al. 2004; Hufnagl and Temming 2011). For the field, such differences in development time also have implications for the spatial origin of the post-larvae that settle in the Wadden Sea. Shrimp larvae drift passively with currents until they become post-larvae (Temming and Damm 2002). At low temperatures, the larvae will drift for longer because development is slower (Daewel et al. 2011). The time period that larvae are exposed to pelagic predators is therefore also extended, possibly leading to higher mortality rates. Wind speed and direction influence the drifting track as well (Daewel et al. 2011) and could cause differences in the timing and abundance of post-larvae that settle in the Wadden Sea.

Post-larval settlement of other crustaceans is known to take place in waves correlated with the moon phase or the amplitude of the high tide. For the post-larval shrimp on the intertidal flats in the westernmost Dutch Wadden Sea, we did not find that median length was correlated with the moon phase or the height of the tide. This rejects a hypothesis for post-larval shrimp settlement to occur in moon or tide-driven

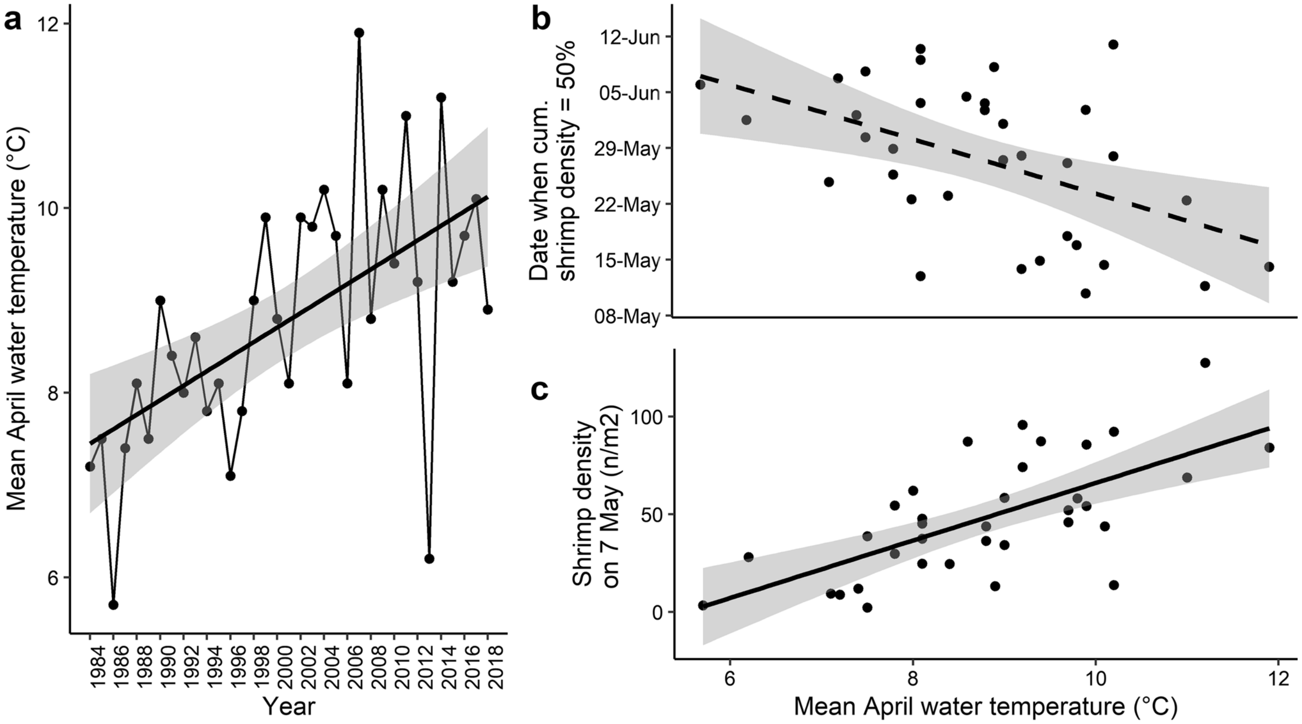


Fig. 5 **a** Average April seawater temperature over time. **b** The time of year when 50% of the cumulative shrimp density has been reached. Linear regression line plotted ($r^2 = 0.24$, $F_{1,33} = 10.55$, $p = 0.003$). **c** the shrimp density on 7 May, plotted against the mean April seawater temperature. Linear regression plotted ($r^2 = 0.44$, $F_{1,33} = 26.06$, $p < 0.001$). In **b** and **c** each point represents a year, the shaded areas mark the 95% CI

Table 1 Comparison of linear regression models describing 1) the timing of settlement: date when 50% of annual cumulative shrimp density is reached and 2) shrimp density on 7 May

Model terms	ac-structure	AIC	r^2	p
50% day ~ water temp. + year		253.82		
50% day ~ water temp. × year		255.64		
50% day ~ water temp		**252.27**	**0.24**	**0.002**
50% day ~ year		256.84		
7 May density ~ water temp. + year		324.65		
7 May density ~ water temp. × year		326.16		
7 May density ~ water temp		**322.68**	**0.44**	**< 0.001**
7 May density ~ year		336.57		
50% day ~ water temp. + year		262.88		
50% day ~ water temp. + year	CompSymm	264.88		
50% day ~ water temp. + year	AR1	264.88		
7 May density ~ water temp. + year		327.63		
7 May density ~ water temp. + year	CompSymm	329.63		
7 May density ~ water temp. + year	AR1	329.63		

Independent variables: year and April seawater temperature

Variance explained (r^2) and the p value of the models with the lowest AIC are indicated in bold

waves. The idea that settlement could especially happen during nocturnal flood tides (Christy and Morgan 1998), could not be evaluated with our data.

Over the course of the sampling season, the mean shrimp length increased from 9.7 to 12.9 mm. This increase might suggest that post-larval shrimp move to the mudflat at larger sizes. However, this seems unlikely, as we did not find a change in the minimal shrimp length over the season. Also, the increase in mean length is too low to be attributed to growth. On the basis of measured individual growth rates of 0.28 mm per day for a 10 mm shrimp in the water of 10 °C (Hufnagl and Temming 2011), the individual increase in body length would be expected to be 12.3 mm over the 44 day study period, i.e. almost four times the 'growth' in the field. Even with this conservative scenario (the mean water temperature in May is actually 12 °C), the growth speed is clearly too high to explain the increase in the mean shrimp length. This suggests that the mean shrimp length decreased because of an increase in the turnover of the population, with the larger juveniles leaving for deeper waters at ever faster rates. Indeed, departure of shrimp from intertidal flats may start at 15 mm (Hufnagl et al. 2014) instead of 20 mm (Beukema 1992), which would have caused a steeper decrease of larger length classes which would have kept the observed increase in mean shrimp length across the season small. Whether the departure of juveniles is triggered by changes in the sensitivity to hydrostatic pressure just as in adults, will require further investigation.

The advanced settlement on intertidal flats was best correlated with the seawater temperatures in April (which increased over the years). The mechanisms underlying this pattern remain to be established, but on the basis of the observational data presented we propose four non-mutually exclusive interpretations of the changes in the timing of shrimp on the mudflat: (1) shrimp settle on the mudflat when they reach a certain 'threshold' length, (2) the settlement of shrimp is controlled by a critical period of 'threshold' temperature sensitivity, (3) the timing of shrimp settlement is a response to food availability on the mudflats and/or (4) shrimp settlement on intertidal flats is behaviour to avoid predation by other species and cannibalism by adult shrimp. Predictions on climate effects on future shrimp lengths at the time of settlement and shrimp densities in spring will differ between the four different hypotheses.

For the first interpretation, assuming a threshold length for settlement of 4.7 mm (i.e. the length when shrimp reach the post-larval phase; Kuipers and Dapper 1984), this length should be the dominant length, at least during the sampling early in the season. However, median lengths as small as 5 mm occurred only on 1% of the sampling days. Either the peak of settlement already passed by the time that sampling started, or settled post-larval shrimp spend time elsewhere before moving onto the intertidal flats. Regardless of the precise threshold length at settlement, in the light of climate change no changes from this threshold length are expected if body length itself triggers settlement. Advancements in the timing of settlement would occur if this length would be reached earlier in the year. With increasing water temperatures, growth rates will increase during all life stages of shrimp (Wear 1974; Criales and Anger 1986; Paschke et al. 2004). This actually may occur, as Beukema and Dekker (1992, 2014) showed advanced shrimp settlement and higher spring shrimp densities after mild winters.

However, by comparing the correlations between shrimp density on 7 May and the water temperature in preceding time periods, we discovered that the water temperature in April shows the strongest correlations. This cannot be explained by greater growth rates at higher water temperatures, but rather hints at the existence of a threshold temperature during a sensitive time window. Here, we assume that shrimp go through a developmental period during which they are sensitive for a threshold in the seawater temperature. When this threshold is reached, the shrimp settle on the mudflat. Under this interpretation shrimp would settle on the mudflat when the temperature conditions are right (rather than when they reach a certain length or life stage). With increasing water temperatures, the temperature threshold may be reached earlier in the year, leading to the observed advancement in the timing that shrimp settle on intertidal mudflats. That the water temperature in the preceding months will lead up to the water temperature in April may then explain why water temperatures during the preceding months also correlate with shrimp densities in May. In the presence of a temperature threshold, shrimp may actually settle on the mudflat at the minimal post-larval length of 4.7 mm after warm winters and at larger sizes after cold winters. Due to the timing of sampling we can not confirm this with our data. Survival and growth rates are lower at low temperatures, but shrimp may still grow in water below 10 °C (Rochanaburanon and Williamson 1976; Hufnagl and Temming 2011). Therefore, during a cold spring, the temperature threshold will be reached later, leading to individuals that settle on the mudflat when they are larger. Again, assuming that in the subtidal shrimp do show growth, in warm springs the temperature threshold would be reached earlier in the year, resulting in smaller individuals that settle on the mudflat.

The third interpretation is that the advance in shrimp settlement is based on increases or peaks in food availability occurring earlier. The diet of shrimp < 20 mm mainly consists of meiofauna (Pihl and Rosenberg 1984; del Norte-Campos and Temming 1994). As a result of increased water temperatures, the phenology of meiofauna may be advanced. Shrimp may follow their prey, with advanced settlement on the mudflats as a result. Assuming that with increased water temperatures the food of shrimp becomes available earlier in the year, shrimp will advance settlement on the mudflat. Additionally, they could still be of a smaller size, as earlier in the growing season shrimp will still be smaller.

Our fourth and last alternative interpretation is an advancement of high predation pressure in the subtidal induces post-larval shrimp to move to intertidal mudflats earlier in the year. Currently, post-larval settled shrimp are thought to be absent in the subtidal—they have rarely been found there in the past. At the same time, because previously used mesh sizes were too wide, sampling may have failed to detect small shrimp < 10 mm properly (Beukema 1992), or started too late. Earlier we already concluded that settled post-larval shrimp may spend time somewhere deeper before moving onto the intertidal flats.

Observational studies (including comparisons between different areas in e.g. the Wadden Sea), and experimental studies on the mechanisms on shrimp settlement, are now required to elucidate why our measurements of 'settlement' are correlated with water temperatures especially in April. Noting that the different interpretations will lead to different scenarios of change in a warming world, without them it will be impossible to interpret the striking changes in phenology. As shrimp are now present in the intertidal earlier in the year, different predators may benefit from their presence. To fully understand the consequences for higher trophic levels, it is necessary to look into the juvenile shrimp abundances over a longer time in the year and identify if new matches or mismatches between shrimp and consumer exist.

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Author contributions EP, LG, TP and RD contributed to the concept and design of the study. RD conducted the data collection together with Jan Beukema and EP ran the statistical analysis. EP wrote the main sections of the manuscript supervised by TP and with input from LG and RD. All authors approved the submitted version.

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Data availability The datasets generated during and/or analyzed during the current study will become available in the Zenodo Repository (http://doi.org/10.5281/zenodo.4792217).

Declarations

Conflict of interest The authors have no conflicts of interests or competing interests to declare.

Ethical approval This research was conducted in accordance with the Netherlands Code of Conduct for Scientific Practice. All applicable international, national, and institutional guidelines for sampling, care, and experimental use of organisms for the study have been followed.

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