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ECOGRAPHY

Research

Exploring larval phenology as predictor for range expansion in an invasive species

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Predicting range expansion of invasive species is one of the key challenges in ecology. We modelled the phenological window for successful larval release and development (WLR) in order to predict poleward expansion of the invasive crab *Hemigrapsus sanguineus* along the Atlantic coast of North America and north Europe. WLR quantifies the number of opportunities (in days) when larval release leads to a successful completion of the larval phase; WLR depends on the effects of temperature on the duration of larval development and survival. Successful larval development is a necessary requirement for the establishment of self-persistent local populations. WLR was computed from a mechanistic model, based on in situ temperature time series and a laboratory-calibrated curve predicting duration of larval development from temperature. As a validation step, we checked that model predictions of the time of larval settlement matched observations from the field for our local population (Helgoland, North Sea). We then applied our model to the North American shores because larvae from our European population showed, in the laboratory, similar responses to temperature to those of a North American population. WLR correctly predicted the northern distribution limit in North American shores, where the poleward expansion of *H. sanguineus* appear to have stalled (as of 2015). For north Europe, where *H. sanguineus* is a recent invader, WLR predicted ample room for poleward expansion towards NE England and S Norway. We also explored the importance of year-to-year variation in temperature for WLR and potential expansion: variations in WLR highlighted the role of heat waves as likely promoters of recruitment subsidising sink populations located at the distribution limits. Overall, phenological windows may be used as a part of a warning system enabling more targeted programs for monitoring.

Keywords: Asian shore crab, dispersal, invasion, larva, metapopulation



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Introduction

Widespread invasions as a consequence of human-mediated introduction of species (Gurevitch et al. 2011) and climate change (García-Molinós et al. 2016) are responsible for much of the current dynamics of natural communities. Both climate model predictions and observations coincide in that various tropical and temperate species will extend (or are extending) their range poleward (Hickling et al. 2006, Burrows et al. 2011, Poloczanska et al. 2013). In addition, introductions of non-native species are currently modifying ecosystems at a global scale (Simberloff 2009, Ehrenfeld 2010, Gurevitch et al. 2011, Hulme 2017) and, in particular, in coastal marine habitats (Ruiz et al. 2000, Levin et al. 2002, Reise et al. 2017). In the light of such extent of ecological change, understanding the major processes driving invasions has become a priority in ecology and conservation (Perrings 2005, Gurevitch et al. 2011).

Range expansion is one of the major characteristics identifying invasions (Gurevitch et al. 2011). Range expansion may be facilitated by specific traits leading to increased competitive ability (Roy 1990, Holdredge and Bertness 2011, but see Vilà and Weiner 2004), environmental tolerance (Kelley 2014) or dispersal ability (Hassall et al. 2008, Simberloff 2009). Dispersal ability is enhanced in those marine bottom dwelling (= benthic) organisms characterised by pelagic dispersive larvae (e.g. crabs, mussels, starfish and sea squirts). Such larvae will drift in the sea (the pelagic habitat), and eventually settle and continue life as a juvenile in a novel benthic habitat. In such organisms, propagule pressure, in particular (sensu Simberloff 2009) depends on the spread and survival of larvae.

Larval production, along with filtering effects, is a main contributor for the establishment of self-sustaining populations, necessary for invasion (deRivera et al. 2007). Theoretical analyses (Fig. 1, Supplementary material Appendix 1) suggest that spatial gradients in larval habitat quality can limit range expansion because a source–sink dynamics (sensu Pulliam 1988, Dias 1996, Bode et al. 2006) is established at the borders of the distribution. At such borders, poor habitat quality creates a limit where populations cannot self-sustain and instead become ‘sinks’, which undergo extinction in the absence of subsidy (Dauphinais et al. 2018). A critical point is therefore defined by the conditions needed for the development of a self-sustained population; one such condition is that the quality of the larval habitat must ensure retention (i.e. that sufficient larvae, produced at a local population, return to the same population).

We focused on understanding the importance of spatial gradients in larval habitat quality, as a way to predict the establishment of self-sustained populations and the poleward expansion of the Asian shore crab *Hemigrapsus sanguineus*. *H. sanguineus* develops through a pelagic larval phase of 3–5 weeks, characterised by several stages; the last stage, called megalopa, colonises (= settle on) rocky shore habitats and metamorphoses into a juvenile. This crab has invaded the

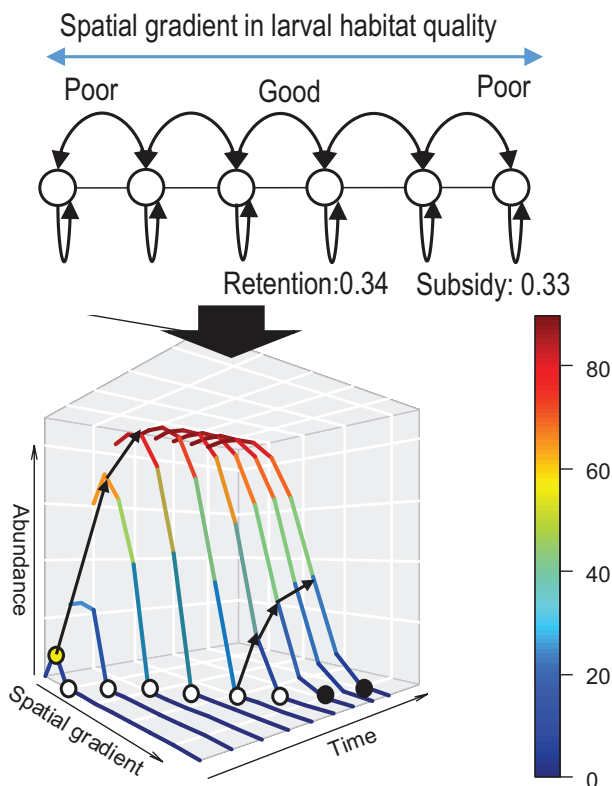
coast of North America and Europe (Dauvin et al. 2009, Epifanio 2013). In North America, *H. sanguineus* was found in Delaware Bay (Atlantic coast) in the 1980s and then expanded northwards covering almost 10 degrees of latitude in the subsequent 30 yr (Stephenson et al. 2009). In Europe, *H. sanguineus* was first recorded in the Dutch delta system in the late 1990s and then spread over the southern North Sea reaching Danish waters by 2012 (Jungblut et al. 2017, Geburzi et al. 2018).

Stephenson et al. (2009) found that the distribution of *H. sanguineus* in the coast of North America and in the native habitat (Pacific coast: China, Japan and Russia) was limited (at the poleward end) to sites characterised by summer water temperatures above 12–13°C. Lord and Williams (2017) re-examined the northern distribution limits in North America (in 2015) and concluded that the range expansion has stalled since 2005. Those field studies and additional laboratory experiments support the hypothesis that range limits depend on the tolerance of the larval stages to low (summer) temperature (lower limit 12–15°C: Epifanio et al. 1998, Stephenson et al. 2009). In north Europe, the current distribution of *H. sanguineus* lies well within the region where summer water temperatures are higher than 15°C, providing sufficient time to complete larval development.

We modelled the range expansion of *H. sanguineus* based on the phenological window for larval release (WLR). WLR is the window of opportunity (measured in number of days) available at each summer for successful larval development from larval release to the megalopa, depending on water temperature. WLR gives an idea on whether the temperature conditions should preclude the establishment of a self-sustaining population (WLR=0). In the past, the likelihood of successful larval development in *H. sanguineus* was established from isotherms and the effect of temperature on larval survival (Stephenson et al. 2009). Isotherms may be used to estimate the breadth of a thermal window for larval development. However, such an approach does not consider possible failures of development because late larval release would extend development beyond the thermal window. Our approach, based on WLR, considers such situations because it accounts for the effect of temperature on developmental rates within a thermal window defined by survival rates. In addition, the calculation of WLR incorporates key properties of the thermal window arising from daily variations in temperature observed in the field.

We had two main specific objectives, first to determine if WLR would correctly predict the range distribution limits in N America; second, concerning north Europe, to determine if predictions of WLR were consistent with spatial distribution and whether it would predict poleward expansion. Calculations of WLR were based on a ‘temperature–time’ model (TTM) predicting the timing of abundance of megalopa on the basis of known dates of larval release, daily time series of temperature, and a statistical model predicting the effect of temperature on larval development time. The statistical model was fitted to data obtained from laboratory

(a) Stepping stone connectivity



(b) No connectivity

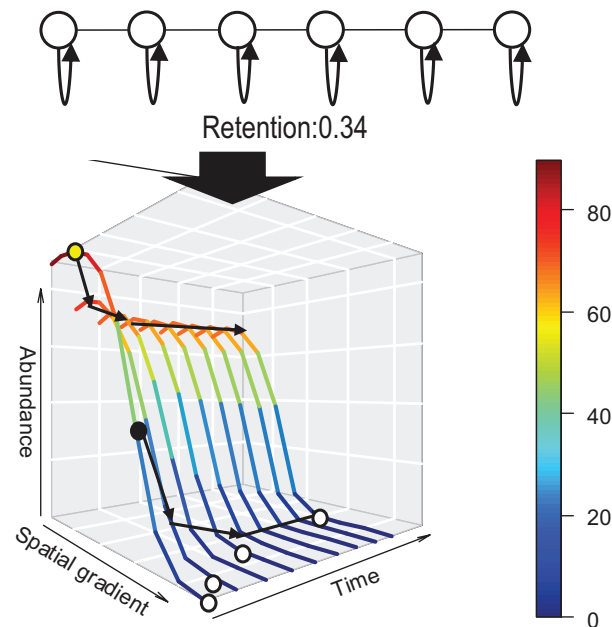


Figure 1. Simulation of range expansion of a metapopulation of a benthic marine invertebrate with dispersive larvae, colonising local habitats along a coastal region. The metapopulation is idealised as a collection of local populations occupying habitats (circles)

experiments quantifying the effect of temperature on larval survival and duration of development. The TTM was previously validated by showing that predictions of timing of megalopa matched observations at the local population. In addition, the application of the TTM to the population of North America was also validated because we confirmed that our experimental results coincided with those carried out with larvae from a population located in the Atlantic coast of N. America (Epifanio et al. 1998). The fact that WLR correctly predicted the timing of settlement in our local population and the northward range distribution limits in N. America, validated the application for north Europe.

Methods

Experiments

The model was based on experiments rearing larvae from four females at four temperatures (15, 18, 21 and 24°C). The lower temperature was chosen for three reasons: First, a previous laboratory study (Epifanio et al. 1998) showed that few larvae would successfully reach the megalopa at 15°C; this was confirmed by our results. Second, our own checks, based on larvae from two females (see Results), showed that larvae reared at 12°C did not reach the megalopa (all larvae died by the fourth or fifth zoal stage). Third, three years of data (see Results), indicated that larvae were released at times when water temperature was higher than 15°C.

Larvae of *H. sanguineus* were obtained from four ovigerous females collected on the intertidal zone of the island of Helgoland (Germany). Females were kept in aquaria (volume = 2 l) with filtered seawater, permanently aerated, at 18°C in a temperature-controlled room (precision $\pm 0.5^\circ\text{C}$)

distributed along an idealised 1-dimensional straight coastline. The coastline is characterised by a spatial gradient in larval habitat quality, decreasing from good to poor from the centre of distribution towards the extremes of the range. The metapopulation expands from the population centre. Larval dispersal is denoted with arrows: larvae either return to the natal habitat (retention), disperse to adjacent habitats (subsidy) or die through over-dispersion (not shown); juveniles experience density-dependent survival; adults reproduce and die (juveniles and adults are non-dispersive stages). (a) Stepping stone connectivity: populations are connected so that about 1/3 of larvae are retained and there is a subsidy of ca 1/3 from each adjacent population (indicated as arrows arriving to black circle). The meta-population grows over time and expands along the spatial gradient, from the population centre of distribution (yellow circle in 3D plot) occupying empty habitats at some point in time (white circles). Arrows show the population trajectory towards a steady state. Variation in abundance is shown as a colour gradient and adjacent bar. (b) No connectivity: after the model is run for several generations, the connectivity is set to 0 (but retention is allowed). The population at the centre of distribution decreases in abundance towards a new steady state (see arrows) but in sink habitats, populations go extinct leading to empty habitats (from black to white circles).

until the hatching of larvae. Freshly hatched larvae were distributed in rearing vessels containing filtered sea water, assigned randomly to temperature treatments and then transferred to the appropriate temperature controlled rooms where the test temperatures were reached gradually (within 24 h). Larvae were reared at a constant density of one individual per 10 ml. The first two females produced a low number of larvae; hence, we reared their larvae in 3 replicates of 10 individual each in 100 ml-vials. Females 3 and 4 produced more larvae and were reared in 4 replicates of 50 larvae in 500 ml vessels. Density is the critical factor driving larval survival in the laboratory, but not so the size of the containers. This was confirmed by the facts that most variation in developmental time occurred between the first and second hatch, reared with the same containers (Supplementary material Appendix 2 Fig. A2), and because on average, our values of developmental time were similar to those found by Epifanio et al. (1998). Larval rearing followed standard methods (Torres et al. 2011; see also Supplementary material Appendix 2).

Duration of development from hatching to the megalopa (average per replicate vessel) was analysed through mixed models (Zuur et al. 2009), with temperature as a continuous predictor and female of origin as a random factor, affecting both intercepts and slopes. Analyses were carried out with the lme4 package (Bates et al. 2015). For duration of development (D), the effect of temperature (T) can be described through exponential or power models (Dawirs 1985, O'Connor et al. 2007, Crickenberger and Wetthey 2018). Hence, we compared an exponential model, $D = a \exp(-bT)$, versus a power model, $D = aT^{-b}$ (constants a and b were estimated by fitting linear models to previously transformed data, using appropriate logarithmic transformation). Comparisons were based on the Akaike information criterion (AIC) and by checking model residuals. The output of this statistical model was then used as a basis for the temperature time model (see below).

Temperature–time model (TTM): development and validation

We developed a model predicting duration of larval development to the megalopa from field data on sea surface temperature. The TTM is based on those developed by Anger (1983) and Dawirs (1985); TTM's have been used by deRivera et al. (2007) to predict invasion of European shore crab larvae in North America and by Giménez (2011) to explore effects of temperature increase in the timing on larval settlement. The model uses daily field temperatures over several consecutive days and the equation of development time as a function of temperature, to predict, for each day, a fraction of development. A complete development (with its duration and end day) is obtained as the day when the sum of the fractions equals or surpasses 100%. Our TTM, in addition, considers intraspecific variation in larval responses due to maternal influences and within brood variation, as it is based on predictions made through a mixed (random/fixed) statistical model (Supplementary material Appendix 3).

The model validation consisted in comparing the output of the TTM with observations of abundance of megalopa of *H. sanguineus* in the intertidal of Helgoland (Supplementary material Appendix 4) and through cross-correlation analysis (Chatfield 2004). For the output of the TTM, temperature data consisted of daily records of seawater temperature for the Helgoland Roads, island of Helgoland, German Bight (source COSYNA data portal, Helmholtz–Zentrum Geesthacht, Wiltshire et al. 2008, Breitbach et al. 2016, Baschek et al. 2017). The TTM uses a time series of the abundance of Zoea I larvae (in individuals per m^3) to establish the date at which virtual larvae are released in the model: the density of Zoea I in the water column at a given date is therefore used as proxy for the timing of larval release. Zoea I were collected at Helgoland Roads with plankton nets (see further details in Supplementary material Appendix 4). We explored two empirically driven scenarios of release of virtual larvae: in scenario-1, 1000 virtual larvae started development at each hatching date of the period when larvae were observed in the field (30 June–25 July). In scenario-2, the number of virtual larvae were constrained by the dates and density of larvae observed in the field; for this scenario, the number of virtual larvae released was determined by fitting a fourth order polynomial equation to the time series of abundance of larvae found in the field (Supplementary material Appendix 6 Fig. A3, year 2018).

Megalopae were collected over the summer of 2018, three times a week, by means of artificial units of habitat (AUH, South 2016). AUHs consisted in three cylindrical floating collectors (height = 25 cm, diameter = 7 cm) made of green plastic garden mesh (aperture = 1 cm) and containing six plastic kitchen sponges or 'tuffies'. Tuffies are used commonly for monitoring settlement of intertidal rocky shore organisms found in filamentous algae (Navarrete et al. 2002, South 2016). Floating collectors were deployed for 24 h at low tide at a boulder shore located at the SW of Helgoland (see Giménez and Dick 2007 for details of location) where *H. sanguineus* is known to occur. Megalopa were classified as belonging to *H. sanguineus* by use of the corresponding identification key (Hwang et al. 1993) and by comparing collected individuals with those obtained from our laboratory cultures. Data on megalopa was pooled for all collectors for each day (max = 34 individuals collected on 8 August, 2018; 124 individuals collected over the settlement season).

Window for larval release (WLR)

The WLR is defined, for a given site, as the number of days of larval release that would allow larvae sufficient time to develop to the megalopa stage within the season. WLR gives the number of opportunities (i.e. potential hatching dates) to achieve development from larval release to the time of when individuals reach the megalopa. We refer to WLR_{15} because it was based on a thermal window defined by the temperature at or higher than 15°C within a year (TW_{15}). TW_{15} is the window, within a year, defined by cold tolerance,

quantified as survival from hatching to the megalopa. We do not have data on the upper thermal tolerance but the temperatures recorded in the data sets never reached the highest temperatures for which complete development is achieved in the laboratory (24°C, this study; 25°C: Epifanio et al. 1998). WLR_{15} is defined in such a way that larger values mean higher chances of sustaining a local population. For instance, assuming a duration of development = 52 d at 15°C, if the temperature were to stay exactly at 15°C for 52 d (and otherwise remain at lower values) we would obtain $WLR_{15} = 1$ d, because only those larvae released at the first day of TW_{15} would be able to reach the megalopa within that window. In real situations, WLR_{15} depends on the breadth of W_{15} and on the actual fluctuations in temperature (i.e. at same width, higher temperatures would lead to a broader WLR_{15}).

We made spatial explicit predictions of the likelihood of *H. sanguineus* to complete the larval development at 16 sites located in the Atlantic coast of N. America, and 19 sites along the North Sea and the Norwegian coast. Predictions for North America were carried out to address the first objective, i.e. to determine if WLR would correctly predict the northern distribution limit for a region where population range expansion has been monitored and is known with high spatial detail (Stephenson et al. 2009, Lord and Williams 2017). Validation was carried out by visual check of the match between model predictions and observations of range limit and by correlations of observed crab densities (Lord and Williams 2017) and values of WLR. We also carried out a validation by calculating the proportion of matches between predictions and observations of presence/absence (Liu et al. 2010); predictions were based on average WLR (over the 3 yr of data) with values of WLR assigned from the two nearest temperature platforms. Predictions were made using two failure thresholds ($WLR = 0$ or $WLR < 5$ d): failure thresholds are usually used in model validation (Crickenberger and Wethey 2018); in our case a failure at $0 < WLR < 5$ would result from high larval mortality rate. In addition, we checked the capacity of averaged WLR in predicting population density through regression and correlation analysis (crab density data in Lord and Williams 2017). The calculation of WLR and its validation was possible because the predicted effects of temperature on duration of development obtained in the experiments matched those obtained for a North American population (see Results) by Epifanio et al. (1998). Predictions for North Europe were carried out to address our second objective, i.e. explore whether WLR will correctly predict the current (northwards) distribution range and whether it would predict poleward expansion.

WLR_{15} was calculated by running the TTM within the thermal window TW_{15} and then computing the average number of days leading to successful development within that window. WLR_{15} was calculated using temperature data from two sources, 'Emodnet' (<www.emodnet.eu>) and 'Seatemperatures' (<www.seatemperature.org>). Emodnet provides data from in situ platforms (e.g. buoys) located near the shore or offshore, with temperature taken hourly or at shorter time scales in surface waters (0–1 m). Seatemperature.

org provides monthly means of sea surface temperature based on NOAA satellite data at coastal towns. We used two sources because the spatial resolution for each data portal varies with region of study, but in addition, the Emodnet platform enabled us to explore the sensitivity of WLR_{15} to year-to-year variations in temperature. In addition, the calculation of WLR_{15} also incorporates uncertainties arising from maternal influences and intra-brood variation in larval responses as it is based on predictions made by the TTM. Details of the platforms used for computing WLR_{15} are given in Supplementary material Appendix 5.

Results

Laboratory experiments with the Helgoland population

Larval survival to megalopa depended strongly on temperature (Fig. 2). At 12°C none of the test larvae reached the megalopa stage, but died instead at the fourth or fifth larval stage. At 15°C, on average 20% of larvae reached the megalopa stage and survival varied among larvae from different hatches (average from 0 to 60%) with considerable variation between the first and the second hatch (Supplementary material Appendix 2 Fig. A2a). Survival from hatching to megalopa was significantly higher in the range 18–24°C (> 40% on average) with lower variation among females (30–60%; Supplementary material Appendix 2 Fig. A2a).

The power model had a better fit than the exponential model in explaining the effect of temperature on duration of development ($\Delta AIC = 31$ in favor of power model; also better residual errors see Supplementary material Appendix 6 Fig. A4). Hence, the best fits were obtained when the logarithmic transformed values of duration of development depended linearly on the logarithm of the temperature (Fig. 3). The power model also contained random terms for the intercept and slopes capturing the variation in the thermal response among hatches (Supplementary material Appendix 6 Table A1).

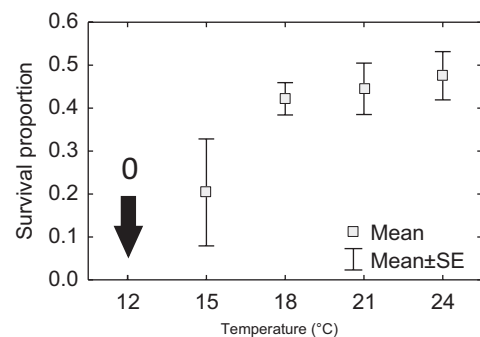


Figure 2. Effect of temperature on average survival of *H. sanguineus* larvae from hatching to megalopa. The error bars, (SE: standard errors) correspond to the variation in survival of larvae hatched from four females. Averages and variation within each female are shown in Supplementary material Appendix 2 Fig. A2a.

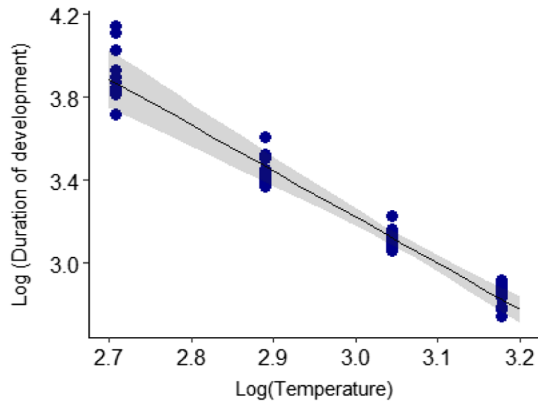


Figure 3. Linearised power model of the effect of temperature (T in $^{\circ}\text{C}$) on duration of larval development (D in days) from hatching to megalopa in *H. sanguineus*. The line is the fixed part of the fitted model while the shaded area gives the confidence interval. The line is given by the following equation: $\log(D) = 9.89 - 2.22 \log(T)$. The full model is given in the Supplementary material Appendix 1 Table A1 and plots for larvae from different females is given in Supplementary material Appendix 2 Fig. A2b.

Validation of TTM

In 2018, zoea I larvae of *H. sanguineus* occurred in low numbers in the plankton samples, but they were found consistently between 6 July to 20 July (Supplementary material Appendix 7 Fig. A4). Larvae were absent from samples taken on 2 and 4 July as well as 29 June. They were also absent in samples taken 23 and 25 July, and from August to October (end of the sampling period).

The modeling scenarios gave a good match between predictions and observations of timing of megalopa in the intertidal (Fig. 4). The model predicted that larvae should reach the megalopa stage between late July and mid to late August, with ranges depending on the scenario. Megalopa started to occur in the intertidal from 20 July, but the main wave of settlement occurred between 30 July and 8 August, matching model predictions. There was a positive and significant cross-correlation between the predicted and observed abundances (Supplementary material Appendix 8 Fig. A5). Significant cross-correlation at negative lags highlight the fact that the observed peak of abundance occurred one time unit before of the predicted peak (Supplementary material Appendix 8 Fig. A5).

Spatial predictions for Atlantic North America

Duration of larval development for our study population (Helgoland, North Sea) was similar to that reported by Epifanio et al. (1998) for a population of the Atlantic coast of N. America (Delaware Bay) at similar temperatures and salinities (Averages: Delaware: 30 PSU; Helgoland: 32 PSU). At 15°C , duration of development differed less than 6% among populations (Delaware: 53 d versus Helgoland: 51 d). Likewise, the average found for the Helgoland populations at 21 and 24°C (22.4 and 17.1 d respectively) matched

very well with those of Delaware at 20 and 25°C (20.8 and 15.6 d). Such similarities enabled us to use our temperature curve to test if predictions from WLR matched the observed distributions.

Predictions of WLR_{15} were consistent with the known patterns of distribution of *H. sanguineus* and with limits of distribution established by Lord and Williams (2017) in N America during a survey carried out in 2015 (Fig. 5a). At the sites where habitats were void of *H. sanguineus*, the predicted WLR were very narrow (Fig. 5b) or there was no window at all because maximal temperatures were lower than 15°C . In 2015, there was an occupied site north of the limit where model outputs based on temperature data from an adjacent platform predicted $\text{WLR}_{15} > 0$ for two of the three tested years. Based on presence/absence, predictions of model accuracy ranged from 75% success (threshold $\text{WLR} = 0$; averaged $\text{WLR} > 0$ is assigned to 4 populations north of the range limit), to 93% (threshold $\text{WLR} = 5$ d). Based on quantitative data, accuracy was high, as we found a significant, positive and strong correlation ($R^2 = 0.82$, Fig. 5c) between average WLR and crab density.

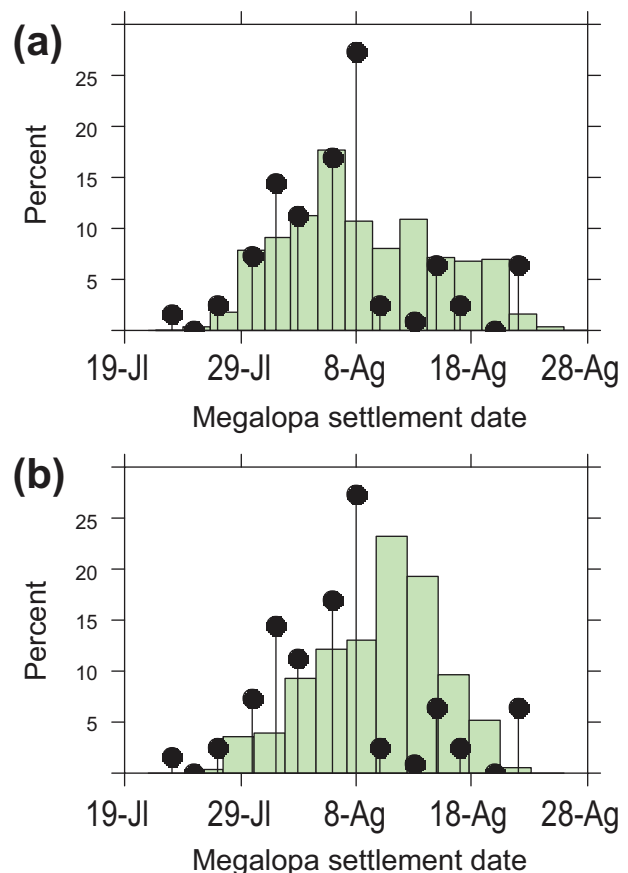


Figure 4. Matching between model predictions (green bars) and observations (black dots) of the temporal distribution of megalopa of *H. sanguineus* in the intertidal of Helgoland. (a) Predictions based on releasing 1000 virtual larvae during the observed window larval release (30 June–25 July). (b) Predictions based on the actual temporal distribution of larvae release.

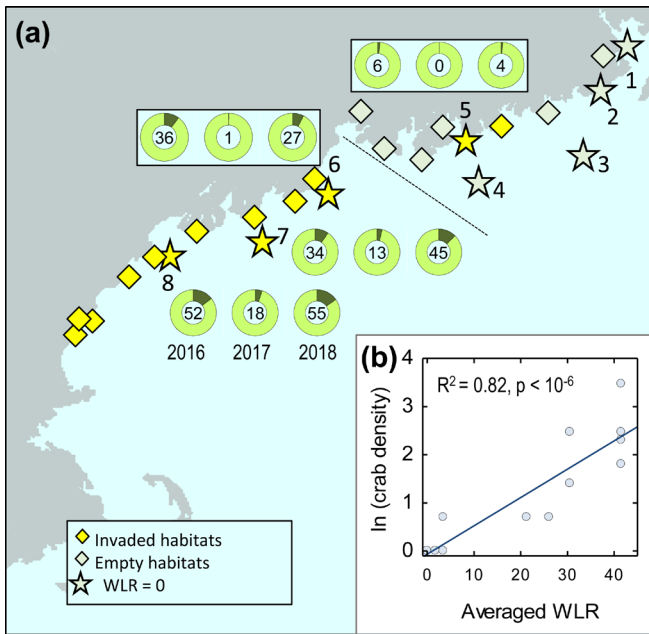


Figure 5. Predicted window of larval release (WLR) across the northern distribution limit of *H. sanguineus* for the Atlantic population of North America for three consecutive years (2016–2018). (a) Distribution of *H. sanguineus* and the position of platforms (stars) providing data of temperature used to compute WLR. Predicted average WLR are represented as pie charts for three consecutive years for platforms 5–8 (note that WLR=0 for platforms 1–4). WLR is given in number of days (from 0 to 55) and as proportion of time (dark green) in the year (remaining time in light green). (b) Correlation between WLR (averaged over 2016–2018) and crab density. Habitats occupancy and crab density were taken from Fig. 2 and Table 2 of Lord and Williams (2017). Additional symbols: for platforms 6 and 7, temperatures in 2017 were > 15 for short periods (platform 6: four periods of 5–8 d; platform 7: 10 consecutive days) and hence WLR is overestimated. Further information on platforms is given in the Supplementary material Appendix 5.

Within the northern limit of distribution, water temperatures predicted $WLR_{15} > 10$ d albeit with strong year-to-year variation. In 2017, reduced temperatures lead to narrower WLR as compared to the other tested years. For platforms 6 and 7, TW_{15} was intermittent in 2017, with periods of time with $T > 15^\circ\text{C}$ were interrupted by long periods of $T < 15^\circ\text{C}$. Hence, the actual values of WLR would be lower as they were to be calculated solely based on periods with $T > 15^\circ\text{C}$ (WLR=0 for platform 6).

Spatial predictions for north Europe

Predictions for WLR_{15} in the North Sea are consistent with the known pattern of distribution of *H. sanguineus* (Fig. 6a), in the sense that $WLR_{15} > 0$ next to the occupied sites. For instance, WLR_{15} , based on average seawater temperatures, predicted ample time for development from hatching to megalopa in the German coast ($WLR_{15} = 30\text{--}90$ d depending on location). Predictions WLR_{15} from daily temperature

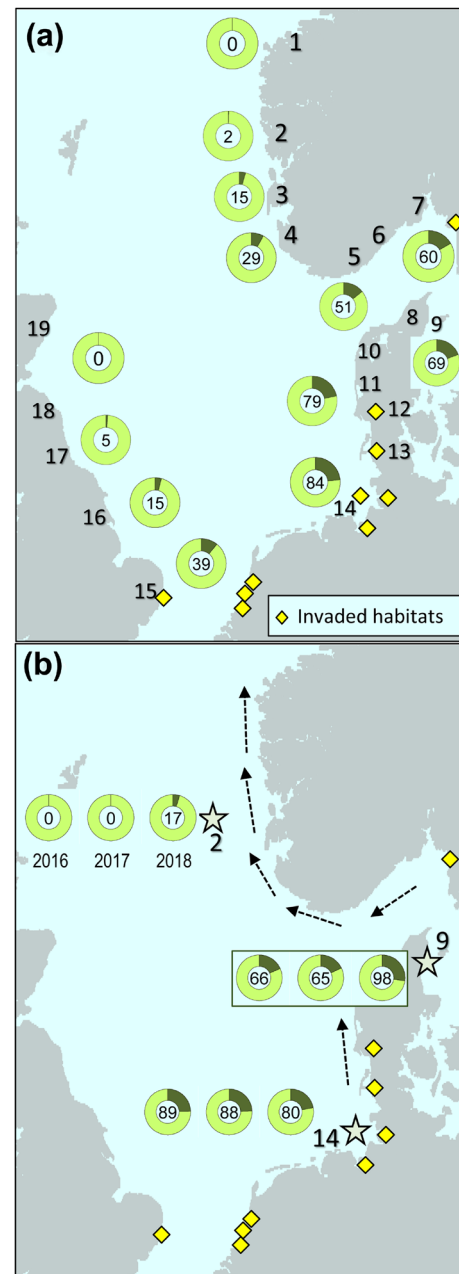


Figure 6. Predicted window of larval release (WLR) across the distribution limit of *H. sanguineus* in NW Europe, given in number of days (from 0 to 98) and as proportion of time (dark green) in the year represented as a pie chart (remaining time in light green). (a) Predictions based on monthly averaged temperatures (source: seatemperature.org) for numbered sites (towns or cities); site names are given in Supplementary material Appendix 5. Diamonds indicate locations where *H. sanguineus* have been found, based on Dauvin et al. (2009) and Jungblut et al. (2017, Fig. 1); lack of diamonds NE England (north of site 15) and Scandinavia (sites 1–7) does not necessarily mean absence, but lack of data. Predictions of WLR are shown only for selected sites (#2–5, 7, 12, 14, 15–17). (b) Predictions based on daily temperatures (source: Emodnet) obtained from platforms (numbered stars) and patterns of coastal circulation (arrows: Jutland Current, Norwegian coastal current). Further information name and geographic location is given in Supplementary material Appendix 5.

observations were also consistent for the two other tested sites (Helgoland and Frederikshavn: compare Fig. 6a and b).

WLR₁₅ predicted a limit of distribution around Bergen in Norway and around New Castle in the UK. The available data on daily temperatures (Fig. 6b) for 2016–2018 led to similar predictions for range limits in Norway (no data were available to check predictions in UK). Such limits are beyond the known limits of distributions (SE England, N Denmark and Swedish coast: Fig. 6).

Predictions of WLR₁₅ based on daily temperature data (Fig. 6b) suggested important temporal variations in the breath of the window for larval development. The summer heatwave of 2018 had an important effect, opening a window for complete development around Bergen and increasing the breath of the window for Fredrikshavn in the Skagerrak. On Helgoland, WLR was narrower in 2018 as compared to the previous years; the breath of the thermal window (TW₁₅ = 116 d) was > 5 d narrower than in the previous years (2016: 121 d, 2017: 127 d).

Discussion

We evaluated if the phenological window of larval release (WLR) would predict distribution limits and poleward expansion of the Asian shore crab *Hemigrapsus sanguineus*. The use of WLR is based on a temperature time model (TTM), validated by showing that predictions of settlement period coincided with observations for the local population. Similar procedures have been carried out in other studies using TTMs (Anger 1983, Dawirs 1985). Our first objective was to determine if WLR would correctly predict distributions limits in the Atlantic coast of North America. This test provided information about the capacity of WLR to predict limits of range distributions in *H. sanguineus*. The application of WLR for the range distribution in N America was validated by the fact that the duration of development for our local population matched that obtained for a population from N America (Epifanio et al. 1998). In consistence with hypotheses made in previous studies (Stephenson et al. 2009, Lord and Williams 2017), WLR correctly predicted the limits of distribution in N America. Both the sharp limits observed in the distribution of *H. sanguineus* and predicted by WLR coincide with a strong temperature gradient in the Gulf of Maine in summer (Kolber et al. 1990).

Our approach to predict the range distribution of *H. sanguineus* may be considered a form process- or fitness-based model (i.e. based on traits determining the fitness of individuals in particular environmental conditions: Morin and Lechowics 2008, Chuine 2010). The use of WLR is consistent with findings identifying phenology as one of the most important traits in shaping species distributions (Chuine 2010, Smith and Hall 2016). Fluctuations in WLR in particular, point towards demographic consequences (Miller-Rushing et al. 2010), as it will set the likelihood for successful reproduction and larval survival in *H. sanguineus*. The use

of WLR enables the integration of information about phenology (timing of larval release and settlement), physiology (larval thermal tolerance) and development (effects of temperature on developmental rates), which constitute a focus of work in phenological research (Forrest and Miller-Rushing 2010). WLR should be more realistic than the use of thermal windows, which can only incorporate effects of temperature on survival. Importantly, the period delimited by WLR based on 15°C is narrower than that delimited by the thermal threshold of 15°C; hence, the use of isotherms may overestimate distribution ranges. The focus on a single window was successful in *H. sanguineus*, most likely because larvae appear

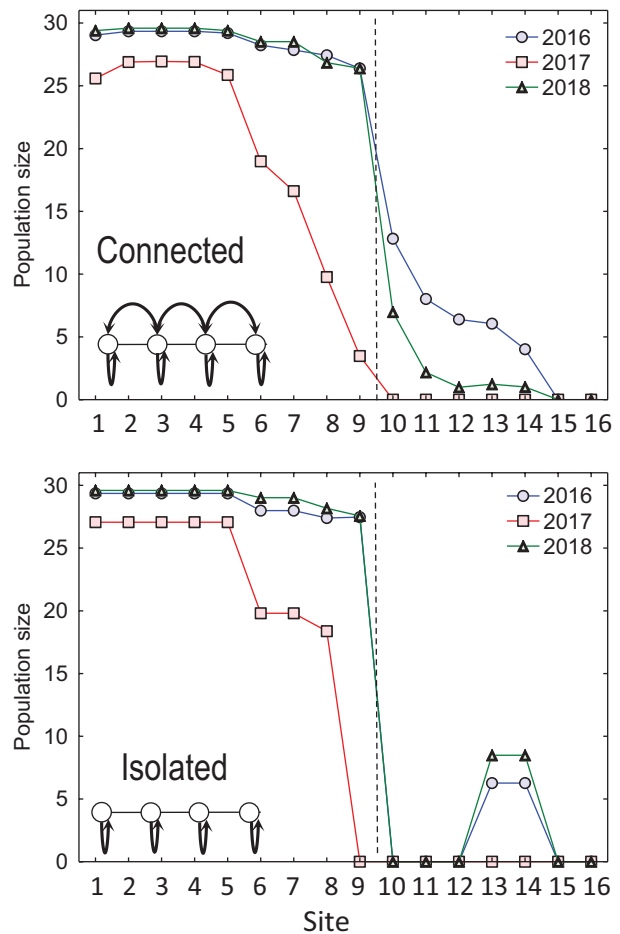


Figure 7. Predictions of distribution range for the coast of North America based on a metapopulation model integrating values of WLR and effects of temperature larval survival predicted for 2016–2018. Upper panel: predictions for a metapopulation connected through stepping stones larval dispersal (coefficient: retention = 0.34, subsidy = 0.33); lower panel: predictions under no connectivity (larvae either return to the parental population or die; retention = 0.34). Models were run for 40 generations with parameters as follows: larval instantaneous mortality rate = 0.18, benthic mortality rates (Beverton–Holt model): density independent term = 0.3, density dependent term = 0.01; fecundity = 1000, initial number of individuals per population = 10 (see Supplementary material Appendix 8 for more details).

to be more sensitive to low temperatures than embryonic or benthic stages (i.e. embryogenesis occur at an earlier time in the year than larvae and adult populations are found at sites with temperatures dropping below 2°C: Stephenson et al. 2009). In a more general context, one may consider the influence of thermal physiology on phenological windows at different life history stages (Briscoe et al. 2012).

Phenological windows may be integrated in a mechanistic model of species distribution. Here, we use a metapopulation model (modified from the one presented in Fig. 1) as a preliminary evaluation of the effects of temperature on distribution range in the coast of USA. The model incorporates the effect of temperature on larval survival and the time of larval release set by WLR (details in Supplementary material Appendix 8). The model, predicts a clear drop of local population size (Fig. 7) around the point where crab densities estimated by Lord and Williams (2017) drop to zero. This prediction is robust to changes in connectivity, although high population connectivity makes the distribution limit less sharp, as sink populations are sustained by larval dispersal. In addition, differences in model predictions, related to the breath of WLR and the level of larval connectivity give also some insights into how temperature increases and larval transport are likely to alter the range of distribution. A further step in the mechanistic predictions of distribution range of *H. sanguineus* may be based on an age-structured metapopulation model (Armsworth 2002, Giménez et al. 2020) incorporating information on benthic and pelagic processes driving survival and migration. A component of such model may incorporate a ‘Lagrangian approach’ to phenology and physiology, whereby the temperature time series, used to calculate WLR and larval survival, is the one being experienced by larvae as they disperse.

The success of WLR in predicting range distributions in North America constituted the validation step for its application on European waters, consistently with standard procedures for mechanistic species distribution models (Peterson et al. 2019). Mechanisms that limit species distribution can vary spatially, but in our case, responses to temperature were similar in larvae from North America and Europe. In Europe, the introduction of *H. sanguineus* has occurred more recently and range expansion has been taking place over the last 10 yr (Jungblut et al. 2018). Hence, our interpretation of the model output is that *H. sanguineus* should expand its range in Europe to S Norway and NE England. Range expansion may occur through maritime transport and larval transport by coastal currents (Fig. 6b). Larval survival of newly occupied habitats should be favoured by summer heatwaves or consistent increase in summer temperatures. Populations at such sites may be established originally as sinks and subsidised intermittently during summer heatwaves, which are likely to occur more frequently in the future (Christidis et al. 2015). Monitoring of the Norwegian coast and that of NE England may determine further expansion and future ecological effects of *H. sanguineus* perhaps detected as a form of source–sink dynamics at the border (Dauphinais et al. 2018);

efforts may focus on warm summers. Monitoring could well start at the first phase of invasion using artificial units of habitats in order to capture megalopa. Artificial units of habitat, such as those used by us can collect up to hundreds of larvae and juveniles, are easy to attach to rocks and can be deployed along large portions of shoreline.

Our predictions of expansion and effects of summer heatwaves are consistent with evidence showing that shifts or fluctuations in distribution limits are driven by climate tolerance (Humphries et al. 2002, Perry et al. 2005, Kelley 2014). Marine organisms in particular, are good in tracking isotherms (Sunday et al. 2012). In addition, fluctuations in range expansion correlate with temperature fluctuations (Behrens Yamada et al. 2005, Diederich et al. 2005, deRivera et al. 2007) and range shifts correlate with climate change (Chen et al. 2011). As temperature increases due to climate change, many sink populations should become self-sustaining and contribute to further expansion.

Our analysis is also consistent with evidence showing that range distributions depend on ontogenetic variations in environmental tolerance (Radchuk et al. 2013, Levy et al. 2015). In particular, environmental tolerance in marine invertebrates appear to be narrow in the larval stage (Przeslawski et al. 2015). However, the establishment of self-sustaining populations may depend on additional factors and processes. Range distributions may be driven by effects of current flow on larval transport (Gaylord and Gaines 2000). Northward larval transport to the Norwegian coast will be favoured by coastal currents (Winther and Johannessen 2006), but currents flowing southwards in the eastern British side of the North Sea may limit northward transport in Great Britain (but see Karlsson et al. 2019). The fact that *H. sanguineus* is already present in the S Scandinavian coast (Sweden: Karlsson et al. 2019), speaks against restrictions in range distribution for that region either in the larval or adult habitats. On the shores of N Europe, the only intertidal competitor is the predatory crab *Carcinus maenas*, but that species already coexists with *H. sanguineus* in North America and N Europe (Lohrer and Whitlatch 2002, Jungblut et al. 2017). A potential limiting factor for the expansion of *H. sanguineus* to E England and S Norway may be adult cold tolerance (< 2°C: Stephenson et al. 2009). However, comparisons of data on winter temperatures for E England and S Norway versus sites where populations are present do not support such hypothesis. Winter seawater temperatures in E England and S Norway (> 7°C: Mathis et al. 2015) are higher than those currently experienced by adults in the German Bight (< 4°C), where populations of *H. sanguineus* persist over the winter (Geburzi et al. 2018). Such difference in winter temperature is likely to result from coastal waters of E England and S Norway being influenced by the inflow of North Atlantic water, bringing water from the warm north–eastern limb of the Atlantic Meridional Overturning Circulation (Otto et al. 1990, Huthnance et al. 2016). Another point is that models are based on records of surface temperature while larvae may occur deeper in the water column. Larvae of *H. sanguineus*

(all stages of development) have been found in surface coastal waters during day and night (Epifanio 2013), but laboratory experiments suggest the existence of tidal and diel vertical migrations (Cohen et al. 2015), which may expose larvae to low temperatures at least for a time in areas with strong stratification. This is not the case at least in the coast of NW England, Netherlands and the German Bight, but summer stratification occurs near the coast in S Norway (Otto et al. 1990). Perhaps, exposure to cooler waters hampers expansion into S Norway if larvae spend considerable time below the thermocline.

A key question is about the future expansion in both invaded ranges. Our analysis does not consider the role of eco-evolutionary processes (Sexton et al. 2009, Donelson et al. 2012, Shama et al. 2014), in particular local adaptation (Hassall et al. 2008, Angert et al. 2011, Peterson et al. 2019) that may explain some mismatches between observations and species distribution models (Fitt et al. 2019). We accounted for intraspecific variation in thermal responses through the incorporation of random terms of the model into the estimations of WLR. Such variation may reflect maternal effects (Giménez 2006) and within-population genetic variation. However, current experimental data and information from the field do not give evidence for spatial variations in larval responses to temperature; otherwise, we would have needed to calculate WLR based on a thermal performance curve specific to the North American population. We found only small differences in the average thermal response of *H. sanguineus* larvae from the North Sea population and another located in North America. In addition, range limits in both North American populations and those in the native range (east Asia) correlate with similar minimum summer temperatures (Stephenson et al. 2009). Both introductions are recent and gene flow maintained by larval dispersal may currently limit the capacity of *H. sanguineus* to evolve larval thermal tolerance; indeed, little genetic spatial difference and high gene flow have been found for the North American populations (Lord and Williams 2017). This is consistent with the fact that evidence of local adaptation is less common in marine than in terrestrial species (Sunday et al. 2012). On the other hand, in north Europe, increasing temperatures in the northern limit of distribution (Burrows et al. 2011) should relax the selecting pressures driving the evolution of larval tolerance to low temperatures. In such scenario, and at least in the short term, the driver of range expansion is likely to be the climate velocity (i.e. the speed of the poleward shifting of the isotherms: Burrows et al. 2011, Pinsky et al. 2013). Climate velocity can surpass the species' ability to occupy the habitat that becomes available (Davis et al. 1986, Schloss et al. 2012). Irrespective of the mechanism, the use of phenological windows could be a valuable tool to model range distributions. An evolutionary process may be modelled through changes in the parameters driving the thermal performance curve.

Data availability statement

Data available from PANGAEA: <<https://doi.pangaea.de/10.1594/PANGAEA.919805>> (Giménez 2020).

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Supplementary material (available online as Appendix ecog-04725 at <www.ecography.org/appendix/ecog-04725>).
Appendix 1.