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Espinosa-Novo, Noé ; Gimenez Noya, Luis; Boersma, Maarten; Torres, Gabriela

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On their way to the North: larval performance of *Hemigrapsus sanguineus* invasive to the European coast. A comparison with the native European population of *Carcinus maenas*

Noé Espinosa-Novo[1*], Luis Giménez[1,2], Maarten Boersma[1,3], Gabriela Torres[1]

[1]Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Biologische Anstalt Helgoland, 27498 Helgoland, Germany.
[2]School of Ocean Sciences, Bangor University, LL59 5AB Menai Bridge, United Kingdom.
[3]University of Bremen, Germany

*Corresponding author:

Noé Espinosa-Novo

Ostkaje 1118

27498 Helgoland

Email: Noe.Espinosa@awi.de

Noé Espinosa-Novo: 0000-0001-8469-3374
Luis Giménez: 0000-0002-1472-2915
Maarten Boersma: 0000-0003-1010-026X
Gabriela Torres: 0000-0003-0970-5990

ABSTRACT

The Asian shore crab *Hemigrapsus sanguineus* has become invasive in North Europe and it co-occurs and competes with the native European shore crab *Carcinus maenas*. Both species develop through a feeding and dispersive larval phase characterised by several zoeal and a settling megalopa stage. Larvae of marine crabs are vulnerable to food limitation and warming has the potential to exacerbate the negative effects of food limitation on survival and growth. We quantified the combined effects of temperature and food limitation on larval performance (survival and growth) of *H. sanguineus* and we compared our results with those reported on performance of *C. maenas* larvae, under the same experimental design and methodology. Larvae from four females of *H. sanguineus* collected on Helgoland (North Sea) were experimentally reared from hatching to megalopa, at four temperatures (range 15-24ºC) and two food conditions (permanent vs daily limited access to food). Larval survival of *H. sanguineus* was low at 15 ºC and increased with temperature, in contrast to the high survival reported for *C. maenas* larvae in the range 15-24 ºC. Food limitation reduced survival and body mass of *H. sanguineus* larvae at all temperatures, but without evidence of the exacerbating effect caused by high temperatures and reported for *C. maenas*. By contrast, high temperature (24ºC) mitigated the negative effect of food limitation on body mass on *H. sanguineus* larvae. Advantages of *H. sanguineus* over *C. maenas* appear especially under the increased temperatures expected from climate change.

Keywords: food limitation, warming, invasive vs native crabs, survival, growth rates

INTRODUCTION

Increasing trade and travel in the last decades has led to biological invasions, i.e. the dispersion and introduction of many species to geographical areas located outside their native range (Hulme 2011; Bailey et al. 2020). Dispersion of organisms due to anthropogenic activities occurs through shipping (ballast water, fouling), construction of corridors, aquaculture, fisheries, and food trade (Carlton 2002, Hulme et al. 2008; Molnar et al. 2008; Katsanevakis et al. 2013). The introduction of a new species can lead to the decline in native species richness and abundances, loss of genetic variation in the native community, and an increase in the homogeneity of the invaded communities (Rahel 2000; Pyšek et al. 2012; Geburzi et al. 2018). Whenever the "introduced" species causes an impact on the host ecosystem, it is considered "invasive". Biological invasions are one of the most important threats to biodiversity after changes in land and sea use, animal exploitation, climate change, and pollution (Brondizio et al. 2019; IPCC 2019). Invasive species affect the dynamics of native communities at different scales (Hulme 2017), by means of different interactions including competition, predation, and introduction of new diseases (Ruiz et al. 2000; Sakai et al. 2001; Jeschke et al. 2012). Biological invasions have been reported for most marine and estuarine habitats in the world (Katsanevakis et al. 2013; Chan and Briski 2017; Pyšek et al. 2020). Many hypotheses have been proposed to explain biological invasions and the success of the invaders (Simberloff and Von Holle 1999; Gurevitch et al. 2011; Kelley 2014), yet there is still little information on the processes involved in dispersion and establishment of alien species in novel habitats (Bailey et al. 2020; Rato et al. 2021).

Global climate change is causing an increase in the number and the impact of biological invasions (Hulme 2017; González-Ortegón et al. 2020; Pyšek et al. 2020), because of the steady increase in temperature (IPCC 2021), and the increased frequency of extreme events (e.g. heatwaves, Meehl and Tebaldi 2004; Smale et al. 2019). These changes combined with other human activities can act together to help the dispersal and establishment of new species. For example, the oyster *Crassostrea gigas* was first introduced in the North Sea for aquaculture purposes and was able to establish there due to above-average summer temperatures that helped the species to spread (Diederich et al. 2004; Smaal et al. 2009). Global warming has also led to the poleward expansion of many species (Sorte et al. 2010; Poloczanska et al. 2013; Giménez et al. 2020).

Global warming could affect both invasive species and their native competitors in different ways. How different species respond to changes in environmental variables (e.g. temperature) will ultimately determine individual performance and species interactions. Increases in temperature cause rises in metabolic demands, which should be met by food supply (Gillooly et al. 2001; Somero 2002). However, for organisms living in the marine pelagic realm, where the food distribution is patchy (Paffenhöfer et al. 1987, McManus et al. 2003) increased temperature combined with food limitation could impair growth and survival. The combined effect of food limitation and increased temperature may particularly impact life history stages characterised by high growth rates (Foster and Hirst 2012; Otto et al. 2020). Crustacean larvae are an example where high growth rates are sustained by high feeding rates, which in turn demand higher food availability (Anger 2001). In such case, one would expect that increased temperatures combined with limited access to food may cause reductions in growth rate and survival (Torres and Giménez 2020). However, the nature of the effect could vary between native and exotic competitors because of differences in thermal optimum ranges (Griffith et al. 2021). Hence, a critical question to understand current invasion and future population spread is how increased temperature combined with food limitation drive the performance of both native and exotic species.

The Asian shore crab *Hemigrapsus sanguineus* is native to the east coast of Asia (20º - 50º N) (Takahashi et al. 1985; Fukui et al. 1989; Hwang et al. 1993). It is one of the most abundant crab species on rocky beaches and occupies the upper and middle intertidal zones (Kikuchi et al. 1981; Fukui 1988). It has successfully invaded the coasts of North America, North Europe, and the Adriatic and Black Seas (Schubart 2003; Micu et al. 2010) via ballast water (Ai-yun and Yang 1991; Kraemer et al. 2007; Epifanio 2013). In northern Europe, *H. sanguineus* was first recorded in France and the Dutch Delta system in 1999 (Breton et al. 2002) and then spread to the North Sea and Scandinavia (Wolff 2005; Kerckhof et al. 2007; Dauvin and Dufossé 2011; Gittenberg et al. 2010; Gothland et al. 2013; Seeley et al. 2015; Karlsson et al. 2019). *H. sanguineus* was occasionally found in the Mediterranean and Black Sea (Schubart 2003; Ben Souissi et al. 2004; Micu et al 2010; Ounifi-Ben Amor et al. 2016a,b; GBIF.org). There are several factors likely to drive or limit the expansion of *H. sanguineus*, including the presence of congeneric competitors (e.g. US North Pacific, Steinberg and Epifanio 2011, Lord 2017) and low summer temperatures (Stephenson et al. 2009). In the Atlantic coast of North America, the northern distribution limit of *H. sanguineus* is determined by the larval thermal tolerance to low temperatures (Epifanio et al. 1998; Stephenson et al. 2009). Hence, as a result of warming, the distribution of *H. sanguineus* is likely to expand further north (Epifanio 2013; Giménez et al. 2020). *H. sanguineus* co-occurs and competes with the shore crab *Carcinus maenas* in Europe and in North America. Both species overlap in diet and habitat use, with juvenile/adults of *H. sanguineus* outcompeting *C. maenas* in the use of space and resources*. H. sanguineus* also predates on *C. maenas* juveniles affecting their recruitment success (Lohrer and Whitlach 2002; Jensen et al. 2002; Geburzi et al. 2018). For example, in Southern New England *H. sanguineus* has significantly reduced the recruitment of *C. maenas* due to direct predation, leading to a decline in densities by 40 - 90 % (Lohrer and Whitlatch 2002). In addition, when in sympatry individuals of *C. maenas* migrate towards the subtidal zone (Geburzi et al. 2018). The above-mentioned factors, help explain the displacement of *C. maenas* from environments where it was previously more abundant.

We compared the performance of *H. sanguineus* and *C. maenas* from the perspective of the larval phase for co-occurring populations of the German Bight (Helgoland, North Sea). We focus on larvae because larval survival and recruitment are critical contributors to the propagule pressure by *H. sanguineus* (Simberloff 2009) and for the persistence of populations of *C. maenas*. Propagule pressure, i.e. a group of individuals of a species arriving in a region to which they are not native, drives the establishment and spreading of invasive populations (Simberloff 2009). Marine larvae in particular, tend to be more sensitive to environmental fluctuations than juveniles or adults (Pandori and Sorte 2019) and larval survival is central to the recovery of populations after environmental disturbances (Cowen and Sponaugle 2009; Pineda et al. 2009; Giménez et al. 2020). In particular, differences in larval survival among co-occurring species may affect the balance of competition, either exacerbating or counteracting the outcome. In theory, counteracting effects may occur in cases of trade-offs between competition and dispersal abilities (Seifan et al. 2013). Because *H. sanguineus* was first reported in the German Bight very recently (2008- Scrosati et al. 2011, 2009- Jungblut et al. 2017), it is not clear yet whether *H. sanguineus* would be able to outcompete *C. maenas* at that local habitat. Unlike *C. maenas*, larvae of *H. sanguineus* cannot develop at temperatures below 13-15 ºC (Epifanio 2013) which characterise the spring and early summers in the German Bight and coastal North Sea (Giménez et al. 2020). For *H. sanguineus*, larvae appear to be released when the temperature surpasses 15 ºC which is early/ mid- June depending on the year (Giménez et al. 2020). In the case of *C. maenas*, larval release starts in May (Harms et al. 1994), but the full larval season of both species partially overlap. We know that under food limitation, zoea I of *H. sanguineus* is more tolerant to short thermal fluctuations than *C. maenas* (Giménez et al. 2021). However, over the entire larval phase and under low temperatures, food limitation may produce a stronger negative effect on survival of *H. sanguineus* than that observed in *C. maenas*.

Here we compared the responses of larvae of *Hemigrapsus sanguineus* and *Carcinus maenas* to food limitation under increased temperature, reared in comparable experimental conditions. We first quantified the combined effects of temperature and food limitation on survival and performance of larvae of *H. sanguineus.* For the first time, we documented growth and survival responses in any population of this species to food limitation over a wide range of temperatures. In particular, we quantified the correlated responses of growth and development, driving size, and reserves at metamorphosis, which for benthic invertebrates, are known to drive the performance of the post-metamorphic stages in the benthic habitat (Giménez et al. 2004; Pechenik 2006; Giménez 2010; Torres et al. 2016). Second, we compared our results on *H. sanguineus* with those obtained by Torres and Giménez (2020) for a co-occurring population of *C. maenas*.

MATERIALS AND METHODS

Animal husbandry, larval rearing and experimental design

Berried females of *H. sanguineus* (carapace width 15.8 - 17.2 mm) were collected on the island of Helgoland (North Sea, German Bight, 54°10'40.9" N 7°53'32.4" E) during their reproductive season (July - September) and transported to the laboratory. Females were kept individually in 2-L aquaria with UV-treated filtered (0.2 µm) seawater (32.5 ‰) permanently aerated, in a temperature-controlled room at 18 ºC (± 0.5 ºC) with a 12:12 h light: dark cycle. Females were fed every 3 days with shrimps (*Crangon crangon*) and water was changed daily to ensure high water quality at hatching.

The experimental setup comprised a factorial design, in which we exposed larvae obtained from each given female to different combinations of temperatures and access to food (following Torres and Giménez 2020). This experimental procedure was repeated four times, i.e. once for each of the hatches obtained from four different females, in order to assess potential variations in responses driven by maternal influence. Freshly hatched zoeae were distributed in 8 treatments (4 replicate vessels per treatment, see below for more details), combination of 2 levels of daily access to food (6 or 24 h / day, provided *ad libitum*) and 4 temperatures (15, 18, 21 and 24 ºC). The different temperatures were chosen based on its natural variability in the German Bight: 15 and 18 ºC represent temperatures recorded during the larval season of *H. sanguineus* (Giménez et al. 2020); this corresponds to summer temperatures around the local population (Wiltshire and Manly, 2004). Temperatures > 20 °C are expected as the consequence of steady warming due to climate change (Schrum et al. 2016), and as the consequence of the expected increment in the frequency of warm summers (Christidis et al. 2015).

Experiments were carried out in temperature-controlled rooms and using natural UV-treated filtered (0.2 µm) seawater. When hatching occurred, 50 larvae were sorted into each of 500-mL rearing vessels (4 replicate vessels per treatment for each of the four females) in UV-treated filtered seawater at the temperature of hatching. Freshly hatched *Artemia* sp. nauplii (Great Salt Lake Artemia, Sanders, USA) were provided as food for the larvae in densities of ~5 nauplii/mL (Torres et al. 2021). In the treatment of limited access to food, *Artemia* sp. nauplii were available for 6 hours each day (between 9 a.m. and 3 p.m., following Giménez and Anger 2005, Torres and Giménez 2020). By contrast, in the treatment of permanent access to food, *Artemia* sp. nauplii were available all day. Water in all treatments was changed daily following standard procedures for larval rearing (Torres et al. 2021). During the daily water change, live larvae were staged and recorded, dead ones were also recorded and removed from the experiments; in addition, we checked that remaining food was present in each rearing vessel.

Body mass and elemental composition (carbon and nitrogen) were measured in freshly hatched larvae (3 replicates, 50 zoea each at the start of each experiment) and in freshly moulted megalopae (sampled within 24 h after moulting). Carbon content is used as a proxy for lipid reserves, used by crustacean larvae to sustain periods of food limitation (Dawirs et al. 1986; Anger and Harms 1990); nitrogen content is used as a proxy for protein content (Dawirs 1996; Dawirs et al. 1986). The number of individual megalopae sampled in each of the 4-replicate rearing vessel was on average 5 (Table S1). Larvae were pipetted onto a filter, rinsed with distilled water, gently blotted dry with filter paper, and stored in pre-weighed tin cartridges at -20 °C for later analysis. To determine the dry weight, samples were freeze-dried for 48 h and weighed using a microbalance (Sartorius SC2, precision 1 µg). Carbon and nitrogen content were then determined using an elemental analyser (vario MICRO cube CHNS analyser, Elementar Analysensysteme).

Data analysis

The response variables were survival, duration of development, body mass, elemental composition (carbon and nitrogen), and instantaneous growth at the megalopa. Survival to each zoeal stage was calculated as the percentage of survivors in relation to the number of organisms at the start of each experiment. Duration of development was calculated as the time elapsed from hatching to reach each developmental stage. Growth rates were estimated as $G = \log (W_f / W_0)/t$. In this formula W_0 is the average mass (dry weight, carbon or nitrogen) at hatching, W_f is the corresponding mass of each individual megalopa collected in each rearing replicate and t is the corresponding duration of development of each individual megalopa.

Mixed modelling was carried out in R (function lme and gls from package nlme, Pinheiro et al. 2018, R Core Team 2013) to assess the responses to the different combinations of food availability and temperatures on survival and duration of development. The models contained temperature and food availability as fixed factors and female of origin as a random factor. We performed backwards model selection (Zuur et al. 2009) in two steps. In a first step, we tested the random terms using restricted maximum likelihood (REML), we compared the different models through the corrected Akaike information criteria (AICc) and ranked them. The model with the lowest AICc was selected for further analysis. When the difference between two models was ΔAICc < 3 and the most complex model had the lower AICc we applied hypothesis testing (likelihood ratio tests). When the models differed significantly ($p < 0.05$), we chose the model with the lowest AICc and when the difference was not significant we chose the simpler model (with the lowest number of parameters). In a second step, the fixed terms were analysed through maximum likelihood (ML). For dry mass, elemental composition, and growth rates at the megalopa we did not get sufficient data in the food limited treatment at 15 °C for female 4 (F4). We therefore, analysed the data using two different starting models: (1) considering all females but without 15 °C and (2) considering all treatment combinations but without F4.

Data for survival was analysed in the logistic (Warton and Hui 2011) and logarithmic scale; as a first step, proportions (p) were re-scaled using the formula $p' = [p (50-1) + 0.5]/50$, to avoid inconsistencies associated to log (0) values. Logarithmically-transformed proportions were used to test the multiplicative model, whereby temperature and food limitation would act independently on the survival rates (Piggot et al. 2015). Survival responses consistent with a multiplicative model cannot be tested when the proportions are expressed in the logistic scale (Torres and Giménez 2020). Duration of development was analysed in the raw and the logarithmical scale to test if the effects were additive, multiplicative or interactive. Body mass and elemental composition were analysed in the raw scale. Tukey´s honestly significant difference tests (Tukey´s HSD) were performed to test differences among the different treatments.

Comparison performance *H. sanguineus* and *C. maenas*

We compared the performance of *H. sanguineus* and *C. maenas* at different temperatures and food conditions through two means. First, we compared the integrative response of body mass and developmental time. We calculated the ratios between the body mass under food limitation and those observed under permanent access to food for each temperature; the same calculation was made for duration of development. For comparison, these standardised values were plotted against those of *Carcinus maenas*. In this plot, the unit corresponds to the values of body mass (and duration of development) under permanent access to food at each temperature.

We also calculated the ratios of survival (S_R) and growth rates (G_R) between species, i.e. as SR $=S_H/ S_C$ and $G_R= G_H/ G_C$, where S_H and S_C are the survival to the megalopa of *H. sanguineus* and *C. maenas*, respectively and G_H and G_C the respective growth rates (from hatching to megalopa). We calculated average ratios and used simulations (details in: Supplementary material, Materials and Methods, Section 2. Data analysis: details on model simulation) to incorporate the intraspecific variation in survival and growth associated to variations within and among families. First, for each species, we simulated 1000 values of the survival and growth rates. Survival was simulated from the statistical model fitted to the responses of both species to the different combinations of temperature and access to food; i.e. there were 1000 values for each combination of species, response variable, temperature, and food condition. Growth was simulated from an additional statistical model which also considers survival as covariate; this model incorporates correlations between average survival and growth associated to female-to-female variation in larval performance. The data and models used for *C. maenas* correspond to Torres and Giménez (2020). The model used for survival of *H. sanguineus* was that of Tables S2; for growth we fitted an additional model based on female-to-female averages (Supplementary material, Materials and Methods, Section 2. Data analysis: details on model simulation). Simulations were performed using the function *simulate* of the package nlme (R Core Team 2013) applied to the best fitted models for each variable. Second, for each combination of temperature and food condition a pair of values of survival and growth was randomly sampled (function *sample,* R Core Team 2013) for each female of each species. The ratio of survival (or growth) was calculated between two randomly chosen females (one per species). This procedure was repeated 4000 times in order to obtain distributions of ratios of survival (and growth) for each combination of temperature and food condition. We then calculated the average of four ratios, comparing the performance of four hatches of *H. sanguineus* and four of *C. maenas*; this calculation takes into account that larvae obtained from four different females were used for each study. In addition, this procedure to calculate the average maintained the correlation between survival and growth. Using the simulated ratios of survival and growth, we calculated the centroid and the 90% confidence ellipses which were plotted for each combination of temperature and food (see Fig. 5).

RESULTS

We first describe the survival, development and growth rates for *Hemigrapsus sanguineus* and we compare them to the data from *Carcinus maenas* already published (Torres and Giménez 2020, PANGAEA: https://doi.org/10.1594/PANGAEA.918056). The graphs showing the results corresponding to already published data of *C. maenas*, are highlighted with a grey background in figures 1, 2 and 3.

Survival, development, and growth

Survival to megalopa in *H. sanguineus* decreased towards lower temperatures and under limited access to food (Fig. 1, left panel); while at 15 °C, food limitation reduced survival by 74 %, at 24 °C the survival reduction was 35 %. Best models retained food availability and temperature operating in additive or interactive ways depending on the stage (Table S3), but with variations among larvae from different females (Table S4). Survival to megalopa under limited access to food ranged from 0 - 74 % depending on temperature and female of origin, with 0 % survival occurring at 15 ºC and 24 ºC for female 3 (Fig. S5). The effects of temperature and limited access to food on survival to zoeae II to IV were small, but increased for survival to ZV and especially to the megalopa (Fig. S6). The sensitivity to temperature varied among larvae from different females; survival at 15 °C was consistently low (13.2 %) but survival at 24 °C ranged from 19 to 92 % (larvae under permanent access to food) depending on the female (Fig. S5).

The combined effects of temperature and food limitation on the overall survival to megalopa (Fig. 1, left panel) were consistent with a multiplicative model (additive model retained in the logarithmic scale: Table S3). The multiplicative model can be illustrated considering the combination of 24 ºC and permanent access to food as the optimal condition. In this case, the observed proportion of survivors under the combination of two stressors experienced simultaneously (15 ºC and limited access to food: 0.05) is close to that expected by the product of the proportions observed when the stressors were experienced in isolation (limited access to food: 0.3; 15 ºC: 0.2). On a female-by-female basis, the effects ranged from synergistic with a strong effect of temperature (F1 and F2) to antagonistic with a strong effect of limited access to food (F3 and F4).

The overall response of *H. sanguineus* was clearly different from that of *C. maenas* (Fig. 1). The increased survival of *H. sanguineus* with temperature irrespective of the food condition contrasts with the reduced survival of *C. maenas* under food limitation and high temperatures. The response of *H. sanguineus* to food limitation and temperature, consistent with a multiplicative model, also differs from the strong interactive effect shown by *C. maenas* where high temperatures exacerbated the effect of food limitation on survival (Fig. 1).

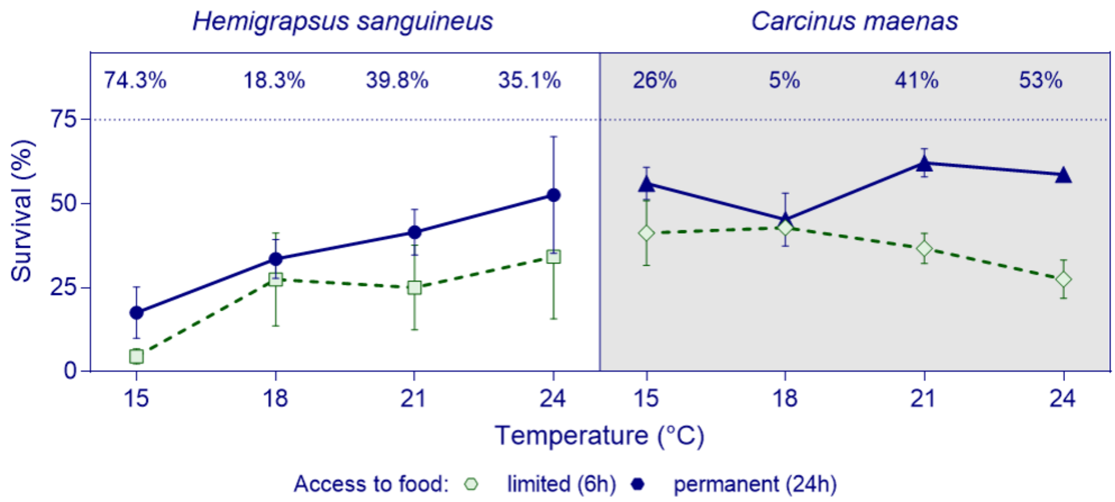

Figure 1. *Hemigrapsus sanguineus* and *Carcinus maenas*. Average survival from hatching to megalopa as a response to temperature and food availability. Data shown as average values ± SE for the four females of origin. Permanent access to food: blue symbols and continuous line; limited access to food: green symbols with dashed line. Percentages on top (only when significantly different): percent difference in survival between permanent and limited access to food treatments for each temperature. Already published data for *Carcinus maenas* is presented in the right panel, grey background (Torres and Giménez 2020).

Duration of development to megalopa in *H. sanguineus* increased with decreasing temperatures in a non-linear pattern (Fig. 2a, left panel); the best model retained the interactive effect of temperature and limited access to food (Table S5). At low temperatures, the effects of food limitation were weak, producing a delay in the metamorphosis of fewer than 3 days (representing less than a 5 % change between the two food conditions). However, at 21 and 24 ºC the delay was longer than 3 days, representing 14 - 16 % change (Fig. 2a, left panel). The effect of food limitation was weak at early stages and then it became stronger in the zoea IV (Fig. S7); best models retained temperature in development to stages ZII and ZIII, temperature and food availability operating in an additive way in development to ZIV, and interactively in development to ZV and megalopa (Table S5). In larvae from all females reared at 15 °C, there was an extra zoeal stage (zoea VI) regardless of food availability.

Carbon growth rates of *H. sanguineus* increased with increasing temperatures in both food conditions; food limitation caused a reduction in carbon growth rates, and the effect was stronger at higher temperatures (Fig. 2b, left panel); best models retained the interaction of food availability and temperature (Table S6). Similar effects were also found in terms of dry mass and nitrogen content (Fig. S8 a, c). Exposure to food limitation resulted in a reduction in body mass, carbon and nitrogen content (Figs. 2c left panel, S8 b, d), but the magnitude of the effect depended on temperature and varied among females. Best models retained food availability and temperature operating interactively (Table S6). Consistently for all females, the effect of food limitation on carbon content was strong in the range 15

- 21 ºC as compared with 24 ºC (e.g. 16 % vs 8 % decrease in carbon content). Similar effects were found for dry mass and nitrogen content (Fig. S8 b, d). Food limitation reduced carbon and nitrogen contents in similar proportions among temperatures resulting in comparable C/N ratios (Fig. 2d, left panel); the exception was 15 ºC where the reduction in nitrogen (19 %) was higher than that of carbon (16 %).

Duration of development and growth of *H. sanguineus* larvae were more affected by temperature which contrasts to those of *C. maenas*, that are more sensitive to food limitation (Fig. 2). In terms of duration of development, larvae of *H. sanguineus* were more sensitive to temperature than *C. maenas*, especially at low temperatures; at 15 ºC *H. sanguineus* reaches the megalopa in ca 70 days while *C. maenas* needs ca 30 days (Fig. 2a). By contrast, limited access to food increased developmental time in a lesser extent in *H. sanguineus* (< 16 % change between the two food conditions) than in *C. maenas* (> 20 %). While growth rates of *H. sanguineus* increased with temperature irrespective of the food condition, those of *C. maenas* decreased with temperature but remained constantly low in the food limited treatment (Fig. 2b). *H. sanguineus* megalopa had higher carbon content and lower C/N ratios than *C. maenas* (Fig. 2d). The weakest effect of food limitation on carbon content found at the highest temperature in *H. sanguineus* contrasts to the pattern found in *C. maenas*, where the effect was weakest at the lowest temperature (Fig. 2c).

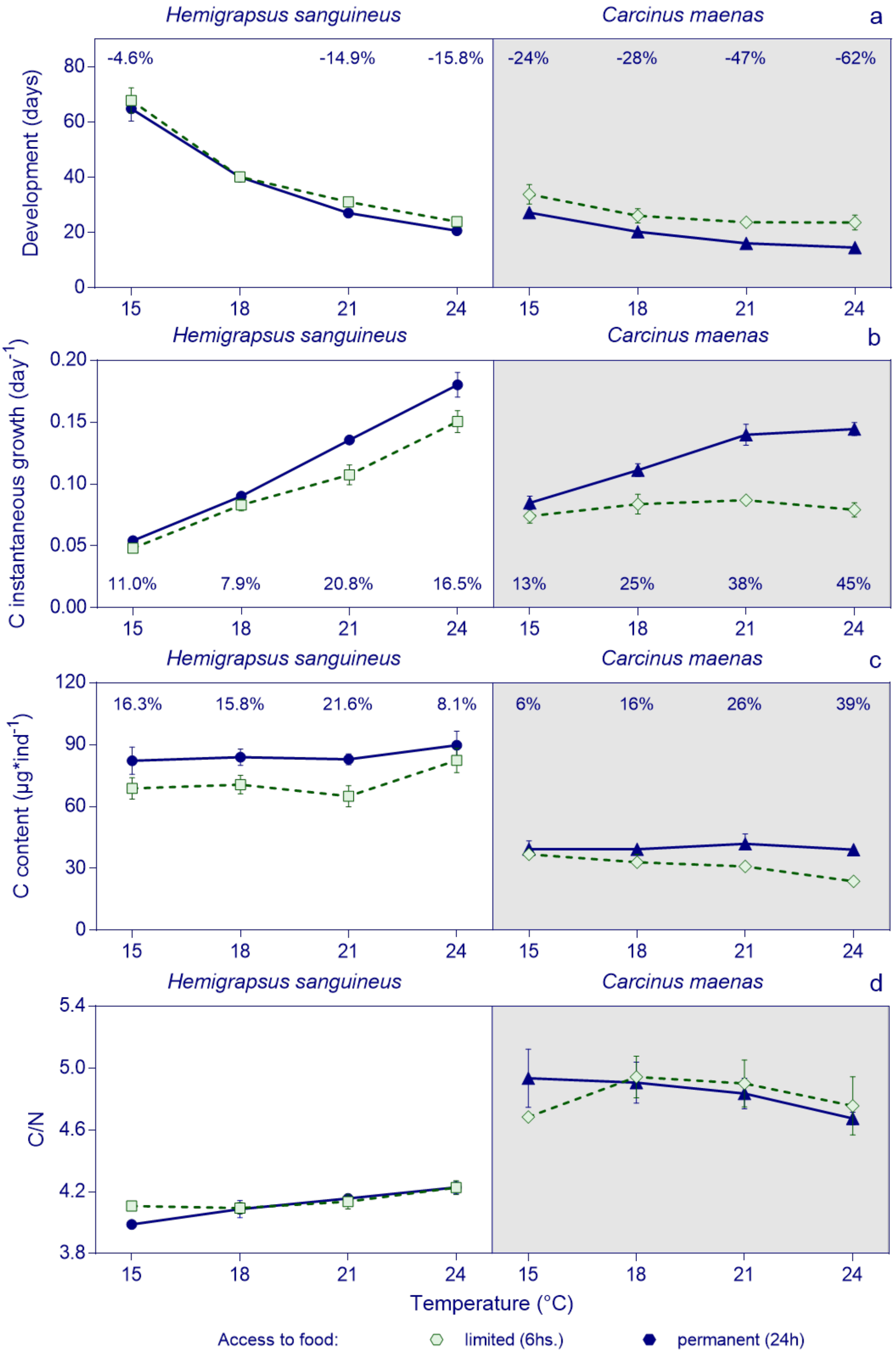

Figure 2. *Hemigrapsus sanguineus* and *Carcinus maenas*. (a) Average duration of development. (b) Average growth rates. (c) Average carbon content. (d) Average C/N ratio. Data corresponds to the responses, from hatching to megalopa, to temperature and access to food. Data shown as average values ± SE. Symbols as in Figure 1. Percentages on top or below (only when significantly different): percent difference in development time, C growth, C content, and C/N between permanent and limited access to food treatments for each temperature.

Integrated growth responses to megalopa of *H. sanguineus* were characterised by a strong decrease in body mass under food limitation rather than a long delay in development. The delay in metamorphosis did not compensate the effects of food limitation on growth rates. At 24 °C and under permanent access to food larvae reached a maximum threshold of body mass (= 260 µg/ ind), and differences between food conditions were small (limited access to food = 240 µg/ ind). However, lower thresholds were reached at lower temperatures, especially under limited food availability (Fig. 3, upper side of graph). In addition, *H. sanguineus* larvae did not compensate for the effect of low temperature on body mass even under permanent access to food (Fig. 3, upper side of graph). Similar patterns characterised the integrated responses in terms of carbon and nitrogen content (Fig. S9).

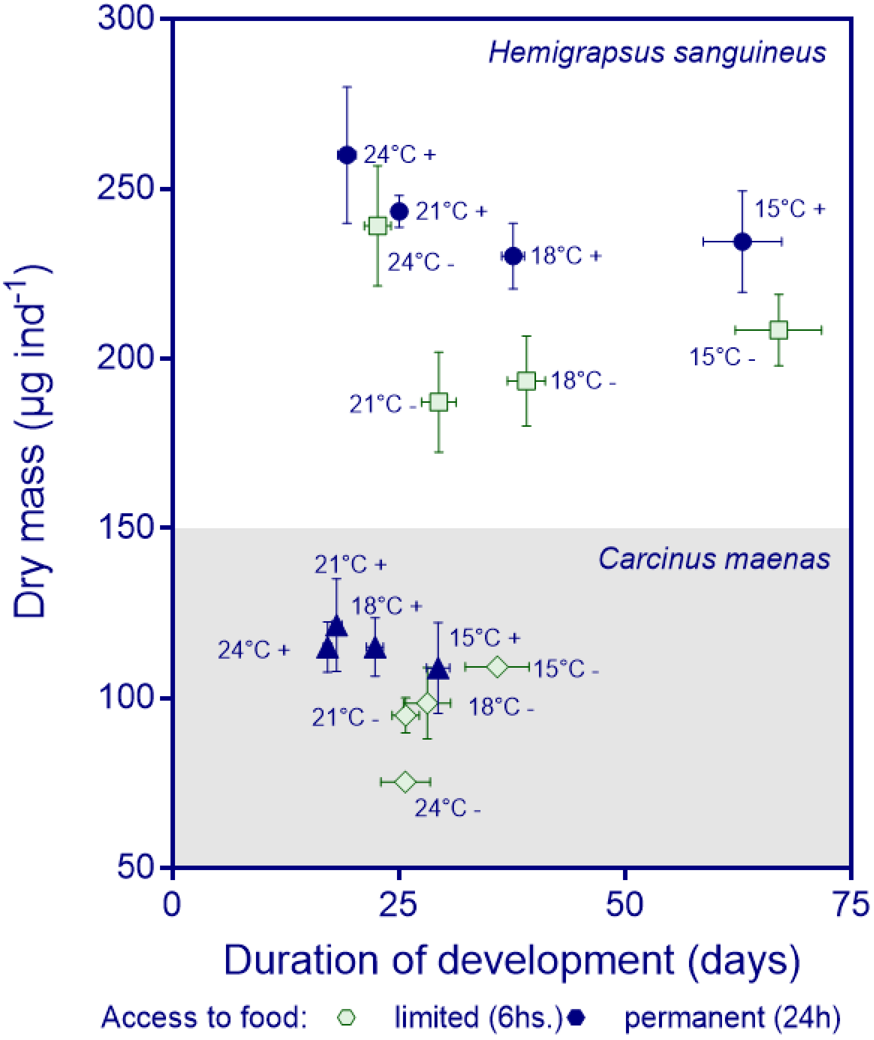

Figure 3. *Hemigrapsus sanguineus* and *Carcinus maenas*. Integrated responses of body mass and duration of development under the different treatments of temperature and food availability. Data shown as average values ± SE for both variables. Symbols: permanent access to food is represented with blue symbols (indicated as `+´) and limited access to food with green symbols (indicated as `-`), temperature is indicated in the graph next to the symbols.

The range of variation in the integrative response of *H. sanguineus* is much higher than that of *C. maenas* larvae (Fig. 3). However, when the duration of development and the body mass are standardised, the opposite pattern arises. Figure 4 compares the effect of food limitation on the integrated responses of body mass and developmental time, for each temperature, of both *Carcinus maenas* and *H. sanguineus*. Each variable (V: body mass or duration of development) was expressed for each temperature (T) as a ratio, R:

$$R_T = \frac{V_{T,L}}{V_{T,P}} \quad (1)$$

where the subindices L and P represent limited and permanent access to food, respectively. In this representation, the condition of permanent access to food is set to one irrespective of the temperature because the formula becomes:

$$R_T = \frac{V_{T,P}}{V_{T,P}} = 1 \quad (2)$$

Figure 4 shows that as compared with *C. maenas*, *H. sanguineus* extended the development in a small fraction in response to limited access to food. In *C. maenas*, the proportional reduction in body mass and delay in metamorphosis became larger with temperature (Fig. 4, see also Torres and Giménez 2020); by contrast in *H. sanguineus* both reduction in body mass and delays in metamorphosis do not show any consistent trend.

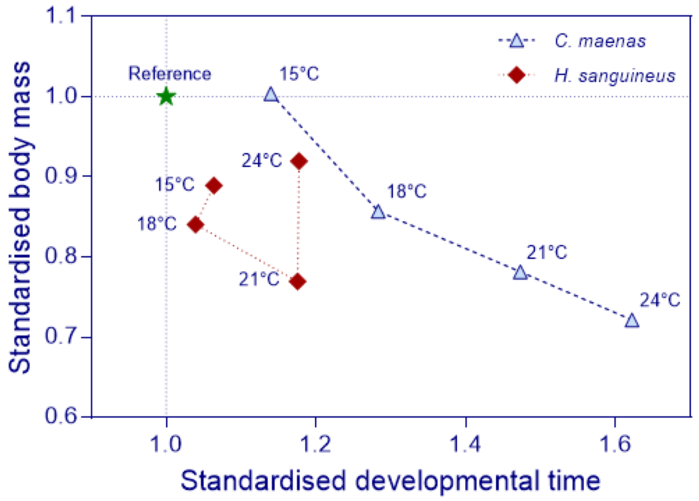

Figure 4. *Hemigrapsus sanguineus* and *Carcinus maenas*. Summary of standardised responses to the different temperatures under food limited conditions (blue triangles and red diamonds, see equation (1)). For the standardised values of body mass and developmental time, the values for permanent food conditions represent the unit (green star, see equation (2)). At the lowest temperature tested, *C. maenas* extended the developmental in response to food limitation; larvae compensated for the limited access to food, metamorphosing with high body mass. *H. sanguineus* did not compensate for the limited access to food and metamorphosed with lower body mass. Symbols: *C. maenas*: blue triangles, *H. sanguineus*: red diamonds. Data for *H. sanguineus* this study, data *C. maenas* from Torres and Giménez 2020.

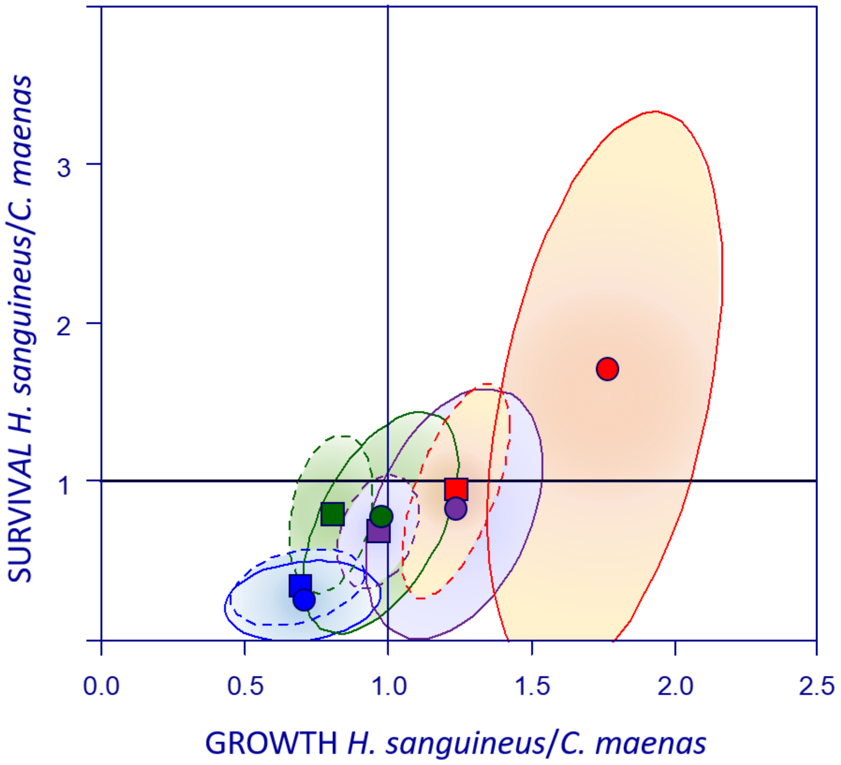

Figure 5. *H. sanguineus* and *C. maenas* simulated survival and growth ratios under different food and temperature conditions. Squares and circles denote centroids of 95% confidence ellipses in shown colour. Data for permanent access to food (circles) shown with ellipses as continuous lines and for limited access to food (squares) as dashed lines. Blue: 15 °C, green: 18 °C, purple: 21 °C and red: 24 °C.

The results of the simulated ratios of survival vs growth rates of both species showed that at most of the temperatures and food conditions (15 °C and 18 °C permanent and limited access to food and 21 °C limited access to food) larvae of *C. maenas* will be favoured; but at higher temperatures and especially under conditions of high access to food, larvae of *H. sanguineus* may be favoured (Fig. 5). The ellipses, indicating the importance of intraspecific variation in the performance of both species, show that *H. sanguineus* might perform better at higher temperatures, but it is not likely to outperform *C. maenas* at the lower temperatures that characterise the German Bight.

DISCUSSION

There were three main findings out of our experiments. First, *Hemigrapsus sanguineus* is able to metamorphose to megalopa under limited daily access to food over a wide thermal range (15 - 24 ºC). Second, within the range of temperatures experienced in the local habitat (German Bight, North Sea), low temperature (15 ºC) appears to be the primary limiting driver of larval performance, in terms of survival and growth. Third, when the performance is quantified in relation to that of *Carcinus maenas*, unfavourable scenarios for *H. sanguineus* are projected for temperature characterising cool summers. In turn, favourable scenarios are projected for summers characterised by long heatwaves and after coastal warming.

Temperature and food limitation

H. sanguineus larvae were able to metamorphose to megalopa under limited access to food over a wide range of temperatures, with some variations among families (i.e. larvae originated from different females). This is consistent with other studies on decapod crustacean larvae and strengthen the general hypothesis that such larvae can reach metamorphosis as long as they access food patches for a short period of time every day (Sulkin et al. 1998; Giménez and Anger 2005; González-Ortegón and Giménez 2014; D´Urban Jackson et al. 2014; Torres and Giménez 2020). Limited daily access to food is expected in habitats characterised by food patchiness (Paffenhöfer et al. 1987; Durham and Stocker 2012; Prairie et al. 2012, Robinson et al. 2021) and in scenarios where larvae perform diel or tidal migrations (Forward et al. 2001; Queiroga and Blanton 2005; dos Santos et al. 2008, Thygesen and Patterson 2019). In temperate latitudes such as the one of the German Bight, access to prey during nigh time should be limited to a few hours because *H. sanguineus* larvae develop in summer when the darker period is restricted to few hours. Hence, *H. sanguineus*, as other species including *C. maenas* should be able to survive the larval phase as long as they access prey for a limited amount of time every day.

Food limitation had important consequences in terms of body mass and reserves at metamorphosis to the megalopa as well as growth rates and developmental time. In species with complex life cycles, traits at metamorphosis are relevant for post-metamorphic survival and are the basis for trait-mediated effects of the pelagic environment on recruitment in the benthic habitat (Giménez 2004; Pechenik 2006; Marshall et al. 2008; Torres et al. 2016). Larvae of *H. sanguineus* under food-limited conditions metamorphosed to megalopae with reduced body mass at all temperatures, suggesting that impacts of food limitation are consistent across the thermal range expected for cool and warm summers. It is important to understand the mechanisms driving body size at metamorphosis as they should mediate effects of warming on species responses (Lowe et al. 2021; Song et al. 2021). While there is a good amount of information on mechanisms driving metamorphosis in species with complex life cycles (Werner 1988; Emlet 1988; Hentschel and Emlet 2000), only a handful of studies have investigated how such mechanisms respond to warming (D'Urban et al. 2014;

Torres and Giménez 2020; Griffith et al. 2021). Body mass is a plastic trait, driven by variations in larval growth rates and developmental time, but body mass should vary within upper and lower thresholds set by fitness costs (Werner 1988; Gotthard and Nylin 1995; Hentschel and Emlet 2000; Gotthard et al. 2000). Beyond the upper threshold, costs are associated to the high growth rates needed to achieve a large body mass (e.g. predation). Longer developmental time contributes to larger body mass but also determines the period when larvae are exposed to pelagic mortality risks (Eckert 2003) and the conditions experienced after settlement (Miron et al. 1999; Jarrett 2003). Because post-settlement conditions fluctuate in seasonal environments, the specific conditions experienced by juveniles are indirectly determined by the duration of the larval phase. For instance, in *H. sanguineus*, late settlement may result in reduced juvenile growth as individuals may miss most of the summer season where growth rates are enhanced by high temperatures in the intertidal zone. During summers, temperatures in the intertidal zone may boost growth because they are much higher than water temperatures given the exposure to sunlight during low tides (Stephenson 1942; Lewis 1964; Somero 2002). In addition, late settlement may expose individuals to cannibalism (Moksnes et al. 1997; Moksnes 2002; Moksnes 2004) or predation by e.g. juvenile *C. maenas*. According to life history theory, costs associated to trait changes should drive the evolution of plastic responses to environmental variation; because of trade-offs associated to such costs, the less responsive traits should be those with higher associated costs (Gotthard and Nylin 1995; Gotthard 2000, 2004). In the case of *H. sanguineus*, larvae responded to food limitation mainly through reduction of growth rates; the extension of development time, found to partially compensate effects of food limitation in *C. maenas* (Torres and Giménez 2020) was rather short. By contrast, *H. sanguineus* larvae showed a strong plasticity to temperature by extending the development from < 20 days at 24 ºC to > 60 days at 15 ºC. Given that at the local population, *H. sanguineus* females appear to release larvae in early summer, only after temperatures reach 15 ºC (Giménez et al. 2020), summers with water temperatures in the range of 15 - 18 ºC would result in late settlement if larvae were to extend further the developmental time. Hence, in the range 15 - 18 ºC and under food limitation, further extension of the larval phase may have higher fitness costs than metamorphosing with a smaller size (but profiting from a warm growing period).

Low temperatures

Our study is in line with others (Stepherson et al. 2009; Giménez et al. 2020), showing that low larval survival occurs at low temperatures (range 12 - 15 ºC). Reduced body mass at metamorphosis found at 15 ºC is expected because body mass at stage, peaks at temperatures where physiological performance is optimal (Anger 1998; Anger 2001). Perhaps the body mass of megalopa of *H. sanguineus* would decrease at temperatures higher than 24 ºC, as expected from the temperature-size rule (Atkinson 1994).

Under low temperature and food limitation, larvae hatching from all females showed a stronger reduction in nitrogen as compared to carbon. This is unlike previously observed responses to stressors in other species (Harms et al. 1994; Torres and Giménez 2020; Torres et al. 2021) where the main characteristic is a stronger reduction in carbon than in nitrogen content. In decapod crustaceans, carbon content is considered a proxy for lipid reserves (Anger and Harms 1990); hence, stress responses of that type are interpreted as a reduction in the accumulation of lipid reserves, but not in the proteins needed to sustain activity or the enzymatic machinery. Given that in decapods, nitrogen is a proxy for protein levels, we hypothesise that the reduction observed in *H. sanguineus* reflects a thermal limitation in the rate of protein synthesis. Protein synthesis accounts for a great proportion of the specific dynamic action (SDA, Brody 1964) in crustaceans, i.e. the energetic costs incurred by physiological processes related to feeding (including e.g. ingestion, digestion, assimilation and synthesis: Jobling 1993; Wieser 1994), which increase after a meal (Houlihan et al. 1990, Robertson et al. 2001). For example, in *Carcinus maenas*, protein synthesis accounts for 20-37 % of the post-meal oxygen rise (Houlihan et al. 1991). Temperature affects rates of protein synthesis in fasted and inactive crustaceans (McMillan and Houlihan 1988; Whiteley et al. 1996; El Haj and Whiteley 1997). Hence, one would expect that rates of protein synthesis are compromised at lower than optimal temperatures, due to limitations in covering the associated costs (Whiteley et al. 1997, 2001). In this study, the lowest temperatures tested are suboptimal for *H. sanguineus,* but not for species that are native to North European Seas (e.g. D'Urban et al. 2014; Torres and Giménez 2020). Hence, the differences between *H. sanguineus* and e.g. *C. maenas*, in how C:N ratios respond to limited access to prey may reflect interspecific differences in the thermal tolerance range.

Performance of *H. sanguineus* relative to *C. maenas*

We found that larval performance (e.g. survival) of *H. sanguineus* at low temperatures is low in relation to that of *C. maenas* also at low temperatures (Fig. 1). This is relevant to understand the outcome of the balance between larval settlement, and competition between *C. maenas* and *H. sanguineus* in the benthos. *C. maenas* larvae can complete larval development at temperatures as low as 12 ºC (Dawirs 1985; Nagaraj 1993). The larval season of both species partially overlap, *C. maenas* larvae are released from May onwards and megalopae settle in the intertidal zone from the end of June until the end of August (Giménez and Dirk, 2007). Interspecific competition occurs because juveniles of both species develop in the intertidal zone during summer (Geburzi et al. 2018) The balance of larval supply and competition of *C. maenas* and *H. sanguineus* must be evaluated considering both spring and summer conditions. For example, a large number of *C. maenas* juveniles would survive competition in years with strong settlement of *C. maenas* followed by weak settlement of *H. sanguineus* due to cool summers (temperature ~ 15 ºC).

We hypothesise that summers characterised by long heatwaves and high temperatures due to warming would increase performance of *H. sanguineus* larvae and exacerbate current competitive advantages already exhibited by the juvenile and adult stages in the benthos (Lohrer and Whitlach 2002; Jensen et al. 2002; Geburzi et al. 2018). Marine heatwaves, i.e. periods of time (> 3 - 5 days) when temperatures are above a predefined threshold (Meehl and Tebaldi 2004; Hobday et al. 2016), can have drastic consequences in structure and functioning of marine ecosystems (Garrabou et al. 2009; Marbà and Duarte 2010; Wernberg et al. 2013; Mills et al. 2013) and those in the German Bight have become more frequent since the 1990's (Giménez et al. 2022). During summer heatwaves such as those occurring in 2018, water temperatures around the local population reached values above 18 ºC (Giménez et al. 2020); temperatures in waters of the coastal Wadden Sea (where *C. maenas* and *H. sanguineus* co-occur) were much higher (BSH, 2019).

Another important aspect considered in our analysis concerns the role of intraspecific variation in performance (IVP). IVP is common in invertebrate larvae (e.g. Appelbaum et al. 2014; Spitzner et al. 2019; Torres et al. 2020), and expected from genetic variation (Marshall et al. 2008; Durrant et al. 2013) or parental effects (Pond et al. 1996; Shama et al. 2014). Important IVP was found in this study as variation in survival, developmental time, and growth among larvae from different females (e.g. Fig. S5), which is also expressed in Figure 5 as wide ellipses. The ellipses are spread across regions where the relative performance switches from being stronger in *H. sanguineus* to become stronger in *C. maenas*. The ellipses surround the area where 90 % of the 1000 simulated events for each factor combination are located. Hence, Figure 5 depicts the importance of the intraspecific variation in the performance of the species, as opposed to what means show; the ellipses show that, for example, there is a possibility for *H. sanguineus* larvae to be able to perform (i.e. survive and grow) better than *C. maenas* at low temperatures. Likewise for *Carcinus maenas*, there is room for their larvae to perform better than those of *H. sanguineus* at high temperatures under food limitation. Species coexistence is one of the important ecological consequences of intraspecific variation (Bolnick et al. 2011; Appelbaum et al. 2014).

In synthesis, larvae from the invasive crab *H. sanguineus* are able to complete their development under a wide range of temperatures and under daily limited access to food (for a period as short as 6 h), with variations among families; hence, *H. sanguineus* larvae should be able to survive starvation periods as long as they can access food patches for a brief time every day. *H. sanguineus* responds to food limitation through lengthening the development to a much smaller degree as compared to *C. maenas*; this occurs at expenses of metamorphosing to megalopa with lower body mass. It remains to be seen how such responses affect the balance of costs and benefits of metamorphosing with lower body mass but still profiting from the warm season increasing juvenile growth rates. *H. sanguineus* shows different responses to high temperatures and food limitation from the native *C. maenas* (Torres and Giménez 2020). Under cool summer conditions, we would expect limited survival of *H. sanguineus* larvae which could favour *C. maenas*. By contrast, under a warming scenario, *H. sanguineus* should benefit through high larval growth and survival rates. Under this scenario, increased rates of survival and growth in the pelagic habitat should enhance propagule pressure of *H. sanguineus*, magnifying the effect produced by being the dominant competitor in the intertidal zone. Overall, our study emphasises the importance of integrative studies comparing the performance among native and invasive species across their life cycles, and extending our study towards the juvenile - adult phase. Such approach will help us to understand and predict effects of warming on species replacement.

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Conflicts of interest: The authors declare that they have no conflicts of interests.

Compliance with Ethical Standards: The research presented in this paper complies with national (Germany) and international laws (guidelines from the directives 2010/63/EU of the European parliament and of the Council of 22nd September 2010) on the protection of animals used for scientific purposes.

Data accessibility: All data for this paper will be available from PANGAEA ®Data Publisher https://www.pangaea.de

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